

Social influences on dispersal and the fat-tailed dispersal distribution in red-cockaded woodpeckers

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“Fat-tailed” distributions of dispersal distances involve long movements that do not appear to follow the normal distribution characterizing most short dispersals. Theorists have offered 2 nonexclusive explanations for such distributions. They suggest that the fat tail is a product of a single perturbed dispersal function, or that there may be multiple movement modes that widen dispersal distributions, or kernels, when considered simultaneously. We evaluated dispersal distances in the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*) using a 22-year data set. Results illustrated that dispersal distances differed between juvenile and helper dispersers but not between sexes. Results further showed fat-tailed dispersal distributions in all social and sex classes. Then within juvenile females, we used radiotelemetry to document 2 fundamentally different dispersal strategies: Woodpeckers forayed from a natal area until breeding vacancies were located, and they made jumps to distant locations where birds continued to search for settlement options. Jumping was a behavior that added long-distance movements to the dispersal kernel and fattened the tail of the distribution. Our results are congruent with growing evidence that dispersal of animals typically does not represent a single process and that dispersers may switch between movement modes based on a complex relationship of internal state, landscape characteristics, motion capacity, and navigational ability. Rare and cryptic movement modes such as jumping may also account for the fat tail in the dispersal distance distributions of other species. **Key words:** dispersal, fat tail distribution, kurtosis, movement ecology, *Picoides borealis*, red-cockaded woodpecker. [*Behav Ecol*]

The “fat-tailed” distribution of dispersal distances is a well-documented phenomenon caused by an overabundance of long-distance dispersals (Clark et al. 1999; Hovestadt et al. 2001; Nathan et al. 2003; Grivet et al. 2005; Petrovskii et al. 2008; Phillips et al. 2008). The concept was first presented to explain vegetation spread following the retreat of Pleistocene glaciers (Reid 1899; Clark et al. 1998) when dispersal distances must have been greater than simple normal distribution models predicted. The distribution of dispersal distances must have had a “fat tail” to account for rapid range expansions. In the ensuing years, researchers found empirical evidence for fat-tailed dispersal kernels in a wide variety of plants (Nathan 2001) and animals (Delgado and Penteriani 2008).

Theorists have been challenged to explain the heavy-tailed portion of these dispersal kernels, however, which result from long-distance movements that do not appear to follow the pattern of most dispersals (Petrovskii et al. 2008). Two non-exclusive explanations predominate. The first posits that the fat tail is a product of a single perturbed dispersal function that is generated by a single dispersal morphology or behavior (Portnoy and Willson 1993; Phillips et al. 2008; Petrovskii and Morozov 2009). The alternate idea is that there are multiple, or stratified, movement modes that widen dispersal kernels when considered simultaneously (Tufto et al. 1996; Turchin 1998; Lindström et al. 2008; Nathan et al. 2008).

In passive movement, such as seed dispersion by wind, fat tails can be explained by peculiarities of turbulent air (Okubo and Levin 1989; Nathan et al. 2002). But mechanisms accounting for the fat tail of the dispersal distribution are more complicated in active movement by insects, birds, and mammals (Nathan 2001). Some plant seeds (e.g., *Crepis sancta*) and insects (e.g., *Prokelisia* planthoppers) develop as 2 morphs. One morph has wings that clearly facilitate long-distance dispersal, and the other wingless morph establishes locally (Denno et al. 1996; Cheptou et al. 2008). When considered together, the dispersal kernels of the short- and long-distance seed and insect dispersers give the composite kernel a fat tail. Among birds and mammals, however, there are no clear morphological or developmental pathways to long- and short-distance dispersal. Rather, the fat dispersal kernels are more likely the product of behavioral traits and individual choices. Those underlying behavioral mechanisms remain unexplained.

