

RED-COCKADED WOODPECKER USE OF SEED-TREE/SHELTERWOOD CUTS IN EASTERN TEXAS

RICHARD N. CONNER, *Wildlife Habitat and Silviculture Laboratory, Southern Forest Experiment Station, U.S. Department of Agriculture, Forest Service, Nacogdoches, TX 75962*

ANNE. SNOW, *Wildlife Habitat and Silviculture Laboratory, Southern Forest Experiment Station, U.S. Department of Agriculture, Forest Service, Nacogdoches, TX 75962*

KATHLEEN A. O'HALLORAN,² *Wildlife Habitat and Silviculture Laboratory, Southern Forest Experiment Station, U.S. Department of Agriculture, Forest Service, Nacogdoches, TX 75962*

Establishment or maintenance of suitable habitat for any wildlife species is an important aspect of its management, especially for endangered species such as the red-cockaded woodpecker (*Picoides borealis*). Populations of the red-cockaded woodpecker are declining over much of the bird's current range, most likely because of the lack of suitable habitat (Carter et al. 1983, Conner and Rudolph 1989, Costa and Escano 1989). Jackson (1982), Locke et al. (1983), and others anecdotally noticed that red-cockaded woodpeckers used residual pines (mature pines left uncut during a harvest) for cavity excavation in seed-tree and shelterwood reproduction cut areas.

Seed-tree and shelterwood reproduction cutting methods remove most trees but leave some residual pines to provide seeds and in some cases shelter for the next generation of pines. Conner and O'Halloran (1987) suggested that shelterwood cuts would produce trees similar to red-cockaded woodpecker cavity trees. Conner and Rudolph (1989) reported that fragmentation caused by clear-cutting was associated with small clan size. Shelterwood cutting may reduce fragmentation if residual pines are not eventually removed, thus reducing the

impact of forest regeneration in areas that contain small red-cockaded woodpecker populations.

The basal area of mature pines left standing in seed-tree areas generally ranges from 1.0-3.0 m²/ha whereas shelterwood areas have 5-9 m²/ha (Baker 1987). Suitable pine basal area for red-cockaded colony sites is generally considered to be 9-18 m²/ha (Hooper et al. 1980, Jackson et al. 1986).

To explore the utility of retaining residual pines for red-cockaded woodpeckers, we examined red-cockaded woodpecker use of 5 seed-tree/shelterwood areas for cavity tree sites. We also compared woodpecker use of the partially cut areas with use of adjacent uncut forest areas.

STUDY AREAS

Five seed-tree/shelterwood (ST/SW) harvested areas ranging in average basal area (2.6-10.0 m²/ha) were selected on the southern portion of the Angelina National Forest, Angelina and Jasper counties, in eastern Texas (Table 1). We selected an equal-sized area of mature uncut pine forest immediately adjacent to each ST/SW area to serve as controls. All study sites were within 0.2 to 2.2 km of existing active woodpecker colonies.

Although tree density and basal area varied within each ST/SW area, areas 2 (\bar{x} = 3.4 m²/ha, SE = 0.5) and 3 (\bar{x} = 2.6 m²/ha, SE = 0.5) could be considered seed-tree areas and areas 1 (\bar{x} = 4.0 m²/ha, SE = 0.5), 4 (\bar{x} = 10.0 m²/ha, SE = 1.0), and 5 (\bar{x} = 4.2 m²/ha, SE = 0.4), shelterwood areas. Longleaf pine (*Pinus palustris*) was the dominant tree species in all harvested stands and in the adjacent uncut forest. Deep loamy sands containing materials of volcanic origin (Tehran and Letney soil types, Neitsch 1982) were the predom-

¹ Wildlife Habitat and Silviculture Laboratory (maintained in cooperation with the School of Forestry, Stephen F. Austin State University), Southern Forest Experiment Station, U.S. Department of Agriculture, Forest Service, Nacogdoches, TX 75962.

² Present address: U.S. Department of Agriculture, Forest Service, Regional Office, Portland, OR 97208.

Table 1. Characteristics of longleaf pine seed-tree/shelterwood cut areas in the Angelina National Forest, eastern Texas.

