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Habitat Relations

Social Composition of Destination Territories and Matrix Habitat Affect Red-Cockaded Woodpecker Dispersal

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ABSTRACT We studied the influence of matrix habitats and destination territory social composition on dispersal choices made by red-cockaded woodpeckers (*Picoides borealis*). We compared matrix habitats and social conditions for 165 dispersals documented between 1995 and 2005 with similarly distanced destinations that went unselected. We modeled data with discrete choice analysis methods, and ranked models using a model selection approach. Model-averaged parameters indicated that juvenile female, and juvenile and helper male red-cockaded woodpeckers dispersed across matrix forests with characteristics similar to those used for breeding. Models differed for sex and social classes, but results generally indicated that birds chose not to transit forests with greater densities of hardwood trees and young pines, and that dispersal was more likely to occur across forests with more large diameter pine trees. Dispersers of both sexes also chose destinations without non-breeding helpers that might present aggressive social challenges to dispersers, particularly males. Juvenile females and helper males also preferred to disperse to territories that were currently occupied by breeding woodpeckers. Previous studies documented the influence on dispersal of travel distance, natal area social interactions and resources, and resources at dispersal destinations. Our results extend factors that affect dispersal movement to include matrix habitats traversed by dispersers and the social composition of destination territories. As such, results have key implications for promoting population connectivity and conservation management of endangered red-cockaded woodpeckers, as well as other resident territorial birds. © 2011 The Wildlife Society.

KEY WORDS cooperative breeding, dispersal, *Picoides borealis*, population connectivity, red-cockaded woodpecker.

Information about dispersal is critical to understanding population dynamics and evolutionary biology, and to designing sound conservation strategies for endangered species (Walters 2000, Clobert et al. 2001, Bullock et al. 2002). Recent work focused on describing individual movements and the evolutionary and ecological factors underlying dispersal patterns (Clobert et al. 2001). Reasons for dispersing are evident (Lidicker 1962, Myers and Krebs 1971). By moving away from natal areas, dispersers can access unsettled or higher quality habitats with lower densities of conspecifics (Kenward et al. 2001, Forero et al. 2002). Dispersal also provides a means by which individuals address temporal fluctuations in habitat quality (Travis and Dytham 1999), and reduce chances of inbreeding as kin are redistributed on the landscape (Pusey and Wolf 1996, Wheelwright and Mauck 1998). Along with these benefits, individuals also incur apparent and real costs to dispersal from novel habitats, predators, resource limitations, and conspecific aggression (Daniels and Walters 2000*a*).

Strategic dispersal choices can minimize risks and maximize benefits (Johnson and Gaines 1990, Williams and Rabenold 2005). Some resident birds make extensive and repeated forays into the surrounding landscape to gather information about potential choices before making informed decisions about dispersal (Kesler and Haig 2007*a*, *b*; Kesler et al. 2010). Initial decisions about dispersal are thus likely rooted in social and resource conditions of the natal area (Stacey and Ligon 1991, Pasinelli and Walters 2002), as well as conditions at dispersal destinations (Emlen 1982, Fischer and Lindenmayer 2007, Schick et al. 2008). The matrix habitats between natal areas and destinations also have the potential to influence dispersal, especially for resident species that make few inter-territory movements (Forsman et al. 1984, Koenig and Dickinson 2004). Open habitat features, including roads (Riley et al. 2006, Tremblay and St. Clair 2009), rivers (Hayes and Sewlal 2004), and forest gaps (Creegan and Osborne 2005), as well as the composition and orientation of landscape features (Levey et al. 2005, Kuefler and Haddad 2006, With et al. 2006), have all been shown to affect animal movements and population connectivity. Social conditions and competition from conspecifics may also influence dispersal, especially in populations of cooperatively breeding species with a pool of non-breeding, adult helpers queuing for breeding opportunities.

Dispersal of cooperatively breeding red-cockaded woodpeckers (*Picoides borealis*) has received considerable attention.