When compared with socially monogamous species (Zack 1990), cooperatively breeding birds often exhibit natal dispersal distributions that include high numbers of individuals that move farther from the mean dispersal distance. These excess long-distance movers add to the tail of the dispersal distance distribution and increase kurtosis, which is a measure of the tail fatness (Zar 1984). Cooperative dispersal distributions further depart from socially monogamous species because they include zero values from delayed dispersers that inherit breeding status on natal territories (Veit and Lewis 1996; Fitzpatrick et al. 1999; Daniels and Walters 2000; Koenig et al. 2000). Median dispersal distances are typically 1–2 territories from natal areas in cooperative breeders, such as red-cockaded woodpeckers (*Picoides borealis*) compared with 4–8 territories in noncooperative species (Walters et al. 2004). Nonetheless, records exhibit for rare long movements in the

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woodpeckers (Ferral et al. 1997; Conner et al. 1997), despite the fact that long-distance dispersal is routinely underestimated because of finite study area sizes (Baker et al. 1995; Koenig et al. 2000; Cooper et al. 2008; Sharp et al. 2008).

We used 2 data sets to explore dispersal behavior in red-cockaded woodpeckers. First, we used long-term dispersal data from a color-banded population of woodpeckers to study dispersal distance and distributions among sex and social classes. Second, we used radiotelemetry to track dispersal behavior of 30 juvenile females with hopes of identifying underlying behaviors that lead to fat-tailed dispersal distribution. In particular, we were interested in those later-dispersing juvenile females that depart 8–11 months after fledging. By studying these females, we observed a previously unknown behavior that can account for the fat-tailed distribution of dispersal distances in red-cockaded woodpeckers.

MATERIALS AND METHODS

Study area

Data on distributions of natal dispersal distances came from a long-term study in the Sandhills of south-central North Carolina (lat 35.108°N, long 79.302°E). The study area encompassed over 110 000 ha and contains roughly 250 groups of red-cockaded woodpeckers, which constitute about half the total Sandhills population. This area includes the western portion of Fort Bragg Army base, horse farms and residential areas to the west, state-owned game lands to the southwest, and intervening areas. The habitat is dominated by mature longleaf pine (*Pinus palustris*) forest and savanna, with ground cover dominated by wiregrass (*Aristida stricta*) and fire-pruned oak (*Quercus* sp.) midstory. Prescribed, military-ignited, and lightning-ignited fires burn the area at 1- to 5-year intervals.

Dispersal records

We used banding records to evaluate red-cockaded woodpecker dispersal distributions at Fort Bragg. Most woodpecker groups within the study area were monitored since 1980, and all were monitored since 1982. All birds within the area were individually color banded. Each breeding season, observers recorded the number of eggs, nestlings, and fledglings produced by each woodpecker social group. Fledglings were sexed with dimorphic crown colors (males have red crowns and females black). Yearly, all group members were identified from their color-band combinations, and the status of each was determined to be either breeder, helper, or floater. Helpers were most often delayed dispersing individuals that stayed on natal territories to help feed young and care for subsequent broods. Floaters were nonbreeding females that remained loosely affiliated with non-natal groups and provided little care. Natal dispersal was based on the first breeding season in which a bird held breeding status. Detailed descriptions of the study area and methods of data collection are provided in Carter et al. (1983), Walters et al. (1988), and Brust et al. (2004).

We evaluated distances traveled by dispersing juvenile and helper red-cockaded woodpeckers between 1981 and 2005 ($n = 956$ juvenile females, 235 juvenile males, 22 helper females, and 223 helper males). Floaters were excluded from the data because their tentative and short-term social bonds were often difficult to assess. As defined elsewhere (Conner et al. 1997), we considered dispersals to be movements that were simultaneously associated with social status transitions from juvenile or helper on a natal territory to breeder on a second territory during the following breeding season. Individuals were also considered to have dispersed if they transitioned to new territories where they held a dominant position,

but did not breed, or where they solitarily occupied territories. Only movements among 275 Sandhills region territories for which we had reliable geographic coordinates were included in dispersal distance analyses. Territory centers were estimated by averaging the geographic coordinates for nest and roost cavity trees used by red-cockaded woodpeckers within a group (geographic data were provided by the Sandhills Ecological Institute, Southern Pines, NC, and Fort Bragg Endangered Species Branch, Fort Bragg). We then estimated dispersal distance by calculating the length of a line linking the centers of origin and destination territories.