Area	Year cut	Size of area (ha)	Distance to closest active colony (km)	Residual pine density ($n = 5/\text{area}$) in 1984 (No./ha)		Average residual tree age ($n = 10/\text{area}$) in 1984 (yrs)		Average cavity tree age (yrs)		No. cavity/start trees excavated 1983-1988
				\bar{x}	S E	\bar{x}	S E	\bar{x}	S E	
1										
2	1975-1975	14.25	0.03	11.21.1	4.7	84.2	9.4	103	4.5	8
4	1975	19.4	0.7	29.9	4.4	86.1	7.9	162	32.2	3
5	1982-1982	11.21.1	1.21	1163-587	11.41.1	11.21.1	7.11			0
\bar{x}		20.1	1.0	52.9	14.9	65.9	8.8	119	11.3 ^a	0

^a Mean and SE of 12 cavity trees present in 1988.

inant soil conditions at all study sites as well as at the red-cockaded woodpecker colonies (colony = cluster of cavity trees used by a social group of woodpeckers) that were nearby. There was little organic material in these sands, and the soils had a low water-holding capacity. Study area 3 was located on a mesic site, and an extensive hardwood under- and midstory had continued to develop over the entire study area throughout the study period; such was not the case in the other areas where bluestem (*Andropogon* spp.) was the predominant ground cover.

METHODS

We located and tagged red-cockaded woodpecker cavity trees on the Angelina National Forest from 1983 through 1988 (see Conner and Rudolph 1989). In mid-April each year, 2 people examined each cavity tree and concurred whether the tree exhibited woodpecker activity or not. We judged cavity trees and colonies to be active if bark bordering resin wells was red (indicating recent pecking [Jackson 1977, 1978]), and clear, fresh resin was flowing from the wells. Locations of cavity trees and woodpecker colonies were mapped to aid in the selection of study areas. It was necessary to know the proximity of all active colonies to our study areas during the entire study to evaluate the likelihood of red-cockaded woodpeckers using each area. Additional information on some woodpecker colonies and cavity trees had been collected from 1978 to 1983 during other studies (Conner and Locke 1982, Locke et al. 1983).

In 1983, after selecting the study areas that were closest to active red-cockaded woodpecker colonies, each residual pine in the 5 ST/SW areas was examined for presence of red-cockaded woodpecker cavities and cavity starts each year through 1988. Although 3 of the 5 ST/SW areas (2, 4, and 5) contained residual pines of younger average age than cavity trees used by red-cockaded woodpeckers (70+ years old, U.S. Fish and Wildl. Serv. 1985) (Table 1), we included them because they provided a range of age classes from

which red-cockaded woodpeckers could select cavity trees. Also, ST/SW areas 1 through 4 contained 2 to 5 relict pines (> 80 years old) per ha.

We also searched the adjacent control areas annually for the presence of cavity trees and cavity starts. Each pair of ST/SW and control areas were equidistant from existing active red-cockaded woodpecker colonies (with at least a breeding male and female) and should have had some probability of being used for new cavity tree locations. Because the density of trees was higher in the uncut control areas, more trees were actually present for woodpeckers to select from than in the ST/SW cut areas. Relict pines (> 80 years old) averaging 4 m²/ha basal area were present in the uncut control areas.

On ST/SW areas and control areas we measured tree and stand characteristics. At 5 randomly selected points in each ST/SW area and each uncut pine control area, 4 dominant trees were selected using the point quarter procedure (Cottam and Curtis 1956). For these dominant trees (20 per area), tree height (measured with a clinometer), tree diameter (dbh), and bark thickness at breast height were measured. Crown depth was measured as the vertical distance between the top of the crown and lowest major branches on the bole of the tree. We measured the radius of the tree crown, determined crown shape, and from these calculated a crown volume for each tree (Conner and O'Halloran 1987). Crown weights (branch wood, branch bark, needles) were calculated from biomass equations using tree height and diameter at breast height as predictor variables (Taras and Clark 1977).

We extracted increment cores from pines at breast height and counted annual growth rings. Five years were added to the number of increments to determine the relative age of trees from the time they germinated. A measure of tree vigor was obtained by counting the number of growth increments in the outer 2 cm of the extracted cores.

In each ST/SW and control area we measured total basal area, pine overstory basal area, and hardwood midstory basal area with a 1 factor metric prism, and estimated percent canopy closure at 5 randomly se-

lected points. Pine overstory density was determined using the point quarter method (Cottam and Curtis 1956). Vegetative characteristics of ST/SW areas were compared to controls with a B-sample t-test.

