INBREEDING DEPRESSION AND ITS EFFECTS ON NATAL DISPERSAL IN RED-COCKADED WOODPECKERS[1]

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Abstract. Natal dispersal is a key life-history component that may be influenced by the fitness consequences of inbreeding. We studied natal dispersal and inbreeding within a large population of cooperatively breeding, endangered Red-cockaded Woodpeckers (*Picoides borealis*). We assessed the costs of close inbreeding, the spatial distribution of related males and its relationship to dispersal distance of females, and the change in dispersal behavior of females in the presence of closely related males. Close inbreeding resulted in a significant loss of fitness, through two separate effects: closely related pairs (kinship coefficient $\geq$ 0.125) exhibited lowered hatching rates and lowered survival and recruitment of fledglings relative to unrelated pairs. Despite a highly predictable spatial clustering of closely related males near the female's natal territory, natal dispersal distance of females was not sufficient to avoid these males as mates. Females changed dispersal behavior in the presence of closely related males on the natal territory: female fledglings were significantly more likely to disperse from natal territories if there were closely related males breeding there in the following year. Females did not change dispersal behavior in the presence of related males that were not on the natal territory. We suggest that dispersal behavior is a trade-off between benefits of short-distance dispersal, e.g., an advantage in competing for scarce breeding vacancies, and the substantial cost of close inbreeding.

Key words: cooperative breeding, inbreeding avoidance, inbreeding depression, natal dispersal, Picoides borealis, Red-cockaded Woodpecker.

INTRODUCTION

Natal dispersal is a complex trait that may be influenced in part by the costs of close inbreeding (reviewed by Pusey 1987, Pusey and Wolf 1996). Evidence of inbreeding depression in wild populations is accumulating (Jiménez et al. 1994, Brown and Brown 1998, Keller 1998), and natal dispersal patterns that reduce close inbreeding have been documented in several species of mammals and birds (Pusey 1987, Wheelwright and Mauck 1998). However, whether such dispersal evolved as a mechanism to avoid inbreeding costs has been debated (Shields 1983, Moore and Ali 1984, Pusey 1987).

If inbreeding incurs high fitness costs, these costs may influence natal dispersal behavior in at least two ways. First, dispersal distance may act to separate kin in space. Studies of sex-biased dispersal (reviewed by Greenwood and Harvey 1982, Pusey 1987) are consistent with this possibility, but lack the detail required for

conclusive evidence because of considerable overlap in dispersal distances between the sexes (Moore and Ali 1984, Wheelwright and Mauck 1998). Second, dispersal behavior may change in the presence of relatives (e.g., birds disperse when relatives are present; Pärt 1996, Wheelwright and Mauck 1998), just as reproductive behavior has been seen to change (Blouin and Blouin 1988, Koenig et al. 1998). This change in dispersal behavior also may be viewed as active mate choice.

Several studies have investigated inbreeding avoidance by comparing observed inbreeding rates within populations to expected values based on simulations of random pairing (Gibbs and Grant 1989, Keller and Arcese 1998, Wheelwright and Mauck 1998). One well-recognized problem in this approach is that the calculation of expected inbreeding depends on assumptions about available mates (van Tierenden and van Noordwijk 1988, Pärt 1996, Keller and Arcese 1998), and may incorporate inbreeding avoidance behaviors into the null model (Pärt 1996). Use of several null models may alleviate

this problem (Keller and Arcese 1998), but a different approach using only observed dispersal behaviors also may be helpful (Pärt 1996).

In this study, we test for effects of inbreeding depression on natal dispersal of Red-cockaded Woodpeckers (*Picoides borealis*). First, we estimate the reproductive costs of inbreeding. We then look for spatial separation of kin by comparing female dispersal distances to the spatial distribution of moderately and closely related males, an approach much more specific than that of documenting sex-biased dispersal. Finally, we assess differences in the dispersal behavior of females in the presence and absence of related males. Specifically, we look for a change in three dispersal behaviors exhibited by female fledglings: the frequency of dispersal from the natal site, the distance dispersed, and the frequency of dispersal to the nearest vacancy. In all but the last analysis, we use only observed dispersal events to avoid making assumptions about which movements are possible (see Daniels 1997 for simulations of random matings).

