- genetics. (B. D. Chepko-Sade, and Z. T. Halpin eds.). Univ. of Chicago Press, Chicago, Illinois.
- Walters, J. R. 1990. Red-cockaded Woodpeckers: a "primitive" cooperative breeder. Pp. 69–101. *in* Cooperative breeding in birds. (P.B. Stacey and W.D. Koenig, eds.). Cambridge Univ. Press, Cambridge, United Kingdom.
- ——. 1991. Application of ecological principles to the management of endangered species: the case of the Red-cockaded Woodpecker. Ann. Rev. Ecol. Syst. 22:505–523.
- ——, S. K. HANSEN, J. H. CARTER III, AND P. D. MANOR. 1988. Long-distance dispersal of an adult Red-cockaded Woodpecker. Wilson Bull. 100:494–496.

D. Pat Ferral, Wildlife Diversity Section, South Carolina Dept. of Natural Resources, P.O. Box 167, Columbia, South Carolina 29202; John W. Edwards, USDA Forest Service, Southern Research Station, Dept. of Forest Resources, Clemson Univ., Clemson, South Carolina 29634 (Present address: Dept. of Agricultural and Applied Economics, Clemson Univ., Clemson, South Carolina 29634-0355.); AND AMY E. Armstrong, Wildlife Diversity Section, South Carolina, Dept. of Natural Resources, P.O. Box 167, Columbia, South Carolina 29202 (Present address: 500 Kinsler Road, Blythewood, South Carolina 29016). Received 16 March 1996, accepted 15 Aug. 1996.

Wilson Bull., 109(1), 1997, pp. 157-160

Long-distance dispersal of Red-cockaded Woodpeckers in Texas.—The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperatively breeding species indigenous to the mature pine forests of the southeastern United States. Continued loss and fragmentation of the mature forests of the South have increased the isolation of extant woodpecker groups throughout the range of this endangered species (USFWS 1985, Conner and Rudolph 1989). Mate replacement following mortality of female and some male breeders is dependent on successful dispersal of young and adult woodpeckers (Walters et al. 1988a). Helper males provide replacements for some male breeders, regardless of cluster isolation.

Dispersal in Red-cockaded Woodpeckers takes two forms, a short-distance form unique to Red-cockaded Woodpeckers, and a longer-distance form like that of other birds (J. R. Walters, pers. commun.). Long-distance dispersal is likely highly sensitive to population density because birds tend to keep moving until they find a breeding vacancy. Isolation of woodpecker groups within a population appears to impair successful short-distance dispersal of woodpeckers and fragmentation of mature pine habitat appears to interfere with successful long-distance dispersal within and between populations to the extent necessary to provide replacement breeders when a member of the breeding pair dies (Conner and Rudolph 1991).

Information on dispersal distances is important in evaluating relationships between cluster isolation and thresholds for successful woodpecker dispersal. Most cases of dispersal involve relatively short distances ($\bar{x} = 4.7$ km for first-year females, and $\bar{x} = 5.4$ for first-year males), generally to the closest neighboring woodpecker groups (Walters et al. 1988a). Dispersing adults generally travel shorter distances ($\bar{x} = 1.8$ km for males and $\bar{x} = 2.1$ km for females) (Walters et al. 1988a).

Long-distance dispersal that involves movement through nonforest habitat and other possible impediments to dispersal have in the past appeared to be rare, and the paths that Redcockaded Woodpeckers take through or around such potential barriers are unknown. Walters et al. (1988b) reported a 90 km dispersal by an adult female in North Carolina that included

possible movements through agricultural lands and hardwood forest habitats. Montague and Bukenhofer (1994) reported a 74 km dispersal of a young female Red-cockaded Woodpecker from the McCurtain County Wilderness Area in Oklahoma to the Ouachita National Forest in Arkansas. In November 1995 a female originally banded in Arkansas was recaptured in Louisiana following a 338 km dispersal (Montague et al., pers. commun.). Walters et al. (1988b) and Reed et al. (1988) stressed the importance of dispersal between populations for the maintenance of genetic variability. The extent to which Red-cockaded Woodpeckers disperse long distances becomes increasingly important for both demographic and genetic reasons as the degree of cluster/population isolation and habitat fragmentation increases. In this paper, we describe six cases of long-distance dispersal by Red-cockaded Woodpeckers within and between populations on the Angelina, Davy Crockett, and Sabine National Forests in eastern Texas.