RESULTS

Red-cockaded woodpeckers excavated 8 new cavity trees and 4 new start trees (cavity not completed) within or on the edge (2 trees in area 3) of 3 of the 5 ST/SW areas (Table 1). These 3 areas had been cut in 1975 and averaged 17.1 ha in size. The mean ages of residual pines in the ST/SW areas at regeneration time ranged from 37 to 71 years, and residuals averaged 66 years in 1984. Red-cockaded woodpeckers selected relicts averaging 119 years old for cavity trees in the 3 ST/SW areas whereas the average age of residual pines sampled in these 3 ST/SW areas was 76 years. Cavity excavation in the residual, relict pines began 7 to 8 years after the cuts took place. Areas 4 and 5 (Table 1) were cut in 1982 and by 1988 had no residual pines excavated as cavity trees. Residual pines in these ST/SW areas averaged 49 years old at the time of the cut.

In 1978, a single cavity tree and a single red-cockaded woodpecker were present 40 m to the south of the ST/SW cut in area 1. In 1981, the single cavity tree was destroyed by fire and the colony site was seemingly abandoned. In 1983, a single start tree was located in 1 of the residual pines in the ST/SW cut, and by 1984, 2 active cavity trees were present and 2 young fledged. In 1985, 6 cavity/start trees were present in the ST/SW area and 2 young were fledged. By 1987, 8 cavity/start trees were present and 2 young were fledged with 3 adult woodpeckers feeding young. In 1988, 4 cavity trees and 4 start trees were still present and the nesting attempt failed to produce young.

Red-cockaded woodpeckers using ST/SW areas 2 and 3 had existing active relict cavity trees available for their use within 200 m of the ST/SW areas. In 1983, a cavity start was excavated in a single residual pine in ST/SW

area 2. In 1986, the cavity was completed, and 2 young were fledged each year in 1987 and 1988 from that cavity tree.

In 1984, there were 2 cavity trees on the edge and 1 in the middle of ST/SW area 3. Adult red-cockaded woodpeckers were present in this area through 1986, and 1 to 2 cavity trees had copious resin flow from active resin wells. In 1985, red-cockaded woodpeckers seemed to be incubating but no young were detected. In 1987, the woodpeckers had abandoned ST/SW area 3. A pair of woodpeckers was present in 1988 and fledged 1 young from a residual pine in the middle of the ST/SW cut.

Searches of the uncut pine forest control areas adjacent to each ST/SW area failed to locate any cavity trees during the entire study period (1983-1988). Total basal area and pine overstory basal area, as well as canopy closure and pine overstory density, were lower ($P < 0.01$) in the ST/SW areas than in the adjacent forest control areas (Table 2).

The characteristics of residual pines within the ST/SW areas also were different from pines in the adjacent uncut areas. Crowns of residual pines in the ST/SW areas were larger on the average than those of pines in the adjacent uncut forests (Table 2). Pines in the ST/SW areas also had larger average dbh and averaged 15 years older than the adjacent uncut forest overstory pines. However, basal area of relict pines in the uncut forest areas adjacent to ST/SW areas selected by red-cockaded woodpeckers (areas 1-3) averaged 4.0 m^2/ha (SE = 0.6).

DISCUSSION

Red-cockaded woodpeckers used residual pines in ST/SW areas for cavity sites. The 2 ST/SW areas that were not used had residual pines with a younger average age (63 and 39 years old) than that normally considered optimum for cavity excavation (95+ years, U.S. Fish and Wildl. Serv. 1985). Also, 1 of these 2

Table 2. Measurements on and around randomly selected trees within seed-tree/shelterwood (ST/SW) cuts (n = 5) of longleaf pine forest and trees in adjacent mature uncut forest control areas (n = 5).

