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## **Genetic and Environmental Influences on Natal Dispersal Distance in a Resident Bird Species**

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# Genetic and Environmental Influences on Natal Dispersal Distance in a Resident Bird Species

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**ABSTRACT:** We analyzed more than 1,600 dispersal events from two populations of a North American cooperatively breeding woodpecker species to determine what factors influence natal dispersal distance and whether distance traveled affects reproduction later in life. We found significant heritability of natal dispersal distance, in both males and females, indicating substantial additive genetic variance for this behavioral trait. Natal dispersal distance additionally was affected by social and ecological factors: individuals dispersing in their first year of life moved longer distances than those staying on their natal site as helpers for a prolonged time prior to dispersal, and increasing territory isolation led to longer dispersal distances. Successful dispersers incurred fitness costs, with lifetime fledgling production (in both sexes) and lifetime production of recruits to the breeding population (in females only) decreasing with increasing natal dispersal distance. We conclude that natal dispersal distance has a genetic basis but is modulated by environmental and social factors and that natal dispersal distance in this species is (currently) under selection.

**Keywords:** natal dispersal, heritability, ecological conditions, fitness costs, evolution.

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Natal dispersal, the movement of an individual from its birthplace to the site of first reproduction, is a key process with a multitude of causes and consequences for individuals, populations, and communities (Clobert et al. 2001). Despite its importance, it is still a poorly understood behavioral trait. In animals, environmental and social factors have often been associated with natal dispersal distance.

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It has also been suggested that natal dispersal patterns are heritable (Howard 1960; Hilborn 1975; Greenwood et al. 1979; Newton and Marquiss 1983; Schroeder and Boag 1988; Hansson et al. 2003; Krackow 2003), but unambiguous empirical evidence for a genetic basis of natal dispersal behavior, and particularly of the distance dispersed, in natural populations of animals is lacking (Chepko-Sade and Tang Halpin 1987; Johnson and Gaines 1990; Krebs 1992; Wheelwright and Mauck 1998; Massot and Clobert 2000; Forero et al. 2002). This is surprising, since additive genetic variance in morphological, behavioral, and physiological traits related to migratory behavior appears to be common (Roff and Fairbairn 2001).

Theoretical models assume natal dispersal to be costly (Johnson and Gaines 1990), for example, in terms of reduced survival or fecundity. Empirical support for this assumption is equivocal, however, as some studies suggest fitness costs of dispersal to be present (Newton and Marquiss 1983; Pärt 1990, 1991; Julliar et al. 1996; Wheelwright and Mauck 1998; Forero et al. 2002), while other studies find no evidence for such costs (Arcese 1989; Spear et al. 1998; Altwegg et al. 2000). Costs of dispersal have been suggested to arise from increased energetic expenditure and increased exposure to predators during the dispersal process and/or from reduced familiarity with ecological and social conditions in novel environments (less efficient resource exploitation, less knowledge of predator communities and their habits; Greenwood 1980; Pärt 1994; Smith and Metcalfe 1997; Bensch et al. 1998).

The aims of this article were to evaluate genetic, environmental, and social factors influencing natal dispersal distance and to investigate potential fitness consequences of dispersal. Specifically, we tested the hypothesis that natal dispersal is heritable by examining if closely related individuals show similar dispersal patterns. Further, we examined the influence of ecological and social factors on natal dispersal distance to evaluate their relative importance compared to genetic factors. Finally, we tested the hypothesis that natal dispersal is costly by determining whether a negative relation existed between distance traveled and fitness. We analyzed dispersal and reproductive

data covering 22 years (1980–2001) from a population of 220 breeding groups of red-cockaded woodpeckers *Picoides borealis* in the Sandhills of south-central North Carolina, U.S.A., and data spanning 16 years (1986–2001) from a population of 50 groups inhabiting Camp Lejeune Marine Base in coastal North Carolina.