The Red-cockaded Woodpecker is an endangered species endemic to mature pine savannas of the southeastern United States. Red-cockaded Woodpeckers breed cooperatively: roughly 50% of fledgling males delay dispersal and remain on the natal territories as helpers, whereas the other fledgling males and almost all fledgling females disperse or die (Walters et al. 1988). The species is well suited for a study of inbreeding depression and natal dispersal for several reasons. First, the social system may increase the likelihood of inbreeding and the evolution of inbreeding avoidance behaviors (Blouin and Blouin 1988). Second, inbreeding avoidance through breeding dispersal has been documented in Red-cockaded Woodpeckers (Walters et al. 1988, Daniels 1997) as well as in several other cooperative breeders (Koenig et al. 1984, Woolfenden and Fitzpatrick 1984, Rabenold 1985). Third, molecular analysis has shown that Red-cockaded Woodpeckers are highly monogamous. The percentage of offspring sired by extra pair fertilization has been estimated at 0.0% (0 of 21, Haig et al. 1993) and 1.3% (1 of 80, Haig et al. 1994). Therefore, a pedigree based on observed pairings provides an accurate representation of the mating system in this species.

METHODS
STUDY AREA AND DATA COLLECTION
The study area, located in the Sandhills of south-central North Carolina, encompasses over 110,000 ha and contains a population of over 500 individuals in roughly 220 groups. All groups within this study area have been monitored since 1982, and most have been monitored since 1980. All known adults have been individually color-banded, and most birds were banded as nestlings. Each breeding season, observers recorded the number of eggs, nestlings, and fledglings produced per group. All members of each group were identified and assigned breeding status based on behavioral observations and relative age. In this way, parentage, location, and status of most individuals were known. Additional groups that were not monitored occur to the south and east of the study area. However, the percent of unbanded adult birds found within the study area is only about 5% per year. Further information on the study species, study area, and methods of data collection is given by Walters et al. (1988). Carter et al. (1983) give a detailed description of the habitats within the study area.

CALCULATION OF KINSHIP
We calculated coefficients of kinship (f) and inbreeding coefficients (F) from a pedigree file containing all known individuals in the study area between 1980–1995 using PROC INBREED (SAS Institute Inc. 1997). 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 kinship coefficient of its parents (Falconer 1989). These were by necessity minimum estimates of kinship and inbreeding, 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, the pedigree was built from 16 years of data, and because estimated generation length in this population is 4 years (Reed et al. 1988), the pedigree contains roughly four generations. We did not standardize the pedigree by excluding individuals with an unknown parent or grandparent because we wished to retain sample sizes of closely related birds; kinship can be detected between two siblings if only one parent is known. Such standardization is valuable when comparing mean inbreeding levels among populations and across species (van Tierenden and van Noordwijk 1988, Keller 1998), but we do not report population-level inbreeding here.

CALCULATION OF NATAL DISPERSAL DISTANCES

We calculated dispersal distances in terms of numbers of territories crossed for females with known birth and breeding locations between 1982 and 1995. Number of territories crossed was a count of actual territories whose estimated centers were within 400 m of a straight line between the estimated territory centers of the natal and first breeding sites. The diameter of nearly all territories in the study area is greater than or equal to 500 m. Territory centers were estimated by the centroid of the minimum convex polygon including all locations of foraging or congregating adults, recorded in universal transverse mercator (UTM) coordinates during regular breeding season monitoring. In calculating the number of territories crossed, the natal territory was not counted but the breeding site was, so that a bird moving next door crossed 1 territory and a bird remaining in the original territory crossed 0 territories. We counted only territories occupied in the year the female appeared in the new location. Unoccupied sites were not considered territories, in part because females rarely remain in sites that have no male present.

REPRODUCTIVE COSTS OF INBREEDING

We tested for lowered reproduction for related pairs using linear regressions of reproductive variables on the kinship coefficient. Only data from 1984–1995 were included because no kinship values above 0 were detected prior to 1984.

