

## SOCIAL AND ENVIRONMENTAL FACTORS AFFECT NATAL DISPERSAL AND PHILOPATRY OF MALE RED-COCKADED WOODPECKERS

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**Abstract.** Natal dispersal behavior can vary considerably among individuals, but the causes of intraspecific plasticity in dispersal are poorly understood. We tested six hypotheses about social and environmental conditions that might influence natal dispersal of males in the cooperatively breeding Red-cockaded Woodpecker (*Picoides borealis*). Further, we examined whether variation in dispersal behavior is heritable. Dispersing from the natal territory during the first year rather than remaining as a helper was associated with four factors. First, dispersing male fledglings were, on average, significantly lower in body mass than their philopatric siblings, indicating an influence of social dominance on dispersal. Second, individuals were more likely to disperse from territories with many male fledglings, independent of the number of adult male helpers per territory, suggesting that sibling (rather than helper–offspring) competition for future reproduction may be the underlying mechanism. Third, the probability of remaining as a helper rather than dispersing was positively associated with quality of the natal territory and with the number of high-quality territories close to the natal site. This suggests an influence of the benefits of philopatry, because many males that initially remain as helpers eventually become breeders on the natal territory or a neighboring territory. Finally, we found evidence that ecological constraints influence dispersal: the probability of dispersing was positively related to the availability of vacant territories in the wider neighborhood of the natal site. Natal dispersal behavior was not influenced by resource competition, measured as group size on the natal territory, or by local density, estimated as the number of active territories in the vicinity of the natal site. Based on comparisons of father–son and brother–brother dispersal behavior, we found no evidence for heritability of philopatric behavior. Dispersal of male fledgling Red-cockaded Woodpeckers can be viewed as conditional on social and ecological factors in the natal territory and in the immediate neighborhood. These factors seem to serve as proximate cues that influence young birds to either disperse or remain as philopatric helpers.

**Key words:** behavioral strategy; cooperative breeding; fledgling tactics; heritability; life history; natal dispersal; philopatry; *Piciformes*; *Picoides borealis*; pine habitat; Red-cockaded Woodpecker; social dominance.

### INTRODUCTION

Natal dispersal is an important life history trait of mobile organisms that may influence many aspects of a species' ecology, such as the dynamics, persistence, and genetic composition of its populations, and the evolution of its social behavior (e.g., Arcese 1989, Johnson and Gaines 1990). Although many studies have focused on the fitness consequences of variation in dispersal behavior (e.g., Newton and Marquiss 1983, Wiley and Rabenold 1984, Stacey and Ligon 1987, Jones et al. 1988, Pärt 1991, Ekman et al. 1999), less attention has been paid to the environmental and social factors influencing dispersal (Koenig et al. 1992). Individuals of a species differ in their dispersal behavior (Lawrence 1987, Russell and Rowley 1993, Herzig 1995, Verhulst et al. 1997), but the causes of intraspecific dispersal plasticity are not well understood.

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The Red-cockaded Woodpecker (*Picoides borealis*) is an endangered species endemic to mature pine forests in the southeastern United States (Jackson 1994). These birds are cooperative breeders and form social units in which nonbreeding adults help the breeding pair to raise their young. A social unit consists of a breeding pair and 0–4 nonbreeding male helpers (Lennartz et al. 1987, Walters et al. 1988). Female helpers are uncommon. A social group inhabits a permanent territory of 50–150 ha (Hooper et al. 1982, DeLotelle et al. 1987) containing a set of cavity trees. Group size is unrelated to home range size (Walters et al., *in press*) but is positively related to the quality of foraging habitat within the home range (James et al. 2001, Walters et al., *in press*). Cavities are excavated in live pine trees and take years to construct. Once completed, they may be used for an equally long period (Conner and Rudolph 1995, Harding 1997). Availability of cavities has been shown to be a critical component of habitat suitability (Walters et al. 1992a, Davenport et al. 2000) and to regulate breeding population size (Walters 1991). Group size is only weakly correlated with the

TABLE 1. Predictions of hypotheses relating to variation in dispersal behavior of fledgling male Red-cockaded Woodpeckers.

Hypothesis	Prediction
1) Social dominance	<b>1a. First-year dispersers are subordinate to helpers.</b>
2) Reproductive competition	<b>2a. Probability of first-year dispersal is positively related to the number of male fledglings on natal site.</b> <b>2b. Brothers differ in their dispersal behavior.</b> 2c. Probability of first-year dispersal is positively related to the number of male helpers on natal site.
3) Resource competition	3a. Probability of first-year dispersal is positively associated with group size.
4) Benefits of philopatry	4a. <i>Probability of first-year dispersal is negatively related to territory quality of natal site.</i> <b>4b. Probability of first-year dispersal is negatively associated with the number of high-quality territories within 1 km of natal site.†</b> 4c. Probability of first-year dispersal is negatively associated with the number of high-quality territories within 3.5 km of natal site.‡
5) Ecological constraints	5a. Probability of first-year dispersal is positively related to the number of vacant territories within 1 km of natal site.† <b>5b. Probability of first-year dispersal is positively related to the number of vacant territories within 3.5 km of natal site.‡</b>
6) Density dependence	6a. Probability of first-year dispersal is related to the number of active territories within 1 km of natal site.† 6b. Probability of first-year dispersal is related to the number of active territories within 3.5 km of the natal site.‡
7) Inheritance	7a. Sons show the same dispersal behavior as their fathers. 7b. Brothers have the same dispersal behavior.

