AN EXPERIMENTAL TEST OF INTERSPECIFIC COMPETITION FOR RED-COCKADED WOODPECKER CAVITIES

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Abstract: To test whether the presence of nest boxes near red-cockaded woodpecker (RCW, *Picoides borealis*) cavity trees reduced cavity use by other species and improved RCW reproductive success on the Francis Marion National Forest in coastal South Carolina, we placed 3 nest boxes in each of 62 experimental clusters and designated 61 clusters as controls. Our observations of nest box and cavity use showed that nest boxes were somewhat effective in reducing cavity use and that eastern bluebirds (*Sialia sialis*) and southern flying squirrels (*Glaucomys volans*) were the most frequent users of nest boxes and cavities. Bluebirds preferred nest boxes to cavities in both years and flying squirrels showed significant preference for nest boxes in 1992. Pretreatment monitoring (1990) of RCW reproductive performance showed no significant differences between control and experimental groups. However, posttreatment monitoring showed that in 1991 RCWs in experimental clusters were significantly more likely to nest than RCWs in control clusters; in 1991 and 1992, they were more likely to fledge ≥1 young. Further; RCWs were less likely to initiate a nest if ≥1 cavity was occupied by a non-RCW species than if no cavities in the cluster were occupied by a non-RCW species. These results indicate that RCW cavities were subject to interspecific competition and that nest boxes may be an effective means of reducing competition, particularly when the number of cavities is limited.

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Key words: cavity use, eastern bluebirds, *Glaucomys volans*, interspecific competition, nest boxes, *Picoides borealis*, red-cockaded woodpeckers, *Sialia sialis*, South Carolina, southern flying squirrels.

The endangered RCW is the only North American woodpecker that excavates cavities in living pines. Cavity trees used by a family group are usually close to each other and called a cluster (Harlow et al. 1983, Hooper 1983, Walters 1990). Red-cockaded woodpeckers depend on their cavities for roosting, nesting, and rearing their young (Ligon 1970). Cavities usually take more than a year to excavate but are used for several years. Although RCWs use a variety of pine species for cavity excavation, not all trees within a species have sufficient heartwood to contain the cavity or are infected with red-heart fungus (*Phellinus pini*) which the RCWs prefer (Hooper 1988, Hooper et al. 1991*a*, Conner et al. 1994). Cavity availability has been proposed as a major factor in the evolution of cooperative breeding in the species (Lennartz et al. 1987, Walters et al. 1988), and lack of suitable cavities is an important factor limiting current population expansion (Copeyon et al. 1991, Heppell et al. 1994).

One factor affecting cavity availability for RCWs is use by other species such as red-bellied woodpeckers (*Melanerpes carolinus*), red-headed woodpeckers (*M. erythrocephalus*), great crested flycatchers (*Myiarchus crinitus*), tufted titmice (*Parus bicolor*), bluebirds, and flying squirrels (Dennis 1971, Jackson 1978, Harlow and Lennartz 1983, Rudolph et al. 1990, Loeb 1993). The effect of cavity use by other species on RCW populations is variable, ranging from minimal in coastal South Carolina (Harlow and Lennartz 1983) and Texas (Rudolph et al. 1990) to more extensive in the Piedmont of Georgia (Lennartz and Heckel 1987) and the North Carolina Sandhills (LaBranche and Walters 1994).

Methods suggested to reduce potential competition for RCW cavities include provisioning nest boxes (Jackson 1978), leaving snags as alternative cavity sites for other primary excavators (Jackson 1978), and putting metal restrictor plates on cavities to prevent enlargement and use by larger species (Carter et al. 1989). Restrictors are not effective for flying squirrels and other small species (Loeb 1993) and snags are not always available. Further, studies of the effectiveness of snags in reducing cavity use have produced mixed results. Everhart et al. (1993) and Harlow and Lennartz (1983) found no relation between snag density in RCW clusters

and use of cavities by other species whereas Kappes and Harris (1995) reported that occupancy rates of RCW cavities by southern flying squirrels and red-bellied woodpeckers were related inversely to snag density in the vicinity of RCW clusters. Bluebirds, flying squirrels, and other species readily use nest boxes (Kibler 1969, Goertz et al. 1975, Pinkowski 1976, McComb and Noble 1981) as well as RCW cavities in many areas, yet the effectiveness of nest boxes in reducing use of RCW cavities by these species never has been tested.