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The bird is a long-term resident species occupying year-round territories as individuals, pairs, or cooperatively breeding groups (Walters 1990, Walters et al. 1992*a*, Conner et al. 2001). Territories are centered on nesting and roosting cavities, and breeders can be assisted by up to 5 delayed dispersers, or helpers, most of which are male (Conner et al. 2001). Female red-cockaded woodpeckers typically disperse as juveniles, and males either disperse from natal sites as juveniles or remain on natal areas as helpers. Although both sexes exhibit protracted dispersal distances, females generally move farther (Walters et al. 1988, Walters et al. 1992*b*, Daniels and Walters 2000*b*, Kesler et al. 2010). A genetic component also affects dispersal distances, and resource and social characteristics of the natal area affect decisions about whether to disperse (Pasinelli and Walters 2002, Pasinelli et al. 2004).

Recent investigations explored the influence of matrix habitats on movement and dispersal for a range of taxa (Stevens et al. 2006, Brudvig et al. 2009, Clark et al. 2010), but empirical data are almost entirely absent from the literature for birds (Walters 1998, Smith and Hellmann 2002; but see Castellon and Sieving 2006, Moore et al. 2008, Coulon et al. 2010). Thus, we studied the influence of matrix habitat composition and the social composition at destination territories on dispersing red-cockaded woodpeckers. We used dispersal records from a long-studied population, in which nearly every bird was individually marked. We tested for influence of forest stand characteristics in the matrix areas between natal territories and dispersal destinations, and studied whether dispersers were more likely to move to occupied territories, and whether they avoided territories with same-sex resident competitors.

STUDY AREA

We used data from censuses of a contiguous population of red-cockaded woodpeckers at Fort Bragg Army Base (79.302° E, 35.108° N), in the Sandhills region of south-central North Carolina, USA. The area was characterized by second-growth longleaf pine (*Pinus palustris*) savanna, which was described in detail previously (Department of Defense 2001). We used data from 2,274 individually marked red-cockaded woodpeckers from 127 breeding territories with known geographic coordinates. The vast majority of birds in the study population were marked with individual-specific color band combinations and continuously monitored since 1983, and all breeding territories were documented for the study area. Methods for monitoring the population were presented elsewhere (Walters et al. 1988, Zwicker and Walters 1999). We restricted data geographically to movements within the contiguous western Fort Bragg population, where forest stand and territory social data were continuously available. We temporally truncated dispersal data for red-cockaded woodpeckers to include only dispersals between 1995 and 2005 to maintain relevance to landscape and vegetation data collected in 2001 (forest stand data provided by P. Wefel, Fort Bragg Forestry).

METHODS

Dispersals and Choice Sets

We used discrete choice analyses to compare chosen dispersal destinations with unselected destinations. We identified red-cockaded woodpeckers that dispersed as juveniles and helpers in census records. As defined elsewhere (Conner et al. 1997), we considered dispersals to be movements associated with social status transitions from first year juvenile or after hatch year helper on a natal territory, to breeder on a second territory during the following season. We also considered birds to have dispersed if they transitioned to new territories where they held a dominant position, but did not breed, or where they solitarily occupied vacant territories. We identified choice sets of territories that were available to each disperser, which included the actual dispersal destination and 4 unused destinations (see Cooper and Millspaugh 1999 for review of selecting choice sets). Unused destinations were territories that were most similarly distanced from the natal territory as the actual dispersal destination, and upon which a same-sex breeding replacement was made during the same time period as the observed dispersal event. Dispersing woodpeckers occasionally re-occupy recently abandoned territories so we also considered unoccupied territories as potential dispersal destinations if they hosted breeding birds within the 5 years prior to the observed dispersal (Doerr et al. 1989, Pasinelli et al. 2004).