We used mean annual number of yearlings produced per pair as an overall measure of reproductive success. We also used several measures of reproductive stages (clutch size, proportion of eggs that hatch, proportion of nestlings that fledge, and proportion of fledglings that survive to age one) so that if an overall effect was present we could determine in which stage(s) it occurred. Each of these five measures of reproductive success was calculated for each nest that produced at least one fledgling. To control for annual variation and to have only one observation per breeding pair, we converted the annual values for each nest to mean deviation of the breeding pair from annual means. To do this, we subtracted annual means from the annual values, summed these deviations by breeding pair, and divided by the number of years the pair produced a successful nest. Average age of the female was included in the regression models

because young females have lowered reproduction (Walters 1990); for birds banded as adults, minimum ages were used. For comparison with other studies, we also report results of linear models using actual annual observations instead of average deviation from annual means per pair, but results of both methods were similar. We also performed two-sample comparisons between reproduction of closely related pairs (f ≥ 0.125) and unrelated pairs using the five measures of reproductive success. If the relationship between the reproductive variables and inbreeding is nonlinear, two-sample comparisons may show inbreeding depression not revealed by the linear models.

In addition, we compared the frequencies with which highly inbred (F ≥ 0.125) and non-inbred female fledglings were recruited into the breeding population. This test provided an alternative approach to analyses of the proportion of fledglings that survived to age one, although it was not performed for males because delayed reproduction of many males reduced sample sizes considerably.

Finally, we tested for differences in the frequency of nest failure and nesting effort between closely related and unrelated pairs. A pair received a yes or no for each of these two variables in each year. Nest failure was scored as yes if eggs were present but no young were fledged from the first nesting attempt of the season; nest effort was scored as yes if any eggs were laid that year. These frequency variables were analyzed using two-tailed Fisher's exact tests.

SPATIAL DISTRIBUTION OF KIN

To assess the spatial distribution of kin in this population, we compared the proportion of related breeding males in the neighborhood of a 1-year-old breeding female to the distance that female dispersed. The neighborhood was defined as all territories whose centers were within 2 km of the center of the territory in question. Neither the natal territory nor the breeding territory was included in these neighborhoods. These tests were restricted to females that dispersed and bred as yearlings in 1993, 1994, and 1995. We 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 to maximize detection of kinship. These and subsequent analyses were

confined to the area within observed female dispersal ranges; in other words, because we used actual dispersal distances in these analyses, kinship of males outside the observed range of female dispersal was not assessed.

CHANGE IN DISPERSAL BEHAVIOR IN THE PRESENCE OF KIN

We first determined whether the possibility of close inbreeding affected the frequency with which female fledglings dispersed from their natal site. We included only those cases, from 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. We judged 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% of helpers are full or half-siblings of the young they help raise (Walters et al. 1988).

Effect of kinship on natal dispersal distance was assessed by comparing dispersal distances of females with the proportion of related males in the neighborhood of the female's natal territory. This natal neighborhood included all territories whose centers were within 2 km of the center of the natal site; neither the natal territory nor the breeding territory was included.

Finally, we compared the tendency of females to disperse to the closest territory vacancy to the kinship of the males on those territories. Available vacancies were identified as any territory with a 1-year-old breeding female or with an unpaired male. Vacancies acquired by older females were considered unavailable to yearlings, because age-based dominance is assumed. Only females that dispersed and bred as yearlings between 1993 and 1995 were included in these last two analyses, for reasons described above.

All statistical tests were two-tailed and the level of statistical significance was set at 0.05. We considered P-values near 0.10 to be indicators of possible effects.