## Methods

### *Definitions, Data, and Sample Sizes*

We defined natal dispersal distance as the distance moved by an individual from its birthplace to the site of first reproduction (Clobert et al. 2001). Methods for monitoring reproduction and censusing the color-banded woodpecker populations as well as descriptions of the study areas are given in detail elsewhere (Walters et al. 1988; Zwicker and Walters 1999). Red-cockaded woodpeckers are cooperative breeders living in groups consisting of a breeding pair and up to five (mostly male) helpers (Conner et al. 2001, p. 117). We focused on those individuals that dispersed to breed, including birds dispersing in their first year of life (hereafter referred to as early dispersers) and, in addition to these early dispersers, those delaying dispersal to become helpers on their natal territory for 1–8 years before breeding elsewhere (helper-first birds), while excluding those individuals that never dispersed and instead bred on their natal territory (Walters et al. 1988). Whether an individual breeds on its natal territory, helps for a period and then disperses to breed, or disperses early without first helping is influenced by social and environmental conditions on the natal territory and its immediate neighborhood but not by genetic factors (Pasinelli and Walters 2002). Hence, inclusion of nondispersers may mask underlying additive genetic variance for natal dispersal distance. A total of 1,618 individuals from 1,324 broods were available for analysis (1,446 young from the Sandhills, 172 from Camp Lejeune).

### *Heritability Analyses*

Heritability of natal dispersal distance was estimated with parent-offspring regressions using only the Sandhills population because there were too few data for the Camp Lejeune population. Since natal dispersal is generally sex biased in birds (Clarke et al. 1997), we calculated separate regressions for each sex of offspring and parent. Heritability was then calculated as twice the slope of the regression coefficient, and the SE of the slope was also doubled (Falconer and Mackay 1996; Roff 1997). Each father and mother, respectively, was used only once, and if more than one offspring per father (or mother) was available, we used the average distance per sex. Midparent-

midoffspring regressions were not calculated since variances of natal dispersal distances differed between the sexes (Roff 1997). Prior to analysis, natal dispersal distance was  $\log_{10}(x + 0.5)$ -transformed, because the distribution of original values was highly skewed. Including the random value 0.5 in the transformation resulted in an improved model fit compared to the standard  $\log x$  transformation. We also examined the possibility of using an “animal model” with restricted maximum-likelihood (REML) estimation procedure to estimate variance components and heritabilities (Groeneveld and Kovac 1990; Knott et al. 1995; Groeneveld 1998), but our data precluded this approach because of their unbalanced structure (i.e., mostly only one surviving offspring per family).

### *Analyses of Environmental and Social Effects*

Of the 1,324 broods, 266 included two or more dispersers (average number of dispersers per family = 1.22, range 1–4). We randomly selected one fledgling per brood for analysis of environmental and social effects, resulting in sample sizes of 795 females and 389 males from the Sandhills population and 84 females and 56 males from the Camp Lejeune population. In a given year, each territory was used only once, but because ecological and social circumstances may vary annually on and around each territory, we used territory years instead of randomly selecting one observation per territory from the entire study period to retain as much information as possible.

Effects of study area (categorical variable), disperser type (early disperser vs. helper-first bird, categorical variable), year, relative nestling mass of the disperser, relative laying date, population size, and territory isolation on natal dispersal distance were analyzed with generalized linear models (Proc GENMOD; SAS Institute 1999–2001). We included natal dispersal distance of father and mother to examine the relative contribution of ecological, social, and genetic components to natal dispersal distance of sons and daughters, respectively. Year was treated as a continuous variable because we were interested in changes of natal dispersal distance over time that might be indicative of a microevolutionary change rather than in differences among years. Results did not differ if year was treated as a categorical variable (data not shown). Relative nestling mass was calculated as the deviation from the mean nestling mass per brood divided by the brood's standard deviation of nestling mass. To examine the effect of laying date on natal dispersal distance, we used relative laying date (of a clutch's first egg; cf. Schiegg et al. 2002), standardized as deviation from the annual median laying date per population. We used population size and territory isolation estimates for the year in which the disperser arrived and first bred in its new territory. However, using pop-

ulation size and territory isolation estimates from the disperser's birth year did not change the results (data not shown). Territories located within 3.5 km of the eastern and southern boundary of the Sandhills study area were excluded from the analysis, since monitoring of territories adjoining our study area to the east and south was not systematically done before 1988. To measure territory isolation, we determined the number of active and vacant territories within 3.5 km of the center of a disperser's natal site. This distance reflects the wider neighborhood of a territory and has been shown to influence whether male fledglings disperse early or remain as helpers (Pasinelli and Walters 2002). Active territories contained either a breeding pair (with or without helpers) or only a single (territorial) male, while vacant territories were not occupied in the year of dispersal but had been occupied at least once during the previous 5 years by a breeding pair or single male. Since females do not disperse to vacant territories (contrary to males), we excluded the vacant territories before calculating territory isolation for female dispersers. Population size was estimated as the number of active territories. We used  $\log_{10}(x + 0.5)$ -transformed natal dispersal distances because this transformation resulted in the best model fit. Separate generalized linear models were calculated for each sex because inclusion of both sexes in one model would have substantially lowered sample size, particularly in males, due to missing natal dispersal distances of one of the parents for most offspring.