*Notes:* First-year dispersers are individuals that disperse within their first year; helpers are those that remain on their natal territory as helpers. **Bold** = supported predictions, *italics* = partially supported.

† Reflects immediate neighborhood of the natal territory.

‡ Within the median dispersal distance of male fledglings (Walters 1991).

number of cavities present on a territory, however (Reed et al. 1988).

The Red-cockaded Woodpecker is particularly well suited for study of factors affecting natal dispersal because its dispersal behavior is distinctly dichotomous (Walters et al. 1988, 1992b, Daniels 1997). Some individuals remain as helpers on the natal territory and wait (for up to 8 yr) for a breeding vacancy on the natal site or in the immediate vicinity. Others disperse within their first year in search of a breeding vacancy, often moving well beyond their natal neighborhood. Most female fledglings disperse, and they will not be considered in this study. Among males, both philopatry and first-year dispersal are common, and dispersal behavior affects demography (Walters et al. 1992b). Males remaining on the natal territory experience higher first-year survival than do those dispersing immediately. In addition, the lifetime reproductive success of individuals delaying dispersal and reproduction can be equal to or higher than that of individuals attempting to reproduce in their second year of life, which show poor reproductive performance during their initial years as breeders. That the variation in dispersal behavior is maintained in males despite this inequity suggests that payoffs of philopatry and first-year dispersal vary in relation to the demographic and ecological circumstances encountered by different individuals.

In this paper, we examine factors affecting the dispersal behavior of fledgling male Red-cockaded Woodpeckers. We use an extensive data set from three populations covering 18 yr and >1400 individual dispersal events. Several explanations for natal dispersal patterns

have been offered, among which inbreeding avoidance, social dominance, competition for mates and for ecological resources, density dependence, and inheritance have received the most attention (Christian 1970, Gauthreaux 1978, Greenwood 1980, Greenwood and Harvey 1982, Waser 1985, Denno and Peterson 1995). Walters et al. (1992b) hypothesized that factors such as dominance rank, quality of the natal territory, and intensity of competition for breeding vacancies might affect the relative fitness benefits of philopatry and first-year dispersal among male Red-cockaded Woodpeckers. Here we test several hypotheses derived from these ideas. The social dominance hypothesis states that subordinate individuals are more likely to disperse than dominant individuals (Christian 1970, Gauthreaux 1978). We therefore predict that dispersers are subordinate to philopatric males (Table 1, prediction 1a), because the payoff of remaining on the natal territory appears to be higher than the benefits of immediate dispersal.

The reproductive competition hypothesis proposes that individuals should disperse if competition for mates or mating opportunities is stronger on their natal territory than elsewhere (Dobson 1982, Dobson et al. 1998). Based on this, we make three predictions. First, the probability of dispersal should be positively related to the number of male fledglings on the natal territory (Table 1, prediction 2a), and second, brothers should differ in their dispersal behavior (Table 1, prediction 2b), because competition for inheriting the natal site will be more severe if many male fledglings are present. Third, the probability of dispersal should be positively

related to the number of male helpers on the natal site (Table 1, prediction 2c), because competition for inheriting the breeding position on the natal territory is stronger if many male helpers are present.

The resource competition hypothesis predicts that individuals should disperse if competition for resources is stronger on the natal territory than elsewhere (Greenwood 1980, Dobson et al. 1998). We therefore expect a positive association between group size, measured as the number of adults plus the number of male and female fledglings, and the probability of dispersal (Table 1, prediction 3a), because each group member consumes resources. However, because group size includes the male fledglings and the male helpers, this prediction is not exclusive of reproductive competition.

The benefits-of-philopatry hypothesis proposes that individuals gain benefits by remaining on the natal territory because of great differences in territory quality (Stacey and Ligon 1987, 1991). We thus predict a negative relationship between the probability of dispersal and quality of the natal territory (Table 1, prediction 4a). This presumes that costs of foregoing reproduction initially (for a prolonged time) will be outweighed by eventually acquiring breeding status on the high-quality natal site. Red-cockaded Woodpecker helpers not only gain breeder status on their natal site, but also monitor the neighboring territories for breeding vacancies (Walters et al. 1988). The benefits of delaying dispersal will be higher if many high-quality territories are within the "assessment sphere" (Zack and Stutchbury 1992) of an individual. Therefore, a second prediction of the benefits-of-philopatry hypothesis is that the probability of dispersal is negatively related to the number of high-quality territories around the natal site (Table 1, predictions 4b and 4c).