Habitat Matrix and Social Composition

We used a geographic information system (GIS; ArcView 3.3 and Arc GIS 9.0, Environmental Systems Research Institute, Inc. [ESRI], Redlands, CA) to evaluate inter-territory distances by calculating the length of a line linking the centers of the origin and destination territories (geographic data provided by the Sandhills Ecological Institute, Southern Pines, NC and Fort Bragg Endangered Species Branch, Fort Bragg). We defined matrix habitats as forest stands that intersected lines connecting dispersal origins with used and unused destinations. We used the GIS to assess forest stand composition in dispersal matrix habitat between origin and destination territories. Forest stand variables aligned with previously published metrics used for evaluating red-cockaded woodpecker breeding habitat (Table 1). In general, the birds require limited midstory vegetation, intermediate densities of medium-sized and large pine trees, and old-growth pines in at least low densities (Carter et al. 1983, James et al. 1997, James et al. 2001, Walters et al. 2002, U.S. Fish and Wildlife Service 2003). Matrix habitat data included mean pine and hardwood tree densities in matrix forest stands in each of 3 size classes that were previously shown to affect breeding in red-cockaded woodpeckers (10.2–25.4 cm dbh, 25.4–35.6 cm dbh, and >35.6 cm dbh; Zwicker and Walters 1999, Walters et al. 2002). When multiple stands comprised matrix habitats, we weighted variable values by the proportion of the matrix line they intersected. All measures were made using ArcView GIS 3.3 and ArcToolbox (ESRI, Redlands, CA), and X-Tools extension (Oregon Department of Forestry, Salem, OR).

Table 1. Variables for forest stand characteristics in matrix habitats and the social composition of destination territories, and associated hypothesized effects on natal dispersal in red-cockaded woodpeckers in North Carolina, 1995–2005.

Variable	Description	Hypothesized effect
Distance	Euclidean distance (km) between natal territory and destination territory center	Greater dispersal distances inhibit dispersal
PTPH_10	Mean number pine trees/ha in the 10–25 cm dbh class	Small pine trees inhibit dispersal
PTPH_25	Mean number pine trees/ha in the 25–36 cm dbh class	Large pine trees facilitate dispersal
PTPH_36	Mean number pine trees/ha in the >36 cm dbh class	Very large pine trees facilitate dispersal
HTPH_10	Mean number hardwood trees/ha in the 10–25 cm dbh class	Small hardwood trees inhibit dispersal
HTPH_25	Mean number hardwood trees/ha in the 25–36 cm dbh class	Medium hardwood trees inhibit dispersal
HTPH_36	Mean number hardwood trees/ha in the >36 cm dbh class	Large hardwood trees inhibit dispersal
Occupancy	Destination occupied by breeding birds	Breeding pair occupancy indicates quality territory, but also potential competition
Juvenile	Destination is occupied by same-sex juvenile	Possible competition for settlement, especially for males that might stay and become helpers
Helper	Male helper member of social group at destination	Male helper at destination presents competition for dispersing males

We used monitoring records from the breeding season preceding observed dispersal events to document the composition of red-cockaded woodpecker social groups at used and unused destinations. We identified whether territories were occupied by a breeding pair, whether each group included a male helper, and whether they had a juvenile of the same sex as the dispersing individual.

Statistical Analyses

We tested the influences on dispersal of matrix habitats and the social composition of dispersal destinations using discrete choice methods (Cooper and Millspaugh 1999, Buskirk and Millsapugh 2006) and a model selection approach (Burnham and Anderson 2002). We composed a complete model set containing all possible combinations of forest stand and destination territory social variables (Table 1). Testing all combinations creates potential for spurious results and multicolinearity (Cook et al. 2001). Multicolinearity among explanatory variables can inflate standard errors of parameter estimates, so we eliminated models with more than 1 pine tree variable or hardwood tree variable. We tested for multicolinearity among variable combinations that were represented in the remaining candidate models (SAS PROC REG; SAS Institute 2004) and found that all fell within reasonable tolerances $\leq$0.4 (Allison 1999). We felt that remaining linear combinations represented reasonable biological explanations. Dispersal distance has been thoroughly evaluated for red-cockaded woodpeckers (Pasinelli et al. 2004, Kesler et al. 2010), so inter-territory distance was also included as a covariate in all models. The set of 129 remaining models included all possible combinations of uncorrelated explanatory variables, the global model, and a null model with only a distance parameter.