#### *Analyses of Fitness Costs*

We used two measures of fitness. First, lifetime fledgling production (LFP) was the total number of fledglings produced during an individual's lifetime. Individuals no longer observed were considered dead, and birds still alive in 2001 were excluded from calculations. Red-cockaded woodpeckers are genetically monogamous (Haig et al. 1994), so LFP is not confounded by extrapair parentage. Second, an individual's lifetime production of recruits to the breeding population (LR) was the total number of offspring produced that survived to breed. Only birds born in the study areas through 1998 were considered, because it takes males on average 2.4 ( $\pm$ SD = 1.3) years ( $N = 665$ ) and females 1.2 ( $\pm$ 0.6) years ( $N = 831$ ) to become breeders. Note that the results did not change when birds born after 1995 were excluded (data not shown). Factors potentially influencing LFP and LR (dependent variables) were analyzed with generalized linear models (Proc GENMOD; SAS Institute 1999–2001) using a log link and assuming a Poisson distribution. Independent variables were untransformed natal dispersal distance (m) and disperser type (categorical variable with two levels: helper first, early disperser), while controlling for effects of year

(categorical variable) and territory quality. Territory quality was estimated with an index based on fledgling production and mortality on each territory over the study period (also see Daniels and Walters 2000; Pasinelli and Walters 2002). The index is calculated as the quotient of the total number of fledglings produced on a territory and the total number of individuals presumed to have died there. Before division, we subtracted the number of fledglings contributed by the specific individual to be analyzed from the total number of fledglings produced on that territory because we were interested in the effects of territory quality on LFP independent of the productivity of the bird in question. Model fit was checked using standard residual analyses (McCullagh and Nelder 1989).

## Results

### *Heritability of Natal Dispersal Distance*

Narrow-sense heritability (Falconer and Mackay 1996; Roff 1997) estimated from parent-offspring regressions of natal dispersal distances ranged from  $-0.16$  to  $0.88$  (table 1). Regressions of father-son and mother-daughter indicated significant heritability when including those individuals that were helpers before dispersing (fig. 1A, 1C). Considering only early dispersers (those dispersing immediately without helping, in both offspring and parents), the father-son regression remained significant ( $P < .001$ ; fig. 1B), while the mother-daughter regression was only marginally so ( $P < .076$ ; fig. 1D). No significant associations were found in the father-daughter and the mother-son comparisons (table 1), presumably due to sex differences in dispersal. There was no evidence for assortative mating of parents with respect to natal dispersal distance (with helper-first birds:  $r = 0.05$ ,  $P = .490$ ,  $N = 230$ ; early dispersers only:  $r = 0.05$ ,  $P = .603$ ,  $N = 110$ ), so heritability estimates obtained from parent-offspring regressions did not need to be adjusted (Roff 1997). Our analyses suggest the presence of substantial additive genetic variance for natal dispersal distance.

Van Noordwijk (1984) showed that resemblance between parent and offspring natal dispersal distances can depend on constraints imposed by the study area. In our study, mean natal dispersal distances of males (2,294 m, 95% confidence interval [CI] = 2,215–2,487 m,  $N = 551$ ) and females (3,307 m, 95% CI = 3,140–3,482 m,  $N = 1,067$ ) were very small compared to size of the study area (110,000 ha, roughly  $40 \times 30$  km), allowing us to sample large variation in dispersal distances, with the longest recorded dispersal movement being 34 km. However, because mean natal dispersal distances were so small, offspring could resemble their parents not because of genes but because of common environment; that is, offspring

**Table 1:** Heritability ( $h^2$ ) of natal dispersal distance in red-cockaded woodpeckers

Regression <sup>a</sup>	$\bar{X}_p$	SD <sub>p</sub>	$h^2$	SE	$V_A$	$V_R$	CV <sub>A</sub>	N	P
Early dispersers: <sup>b</sup>									
Father-son	3.47	.43	.88	.25	.16	.02	11.67	43	.001
Father-daughter <sup>c</sup>	3.49	.39	-.04	.18	0	.16	0	105	.853
Mother-son <sup>c</sup>	3.51	.34	-.12	.25	0	.13	0	67	.623
Mother-daughter	3.50	.36	.17	.10	.02	.11	4.27	330	.076
Helper-first birds:									
Father-son	3.32	.43	.30	.15	.05	.13	7.04	122	.048
Father-daughter <sup>c</sup>	3.36	.41	-.11	.14	0	.17	0	200	.446
Mother-son <sup>c</sup>	3.52	.34	-.16	.16	0	.11	0	156	.333
Mother-daughter	3.49	.36	.19	.10	.03	.11	4.53	341	.048