RESULTS

REPRODUCTIVE COSTS OF INBREEDING

Reproduction of related pairs. Kinship had a significant negative effect on the mean annual
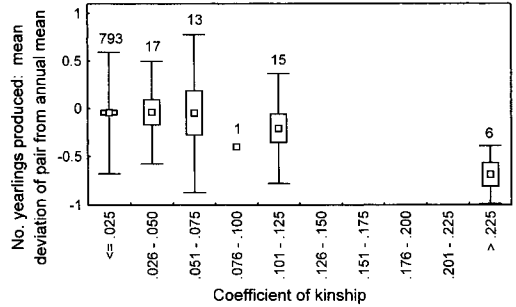

FIGURE 1. Box plots of the annual number of yearlings produced per pair (expressed as mean deviation of the pair from annual mean), categorized by the coefficient of kinship of the breeding pair. Box plots indicate the mean (inner open square), the mean ± the standard error (open rectangle), and the mean ± the standard deviation (whiskers). Sample size for each category is given above the whisker, and outliers are not illustrated.

number of yearlings produced per pair (Fig. 1, Table 1). This relationship was present in the linear regression using one average value for each pair (Fig. 1, Table 1), the regression using annual observations (Table 1), and a two-sample comparison between closely related and unrelated pairs (f $\geq$ 0.125 and f = 0, respectively; Mann-Whitney U-test, n = 21, 767, respectively; mean deviation from annual means for related pairs = −0.34, unrelated pairs −0.04; z = −2.24, P < 0.03). Closely related pairs produced 44% fewer yearlings per year than did unrelated pairs (0.40 vs. 0.71, including nest failures).

This substantial difference in overall reproduction was the result of two separate effects: reduced survival of inbred fledglings to age one (Table 1), and lowered hatching rates for closely related pairs (closely related and unrelated pairs; Mann-Whitney U-test, n = 20, 666, respectively; mean deviation from annual means = −0.10, −0.01, respectively; z = −2.29, P < 0.02). Lowered hatching was not clearly evident in linear regressions (Table 1); however, the relationship between kinship and hatching rate did not appear to be linear (Fig. 2) and so the two-sample comparison provides a better illustration of the effect. Specifically, hatching rate for moderately related pairs (0.125 > f > 0) appeared to be slightly higher than that of unrelated pairs (Fig. 2), and the sample of moderately related pairs was fairly large (n = 70). However, if the relationship between fitness and inbreeding is

TABLE 1. Effect of kinship on the reproduction of breeding pairs, as shown by linear regression. Reproductive variables are expressed as (A) mean deviation of the pair from annual means and (B) actual annual observations for pairs. Age of the female was included as a term in the models when its effect was significant ($P < 0.10$).

Trait	Kinship			Mean age of female			n[a]
	Slope	F	P	Slope	F	P	
A. Mean Deviation of the Pair from Annual Means							
#Yearlings	−1.96	6.40	0.01	0.03	7.01	0.01	845
Clutch size	−0.25	0.10	0.8	0.07	32.06	0.001	745
Prop. eggs that hatched	−0.37	2.46	0.1				745
Prop. nestlings that fledged	0.29	1.50	0.2	0.01	9.45	0.002	745
Prop. fledglings surviving to age 1	−0.83	4.33	0.04				845
B. Annual Observations for Pairs							
#Yearlings	−2.25	9.48	0.002	0.04	16.24	0.001	1,523
Clutch size	−0.28	0.15	0.7	0.09	69.33	0.001	1,178
Prop. eggs that hatched	−0.27	1.48	0.2				1,178
Prop. nestlings that fledged	0.12	0.31	0.6	0.01	3.32	0.07	1,178
Prop. fledglings surviving to age 1	−0.95	7.18	0.01				1,523

[a] First and last measures in each set of models include nests for which clutch size was inferred rather than precisely known.

nonlinear, the square of the inbreeding coefficient is expected to explain significant variation in the fitness measure (Ablanalp 1990). In our analyses, the square of the inbreeding coefficient was not a significant regressor for any reproductive variable, and so our suggestion of nonlinearity between hatching rate and inbreeding requires further investigation before it is confirmed.

Survival of fledglings of closely related pairs was reduced by 29% (30% of young fledged by closely related pairs survived to age one, vs. 42% of young fledged by unrelated pairs); hatching rates of closely related pairs were reduced by 13% (59% of eggs produced by closely related pairs hatched, vs. 68% of eggs produced by unrelated pairs). Clutch size and survival of nestlings to fledging were not related to kinship of the breeding pair (Table 1). Clutch size, nestling survival, and number of yearlings produced were influenced by age of the female (Table 1).