The longest dispersal we observed (75 km straight-line distance) was made by a female Red-cockaded Woodpecker (#1) banded in her natal cluster as a juvenile on 17 October 1989 on the Angelina National Forest (Fig. 1). She was recaptured on 22 September 1993 and again on 13 September 1995 in the Davy Crockett National Forest. If she traveled in a straight line, her dispersal path would have crossed a 5-km wide portion of the Sam Rayburn Reservoir. To avoid the reservoir, her minimal-distance dispersal path would have crossed more than 20 km of agricultural lands, several major highways, and been in excess of 80 km.

Our second longest dispersal (66 km) was made by a male (#2). He was banded as a juvenile in his natal cluster on the Angelina National Forest on 18 September 1990. He was recaptured on 16 October 1991 in the Davy Crockett National Forest (Fig. 1). A straight line dispersal route for this male would have involved crossing a 4 km section of Sam Rayburn Reservoir, > 20 km of agricultural lands, and several major highways. It is interesting to note that this male was the same male that had fallen from its nest cavity as a nestling and was replaced by us on 31 May 1990 (Schaefer et al. 1991). The 66 km dispersal made by this male represents the longest dispersal distance ever reported for a male Redcockaded Woodpecker. Walters et al. (1988a) observed a maximum dispersal distance of 21.1 km for a fledgling male during their study in the North Carolina Sandhills. Lay and Swepston (1973) reported a 42-km dispersal by a 2+ year-old male Red-cockaded Woodpecker on the Angelina National Forest.

Another male Red-cockaded Woodpecker (#3) made a 49 km dispersal from the Angelina National Forest to the Sabine National Forest. He was banded as a juvenile in his natal cluster on 29 September 1994 and recaptured on the Sabine National Forest on 28 September 1995 (Fig. 1). A straight-line dispersal path would have included > 15 km of agricultural lands.

Three additional cases of long-distance dispersal by females occurred within the Angelina National Forest (Fig. 1). A female (#4) was banded on 19 May 1994 as a nestling on the Sam Houston National Forest. She was recaptured as a juvenile on 12 December 1994 and translocated to the Angelina National Forest on 13 December 1994 where she was released into a cluster containing a single male. On 24 August 1995 female #4 was recaptured on the Angelina National Forest after dispersing a least 30 km (straight-line distance). This 30 km distance included a 7 km span of Sam Rayburn Reservoir. To avoid crossing this large reservoir, she would have had to travel > 80 km (Fig. 1). Another female Red-cockaded Woodpecker (#5) was banded as a juvenile in her natal cluster on 10 September 1991 on the Angelina National Forest. She was recaptured on 26 August 1995 in another area of the Angelina National Forest 28 km from her natal cluster. To avoid an 8 km span of the Sam Rayburn Reservoir she would have had to fly > 80 km (Fig. 1). Another female (#6) was banded as a juvenile in her natal cluster on 6 December 1989 on the Angelina National Forest and was recaptured on 29 August 1994 in a different forest compartment. A straight-

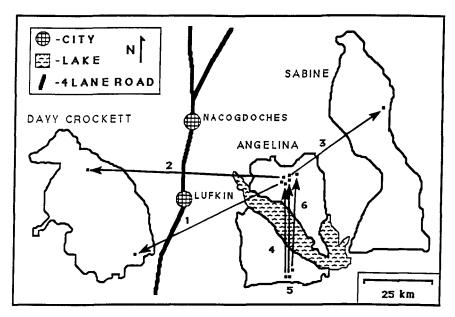


Fig. 1. Six instances of long-distance dispersal by Red-cockaded Woodpeckers on the Angelina, Davy Crockett, and Sabine National Forests in eastern Texas from 1989 to 1995. The dispersal lines represent the straight-line distances between clusters where woodpeckers were initially captured and sites of subsequent recapture. Numbers associated with dispersal lines on the map correspond to Red-cockaded Woodpecker numbers in the text.

line dispersal of 36 km would have included a 9 km span of the Sam Rayburn Reservoir. Otherwise, a dispersal of > 85 km would have been required to avoid crossing the reservoir (Fig. 1).

Although the cases of dispersal we observed are not as long as the 90 km distance reported by Walters et al. (1988b), they suggest that long-distance dispersal may occur on a fairly regular basis. Our observations also indicate that Red-cockaded Woodpeckers have the ability to cross or circumnavigate large, non-forest landscape features such as agricultural lands and reservoirs. This is particularly important for the maintenance of genetic diversity in small, satellite populations of woodpeckers (Haig et al. 1993). We do not know if the long-distance dispersal results in a higher mortality rate to dispersing individuals.