The distribution of log-transformed dispersal distances was nearly symmetrical about the mean, indicating that the mean of transformed data approximates the median on both the transformed and the original scales (see Ramsey and Schafer 1997). Thus, we report observed median distance values for each age and sex class and test for differences in dispersal distances using an analysis of variance (ANOVA) test of log-transformed dispersal distance (proc ANOVA; this and subsequent statistical tests were conducted with Statistical Analysis Software, SAS 9.2, Cary, NC). A Bonferroni correction was used to accommodate the multiple simultaneous tests. We then tested for departures from normality in each of the dispersal distributions with an Anderson–Darling test (SAS proc univariate).

Our data for active dispersal in red-cockaded woodpeckers included a distribution that peaks near the median dispersal distance. Thus, rather than the shape parameter used by some (Veit and Lewis 1996; Clark 1998; Clark et al. 1998), we elected to use the kurtosis statistic to assess excess long-distance dispersal occurrences. Kurtosis was previously referenced with regard to tail fatness of dispersal kernels (Clark et al. 1998; Phillips et al. 2008). We used the sample kurtosis metric (SAS proc univariate), which is the fourth moment about the mean of the distribution, and it measures peakedness and observations at the outer ranges of the distribution (Zar 1984). Excess distant observations give the kernel fat or heavy tailedness, with higher kurtosis values representing increasingly fatter-tailed distributions. Kurtosis values exceeding 0 are leptokurtic and thus have a greater peakedness and fatness in the tails than a normal distribution.

Radiotelemetry

Radiotelemetry investigations of dispersal behavior were conducted on western Fort Bragg in 2006 and eastern Fort Bragg in 2007. Specifically, we were interested in studying the exploratory foraging behavior that preceded dispersal and subsequent dispersal decisions. We considered that birds foraged when they departed from the natal area, explored the surrounding landscape, and then returned before sunset to rejoin the natal social group and roost in the natal territory. Dispersal occurred when birds roosted in a location other than the natal area (e.g., Kesler and Haig 2007).

Juvenile female red-cockaded woodpeckers were banded as nestlings with individual-specific color combinations and numbered aluminum leg bands. Then during the subsequent spring (March to April), the birds were recaptured on natal areas using hoop nets placed over roost cavity entrances. Each bird was fitted with a radio transmitter (1.4 g, PD-2; Holohil Ltd, Ontario, Canada) that was top mounted on the center 2 retrices with ethyl cyanoacrylate glue.

We attempted to relocate radio-marked woodpeckers daily. Study subjects were ordered in a list by geographic location, and then a single individual was randomly selected to be the first daily observation. Birds were located using hand-held yagi antennas in list order until an individual was observed departing from the natal area for a foraging movement. A geographic information system database (ArcView 3.3; ESRI, Redlands,

CA) was used to verify foray occurrence, although the behavior was often clearly evidenced by juveniles that broke away from the natal social group and crossed multiple territories. Birds were considered to be on forays when they were twice as close to a cavity tree on a non-natal territory as they were to a cavity tree on their natal territory and were not with other members of their natal group. During forays, we attempted to collect foray route information at least every 30 min, and we continued tracking foraging birds until sunset or until the birds returned to the natal group. Tracks and locations were recorded with global positioning systems (Garmin Ltd, Olathe, KS). If radio-marked birds were not initially found with the natal group, we drove throughout the study area using vehicle-mounted omnidirectional antennas until the foraging individuals were located. When birds were not located within 2 h, the search radius was extended and a tracking attempt was made each day until the birds were found. Although some individuals were not relocated for several days after making gross movements away from natal areas, we did eventually find every bird. Therefore, we believe that none of the radio-marked woodpeckers dispersed beyond the bounds of the study area during our monitoring period. Radiotelemetry observations ceased when transmitters failed or with the onset of the breeding season and egg laying.