The ecological constraints hypothesis holds that constraints to independent breeding, e.g., a shortage of suitable habitat, prevent dispersal of grown offspring from their natal territory (Brown 1974, Stacey 1979, Koenig and Pitelka 1981, Emlen 1982, Hatchwell and Komdeur 2000). We therefore expect to find the probability of dispersal to be positively related to the number of vacant territories in the neighborhood of the natal territory (Table 1, predictions 5a and 5b).

Density-dependent dispersal occurs in a variety of animals, and both positive (Nilsson 1989, Denno and Peterson 1995, Negro et al. 1997) and negative (Jones et al. 1988, Wolff 1997, Diffendorfer 1998) relationships between population density and dispersal rate exist. Because a young bird in its natal territory is incapable of assessing territory density of the entire population, we use the number of active territories in the neighborhood of the natal site as a measure of local density and predict that it will be related to the probability of dispersal (Table 1, predictions 6a and 6b).

Finally, if dispersal behavior is heritable (Howard 1960), closely related individuals should show more similar dispersal patterns (Hilborn 1975, Schroeder and



PLATE 1. A Red-cockaded Woodpecker arrives at the entrance to its nest cavity to deliver food to its brood. Note the resin barrier that protects the cavity. Photographed by John Hammond at Camp Lejeune Marine Base, North Carolina (USA).

Boag 1988). This hypothesis predicts that sons will have the same dispersal behavior as their fathers (Table 1, prediction 7a) and brothers will practice the same dispersal behavior (Table 1, prediction 7b) more often than expected by chance. We did not consider an inbreeding avoidance hypothesis, because avoidance of close inbreeding on the natal territory is resolved by female movement in Red-cockaded Woodpeckers (Walters et al. 1988, Daniels and Walters 2000a, b).

#### METHODS

Data were collected in three populations, all of which were associated with longleaf pine (*Pinus palustris*) communities with diverse ground covers and a sparse hardwood midstory. The Sandhills study area in south-central North Carolina, USA encompasses ~110 000 ha and contains ~220 groups of individually marked birds. This study area is described in detail in Walters et al. (1988). The other two study areas are located in the coastal plain along the southeastern coast of North Carolina. The population in Croatan National Forest inhabits 63 907 ha and consists of ~50 groups of color-banded Red-cockaded Woodpeckers, whereas the population in Camp Lejeune Marine Base inhabits 34 425 ha and contains 40–50 groups of individually marked birds. Details of habitat composition of the Coastal Plain study sites are given in Zwicker and Walters (1999).

Data used in this study were collected from 1980 to

1997 in the Sandhills population, and from 1986 to 1997 and 1989 to 1997 in the Camp Lejeune and Croatan populations, respectively. Individuals were banded with a unique combination of color bands and a uniquely numbered aluminum band. Most birds were banded as nestlings. Composition of all groups was determined during each breeding season, and the status of each individual (i.e., breeder, helper, floater) was assigned using criteria in Walters et al. (1988). Reproduction of each group was monitored by visiting the cavity trees every 9–14 d from April to mid-July. Nestlings were banded and weighed (to the nearest 0.1 g) 6–10 d after hatching. Fledging occurs 26–29 d after hatching, and the number of fledglings per brood was determined by following the groups after the expected fledging date. The sex of each fledgling was identified by the presence (male) or absence (female) of a red crown patch.

Dominance relationships within broods were assessed from differences in relative nestling mass. Relative nestling mass of an individual was calculated as the deviation from the mean nestling mass per brood, divided by the brood's standard deviation of nestling mass.

Territory quality was assessed in two ways. In this species, reproductive success is highly correlated with group size, an effect that is due partly to positive effects of helpers on reproduction and partly to territory quality (Heppell et al. 1994). That is, some (higher quality) territories consistently produce more fledglings, and because a portion of fledglings remains as helpers, these territories tend to contain larger groups. Territory quality, as indicated by group size and/or productivity, has been related to the quality of foraging habitat (James et al. 2001; Walters et al., *in press*) and the number of cavities (Davenport et al. 2000). We used the number of active and possibly active cavities per territory per year as our first measure of territory quality. This was calculated for the Sandhills and Camp Lejeune populations, but no data were available for Croatan. Territories in the study areas average ~85 ha per group (Walters et al., *in press*), and we did not have the extensive habitat data necessary to assess foraging habitat quality for the >300 groups included in the study. Data from a sample of groups indicate that most have no high-quality foraging habitat within their territory, many have a small amount, and only a few have a substantial amount (Walters et al., *in press*). Because we were unable to use foraging habitat quality, we instead employed an indirect measure of territory quality based on natality and mortality rates for each territory (also see Ligon and Ligon 1990, Daniels and Walters 2000b) that reflects the effects of foraging habitat quality on group size and productivity. We calculated a territory quality index as the quotient of the average annual productivity (total number of fledglings produced on the territory, divided by the number of years that territory had been monitored) and the average annual adult mortality (the number of adults pre-

sumed to have died on the territory divided by the total number of adult bird-years).