Variables	ST/SW cut		Mature forest	
	\bar{x}	SE	\bar{x}	SE
Tree				
Crown depth (m)	9.4	0.6	6.6	0.3***a
Crown weight (kg)	357.8	58.5	230.5	31.2
Crown volume (m ³)	228.7	28.6	135.9	21.4**
Diameter at breast height (cm)	42.2	2.7	35.8	7.9*
Age (yrs)	65.9	8.8	50.7	...
Bark thickness (cm)	1.9	0.1	1.7	0.0*
Tree height (m)	23.2	1.1	23.3	1.1
Growth increments outer 2 cm (No.)	9.7	1.2	11.6	1.8
Stand				
Total basal area (ma/ha)	4.9	1.5	21.6	0.8***
Basal area of overstory (m ² /ha)	4.8	1.3	19.4	1.4***
Basal area of hardwood midstory (m ² /ha)	0.1	0.1	1.0	0.5
Basal area of canopy	9.5			3.3**
Percent pine closure	52.9	14.4	30.0	48.3**

* Means compared by 2-sample t-test.

• p < 0.05.

** p < 0.01.

*** p < 0.001.

ST/SW areas (area 5, the youngest) may have been too far (2.2 km) from active red-cockaded woodpecker colonies for use by woodpeckers.

Red-cockaded woodpeckers may yet select ST/SW area 4 because it is 700 m from an active colony and contains relict pines. Areas 1 through 3 were not colonized for 7 to 8 years after the reproduction cut. Only 6 years had passed since ST/SW area 4 was cut.

The formation of totally new woodpecker colonies was not observed. All 3 instances of ST/SW area use appeared to involve a colony shift rather than formation of a new colony. Red-cockaded woodpeckers using ST/SW areas 2 and 3 had existing cavity trees still available for use in their old colony sites when they initiated cavities in residual pines in the ST/SW areas and used them for nest trees. Hardwood basal area of both of the existing colony sites (about 2 m²/ha) was not excessive (U.S. Fish and Wildl. Serv. 1985).

Red-cockaded woodpeckers selected residual pines in the ST/SW areas in preference to overstory pines in the uncut mature pine control areas that were adjacent to the ST/SW

areas. Relict pines were present in the uncut mature areas adjacent to the used ST/SW areas. These could have provided potential cavity trees had the woodpeckers chosen to excavate cavities in the uncut areas.

Differences between the residual pines in the ST/SW areas and mature pines in the uncut control areas were similar to those observed by Conner and O'Halloran (1987) when they compared red-cockaded woodpecker cavity trees to randomly available mature pines in the Angelina National Forest. That study detected significantly larger crowns and dbh's in cavity trees. Hence, some pines left as residuals were similar to those that red-cockaded woodpeckers selected as cavity trees in the forest in general.

The average age of 119 years of residual pines with cavities is about 50 years older than the average age of all residual pines in the ST/SW areas and close to the average age (126 years) of longleaf pine cavity trees reported by Conner and O'Halloran (1987). The age of these recently excavated cavity trees supports the suggestion by Conner and Rudolph (1989)

that 120-year rotation ages would benefit the woodpecker.

Jackson (1982) suggested a high risk of wind damage and lightning strike on cavity trees associated with red-cockaded woodpecker use of seed-tree areas. During the period of our study (1983 through 1988) neither wind damage nor lightning strike occurred to any of the cavity trees examined. If 6 to 9 m^2/ha basal area of residual pines is left after cutting, the likelihood of wind damage and lightning strike to cavity trees should be reduced (Taylor 1977).

MANAGEMENT IMPLICATIONS

If a decision to harvest has been made, shelterwood cuts, instead of clear-cutting, may provide a relatively immediate and continuous supply of potential cavity trees if pines 80 to 120 years old are left as the residuals. It would also create the open pine Savannah habitat preferred by the woodpecker (Jackson et al. 1979, Hooper et al. 1980), and leave some foraging habitat while reducing the hazard of the residual stand to southern pine beetles (*Dendroctonus frontalis*) (Gara and Coster 1968). For shelterwood cuts to have any real value as potential colony sites, pine overstory basal area must, at least, approach 9 m^2/ha (Conner and Rudolph 1989). If stand regeneration is necessary, for the benefit of red-cockaded woodpeckers, we suggest that irregular shelterwood cutting (Smith 1986) of 80- to 120-year-old longleaf pines to a basal area of 6-9 m^2/ha and loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines to a basal area of 7 m^2/ha be considered instead of clear-cutting in pine stands that are within 1,200 m of active woodpecker colonies (see Conner and O'Halloran 1987, Conner and Rudolph 1989). We suggest a residual basal area range of 6-9 m^2/ha for longleaf pine to allow for site quality differences with the understanding that the highest basal area possible be left that would still permit development of the regenerating stand. Basal areas <9 m^2/ha are less than ideal for colony sites, but

our recommendations consider the silvicultural needs of natural regeneration. The 1,200-m distance would provide habitat for the existing active colonies as well as for recruitment of new colonies (U.S. Dep. of Agric. 1985). However, Walters et al. (1988) were skeptical of the utility of recruitment stands to provide habitat for the formation of new red-cockaded woodpecker colonies.