Highly inbred female fledglings became breeders less often than expected (Table 2). This result reaffirms the negative effect of pair kinship on survival of fledglings to age one.

In addition to the above effects, closely related pairs when compared to unrelated pairs showed a slight tendency toward more nest failures (Fisher's exact test, $n = 2,130$, $P = 0.1$) and lower nesting effort (i.e., years in which eggs were laid; Fisher's exact test, $n = 1,885$, $P = 0.08$).

SPATIAL DISTRIBUTION OF KIN AND NATAL DISPERSAL DISTANCE

Closely related males were not randomly distributed throughout the territories within female dispersal range, but were clustered near the natal territory. For 109 1-year-old breeding females in 1993, 1994, and 1995 combined, the proportion
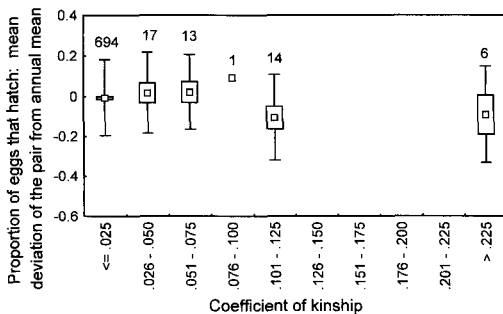

FIGURE 2. Box plots of the annual proportion of eggs that hatch (expressed as mean deviation of the pair from annual mean), categorized by the coefficient of kinship of the breeding pair. See Figure 1 for explanation of symbols.

TABLE 2. Recruitment of female fledglings by level of inbreeding (F). Expected frequencies in parentheses.

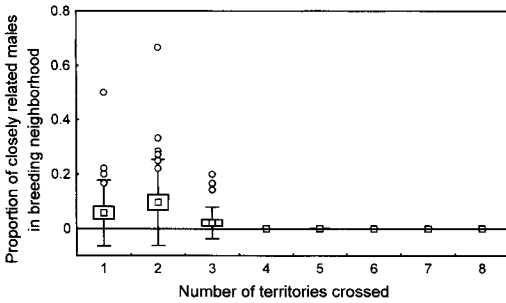|	Became breeder	Disappeared	P[a]
F = 0	465 (451)	976 (989)	0.01
F ≥ 0.125	4 (11)	29 (23)	

[a] Two-tailed Fisher's exact test.

FIGURE 3. Box plots of the proportion of closely related males (f ≥ 0.125) in the neighborhood of the breeding female (natal and breeding sites of the female excluded), categorized by the female dispersal distance in number of territories crossed (n = 109). Outliers (> mean + 4 SE) are indicated by open circles.

of closely related breeding males in the neighborhood of the breeding female was inversely correlated with the distance that the female dispersed (Fig. 3, Spearman rank correlations, r_s = −0.27, n = 109, P < 0.01). Also, females that paired with close relatives had dispersed a shorter distance than females pairing with unrelated males (Mann-Whitney U-test, n = 23, 434, mean = 1.6, 2.9, respectively; z = −2.99, P < 0.001). Thus, increasing dispersal distance decreased the likelihood of close inbreeding, because closely related males were not randomly distributed throughout territories within the observed dispersal range of females.

Despite the clustering of closely related males near the natal territory and costs of inbreeding documented above, natal dispersal distances of females were surprisingly short (Fig. 4). For 603 females that dispersed within the study area between 1982 and 1995, median dispersal distance was 2 territories, mean distance was 2.8 territories, and the most common dispersal distance was 1 territory. Females would have to move at least 4 territories to avoid all chance of mating with closely related males (Fig. 3); however, the majority of females (73%) moved less than 4 territories (Fig. 4).