To determine the number of vacancies available to a fledgling, we counted the vacant territories whose centers were located within 1 km and 3.5 km, respectively, of the center of the fledgling's natal territory. We chose these distances because they reflect the immediate neighborhood of a territory (1 km) and because they are within the median dispersal distances of male fledglings (3.5 km) (Walters 1991). Among the vacancies we included territories not occupied in the birth-year of the fledgling, but which had been occupied at least once within the past 5 yr by a breeding pair or a single territorial male. To determine availability of high-quality territories, we counted the number of high-quality territories within 1 km and 3.5 km of the natal site. Territories were classified as high-quality on the basis of their quality index being greater than or equal to half of the index of the best territory per population. Local population density was estimated as the number of active territories within 1 km and 3.5 km of the natal site. A territory was considered active if it contained a breeding pair (with or without helpers). As territory centers for Camp Lejeune, we used the Universal Transverse Mercator coordinates of the nesting cavity tree in a particular year. Because of missing data for nesting cavity trees, we estimated territory centers for the Sandhills population as the arithmetic mean of the Universal Transverse Mercator coordinates of all foraging locations obtained from each group during regular breeding season monitoring. No spatial data were available for Croatan.

#### *Sample sizes and statistical analyses*

In total, 1437 male fledglings from 1281 broods were observed in their second year of life. Among these were 382 that had dispersed in their first year and 1055 that had remained on their natal territory as helpers. 1130 territories had only one surviving fledgling (215 dispersers and 915 helpers), whereas 146 territories produced two survivors (110 with one disperser and one helper each, 24 with two dispersers and 12 with two helpers) and five territories had three survivors (four with two dispersers and one helper, one with one disperser and two helpers). From each of these 151 territories with two or three fledglings surviving to the next breeding season, one individual was randomly selected to be used in the analyses, resulting in a sample size of 292 first-year dispersers and 989 philopatric males. Each territory was used only once in a given year, but the same territory may have been considered in several years. We used territory-years instead of randomly selecting one observation per territory from the entire study period to retain as much information as possible, because ecological and social circumstances on each territory vary between years.

Each hypothesis was first examined separately, and because results did not differ among study areas, we

pooled the data from the three areas. Using PROC LOGISTIC (SAS Institute 1999), dispersal behavior (0, helper; 1, disperser) was regressed on the variables relating to the predictions of hypotheses 2–6 (Table 1). Differences in nestling mass between helpers and dispersers (Table 1, hypothesis 1) were investigated with *t* tests. First, we used a paired *t* test to compare relative nestling mass of fledglings from the same brood exhibiting different dispersal behavior. For the five broods with three fledglings, we randomly selected one of the two individuals that exhibited the same dispersal behavior. Second, based on broods not used in the previous analysis and having at least two male fledglings, we used a two-sample *t* test to compare relative nestling mass of early dispersers and philopatric males from different broods. Most of these broods had only one individual surviving to the next breeding season; for the 36 broods with two fledglings exhibiting the same dispersal behavior, we randomly selected one individual to include in the analysis. Predictions relating to heritability of dispersal behavior (Table 1, hypothesis 7) were analyzed with  $\chi^2$  tests. Each father was used only once, and if more than one male offspring per brood was available, we randomly selected one. Male fledglings may remain and breed on their natal territory not because dispersal behavior is heritable, but because they prefer to stay on a high-quality territory. We therefore also compared the dispersal behavior of fathers and sons by simultaneously controlling for quality of the fledgling's natal territory (high or low), using the Cochran-Mantel-Haenszel test in PROC FREQ (SAS Institute 1999).

In a second step, we used multiple logistic regression with backward elimination to simultaneously investigate the influence of several factors on dispersal behavior (Dobson and Jones 1985). Dispersal behavior was again the response variable (0, helper; 1, disperser). Explanatory variables were relative nestling mass, number of male fledglings on the natal territory, number of male helpers on the natal territory, group size (adults + all fledglings), territory quality (based on the quality index described previously), and numbers of high-quality territories, active territories, and vacant territories within 1 km and 3.5 km of the natal site. Dispersal behavior of the father was excluded from this analysis because of missing data. High correlations among independent variables can bias the results of multiple regressions (Chatterjee and Price 1991); thus, we first calculated Spearman rank correlations between all independent variables and identified two pairs of highly ( $r_s > 0.6$ ) correlated variables: number of male helpers with group size, and number of high-quality territories within 3.5 km with number of active territories within 3.5 km. We performed the logistic regression using all variables and also by first including one variable, and then the other, of each pair of highly correlated variables. Because the results were identical in all three cases, multicollinearity does not seem to