The daily maximum distance from natal territory centers was used to estimate daily foray distances. Foray distance distributions were relatively normal, so we report mean values and make comparisons with mixed models ANOVA, which accounts for repeated observations of single individuals (SAS proc mix). When on forays, birds were considered to have visited other territories if they were observed within 150 m of an associated nesting or roosting tree. To evaluate the area transited by foraging birds, we calculated the minimum convex polygons (MCP; Kenward 2001) from each individual's foraging locations using the Animal Movement Extension (Hooge and Eichenlaub 1997). Comparisons were made between MCP areas with 2 sample *t*-tests for equal means (Ramsey and Schafer 1997). We present *P* values whenever appropriate, using an α value of 0.05.

RESULTS

The dispersal distance distribution derived from long-term banding data for each age and sex class of red-cockaded woodpeckers is illustrated in Figure 1. Median dispersal distances for juvenile males, helper males, juvenile females, and helper females, respectively, were 2.94, 1.27, 3.31, and 1.88 km. The ANOVA test of log-transformed dispersal distances indicated that there were significant differences between social classes but not between sexes. Juvenile males and females dispersed farther than helpers of the same sex ($P < 0.05$ for both). However, dispersal distances for juvenile males did not differ from juvenile females, and helper males did not differ from helper females ($P > 0.05$ for both). These results support the idea that the dispersal strategies of juvenile birds differed from helpers and that dispersal distance was not sex biased. The Anderson-Darling test for normality demonstrated that each dispersal distribution departed significantly from normal ($P < 0.01$ for all). Furthermore, the skewed distributions and the kurtosis statistics that greatly exceeded 0 illustrated the fat-tailed distribution of the red-cockaded woodpecker dispersal kernels for juvenile males and females (4.3 and 11.5, respectively) and for helper males and females (19.1 and 5.3, respectively).

Juvenile female forays

To study behaviors underlying the dispersal process, we used radiotelemetry to track the exploratory foraging movements

and dispersal of 30 juvenile female red-cockaded woodpeckers. Dispersal was a prolonged process that included foraging, departure from natal areas, and settlement elsewhere, and it occurred over a period of months. Some juvenile females apparently dispersed during the late summer, fall, or winter because many of the birds marked on natal areas during the previous season were not present in March when we attempted recapture and radio marking. Banding records indicated that there were >70 juvenile females banded in 2005 and 2006, and during the following years, we relocated 17 and 13, respectively. Some of the birds that we were not able to locate in natal areas were later observed elsewhere, indicating that they dispersed before our February and March searches.

Among radio-marked birds, we observed 255 forays (243 with reliable geographic coordinates) from natal areas and most followed a similar pattern. Radio-marked females left their natal group, transited the landscape, and often visited other territories (mean 0.9 and range 0–7 territory visits per foray) where they interacted with the groups inhabiting those territories. They then returned to rejoin the natal group. The frequency of such forays increased as the breeding season approached. In 2007, both natal territory occurrences and foraging observations were collected. During the first week of March, 12% of the study subjects forayed each day. By the second week of April, 33% forayed, and 54% of the birds forayed each day by the third week of May. The distribution of foray distances that originated from natal areas (i.e., daily maximum distance from natal territory, mean 2.2 km, and range 0.2–8.9 km) contrasts strongly with the long-term natal dispersal distance distribution for juvenile females (Figure 2). Rather than displaying the fat-tailed characteristics of the dispersal function, foray distances from natal territory origins were relatively light tailed (kurtosis 1.22).