The intensive six-year demographic study by Walters et al. (1988a) in North Carolina involved monitoring a population of over 500 banded Red-cockaded Woodpeckers, and initially, only one individual (a female) was detected dispersing over 30 km (31.5 km) prior to the 90 km dispersal reported later (Walters et al. 1988b). The six cases of long-distance dispersal we observed were detected from 122 banded woodpeckers over a similar six-year period. Obviously, the observations we report here do not represent all instances of long-distance dispersal by Red-cockaded Woodpeckers on the National Forests in Texas, but are only those detected under a limited banding and recapture program. Most woodpeckers were banded to assist with the U.S. Forest Service's translocation program to augment clusters that contained only a single woodpecker, and not as a major demography study such as that of Walters et al. (1988a). Thus, what we have observed likely under represents long-distance

dispersal by Red-cockaded Woodpeckers among the small, isolated populations in eastern Texas.

The apparent higher frequency of long-distance dispersal we detected among the small, isolated populations in eastern Texas suggests the possibility that long-distance dispersal may be more prevalent within small populations where population density is low than within larger, dense populations such as those reported in the North Carolina Sandhills (Walters et al. 1988a). Thus, small, isolated populations may not be as genetically isolated as previously thought and loss of genetic variability may not be as great as has been assumed when defining minimum viable population size based on genetic criteria. However, long-distance dispersal by woodpeckers into large, dense populations appears to have a higher probability than long-distance dispersal into small, isolated populations because of the different sizes of the respective "target" populations.

Acknowledgments.—We thank R. Mize, S. Best, D. Carrie, and L. Carolan for assistance with some field aspects of the study, and J. R. Walters, F. C. James, P. D. Doerr, and R. G. Hooper for constructive comments on an early draft of the manuscript.

LITERATURE CITED

- CONNER, R. N. AND D. C. RUDOLPH. 1989. Red-cockaded Woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests. U.S.D.A. For. Serv., Res. Pap. S0–250.
- AND ———. 1991. Forest habitat loss, fragmentation, and Red-cockaded Woodpecker populations. Wilson Bull. 103:446–457.
- HAIG, S. M., J. R. BELTHOFF, AND D. H. ALLEN. 1993. Population viability analysis for a small population of Red-cockaded Woodpeckers and an evaluation of enhancement strategies. Cons. Biol. 7:289–301.
- LAY, D. AND D. W. SWEPSTON. 1973. Red-cockaded Woodpecker final report. Credit Fed. Aid Proj. W103R. Tex. Parks Wildl. Dept., Austin, Texas.
- Montague, W. G. and G. A. Bukenhofer. 1994. Long range dispersal of a Red-cockaded Woodpecker. Proc. Arkansas Acad. Sci. 48:259–260.
- REED, J. M., P. D. DOERR, AND J. R. WALTERS. 1988. Minimum viable population size of the Red-cockaded Woodpecker. J. Wildl. Manage. 52:385–391.
- Schaefer, R. R., D. C. Rudolph, and R. N. Conner. 1991. The response of an adult Red-cockaded Woodpecker to a fallen nestling. Wilson Bull. 103:514–515.
- U.S. FISH AND WILDLIFE SERVICE. 1985. Red-cockaded Woodpecker recovery plan. U.S. Fish and Wildlife Service, Atlanta, Georgia.
- WALTERS, J. R., P. D. DOERR, AND J. H. CARTER III. 1988a. The cooperative breeding system of the Red-cockaded Woodpecker. Ethology 78:275–305.
- —, S. K. HANSEN, J. H. CARTER III, P. D. MANOR, AND R. J. BLUE. 1988b. Long-distance dispersal of an adult Red-cockaded Woodpecker. Wilson Bull. 100:494–496.

RICHARD N. CONNER, D. CRAIG RUDOLPH, RICHARD R. SCHAEFER, AND DANIEL SAENZ. Wildlife Habitat and Silviculture Laboratory (maintained in cooperation with the College of Forestry, Stephen F. Austin State Univ.), Southern Research Station, U.S.D.A. Forest Service, Nacogdoches, Texas 75962. Received 23 Jan. 1996, accepted 15 Aug. 1996.