Males moderately related to a given female were not clustered near her 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 (Fig. 5; n = 109, r_s = −0.05, P > 0.5). In addition, dispersal distance of females pairing with moderately re-
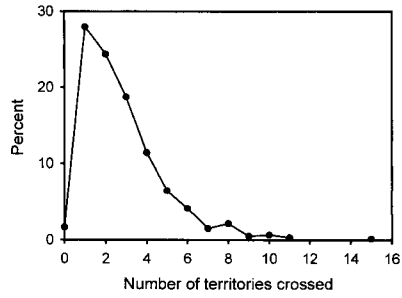

FIGURE 4. Distribution of natal dispersal distances, in number of territories crossed, for 603 female Red-cockaded Woodpeckers, 1982–1995.

lated males did not differ from that of females pairing with unrelated males (Mann-Whitney U-test, n = 74, 434, respectively; mean = 2.7, 2.9, respectively; z = −0.69, P > 0.5). Increasing dispersal distance did not decrease the likelihood of mating with moderately related males, because these males were distributed throughout the range of observed female dispersal distances.

CHANGE IN DISPERSAL BEHAVIOR IN THE PRESENCE OF KIN

Frequency of dispersal from the natal site. Dispersal of female fledglings from the natal site was affected by the presence of close kin (Table 3). A female was less likely to leave the natal site if there was no closely related breeding male present in the following year.

Change in natal dispersal distance. There was no correlation between dispersal distance and the proportion of closely related males neighboring the natal site (Fig. 6, n = 109, r_s =
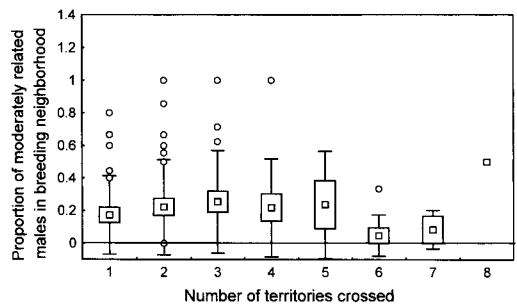

FIGURE 5. Box plots of the proportion of moderately related males (0 < f < 0.125) in the neighborhood of the breeding female (natal and breeding sites of the female excluded), categorized by female dispersal distance in number of territories crossed (n = 109). Outliers (> mean + 4 SE) are indicated by open circles.

TABLE 3. Frequency of dispersal of female Red-cockaded Woodpeckers from the natal territory, with and without a chance of inbreeding on that territory. Expected values in parentheses.

	Female dispersed	Female did not disperse	P^a
With chance of in-breeding	158 (153.5)	3 (7.5)	0.001
Without chance of inbreeding	27 (31.5)	6 (1.5)	

[a] Two-tailed Fisher's exact test.

-0.06, $P > 0.5$). Females did not disperse farther when more closely related males were nearby.

Frequency of occupying the closest vacancy. Kinship of males in the closest vacancy had no effect on whether or not the female occupied that vacancy (Table 4). Females did not appear to bypass the nearest vacancy to avoid mating with a closely related male.

DISCUSSION

In this study, we documented substantial inbreeding depression in Red-cockaded Woodpeckers. We then revealed a change in natal dispersal behavior in the presence of close kin, showing clearly that natal dispersal in this species is, in part, influenced by costs of close inbreeding. Dispersal is a complex trait, however, and not all aspects of dispersal serve to avoid inbreeding. Specifically, the frequency with which females disperse from their natal territory was influenced by costs of inbreeding, but these costs did not affect dispersal distance once females had left their natal site. This suggests that dispersal behavior is a compromise between costs of close inbreeding and benefits of short-distance dispersal. These results are discussed in detail below.

INBREEDING DEPRESSION

Close inbreeding results in substantial loss of fitness in Red-cockaded Woodpeckers. Two separate effects of close inbreeding on the reproduction of pairs were revealed: lowered hatching rates and lowered survival and recruitment of fledged young. Additional effects are suggested by the trend toward more nest failures and reduced nest effort for closely related pairs. Selection against close inbreeding is clearly operating in this population.
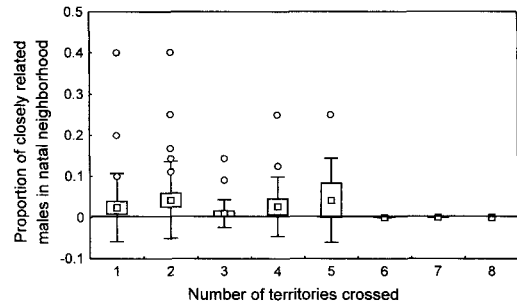

FIGURE 6. Box plots of the proportion of closely related breeding males ($f \geq 0.125$) in the neighborhood of the female's natal territory (natal and breeding sites of the female excluded), categorized by female dispersal distance in number of territories crossed ($n = 109$). Outliers (> mean + 4 SE) are indicated by open circles.