Note: Natal dispersal distance  $\log_{10}(x + 0.5)$ -transformed prior to analyses to optimize model fit.  $\bar{X}_p$  and SD<sub>p</sub> = mean and standard deviation of parental dispersal distance. Total phenotypic variance ( $V_p$ ) partitioned into additive genetic variance ( $V_A$ ) and residual variance ( $V_R$ ). CV<sub>A</sub> calculated as  $100\sqrt{V_A/\bar{X}_p}$ ; where  $h^2 < 0$ ,  $V_A$  was set to 0 (cf. Houle 1992). N = number of parent-offspring pairs; P values refer to regressions. Early dispersers are only individuals moving in their first year of life; helper-first birds included individuals that were helpers before eventually dispersing to breed.

<sup>a</sup> Calculated separately for each sex of offspring and parent, since natal dispersal is generally sex biased in birds (Clarke et al. 1997).

<sup>b</sup> Refers to both offspring and parents; that is, helper-first birds excluded.

<sup>c</sup>  $h^2$  and SE corrected for unequal variances between sexes (Roff 1997).

may have about the same options in terms of territories to which to disperse as had their parents, and this constraint might cause the resemblance shown above. We tested this possibility by regressing natal dispersal distances of sons and daughters on those of nonrelated male and female individuals, respectively, from adjacent territories, expecting significant associations between natal dispersal distances of these unrelated individuals if environmental constraints existed. Neighbors selected for analyses were those closest in distance to the individual and territory in question, and if more than one individual on a next-door territory was available, one was randomly chosen (irrespective of disperser type). The regression slopes were not significantly different from 0 in either case (males: with helper-first birds,  $b = -0.04$ , SE = 0.07,  $P > .55$ ,  $N = 100$ ; early dispersers only,  $b = 0.09$ , SE = 0.19,  $P > .62$ ,  $N = 32$ ; females: with helper-first birds,  $b = 0.02$ , SE = 0.05,  $P > .74$ ,  $N = 317$ , early dispersers only:  $b = 0.03$ , SE = 0.05,  $P > .50$ ,  $N = 308$ ). Median distances between territories of offspring and nearest neighbors for males and females were 692 m ( $N = 100$ ) and 665 m ( $N = 317$ ), respectively, so given an average territory size of 80 ha (Walters et al. 2002), nearest neighbors and subjects probably experienced similar environments. We conclude that the heritability estimates from the father-son and mother-daughter regressions in table 1 are unlikely to arise from constraints imposed by the study area.