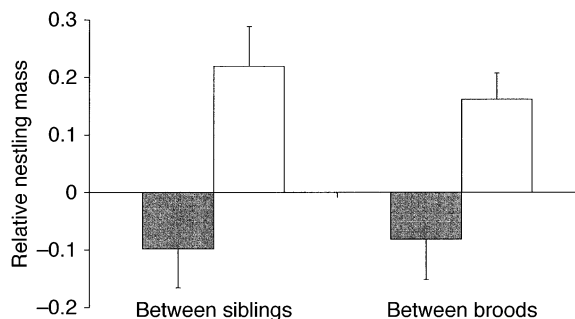


FIG. 1. Mean relative nestling mass (+1 SE) of individual male Red-cockaded Woodpeckers dispersing from (shaded bars) or remaining on (white bars) the natal territory in their first year of life. "Between siblings" columns compare nestlings of the same brood ( $n = 114$ ); "between broods" columns compare nestlings of different broods, using only one nestling per brood ( $n = 120$  dispersing, 280 remaining). Relative nestling mass is calculated as  $(\text{individual mass} - \text{mean mass}_{\text{brood}}) / \text{standard deviation of mass}_{\text{brood}}$ .

be problematic, and we only present the result of the analysis with all variables. The criterion for backward elimination of an independent variable was set at  $\alpha > 0.05$ . The significance of each variable and interaction was assessed with the likelihood ratio test. This analysis was restricted to the Sandhills and Camp Lejeune populations because of missing data from the Croatan population for variables referring to the spatial distribution of territories.

## RESULTS

### *Social dominance*

Fledglings that dispersed in their first year of life were significantly lower in body mass during the nestling stage than their siblings that remained as helpers on the natal territory (Fig. 1; paired *t* test,  $t = 2.7$ ,  $P = 0.0047$ ,  $n = 114$ ). Similarly, comparing nestlings from different broods, dispersers were significantly lighter in mass than helpers (two-sample *t* test,  $t = 2.9$ ,  $P = 0.0019$ ,  $n_{\text{disp}} = 120$ ,  $n_{\text{help}} = 280$ ).

### *Reproductive competition*

Dispersal was more likely to occur from territories with many male fledglings (logistic regression, likelihood ratio test,  $\chi^2 = 29.4$ ,  $df = 1$ ,  $P < 0.0001$ ,  $n_{\text{disp}} = 292$ ,  $n_{\text{help}} = 989$ ), whereas there was no association between the probability of dispersal and the number of male helpers per territory ( $\chi^2 = 0.8$ ,  $df = 1$ ,  $P = 0.376$ ). The interaction between number of male fledglings and number of male helpers was not significant either ( $\chi^2 = 0.4$ ,  $df = 1$ ,  $P = 0.507$ ), indicating that the relationship between the likelihood of first-year dispersal and the number of male fledglings did not depend on the number of male helpers present. The positive relationship between the probability of first-year dispersal and the number of male fledglings is not simply due to a higher chance of observing a disperser sur-

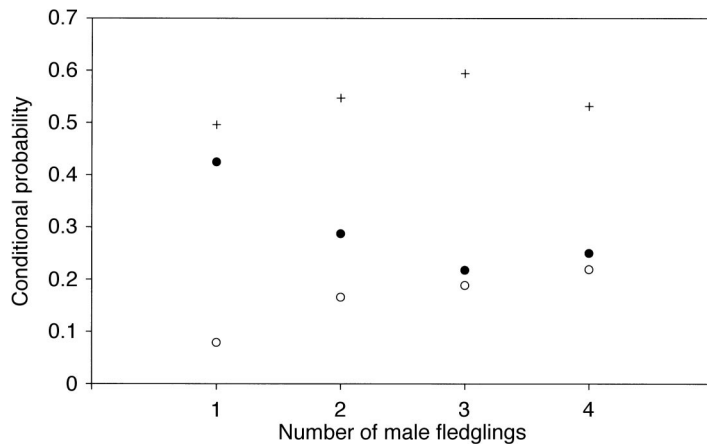


FIG. 2. Probability of a male fledgling Red-cockaded Woodpecker dispersing from the natal territory (open circles), staying on the natal territory (solid circles), or dying (crosses) in its first year of life, as a function of the number of male fledglings per brood. Data are from 3032 fledglings from 2206 broods.

living to the next breeding season because there are more male fledglings to start with. The probability that an individual would stay on the natal territory decreased as a function of male brood size, whereas the probability that an individual would disperse increased; the probability that it would not survive did not change (Fig. 2). Brothers exhibited opposite dispersal behavior in 111 out of 151 broods in which two males survived to age 1 yr, which is significantly more often than the 75.5 cases (151/2) expected by chance ( $\chi^2 = 33.4$ ,  $df = 1$ ,  $P < 0.0001$ ). This indicates that the social interaction between brothers influenced their dispersal behavior.