We then fit matrix tree stand and destination social data for choice sets of used and unused dispersal destinations with the conditional logit option in SAS's discrete choice procedure (PROC MDC; SAS Institute 2004). We ranked models with Akaike's Information Criterion with correction for sample size (AIC_c) in order of lowest to highest AIC_c value. We calculated model weights (w_i) to represent the plausibility of each model (Burnham and Anderson 2002). For the subset of models within 2 AIC_c units of the top-ranked model (i.e., $\Delta AIC_c < 2$), we calculated model-averaged parameter estimates, unconditional standard errors, and variable influence metrics (sum of containing model weights; Burnham and Anderson 2002, Arnold 2011; Table 1). We randomly selected 1 individual when records existed for multiple natal dispersals from the same territory and during the same year. We treated dispersal choice sets for juvenile males ($n = 17$), helper males ($n = 44$), and juvenile females ($n = 104$) separately, and we excluded helper females because of the limited number of dispersal observations ($n = 7$). Red-cockaded woodpeckers occasionally inherit territories from parents. We excluded all such observations from the data because they prevented the evaluation of matrix habitats. We considered that differences were statistically significant at $\alpha \leq 0.05$ and suggestive at $\alpha \leq 0.10$, and we report 95% confidence intervals wherever appropriate.

Traditional measures of model fit are not appropriate for conditional logistic modeling (Hosmer and Lemeshow 2000, Boyce et al. 2002). Thus, we assessed model fit for each age and sex class using 5-fold cross validation. We divided data for each sex and social class into 5 sets, fit competing models to 4 of 5 training sets, and then tested model fit on the remaining unused validation set (e.g., Buskirk and Millsapugh 2006). We then used the linear combination of model-averaged explanatory variables to estimate a probability of selection for each territory; greater values indicated a greater probability of woodpeckers choosing a territory for dispersal. We repeated this approach until each of the 5 subsets was used as a validation set. We further used a chi-square test to determine whether model predictions ranked actual dispersal destinations higher than unused destinations within each choice set and we present predicted odds of choosing a dispersal destination over any of the other territories in the choice set.

RESULTS

Dispersal choices made by red-cockaded woodpeckers corresponded with higher quality forest stands in the matrix habitats between natal areas and dispersal destinations, and

with woodpecker occupancy and social composition at potential destination territories (Fig. 1). Parameter estimates and 95% confidence intervals strongly supported the influence of destination territory distance on dispersal choices in red-cockaded woodpeckers, validating previous reports and our decision to include distance as a covariate in all models. However, the null model, which including only a variable for dispersal distance, did not fall within the set of competing models for juvenile females, juvenile males, or helper males (respectively, $w_i < 0.01$, $w_i = 0.03$, $w_i < 0.01$). Thus, models including matrix habitat and social variables better represented the dispersal choices made by red-cockaded woodpeckers than distance alone. The distance between natal territories and unused territories differed from actual dispersal distances in the same choice sets by a mean of 1.4 km (SD 1.9) for juvenile females, 1.4 km (SD 1.3 km) for juvenile males, and 1.0 km (SD 1.1 km) for helper males.

Results yielded a suite of competing models ($\Delta AIC_c < 2$) sharing many of the same variables for each sex and social class (Table 2). In addition to the distance covariate included in all models, the set of 7 competing models for juvenile females included variables for the smallest and largest pines and hardwoods in matrix habitats, and for dispersal destination occupancy and helper presence. The set of 3 competing models for juvenile male dispersal included variables for the medium and large classes of hardwood trees, and for helper occupancy on potential dispersal destinations. Helper male disperser models in the competing set of 12 models included variables for pine and hardwood trees in the small and medium size classes, and for breeder and helper occupancy on dispersal destinations.