We also observed a previously unknown dispersal behavior in 7 red-cockaded woodpeckers that may account for the discrepancy in the light-tailed distribution of foray distances and the fat-tailed distribution of natal dispersal distances. Following Suarez et al. (2001), we termed the behavior "jumping." Jumper female woodpeckers made forays to territories surrounding natal areas. Prior to jumping, they forayed with high frequency in the direction of the jump, but they stayed within normal foraying range and returned to natal areas each night. Jumpers then left the natal territory as if on a foray but entered an alternate long-distance movement mode and then continued traveling well beyond where they forayed previously. The birds eventually stopped in distant locations from which they did not return (Figure 3).

Among jumpers, the mean foray distance from natal territories was 2.5 km before jumping ($n = 47$), which was similar to the mean foray distance for nonjumpers (2.1 km, $P = 0.4086$, $n = 196$). After jumping, however, birds remained at a mean distance of 9.9 km from their natal territories (mean distance for all postjump observations of 7 jumpers, $n = 89$). Jumping thereby added substantial weight to the tail of the dispersal distribution for our study population. After jumping, 6 birds reentered the localized exploration movement mode that characterized forays from natal areas, and one bird was not relocated until it was already settled on a destination territory. Jumpers visited a mean of 0.8 (range 0–7) territories per day in the natal neighborhood during forays before jumping, and then they visited 0.6 (range 0–4) territories per day in relocation sites after jumping.

Further evidence of multiple movement modes in juvenile female dispersers comes from the areas explored during forays. MCP ($n = 7$) around all observed locations of jumpers and nonjumpers differed significantly in area (respectively, 3338 and 626 ha; $P < 0.001$). However, polygons encircling foray areas traversed prior to jumps were similar in size to areas