#### Resource competition

Probability of first-year dispersal was positively related to group size, measured as the number of adults plus fledglings on the natal territory (logistic regression, likelihood ratio test,  $\chi^2 = 16.2$ ,  $df = 1$ ,  $P < 0.0001$ ,  $n_{\text{disp}} = 292$ ,  $n_{\text{help}} = 989$ ). However, group size includes the male fledglings, so this result might reflect an effect of reproductive competition among male fledglings on dispersal strategy rather than an effect of group size. After statistically controlling for the influence of the number of male fledglings (Type I analysis with PROC GENMOD in SAS), we found no significant relationship between group size and dispersal probability ( $\chi^2 = 0.6$ ,  $df = 1$ ,  $P = 0.458$ ). Thus, resource competition with other group members generally does not seem to influence dispersal behavior, although we cannot rule out the possibility of resource competition with other male fledglings specifically, which is confounded with reproductive competition in our analyses.

#### Benefits of philopatry

Probability of first-year dispersal was negatively related to the number of high-quality territories within 1 km of the natal site (logistic regression, likelihood ratio test,  $\chi^2 = 6.7$ ,  $df = 1$ ,  $P = 0.0095$ ,  $n_{\text{disp}} = 209$ ,  $n_{\text{help}} = 740$ ), but not to the number of high-quality territories

within 3.5 km of the natal site ( $\chi^2 = 2.9$ ,  $P = 0.0864$ ). We found no relationship between the probability of first-year dispersal and the quality of the natal territory, either for the site quality index ( $\chi^2 = 2.2$ ,  $df = 1$ ,  $P = 0.142$ ) or for the number of active and possibly active cavities as a measure of quality ( $\chi^2 = 0.14$ ,  $df = 1$ ,  $P = 0.712$ ). Thus, the presence of high-quality territories close to the natal site seems to favor remaining on the natal territory, whereas the quality of the natal site does not seem to affect dispersal behavior.

#### Ecological constraints

Probability of first-year dispersal was positively related to the number of vacant territories located within 3.5 km of the natal territory (logistic regression, likelihood ratio test,  $\chi^2 = 4.9$ ,  $df = 1$ ,  $P = 0.0267$ ,  $n_{\text{disp}} = 262$ ,  $n_{\text{help}} = 907$ ), whereas no association was found with the number of vacancies within 1 km ( $\chi^2 = 0.23$ ,  $P = 0.629$ ). Thus, young male Red-cockaded Woodpeckers dispersed more often if there were more vacancies in the wider neighborhood of their natal site.

#### Density dependence

The probability of first-year dispersal was not related to local density, measured as the number of active territories within 1 km (logistic regression,  $\chi^2 = 2.6$ ,  $df = 1$ ,  $P = 0.1058$ ,  $n_{\text{disp}} = 258$ ,  $n_{\text{help}} = 896$ ) and 3.5 km of the natal site ( $\chi^2 = 2.8$ ,  $df = 1$ ,  $P = 0.0957$ ), respectively. This suggests that dispersal behavior is not density dependent.

#### Heritability

We did not find any significant association between dispersal behavior of fathers and their sons (Table 2a). Because the number of male fledglings on the natal site seems to influence the fledglings' dispersal behavior, we redid the analysis of father-son dispersal behavior by considering only broods in which both the offspring and its father were raised in broods in which they were the only male fledgling. However, we again failed to detect a significant association between the dispersal

TABLE 2. Dispersal behavior of male fledgling Red-cockaded Woodpeckers in relation to dispersal behavior of their fathers.

Offspring	Father	
	Disperser	Helper
A) All data ( $\chi^2 = 0.2$ , $df = 1$ , $P = 0.636$ )		
Disperser	27 (25)	48 (50)
Helper	96 (98)	194 (192)
B) Offspring and father as sole male† ( $\chi^2 = 2.7$ , $df = 1$ , $P = 0.103$ )		
Disperser	9 (6)	17 (20)
Helper	23 (26)	93 (90)

Notes: Expected values are in parentheses. Dispersers are males that disperse within their first year; helpers remain on the natal territory.

† Data are from cases in which both the offspring and the father were raised in broods in which they were the only male fledgling.

behavior of fathers and sons (Table 2b). Furthermore, when controlling for habitat quality (high or low) of the fledgling's natal site, we did not find any significant association between dispersal behavior of fathers and their sons (Cochran-Mantel-Haenszel test,  $CMH = 0.28$ ,  $df = 1$ ,  $P = 0.594$ ). Red-cockaded Woodpeckers are genetically monogamous (Haig et al. 1994), so the lack of association between dispersal behavior of fathers and their offspring is not due to confounding effects of extra-pair paternity. We did not detect similarity indicative of heritability in dispersal behavior of brothers either. In fact, brothers showed opposite dispersal behavior more often than expected by chance (test reported previously in *Results: Reproductive competition*).