The relative importance of variables within model sets, and model-averaged parameter estimates illustrated the influence of forest stand characteristics in matrix habitats on male and female dispersers. Model-averaged parameter estimates indicated that juvenile males dispersed across matrix habitats with lesser hardwood tree densities in the medium and larger size classes (Table 2). Dispersing helper males also avoided matrices with greater densities of small and medium diameter hardwood trees, and those with high densities of the smallest diameter pines. Model averaged estimates also indicated greater probabilities of use by helper males of matrix habitats with medium-sized pines. Juvenile female dispersers also chose to transit matrix habitats with fewer pine trees in the smallest size class, and those with greater densities of large pines. Models in the top-ranked set for dispersing juvenile females also included the smallest and

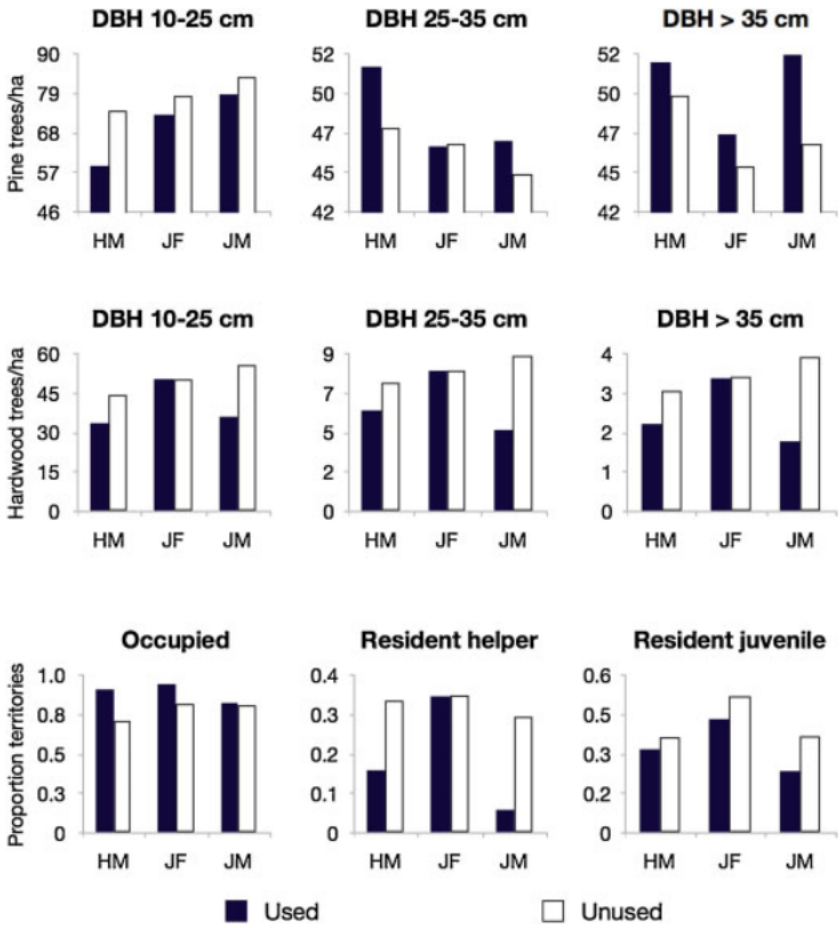

Figure 1. Mean observed values for matrix habitats and social conditions at red-cockaded woodpecker dispersal destinations, and for unselected territories within the choice sets in North Carolina, 1995–2005. Data reflect dispersals of 44 helper males (HM), 17 juvenile males (JM), and 104 juvenile females (JF). All data were used to compile columns, and thus do not account for differences among choice sets included in discrete choice analyses. Note that the *y*-axes for pine tree densities are truncated.

Table 2. Results from discrete choice analysis of dispersal in red-cockaded woodpeckers in North Carolina, 1995–2005. Model-averaged parameter estimates ($\hat{\beta}$), unconditional confidence intervals, and cumulative model weights ($\sum w_i$) are reported for the set of competing models.