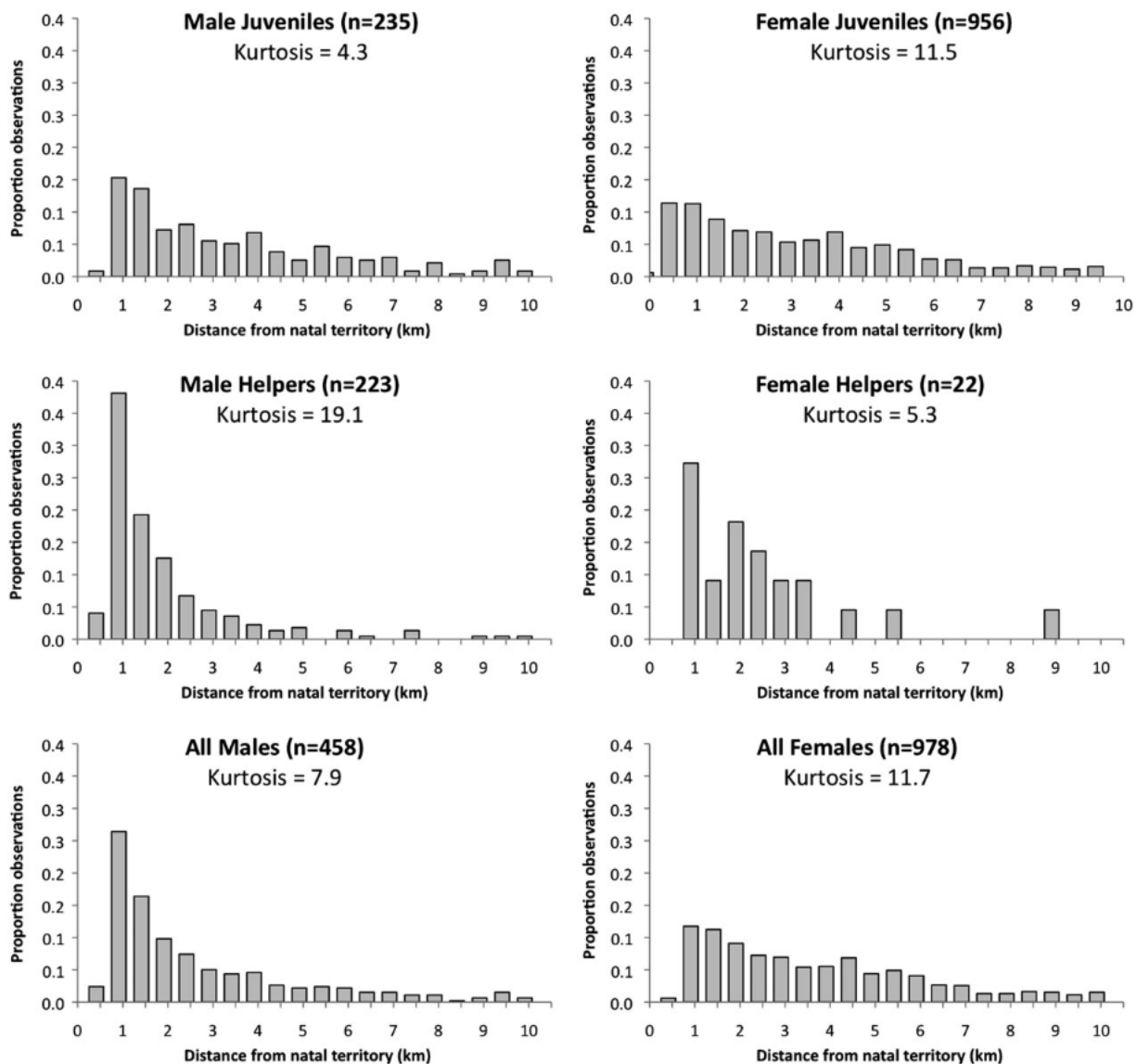


Figure 1
Dispersal distance distributions of red-cockaded woodpeckers recorded during 1981–2005 in the Sandhills region of North Carolina.

used by nonjumpers (642 and 605 ha, $P = 0.89$). There was no difference in the size areas used by jumpers before (642 ha) and after (496 ha) their jump ($P = 0.62$).

Most dispersals occurred after a number of forays and immediately prior to the beginning of egg laying when birds joined other social groups. Radiotelemetry observations concluded with breeding, but later resightings of banded birds provided dispersal information. Five nonjumpers dispersed to settlement territories from natal clusters. One became a breeder, 3 were affiliated auxiliary group members, and 1 became a helper on the destination territory. Additionally, 2 woodpeckers continued making forays and returning to natal areas where they became helpers during the first year. Four of the 7 jumpers were classified as group members at destinations during the first breeding season. The social status of the birds included 1 breeder, 2 auxiliary group members, and 1 bird with social status that could not be determined. Additionally, 2 birds were known to have been predated during our telemetry observations, and 17 birds were not resighted during the next breeding season.

DISCUSSION

In the Sandhills region of North Carolina, juvenile male red-cockaded woodpeckers dispersed the greatest distances, followed by juvenile females and helper males and females. Male and female dispersal distances differ in many species (Greenwood 1980; Clarke et al. 1997; Clobert et al. 2001; Bullock et al. 2002), including red-cockaded woodpeckers (Pasinelli and Walters 2002; Figure 1), and inbreeding avoidance through differential displacement of opposite-sex kin is the most frequently cited reason for the dichotomy (Harvey and Ralls 1986; Pusey 1987; Kerth et al. 2002). However, male and female dispersal distances are not differentiated enough to prevent inbreeding in red-cockaded woodpeckers (Daniels and Walters 2000), and our results showed major differences between juvenile and helper social classes. Dispersal may thus be governed by factors more proximate than inbreeding. Similar observations have been reported for other cooperatively breeding species, which caused some to suggest that the availability of breeding vacancies plays a greater role in dispersal decisions (Stacey and Koenig 1990;