Reduced hatching rates. Reduced hatching rate has become a classic component of inbreeding depression in birds. It has been documented in Great Tits (*Parus major,* Bulmer 1973, Greenwood et al. 1978, van Noordwijk and Scharloo 1981), Blue Tits (*P. caeruleus,* Kempenaers et al. 1996), Great Reed Warblers (*Acrocephalus arundinaceus,* Bensch et al. 1994), Song Sparrows (*Melospiza melodia,* Keller 1998), and many types of domestic birds (reviewed by Abplanalp 1990). Reduced hatching rates for related pairs of Great Tits may be compensated for by increased nestling survival (van Noordwijk and Scharloo 1981), but no such compensation was found for Blue Tits (Kempenaers et al. 1996), Great Reed Warblers (Bensch et al. 1994), Song Sparrows (Keller 1998), or Red-cockaded Woodpeckers (this study).

In several domestic birds, maternal inbreeding (inbreeding of the breeding female) influences hatching rate, but typically the effects are not as

TABLE 4. The number of times a one-year-old dispersing female occupied the nearest vacancy, by the kinship of the male in that territory. Expected values in parentheses.

	Did the female occupy the nearest vacancy?		
	Yes	No	P^a
Was that male closely related?			
Yes	2 (2.5)	9 (8.5)	1.0
No	23 (22.5)	78 (78.5)	

[a] Two-tailed Fisher's exact test.

severe as those of embryo inbreeding (embryos produced by related pairs; Abplanalp 1990). In wild birds, lowered hatching has been commonly linked to embryo inbreeding (Greenwood et al. 1978, Bensch et al. 1994, Kempenaers et al. 1996), but two studies have documented an effect of maternal inbreeding (van Noordwijk and Scharloo 1981, Keller 1998). Keller (1998), in his study of inbreeding depression in Song Sparrows, found an effect in eggs of inbred females but not in eggs of related pairs; he called for more detailed research to clarify the mechanisms underlying reduced hatching.

We suggest that, for our study population, the relationship between hatching rate and embryo inbreeding may not be linear. Domestic birds have exhibited linear and nonlinear (both accelerated and slowed) effects on reproduction with increased inbreeding (Abplanalp 1990). We therefore agree with Keller (1998) that further research into underlying mechanisms is warranted.

Lowered survival. Evidence of inbreeding depression in post-fledging survival is accumulating. Survival effects are common in domestic birds (reviewed by Abplanalp 1990). In wild birds, lowered survival of inbred individuals has been shown in Song Sparrows (Keller et al. 1994, Keller 1998), Mexican Jays (*Aphelocoma ultramarina,* Brown and Brown 1998), Moorhens (*Gallinula chloropus,* McRae 1996), and Red-cockaded Woodpeckers (this study). Effects of inbreeding on survival may become more severe during environmental stress (Jiménez et al. 1994, Keller et al. 1994).

We found substantial costs of inbreeding in one of the largest remaining populations of Red-cockaded Woodpeckers. How inbreeding depression impacts the many small, isolated populations of this endangered species (see James 1995) is an issue of extreme importance.

NATAL DISPERSAL AND INBREEDING AVOIDANCE

Spatial distribution of kin and dispersal distance. We documented a tightly clustered spatial distribution of close relatives not found in other studies of kin structure (e.g., van Tierenden and van Noordwijk 1988, Wheelwright and Mauck 1998). In our study, males closely related to a given female were not distributed randomly throughout the population but were clustered near the female's natal site. No closely related males were found farther than three territories from the female's natal site. In contrast, males moderately related to a given female were not clustered near the natal site but were found throughout the observed range of female dispersal.