	F juvenile ($n = 104$)		M juvenile ($n = 17$)		M helper ($n = 44$)	
Variable[a]	$\hat{\beta}$ (95% CI)[b]	$\sum w_i$	$\hat{\beta}$ (95% CI)[b]	$\sum w_i$	$\hat{\beta}$ (95% CI)[b]	$\sum w_i$
Distance	−0.642 (−0.643, −0.642)	1.00	−1.315 (−1.316, −1.314)	1.00	−1.722 (−1.723, −1.721)	1.00
PTPH_10	−0.01 (−0.03, 0.01)	0.09			−0.03 (−0.09, 0.04)	0.48
PTPH_25					0.06 (−0.08, 0.19)	0.25
PTPH_36	0.05 (−0.01, 0.10)	0.59				
HTPH_10	0.01 (−0.01, 0.03)	0.10			−0.05 (−0.10, 0.01)	0.51
HTPH_25			−0.28 (−0.75, 0.19)	0.20	−0.10 (−0.31, 0.12)	0.06
HTPH_36	0.05 (−0.13, 0.23)	0.09	−0.80 (−1.86, 0.27)	0.37		
Occupancy	1.44 (0.53, 2.35)	1.00			1.66 (0.36, 2.97)	1.00
Helper	−0.29 (−0.79, 0.20)	0.29	−2.94 (−5.86, −0.01)	1.00	−0.87 (−1.84, 0.10)	0.64

[a] PTPH = Pine trees/ha. HTPH = Hardwood trees/ha. The number after the underscore represents the smallest dbh in the size class. Variables only appear in the table if they are included in the set of competing models.

[b] Model-averaged parameter estimates and unconditional 95% confidence intervals are presented for parameters included in the conditional logistic regression models with $\Delta AIC_c < 2$, for the 129 combinations of independent explanatory variables.

largest classes of hardwood trees, although the associated 95% confidence intervals substantially overlapped with zero. Together, model construction and parameter estimates indicated that dispersal occurred across habitats generally considered high quality for red-cockaded woodpeckers.

Model averaged parameter estimates and associated 95% confidence intervals suggested the social composition of potential destination territories strongly influenced dispersal choices in red-cockaded woodpeckers. Juvenile females, juvenile males, and helper males were all less likely to disperse to territories with resident helpers. Helper males and juvenile females chose territories that were already occupied over those that were unoccupied. The presence of resident same-sex juveniles at dispersal destinations during the previous year had no effect on dispersal choices.

Models preformed well, given that the fit analyses tested for the correct identity from sets of 5 possible destinations in each choice set. Results from the 5-fold analysis of subsets of the data indicated that for juvenile males, the odds of correctly identifying actual dispersal destinations was 2.65 times what would be expected if the model randomly chose dispersal destinations ($\chi^2_4 = 14.5$, $P = 0.006$). Results were similarly significant for helper males (odds 3.40; $\chi^2_4 = 233.4$, $P < 0.001$). The model averaged results for juvenile females were also convincing, as the odds of selecting the dispersal destination over any of the other 5 territories in the choice was 1.49 ($\chi^2_4 = 10.1$, $P = 0.038$). Each choice set included 5 destinations, and the observed assignment rates were substantially different from the 20% that would be expected if models randomly assigned dispersal destinations. Linear combinations of model averaged estimates for juvenile males correctly identified 53% of the dispersal destinations from among the 5 territories in each choice set, and ranked the dispersal destination as first or second choice in 77% of the tests. For helper males, the model averaged linear combinations correctly identified dispersal destinations in 68% of the test sets and ranked used destinations as first or second choice in 94% of the test sets. The juvenile female models correctly identified 30% of the dispersal destinations, and ranked destinations as first or second in 51% of the test sets.

DISCUSSION

Previous investigations of dispersal in red-cockaded woodpeckers evidenced the influences of destination distance, and social conditions and resources within the natal territory (Daniels and Walters 2000*a*, Pasinelli and Walters 2002, Pasinelli et al. 2004, Kesler et al. 2010). Our results provided support for 2 additional factors affecting where birds disperse, including the matrix habitats between natal origins and dispersal destinations, and the social composition of conspecific groups at potential dispersal destinations. Previous studies of cooperatively breeding brown treecreepers (*Climacteris picumnus*) showed sex differences in sensitivity to landscape features (Walters et al. 1999, Cooper et al. 2002, Cooper and Walters 2002*a*). Results from our modeling analysis also supported slightly different variable combinations in the dispersal models for each age and sex class of red-cockaded woodpeckers. However, red-cockaded woodpeckers are habitat specialists, requiring open old growth pine stands for survival and reproduction (Walters 1990, Conner et al. 2001) and all 3 of our resulting models, and the included parameter estimates, indicated that those same general habitat characteristics promote inter-territory dispersal movements across matrix areas.