There are instances when shelterwood cutting would be inappropriate, as with conversion of slash pine (*Pinus elliotii*) stands back to longleaf pine. Such stands often have a few residual longleaf pines. These few pines should be retained as a possible seed source during seedling planting and to provide old growth pines for red-cockaded woodpeckers in the future.

In forests where at least 50 woodpecker groups occur and the habitat is not fragmented, residual pines could be left standing as long as silviculturally practicable. In forests where populations are ≤ 50 woodpecker groups and known to be declining, we suggest that residual pines be left standing in perpetuity to provide additional benefit to the woodpecker. Our use of the value "50 woodpecker groups" is based upon our observations of decline and problems with populations where <40 groups are present (Conner and Rudolph 1989). If isolation and extensive forest fragmentation exist, the value may have to be increased.

Retaining residual pines at 9 and 7 m^2/ha basal area in perpetuity is experimental and would impact timber production. In loblolly pines, residuals may have to be thinned back periodically to 7 m^2/ha as their postharvest growth may exceed basal areas that would permit stand regeneration and growth (J. B. Baker, Southern Forest Exp. Stn., Monticello, Arkansas, pers. commun.). In longleaf pine, germination and maturation of seedlings around residuals can be reduced (Walker and Wiant 1966, Boyer 1975). The zone of reduced growth near the base of longleaf pine residuals might be beneficial because young pines would

not grow near cavity trees. In loblolly shelterwood cuts, germination and growth of pines close to residual pines will occur because loblolly is relatively shade tolerant (Baker and Balmer 1983). Clumping of residuals (at least 3 clumps/ha) should be considered because it would create larger openings that would enhance pine survival and growth following germination, and imitate the clusters of mature pines that compose many of the current woodpecker colonies.

SUMMARY

Red-cockaded woodpecker use of 5 seed-tree/shelterwood cut areas was studied from 1983 to 1988. Residual pines (pines left standing) in 3 of the study areas were used by woodpeckers for cavity trees ($n = 12$), whereas none of the pines in the adjacent uncut mature forest control areas were used for cavity tree excavation. Over the 5-year study period there were 6 successful nestings in residual pine cavity trees. Seed-tree/shelterwood cutting may have duplicated the growth history of other previously studied cavity trees by creating a release from suppressed growth conditions (Conner and O'Halloran 1987). Woodpeckers also may have preferred these areas because of openness and initial absence of hardwood midstory. This study suggests that if a timber regeneration cut is necessary around active red-cockaded colonies, irregular shelterwood cutting would benefit the woodpecker by providing more nesting habitat than clear-cutting.

Acknowledgments.—We thank J. B. Baker, W. D. Boyer, J. A. Jackson, M. R. Lennartz, and D. C. Rudolph for constructive comments on an early draft of the manuscript.