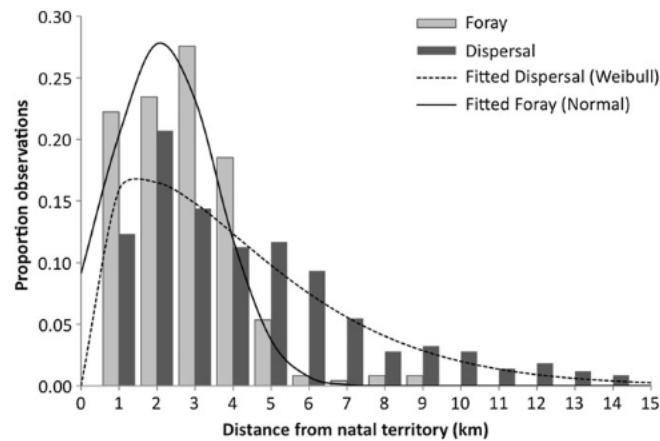


Figure 2

Distribution of 243 forays made by 30 radio-marked juvenile female red-cockaded woodpeckers that originated from natal areas in 2006 and 2007, and distribution of 956 observed natal dispersal distances recorded during 1981–2005. Fitted normal and Weibull functions are included for natal forays and observed dispersals, respectively.

Ligon 1999; Ekman et al. 2004; Koenig and Dickinson 2004). The distance pattern we observed is also congruent with hypotheses suggesting that helpers delay dispersal in order to gain access to higher quality territories in the natal neighborhood, whereas juveniles on poorer quality territories, and perhaps subordinate juveniles on high quality territories, disperse and seek breeding opportunities in the greater landscape (Walters 1990; Stacey and Ligon 1991; Pasinelli and Walters 2002).

Results from banding records indicated shorter median dispersal distances in juvenile male red-cockaded woodpeckers than had been reported in previous publications from the Sandhills region (2.9 vs. 4.5 km in Walters et al. 1988). Substantial effort has been invested in increasing the number of nest and roost cavities available to the birds in recent years (Conner et al. 2001; U.S. Fish and Wildlife Service 2003). These sets of new cavities in uninhabited areas, or recruitment clusters, have also increased the number of breeding opportunities encountered by dispersing individuals. Thus, dispersing juvenile males may not need to move as far as they formerly did to locate vacant territories (Walters et al. 1992). In contrast, juvenile female and helper male dispersal distances were similar to previous estimates. Helper males have an area-restricted search in which they query nearby neighborhood territories. These nearby movements would be unlikely to shorten because of the higher cluster density, and if there

was a shift, our data structure would be unlikely to detect a small change.

The dispersal kernels for all age and sex classes were characterized by leptokurtosis and fat tails. Male red-cockaded woodpeckers are much more likely than females to remain on natal areas as helpers for a second year, and the juvenile male dispersal kernel had lower kurtosis than the juvenile female kernel. Perhaps, males were less likely to make long-range dispersal jumps because they had the option of remaining as helpers. Male helpers also showed strong leptokurtosis, and helpers were previously observed making long-distance jumps when breeding groups broke up. Additionally, our telemetry results suggested that dispersal occurred through the first breeding season, which muddies social classification boundaries and indicates that juvenile dispersal behaviors may occasionally hold over into birds classified as helpers. Long-term records for individually marked birds also support leptokurtosis, as movement distances of 200 km were previously reported (Conner et al. 1997; Ferral et al. 1997). These were nearly 2 orders of magnitude greater than the median dispersal distance and would almost certainly be more pronounced if researchers had the capacity to correct for the finite scope of study areas (Cooper et al. 2008).

We observed a previously unknown jumping behavior that moved dispersers well beyond the normal foray ranges and thus fattened the tail of the dispersal kernel. Jumping red-cockaded