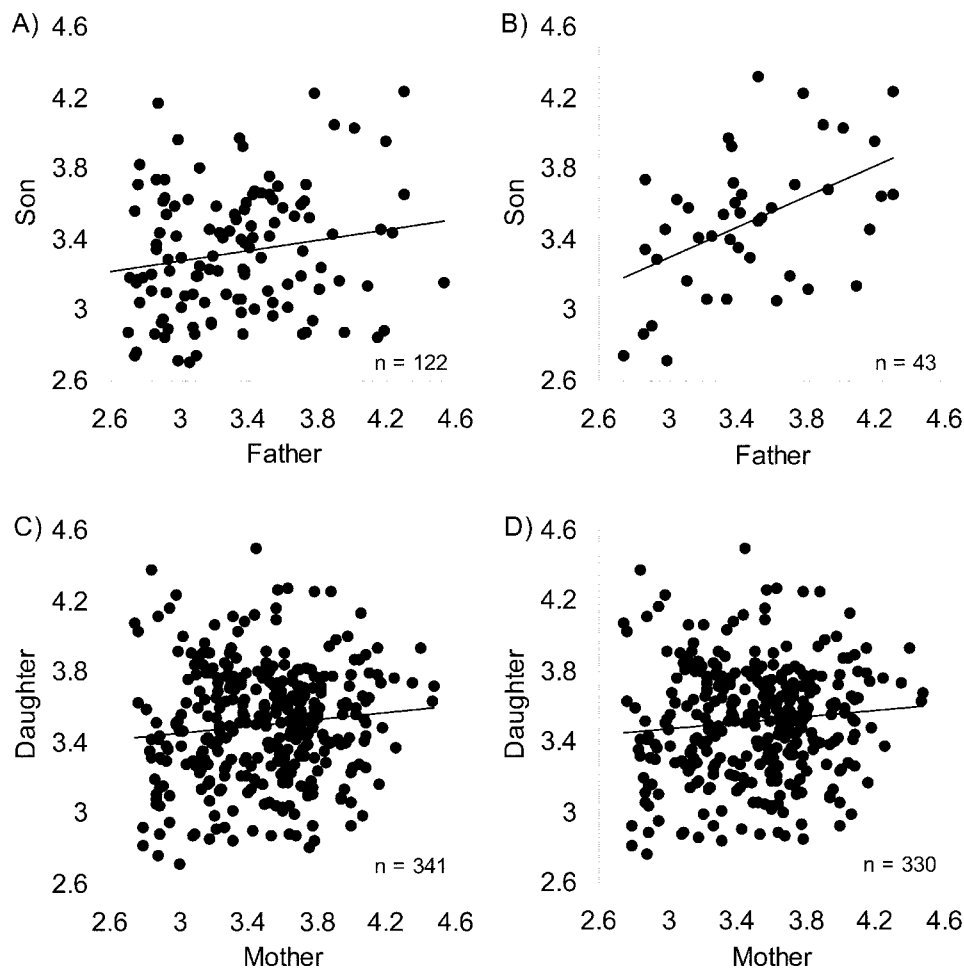
*Ecological and Social Factors*

To simultaneously examine the relative importance of genetic, environmental, and social influences on natal dis-

persal distance, we included natal dispersal distances of male or female parents in the generalized linear models attempting to explain variation in dispersal distance, since paternal and maternal natal dispersal distances were significantly linked to offspring natal dispersal distance. In addition to genetic factors, ecological and social conditions influenced natal dispersal distance in males (table 2). Increasing territory isolation led to longer natal dispersal distances. Further, natal dispersal distances significantly differed between disperser classes, with individuals having been helpers before dispersing moving shorter mean distances (1,539 m, 95% CI = 1,336–1,774 m,  $N = 67$ ) than early dispersers (3,041 m, 95% CI = 2,543–3,635 m,  $N = 86$ ). In females, we again found a marginally significant effect of mother’s dispersal distance on natal dispersal distance of the offspring but no significant effects of ecological or social factors (table 2). Thus, these analyses confirm that natal dispersal distance appears to have a genetic basis and that these genetic effects are stronger in males than in females. The analyses further suggest that ecological (isolation of territories) and social (disperser type) factors are important for males but not for females during the dispersal process.

*Fitness Costs*

In both sexes of red-cockaded woodpeckers lifetime fledgling production (LFP) was negatively related to natal dispersal distance (males: estimate  $\pm$  SE =  $-0.011 \pm 0.005$ ; females:  $-0.008 \pm 0.004$ ; table 3), while controlling for effects of disperser type (males:  $-0.022 \pm 0.041$ ; fe-



**Figure 1:**  $\text{Log}_{10}(x + 0.5)$ -transformed natal dispersal distances (km) of sons and daughters regressed on those of fathers and mothers, respectively. A, C, Helper-first birds (individuals that were helpers before eventually dispersing to breed); B, D, early dispersers (only offspring and parents moving in their first year of life). For regression statistics see table 1.

males:  $-0.052 \pm 0.092$ ), quality of breeding territories (males:  $-0.200 \pm 0.028$ ; females:  $-0.063 \pm 0.023$ ), and years (table 3). Excluding helper-first birds did not change the results in females (data not shown), while in males, the relation between LFP and natal dispersal was no longer significant when helper-first birds were excluded ( $\chi^2 = 0.27$ ,  $df = 1$ ,  $P = .605$ ,  $N = 280$ ). A negative relationship of lifetime production of recruits to the breeding population (LR) with natal dispersal distance existed in females (estimate  $\pm$  SE =  $-0.022 \pm 0.010$ ) but not in males ( $0.003 \pm 0.013$ ), both for all birds (table 3) and for early dispersers only (data not shown). Again, we controlled for effects of disperser type (males:  $0.082 \pm 0.119$ ; females:  $0.141 \pm 0.321$ ), territory quality (males:  $-0.084 \pm 0.077$ ; females:  $0.005 \pm 0.056$ ), and years (table 3). Longevity was not related to natal dispersal distance (males:

estimate  $\pm$  SE =  $-0.003 \pm 0.005$ ,  $\chi^2 = 0.4$ ,  $df = 1$ ,  $P = .547$ ,  $N = 521$ ; females:  $-0.003 \pm 0.004$ ,  $\chi^2 = 0.5$ ,  $df = 1$ ,  $P = .466$ ,  $N = 1,009$ ). Thus, the significant effects on LFP and LR are due to fecundity, not length of the reproductive life span. We conclude that the distance moved during natal dispersal is under negative directional selection that possibly is more pronounced in females than in males.

### Discussion

This article presents evidence that in red-cockaded woodpeckers the distance moved during natal dispersal has a genetic basis. Social and ecological factors have regularly been found to influence natal dispersal (Massot and Clobert 2000; Clobert et al. 2001; Merilä and Sheldon 2001;

**Table 2:** Relative contributions of ecological, social, and genetic factors to natal dispersal distance

Parameter	Males ( <i>N</i> = 129)					Females ( <i>N</i> = 368)				
	df	Estimate	SE	$\chi^2$	<i>P</i>	df	Estimate	SE	$\chi^2$	<i>P</i>
Site	1	-1.182	.874	1.83	.176	1	.103	.548	.04	.851
Year	1	.001	.008	.02	.898	1	-.001	.005	.08	.780
Disperser type	1	.260	.065	16.17	.0001	1	.170	.112	2.33	.127
Relative nestling mass	1	-.068	.047	2.12	.146	1	.007	.028	.06	.811
Relative laying date	1	.001	.003	.02	.885	1	.002	.002	1.16	.281
Population size	1	-.007	.005	2.19	.139	1	-.000	.003	.00	.949
Territory isolation	1	-.008	.004	4.95	.026	1	.002	.003	.76	.383
Parental dispersal distance	1	.163	.079	4.20	.041	1	.092	.055	2.83	.092

Note: Generalized linear model with offspring natal dispersal distance ( $\log_{10}[x + 0.5]$ -transformed, to optimize model fit) as dependent variable, site (Sandhills/Camp Lejeune), disperser type (helper first/early disperser) as categorical independent variables, year, relative nestling mass ( $[\text{individual mass} - \text{mean mass}_{\text{brood}}] / \text{SD mass}_{\text{brood}}$ ), relative laying date (laying date of first egg of brood - median laying date of first egg of all broods per year and study site), population size (number of active territories), territory isolation (number of active and vacant [only in males] territories < 3.5 km from the center of a disperser's natal site in year when disperser first bred), and natal dispersal distance of the parent ( $\log_{10}[x + 0.5]$ -transformed) corresponding in sex to the offspring as continuous independent variables.  $\chi^2$  and *P* values refer to likelihood ratio tests of Proc GENMOD (SAS Institute 1999–2001) with normal error distribution and identity link function.

Roff and Fairbairn 2001; Meffert et al. 2002), while inheritance of natal dispersal tendency has only recently been suggested to exist (Hansson et al. 2003; Krackow 2003), and no study has so far unambiguously shown heritability

**Table 3:** Effects of disperser type, natal dispersal distance, territory quality, and year on lifetime fledgling production (LFP) and on lifetime production of recruits to the breeding population (LR)

Parameter	df	Males		Females	
		$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
<b>LFP:</b>					
Disperser type	1	.30	.586	.31	.576
Distance	1	5.24	.022	4.37	.037
Quality	1	51.97	<.001	7.61	.006
Year	19	234.01	<.001	213.21	<.001
<b>LR:</b>					
Disperser type	1	.47	.492	.20	.653
Distance	1	.07	.785	6.06	.014
Quality	1	1.17	.278	.01	.934
Year	17	67.06	<.001	144.46	<.001