LITERATURE CITED

- BAKER, J. B. 1987. Silvicultural systems and natural regeneration methods for southern pines in the United States. Pages 175–191 in *Proc. of the seminar on forest productivity and site evaluation*. Council of Agric., Taipei, Taiwan (ROC).
- , AND W. E. BALMER. 1983. Loblolly pine. Pages 148–152 In R. M. Burns, tech. compiler. *Silvicultural systems for the major forest types of the United States*. U.S. Dep. Agric., For. Serv., Agric. Handbook No. 445.
- BOYER, W. D. 1975. Timing overstory removal in longleaf pine. *J. For.* 73:578–580.
- CARTER, J. H., III, R. T. STAMPS, AND P. D. DOERR. 1983. Status of the red-cockaded woodpecker in the North Carolina sand hills. Pages 24–29 in D. A. Wood, ed. *Red-cockaded woodpecker symposium II*. Fla. Game and Fresh Water Fish Comm., Tallahassee.
- CONNER, R. N., AND B. A. LOCKE. 1982. Fungi and red-cockaded woodpecker cavity trees. *Wilson Bull.* 94:64–70.
- , AND K. A. O'HALLORAN. 1987. Cavity-tree selection by red-cockaded woodnecks as related to growth dynamics of southern pines. *Wilson Bull.* 99:398–412.
- , AND D. C. RUDOLPH. 1989. Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests. U.S. For. Serv. Res. Pap. SO-250. 15pp.
- COSTA, R., AND R. E. F. ESCANO. 1989. Red-cockaded woodpecker status and management in the southern region. U.S. For. Serv. Tech. Publ. R8-TP-12. 71pp.
- COTTAM, G., AND J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451–460.
- GARA, R. I., AND J. E. COSTER. 1968. Studies on the attack behavior of the southern pine beetle. III. Sequence of tree infestation within stands. *Contrib. Boyce Thompson Inst.* 24:77–85.
- HOOPER, R. G., A. F. ROBINSON, AND J. A. JACKSON. 1980. The red-cockaded woodpecker: notes on life history and management. U.S. For. Serv. Gen. Tech. Rep. SA-GR9. 8pp.
- JACKSON, J. A. 1977. Determination of the status of red-cockaded woodpecker colonies. *J. Wildl. Manage.* 41:448–452.
- , 1978. Pine bark redness as an indicator of red-cockaded woodpecker activity. *Wildl. Soc. Bull.* 6:171–172.
- , 1982. Use of seed tree cuts as colony sites by red-cockaded woodnecks. *Miss. Kite* 12:6–7.
- , R. N. CONNER, AND B. J. S. JACKSON. 1986. The effects of wilderness on the endangered red-cockaded woodpecker. Pages 71–78 in D. L. Kulhavy and R. N. Conner, eds. *Wilderness and natural areas in the eastern United States: a management challenge*. School of Forestry, Stephen F. Austin State Univ., Nacogdoches, Tex.
- , M. R. LENNARTZ, AND R. G. HOOPER. 1979. Tree age and cavity initiation by red-cockaded woodpeckers. *J. For.* 77:102–103.
- LOCKE, B. A., R. N. CONNER, AND J. C. KROLL. 1983. Factors influencing colony site selection by red-cockaded woodpeckers. Pages 46–50 in D. A. Wood, ed. *Red-cockaded woodpecker symposium II proceedings*. Fla. Game and Fresh Water Fish Comm., Tallahassee.

- NETSCH, C. L. 1982. Soil survey of Jasper and Newton counties, Texas. U.S. Dep. of Agric., Soil Conserv. Serv., U.S. Dep. of Agric., For. Serv., and Texas Agric. Exp. Stn. 198pp.
- SMITH, M. S. 1986. The practice of silviculture. Eighth ed. John Wiley and Sons, Inc., New York, N.Y. 527pp.
- TARAS, M. A., AND A. CLARK. 1977. Aboveground biomass of **longleaf** pine in a natural sawtimber stand in southern Alabama. U.S. For. Serv. Res. Pap. SE-162. 32pp.
- TAYLOR, A. R. 1977. Lightning and trees. Pages 831-849 *in* R. H. Golde, ed. Lightning. Vol. 2. Academic Press, New York, N.Y.
- U.S. DEPARTMENT OF AGRICULTURE. 1985. Wildlife habitat management handbook, Ch. 400, section 420—**red-cockaded** woodpecker. FSH 2609.23R—Southern Region U.S. Dep. of Agric., For. Serv., Atlanta, Ga.
- U.S. FISH AND WILDLIFE SERVICE. 1985. Red-cockaded woodpecker recovery plan. US. Fish and Wildl. Serv., Atlanta, Ga. 88pp.
- WALKER, L. C., AND H. V. WIAINT, JR. 1966. Silviculture of **longleaf** pine. School of Forestry, Stephen F. Austin State Coll., Nacogdoches, Tex. Bull 11. 105pp.
- WALTERS, J. R., P. D. DOERR, AND J. H. CARTER, III. 1988. The cooperative breeding system of the red-cockaded woodpecker. *Ethology* 78:275-305.

Received 17 November 1989.

Accepted 1 September 1990.