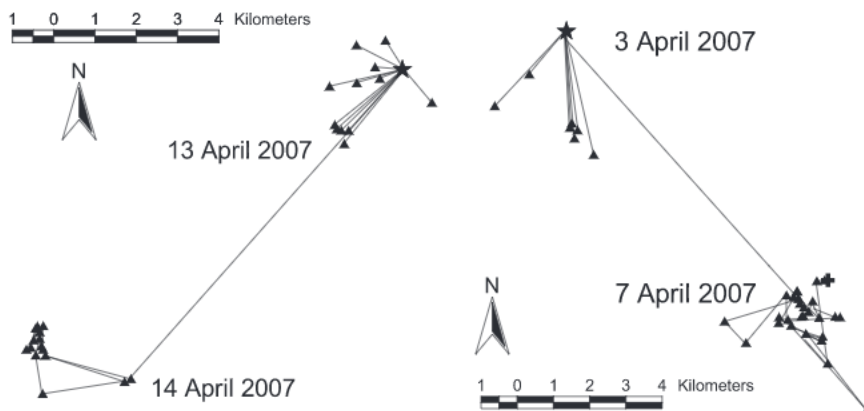


Figure 3

Example of jumping behavior in red-cockaded woodpeckers 1991-97249 (left) and 1951-97068 (right) on eastern Ft. Bragg, NC. Natal territory locations are denoted by stars, and daily foray distances from natal territories are denoted by triangles. Birds initially made daily forays to nearby territories and then returned to natal areas by sunset. After regular forays, 1991-97249 jumped 9.9 km and 1951-97068 jumped 9.6 km to new areas where they then continued short-distance foray movements.

woodpeckers first explored the neighborhood surrounding natal areas, a behavior that has been documented in several cooperative breeders (Woollfenden and Fitzpatrick 1984; Hooge 1995; Kesler and Haig 2007). Jumpers then made extreme unidirectional movements that extended past the areas accessed by birds foraging from natal areas. These long-distance movements observed with radiotelemetry, and the subsequent dispersal settlements, exaggerated the tails of dispersal kernels so that they were more likely to resemble those generated from banding records. Previous work on invasive species illustrated that jumping may be a primary mechanism of human-mediated species invasions (Suarez et al. 2001), and the same process might also apply to natural range expansions of Pleistocene plants, which initiated interest in the fat-tailed distribution of dispersal (Reid 1899; Clark et al. 1998).

When placed in the context of a conceptual framework for movement (Nathan et al. 2008), it is unclear whether red-cockaded woodpeckers switch between a short-distance exploratory movement mode and long-distance jumping mode because of intrinsic motivations or extrinsic influences. Jumping red-cockaded woodpeckers first explored the local neighborhood and only then made long jumps. The pattern suggests that the change in movement behavior was initiated by external factors and that jumping behavior may represent a response to limited dispersal opportunities within the natal foraging range—jumping might be an avian counterpart to saturation dispersal previously described in microtine rodents (Lidicker 1975). However, internal motivations might also play a role as birds seemed to contemplate jumps when they preceded long-distance moves with repeated daily forays in the jump direction. The birds were clearly not limited by navigation or motion capacities because most made multiple forays throughout the study area and readily returned to natal territories by nightfall. Our observations bolster suggestions that dispersal movement and spatial learning are intertwined and that behavior is crucial to dispersal distributions (Delgado and Penteriani 2008; Delgado et al. 2009). The distinct juvenile dispersal strategies are congruent with growing evidence that dispersal typically does not represent a single process (Lidicker and Patton 1987; Nathan et al. 2001; Bowler and Benton 2005) and that dispersers may switch between movement modes based on the complex relationship between internal state, landscape characteristics, motion capacity, and navigational ability (Nathan et al. 2008).

Our results suggested that red-cockaded woodpeckers employ at least 3 dispersal strategies, including dispersal based on forays from natal areas as juveniles, dispersal after jumping to locations far from natal clusters as juveniles, and short-distance delayed dispersal as adult helpers after remaining on a natal territory for extended periods. We speculate that the dispersal repertoire of many species includes differential dispersal strategies, which can include rare behaviors that result in occasional long-distance movements. When amalgamated into species, age, or sex classes, dispersal distances would then represent a summation of several different types of dispersal behavior, each characterized by a different distance distribution. Such behavior could be condition dependent, but in red-cockaded woodpeckers, it may also include a genetic component as juvenile dispersal distances are apparently heritable (Pasinelli et al. 2004). Finally, our results provide a conceptual and quantitative framework for further exploring rare long-distance dispersal events.

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