Surprisingly, despite the predictable spatial distribution of close relatives and the documented cost of close inbreeding, females did not disperse far enough to avoid close relatives as mates. In fact, although females had to move only four or more territories to avoid all chance of close inbreeding, most females moved just one or two territories. Thus, in this population, inbreeding does not affect the distance that females disperse once they have left their natal site. Dispersal distance is sex-biased (Walters et al. 1988, Daniels 1997) but does not produce spatial separation of kin.

Change in dispersal behavior in the presence of close kin. The frequency of dispersal of females from their natal territories changed with the presence or absence of a closely related breeding male. Females rarely remained on their natal territory, but they remained more often than expected if there was no chance of close inbreeding in the following year. Thus, inbreeding influences the dispersal of females from their natal territories.

However, female Red-cockaded Woodpeckers did not change dispersal behavior in response to closely related males that were not on the natal territory. Females did not increase dispersal distance in response to an increasing proportion of closely related males nearby, nor did they avoid nearby vacancies because there were closely related breeding males in those territories.

Wheelwright and Mauck (1998), in their detailed study of natal dispersal and inbreeding avoidance in Savannah Sparrows (*Passerculus sandwichensis*), reported a change in some dispersal behaviors in the presence of close kin. However, these changes were not sufficient to explain the complete lack of close inbreeding (kinship coefficient > 0.125) in their study population, a rate well below that expected based on random simulations. No spatial separation of kin existed, and the authors invoked an unidentified inbreeding avoidance mechanism.

In contrast, Keller and Arcese (1998) found no evidence for inbreeding avoidance in the Song Sparrows of Mandarte Island, British Columbia, despite substantial inbreeding costs in

this population (Keller et al. 1994, Keller 1998). They suggested that variation in inbreeding avoidance behaviors among species is influenced by variation in survival rates, and compared Song Sparrows to Acorn Woodpeckers (*Melanerpes formicivorus*) as an illustration (Keller and Arcese 1998). Red-cockaded Woodpeckers are similar to Acorn Woodpeckers in both survival and level of inbreeding avoidance, and so appear to fit Keller and Arcese's (1998) model. We agree that costs of inbreeding must be compared to costs of inbreeding avoidance (Bengtsson 1978, Waser et al. 1986, Keller and Arcese 1998), and discuss this point below with respect to cooperative breeders.

Why do females disperse such short distances? 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 (Zack 1990).

Studies of the delayed dispersal exhibited by males of this species, and of cooperative breeding in general, have attributed this behavior to unusually high variation in territory quality (Stacey and Ligon 1991, 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, by remaining on the natal territory, can better acquire a breeding position in a high-quality territory (Koenig et al. 1992, Walters et al. 1992).

We suggest that, although only male Red-cockaded Woodpeckers exhibit delayed dispersal, intense competition for breeding vacancies may affect natal dispersal of females as well. Females may occupy breeding positions in nearby territories because such positions are easier to obtain. The cost of mating with a close relative due to inbreeding depression may be less than the cost of travelling longer distances or competing with residents of more territories. The likelihood of mating with close kin appears fairly small, even for females dispersing fewer than four territories. For these females, the average proportion of closely related males within the natal neighborhood is less than 1 in 10 (Fig. 1).

KIN RECOGNITION

Our study provides evidence that females are able to recognize close kin on the natal territory,

but no evidence that females can recognize close kin that are off the natal territory. Familiarity (i.e., association, reviewed by Holmes and Sherman 1983), therefore, is the likely mechanism for kin recognition. Young females are by definition familiar with kin on the natal territory but may not be familiar with close relatives off the natal territory. Breeding females of this species exhibit a similar ability to recognize close kin; they almost always disperse if, after their mates have died, their sons inherit the breeding position (Walters et al. 1988, Daniels 1997). Kin recognition by breeding females is more sophisticated than simple familiarity: females faced with familiar but unrelated helpers as potential new mates rarely dispersed (Walters et al. 1988, Daniels 1997). Further research into kin recognition in this species is warranted.

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