Early work with animal movement conceptualized landscapes as suitable habitat patches situated among oceans of inhospitable matrices (MacArthur and Wilson 1967, Saunders et al. 1991, Soulé et al. 1992). However, recent publications discussed matrices with variable resistances to movement, rather than as complete barriers (Ricketts 2001, Castellon and Sieving 2006). Red-cockaded woodpeckers were not entirely prevented from dispersing across matrix habitats different from those used for breeding, so our results fit the modified concept of movement based on habitat resistance.

Dissected landscape features and habitat fragmentation have also been cited as threats to biological diversity (Noss 1991) because of their potential to degrade habitat quality, increase predation, and disrupt dispersal (Donovan et al. 1995, Walters et al. 1999, Brooker and Brooker 2002,

Cooper and Walters 2002*b*, With et al. 2006). Open habitat features, including roads (Riley et al. 2006, Tremblay and St. Clair 2009), rivers (Hayes and Sewlal 2004), and forest gaps (Conner and Rudolph 1991, Creegan and Osborne 2005), as well as the composition and orientation of landscape features (Robinson et al. 1995, Levey et al. 2005, Kuefler and Haddad 2006, With et al. 2006), have all been shown to affect animal movements and population processes. Similarly, our preliminary exploration of red-cockaded woodpecker dispersal in the greater Fort Bragg area indicated potential habitat fragmentation effects on female movement (D. Kesler, University of Missouri, unpublished data). However, we were unable to assess the effects of forest gaps in the western Fort Bragg study area used in this analysis because it is a largely continuous forest block. We therefore suggest that additional research should be aimed at the effects of forest gaps on dispersal in resident bird species, including red-cockaded woodpeckers. A real-time investigation of disperser movements would almost certainly provide key insights into the proximate factors associated with dispersal in red-cockaded woodpeckers, and might reveal the basis of the sex difference in landscape effects.

Dispersing red-cockaded woodpeckers of both age and sex classes chose destinations based on the social composition of occupant groups, as the presence of helpers negatively influenced choices. Social conditions at dispersal destinations are likely key to resident species, like the red-cockaded woodpecker, that rarely settle in unoccupied areas. All 3 sex and social classes avoided destinations already occupied by male helpers, which may reflect attempts to avoid competition and aggression with resident non-breeding birds. Helper male woodpeckers frequently stay on natal areas until they inherit the territory from the dominant male, or until they fill a breeding vacancy in a nearby location (Walters 1990). The extraterritorial male dispersers we studied might have been unprepared to compete with resident helpers that were already queued for a vacancy, and thus chose to settle elsewhere. We were somewhat surprised that the presence of helpers did not have a positive effect on dispersing juvenile females as helpers augment female reproductive success (Walters 1990). This suggests that male helpers play a role in competition among females over breeding vacancies, or the presence of helpers may be correlated with some other variable that affects dispersal of juvenile females such as territory quality. None of the dispersers were dissuaded by the presence of same-sex juveniles. Indeed, we have frequently observed helpers to disperse to become breeders on territories that retained natal juvenile males that subsequently became their (unrelated) helpers. In contrast, we have never observed a dispersing bird to acquire a breeding position and coexist with a previously present adult helper (J. Walters, Virginia Tech, unpublished data).

MANAGEMENT IMPLICATIONS

The red-cockaded woodpecker was among the first species listed as endangered in the United States (United States of America 1973), and recovery programs aimed at promoting population-level processes have been widely developed (U.S. Fish and Wildlife Service 2003). Our results provide support for the idea that habitats deemed suitable within the breeding areas also promote dispersal at the landscapes level, which can work in concert with breeding bird distributions to facilitate population connectivity (Schiegg et al. 2002). Further, our findings suggest that corridors of pine forests that are managed for breeding habitat conditions might also serve to encourage movements among isolated areas, which would improve population connectivity at a regional scale. Lastly, conservation practitioners may already possess key information needed to broadly promote population connectivity if dispersal patterns in other species are also enhanced by matrix habitats that resemble high-quality breeding sites.

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