Note: LFP: total number of fledglings produced during an individual's lifetime,  $N_{\text{males}} = 521$ ,  $N_{\text{females}} = 1,009$ . LR: an individual's total number of offspring produced that survived to breed,  $N_{\text{males}} = 347$ ,  $N_{\text{females}} = 753$ . Note that the apparent skew in sex ratio of recruits results from exclusion of males that bred on their natal site (i.e., no natal dispersal occurred). Generalized linear models (Proc GENMOD; SAS Institute 1999–2001) with log link function and response probability distribution defined as Poisson. Disperser type = categorical variable with two levels (helper first/early disperser); distance = natal dispersal distance; quality = index of territory quality (see text); year = categorical variable.  $\chi^2$  and *P* values refer to likelihood ratio tests of Proc GENMOD (SAS Institute 1999–2001).

of distance moved. Whether or not this previous lack of evidence reflects differences in the ecology of the species studied is unclear. We suspect, however, that in many cases neither the geographical nor the temporal scales of the studies were sufficient to allow detection of heritability of natal dispersal distance (see also Van Noordwijk 1984; Arcese 1989) and thus suggest that natal dispersal distance may have a genetic basis in other species as well. Consistent with this assertion, natal dispersal seems to be linked with postfledging exploratory behavior (Dingemanse et al. 2003), which has recently been shown to be heritable (Dingemanse et al. 2002).

We found a fairly large difference in heritability of natal dispersal distance between early-dispersing males compared with early-dispersing and helper-first males combined ( $z = 1.99$ ,  $P = .023$ ; for details of calculation of test statistic, see Jensen et al. 2003, p. 1299), suggesting that heritability is primarily expressed in early dispersers. We previously established that the decision of whether to become a helper or to disperse from the natal site in the first year is conditional on social and environmental conditions on and around the natal territory (Pasinelli and Walters 2002). Therefore, the expression of additive genetic variance for natal dispersal distance could be partly inhibited by extrinsic factors in those individuals “choosing” to stay as helpers.

Pre- and postnatal conditions have been shown to affect natal dispersal (Massot and Clobert 2000) but are unlikely to account for the parent-offspring similarities we report. Prenatal effects mediated via the mother may result in variation of egg steroid levels among offspring (Schwabl 1993), but such variation in hormone levels appears to

affect primarily the probability and timing of natal dispersal rather than distance moved (Dufty and Belthoff 2001). Moreover, strong maternal effects are expected to act on male and female offspring in a similar way, but heritability estimated from mother-daughter and mother-son regressions were quite different (with helper-first birds:  $z = 1.86$ ,  $P = .032$ ). Our nearest-neighbor analyses rule out one postnatal component, possible constraints imposed by the study area (Van Noordwijk 1984), as a likely explanation of the similarity in parent and offspring natal dispersal distances reported here. In addition, if strong environmental constraints were driving the significant relationships we observed, we would have expected to find significant regressions in the father-daughter and mother-son comparisons, which was not the case. Parental aggression during the postfledging period is unlikely to induce natal dispersal behavior in this species because the regular presence of primary helpers on the parental territory implies tolerance of parents toward their young (Walters et al. 1988, 1992). Further, we found no evidence that nestling body mass influenced distance moved later in life, suggesting that neither parental provisioning patterns nor individual quality, estimated by nestling weight, played a role in determining natal dispersal distance. Individual quality may still be important, though, because dispersing young likely compete among each other for territories, but we do not have the data to assess this possibility because this requires knowledge of not only the quality of individuals but also their encounters during dispersal.

Our finding of a substantial heritable component for natal dispersal distance does not imply that the distance traveled is inflexible. Rather, the movements of individuals appear to be modulated by social and environmental factors, as suggested by the influences of disperser type and territory isolation. Competition for breeding vacancies appears to be more intense among males than among females, one manifestation of which is the much higher frequency of helping among males (Walters et al. 1992). A male's decision to leave his natal territory in his first year rather than stay to become a helper is influenced only by ecological and social conditions and not at all by genetic factors (Pasinelli and Walters 2002). Males that disperse early are in a poor competitive position; that is, they are low ranking within their own brood and family group and experience large numbers of other males in their neighborhood (Pasinelli and Walters 2002). Thus, the situation in which genetic influence on dispersal distance is greatest, early dispersal by males, appears to enable these early dispersers to escape local competition, reminiscent of dispersal by rodents to escape high population densities (Krebs 1992). Thus, natal dispersal behavior in red-cockaded woodpeckers, and probably in many other vertebrates as well, appears to be a plastic trait, with

distance eventually moved representing a mixture of pre-disposed and conditional factors.