#### Multiple causes of dispersal

To examine whether the dispersal behavior of young male Red-cockaded Woodpeckers was simultaneously affected by several factors, we performed a multiple logistic regression with backward elimination. The analysis corroborated the results of the single-factor tests. The probability of first-year dispersal was posi-

tively related to the number of male fledglings per brood and to the number of vacancies within 3.5 km of the natal site; it was negatively related to relative mass as a nestling and to the number of high-quality territories within 1 km of the natal site (Table 3). Thus, social dominance (Table 1, prediction 1a), reproductive competition (Table 1, prediction 2a), benefits of philopatry (Table 1, prediction 4b), and ecological constraints (Table 1, prediction 5b) were again supported. The only difference between the single-factor tests and the multiple regression was that, in the latter, the quality of the natal territory was negatively related to the probability of first-year dispersal. In other words, fledglings were more likely to disperse from territories of lower quality, which further supports the benefits-of-philopatry hypothesis (Table 1, prediction 4a). Using forward instead of backward selection produced exactly the same results. That dispersal occurred more often in large broods (with many male fledglings) depended neither on the number of male helpers present nor on the quality of the natal territory (nonsignificant interaction terms number of male fledglings  $\times$  number of male helpers [ $P > 0.90$ ] and number of male fledglings  $\times$  quality of natal territory [ $P > 0.66$ ]).

#### DISCUSSION

Dispersal and philopatry of young male Red-cockaded Woodpeckers during their first year of life appeared to be influenced by social factors and environmental conditions on and around the natal site. At least four factors were involved: social dominance relationships and reproductive competition among male fledglings, as well as the distribution of high-quality territories and vacant territories in the neighborhood of the natal site. These factors simultaneously influence the probability of first-year dispersal, showing that natal dispersal "decisions" of young animals can be due to multiple causes, as suggested by Dobson and Jones (1985) and Wheelwright and Mauck (1998).

#### Social dominance

Dominance relationships among siblings have been shown to influence natal dispersal behavior in a variety

TABLE 3. Influence of multiple factors on first-year dispersal behavior in fledgling male Red-cockaded Woodpeckers.

Parameter	Estimate	1 SE	$\chi^2$	$P$
Intercept	-1.930	0.269	51.33	<0.0001
No. male fledglings	0.700	0.110	40.65	<0.0001
No. high-quality territories within 1.0 km	-0.399	0.120	11.01	0.0009
Relative nestling mass	-0.293	0.104	7.99	0.0047
Quality of natal territory	-0.082	0.033	6.26	0.0123
No. vacant territories within 3.5 km	0.044	0.019	5.36	0.0206

Notes: Results of backward stepwise logistic regression with fledgling type (helper, 0; disperser, 1) as dependent variable, relative nestling mass, no. male fledglings, no. male helpers, group size (adults + all fledglings), territory quality, no. high-quality territories, no. active territories, and no. vacant territories within 1 and 3.5 km of the natal site, respectively, as independent variables, and three interactions: no. male fledglings  $\times$  no. male helpers, no. male fledglings  $\times$  territory quality, and no. male helpers  $\times$  territory quality. Only significant variables are shown. Model:  $\chi^2 = 74.30$ ,  $df = 5$ ,  $P < 0.0001$ .

of animals: spiders, Kim (2000); birds, De Laet (1985), Ellsworth and Belthoff (1999), and Altwegg et al. (2000); mammals, Gauthreaux (1978), and Gese et al. (1996). Dominant individuals are assumed to have priority of access to resources on the natal territory, which can have two consequences for dispersal behavior. First, dominant individuals might mature faster than subordinates, and therefore might have the opportunity to disperse earlier; second, dominant individuals might force siblings to disperse, either by direct aggression or by controlling limited resources. That early dispersers are, on average, lighter in body mass than philopatric males in Red-cockaded Woodpeckers suggests dispersers to be subordinate, supporting the second explanation. This conclusion rests on the assumption that differences in nestling mass measured between day 6 and day 10 translate into dominance relationships among fledglings, conferring competitive advantages to dominant fledglings. We do not have data to support this assumption, but there is indirect evidence from other species showing that differences in nestling mass are not likely to change in the course of the nestling period (e.g., Krebs 1999, Forbes and Glassey 2000), and that mass differences among nestlings do indeed reflect dominance relationships (Stanback 1994, Ellsworth and Belthoff 1999, Krebs 1999). Fights among fledgling Red-cockaded Woodpeckers can be regularly observed (Conner et al. 2001), suggesting aggression of dominant fledglings as a proximate mechanism promoting first-year dispersal of subordinates. Similar results have been found in other bird species in which some juveniles exhibit delayed dispersal (De Laet 1985, Strickland 1991). In contrast, for species in which first-year dispersal is the rule, large young seem to disperse earlier (Nilsson and Smith 1985, Ellsworth and Belthoff 1999).