Our results further suggest that distance traveled affects fitness later in life. In both sexes, individuals produced fewer offspring over their lifetime with increasing natal dispersal distance. One explanation for this pattern may be that familiarity with the environment decreases as individuals progressively leave their natal neighborhood, leading to reduced LFP for individuals moving longer distances. Reduced familiarity has been shown to negatively influence foraging behavior, territory establishment, predator detection, and mate attraction in birds (Greenwood 1980; Pärt 1994; Smith and Metcalfe 1997; Bensch et al. 1998). Effects of familiarity should be strongest in the first brood of an individual's life and with increasing distance from the natal site because familiarity should increase in subsequent years and with proximity of the breeding territory to the natal site. We tested this possibility by excluding the first broods of individuals in the calculation of LFP and repeating the analyses relating LFP to natal dispersal distance. However, the negative relation between LFP and natal dispersal distance persisted (data not shown), suggesting that potential fitness losses due to unfamiliarity during first broods are not primarily responsible for the overall reduced LFP of individuals moving longer distances. Alternatively, individuals moving longer distances may be of lesser quality than those dispersing over short distances. However, we found no relation between relative weight as a nestling and distance moved during natal dispersal, suggesting that this aspect of individual quality does not affect natal dispersal distance or that relative nestling weight does not accurately reflect individual quality. Finally, fitness costs of dispersal may be due to outbreeding depression, although the evidence for outbreeding depression is so far rather modest in birds (cf. Marr et al. 2002) and may be unlikely to occur at the spatial scale examined here.

Overall, our analyses on the relation between fitness estimates (LFP and LR) and distance traveled support the widespread notion, derived from theoretical considerations, that natal dispersal is costly (Johnson and Gaines 1990). In our calculation of LFP, we did not include potential inclusive fitness benefits incurred by those individuals that stayed and helped before dispersing. Had we done this and found a negative relation between LFP and distance dispersed, then it would be impossible to separate effects of helping from those of dispersing on fitness, because the negative relation may have resulted from inclusive fitness benefits enjoyed by helpers or by advantages of their short dispersal distances. Omitting inclusive fitness calculations, as done here, and still finding a negative relation between LFP and distance moved strongly suggest costs of natal dispersal.



Our analyses include only successful dispersers and thus exclude potential costs associated with the dispersal process itself, which are substantial in this species in terms of reduced survival of dispersers compared to philopatric individuals (Walters et al. 1992; Daniels and Walters 2000). These costs are not known to vary with distance moved, however. When these costs are combined with those reported here, the cost of dispersal in red-cockaded woodpeckers appears to be high indeed. The idea that natal dispersal is costly has so far received equivocal empirical support from comparisons of reproduction and/or survival of philopatric versus dispersing individuals (Small et al. 1993; Bélichon et al. 1996 and references therein; Bensch et al. 1998; Wheelwright and Mauck 1998; Altwegg et al. 2000).

Our fitness analyses suggest that natal dispersal distance is under (negative) directional selection, particularly in females. Together with our findings from the heritability analyses, we would expect a change of natal dispersal distance to occur over time, which was not observed in this study (year effect not significant; table 2). Such an absence of a microevolutionary change despite (apparent) directional selection on a heritable trait has been observed in other studies as well (see Merilä et al. 2001a, 2001b). We suggest that because both environmental variation, mediated through territory isolation, and social variation, mediated through disperser type, influence natal dispersal distance as indicated above, an evolutionary response of this behavioral trait may be masked. Further analyses are needed to clarify the observed lack of change in natal dispersal distance over time in this species.

Traits closely associated with fitness usually show low heritabilities (Roff 1997) because natural selection presumably erodes genetic variation in these traits. Our results lend support to these ideas since we found a reduction in heritability from early-dispersing males to all males (i.e., including the helper-first birds) to females and an increase in fitness costs of natal dispersal distance from early-dispersing males to females. Thus, genetic variation for natal dispersal distance appears to be lowest in the class (females) that bears the highest fitness costs.

Studies examining long-term fitness consequences of natal dispersal distance in long-lived species are still extremely rare (Spear et al. 1998; Forero et al. 2002). Fitness consequences of natal dispersal may vary across species and even across populations within species. Clearly, more studies are needed to better understand the evolutionary significance of different dispersal patterns in relation to varying environmental and social circumstances. Long-term studies examining fitness consequences will continue to provide valuable insights into the evolution of natal dispersal, as will experimental studies separating fitness consequences of individual traits and dispersal itself, al-

though the difficulties of studying dispersal behavior hold great challenges for experimental approaches (Koenig et al. 1996).

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