The interaction between dispersal behavior and presumed rank of young male Red-cockaded Woodpeckers suggests a difference in the relative payoffs of staying vs. leaving the natal site. In species in which remaining on the natal site for some time is advantageous, e.g., in terms of winter survival, dominant individuals seem to choose to delay dispersal. Examples include many cooperative breeders (Koenig et al. 1992), as well as some noncooperatively breeding species (De Laet 1985, Strickland 1991, Ekman et al. 2000). If, on the other hand, remaining on the natal site is not an option, e.g., because of parental eviction, dispersing as early as possible seems advantageous in order to obtain the best available vacant territory (Nilsson 1989, Ellsworth and Belthoff 1999). Our results suggest that philopatry is the preferred option of young male Red-cockaded Woodpeckers, as do fitness calculations comparing philopatric individuals with those that disperse early (Walters et al. 1992b).

#### *Reproductive competition*

The probability of first-year dispersal in this study was positively related to the number of brothers per

brood, and brothers practiced different dispersal strategies more often than expected. Together, these results suggest that, in broods with many males, dispersal is a better option than staying on the natal site for all but one of the males. By dispersing, a young male avoids future reproductive competition with the brother that remains and tries to acquire a breeding position elsewhere. That the dominant individuals tend to remain is also suggestive of competition. The effect of brood size was independent of the numbers of helpers present on the natal territory, indicating that competition with age mates, and not with older relatives, for future reproduction is the underlying mechanism. Our results corroborate earlier studies suggesting an influence of reproductive competition on dispersal behavior (Waser 1985, Johnson and Gaines 1990, Koenig et al. 1992, Dobson et al. 1998, Travis et al. 1999). However, we cannot rule out the possibility that our results are due to competition with age-mates for critical resources rather than reproductive competition.

#### *Benefits of philopatry and ecological constraints*

Our study suggests that both ecological constraints (Brown 1974, Stacey 1979, Koenig and Pitelka 1981, Emlen 1982) and benefits of philopatry (Stacey and Ligon 1987, 1991) influence dispersal behavior of male Red-cockaded Woodpecker fledglings in their first year of life. Specifically, the probability of first-year dispersal is positively related to the availability of vacant territories in the wider neighborhood, lending support to the ecological constraints hypothesis and agreeing with earlier findings (Walters et al. 1992a). Vacancies within 3.5 km of the natal site, but not those within 1 km, appeared to influence dispersal, suggesting that young birds may be aware of the social environment over a fairly wide area when they "decide" to leave the natal territory, perhaps through extra-territorial forays and prospecting behavior, as occurs in other species (Hooge 1995, Reed et al. 1999). Alternatively, this result might reflect a higher survival probability of dispersers if there are more vacant territories within 3.5 km, rather than an influence of these vacancies on dispersal behavior in the first place. A final possibility is that fledglings may be able to assess availability of vacancies indirectly from the frequency of floaters and other intruders on their territory.

On the other hand, dispersal behavior also appears to be influenced by the availability of high-quality territories in the immediate vicinity of the natal site and by the quality of the natal territory itself, which is in accordance with the benefits-of-philopatry hypothesis. In our study, there was no correlation between the numbers of high-quality territories and vacant territories within 1 km of the natal site, indicating that a large number of high-quality territories did not simply reflect a low availability of vacant territories. We therefore conclude that the tendency for male fledglings to remain on the natal territory in their first year of life is



influenced by the quality of the breeding sites that such individuals may eventually acquire, namely the natal site and territories in the immediate neighborhood of the natal site. From one breeding season to the next, 15% of Red-cockaded Woodpecker helpers gain breeder status on their natal site, and an additional 12% do so on territories within a median distance of 1 km from the natal site (Walters et al. 1988). Therefore, the chances of an individual eventually acquiring a high-quality site by delaying dispersal will be higher the better the natal territory is and the more high-quality territories are located in the immediate neighborhood of the natal site.

#### *Natal dispersal as conditional behavior*

We found no evidence that variation in dispersal behavior is heritable. Instead, dispersal alternatives observed in young male Red-cockaded Woodpeckers can be viewed as conditional on sibling competition and ecological conditions in both the natal territory and its neighborhood. Delaying dispersal and remaining on the natal territory as a helper seem to be advantageous under particular circumstances, namely for a dominant male fledgling raised on a high-quality territory surrounded by many other such territories. Dispersing immediately appears to be advantageous when these circumstances do not exist, that is, for subordinate male fledglings and for males fledged in poor-quality territories and neighborhoods. Given the particular circumstances on any natal territory, both dispersal alternatives may enable individuals to maximize their fitness (Cade 1984, Waser and Jones 1989). Further, as long as each alternative is advantageous for at least some individuals, both will be maintained by selection. Although Walters et al. (1992b) found that the average fitness of philopatric individuals probably exceeded that of first-year dispersers, our results indicate that these averages may not accurately represent expected fitness payoffs for every individual. We suggest that dominant individuals in high-quality habitat that are philopatric enjoy the highest fitness. Although subordinates and individuals fledged in poorer quality habitat cannot do as well as these individuals, irrespective of their dispersal behavior, they can do better by dispersing early than by staying on the natal territory as helpers.

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