In September 1989 Hurricane Hugo destroyed 87% of the active RCW cavities on the Francis Marion National Forest in coastal South Carolina (Hooper et al. 1990). Although natural cavities were replaced by almost 1,000 artificial cavity inserts (Allen 1991) and drilled cavities (Copeyon 1990, Taylor and Hooper 1991) from 1990 to 1993, the number of cavities per cluster site was still considerably below pre-Hugo levels (Watson et al. 1995). Our observations during the nesting season immediately following Hurricane Hugo suggested that use of cavities by other species may have reduced the reproductive potential of the RCW population by as much as 25% (R. Hooper, unpubl. data). The shortage of RCW cavities on the Francis Marion National Forest following Hurricane Hugo and the high use of these cavities by other species provided an excellent opportunity to test the effectiveness of providing supplemental nest boxes to reduce RCW cavity use by other species and to understand the role of interspecific competition in RCW ecology. The objectives of this study were to: (1) determine if other species used nest boxes placed in RCW clusters and decreased their use of RCW cavities, and (2) test whether the presence of nest boxes improved RCW reproductive success.

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STUDY AREA

We conducted the study in 1990-92 on the Francis Marion National Forest, Charleston and Berkeley counties, in the Lower Coastal Plain physiographic region of South Carolina. The RCW clusters included in this study were in loblolly (*Pinus taeda*) and longleaf (*P. palustris*) stands distributed throughout the entire forest. The forest contained a mixture of 51% loblolly pine stands, 19% longleaf pine stands, 25% hardwood stands, and 3% mixed pine-hardwood stands (U.S. For. Serv. 1985). Before Hurricane Hugo, the area supported a large and increasing population of RCWs (Hooper et al. 1991*b*). In 1987-88, there were an estimated 477 RCW family groups; after Hurricane Hugo, there were 240 cluster sites with ≥1 cavity tree and ≥1 RCW (Hooper et al. 1990).

METHODS

In 1990 we used a stratified random sampling design to select 122 sites in 3 hurricane damage classes as described by Watson et al. (1995): 66 in the heavily damaged zone (>90% of RCW cavities destroyed), 34 in the moderately damaged zone (average of 65% of RCW cavities destroyed), and 22 in the low damage zone (average of 38% of RCW cavities destroyed). The number of sites in each damage class was proportional to the total number of cluster sites in each damage class. Within each damage class, half of the cluster sites were designated randomly as control sites and the rest as experimental sites. The subsequent death of cavity trees and loss of birds forced us to drop some cluster sites from the study and replace them with others, somewhat varying the number of clusters in each group during the study. We placed 3 bluebird nest boxes (28 X 18 X 18 cm; hole diam 4.0 cm) 6 m high on living pines in each experimental site. We chose bluebird boxes because we felt they would be used by the most common potential cavity competitors in the area. Although the boxes were somewhat shorter than nest boxes routinely used for southern flying squirrels (Sonenshine et al. 1973), they were similar in size to those used successfully in several southern flying squirrel studies (Muul 1968, Stojeba 1978). One of the most important factors determining suitability of nest boxes for southern flying squirrels is a small entrance diameter (Stone et al. 1996) and the bluebird boxes we used satisfied this requirement. Where possible, we placed boxes on trees that were from 20 to 50 m from a RCW cavity tree to reduce direct interactions with RCWs but at the same time, offered a choice between the nest box and RCW cavity. No nest boxes were placed in control sites.

We installed nest boxes in early December 1990 and used a light and a mirror to inspect all boxes and cavities in experimental clusters and all cavities in control clusters once in January-February 1991, twice during the 1991

Table 1. Results of P-way ANOVA testing the effects of hurricane damage level, treatment (nest boxes vs. control), and the interaction term on number of RCW cavity trees, cavities, and group size on the Francis Marion National Forest, South Carolina.

	1991				1992			
Source	df	MS	*F*	*P*	df	MS	*F*	*P*
No. of trees								
Damage	2	10.0487	8.46	0.0004	2	8.658	6.24	0.0027
Treatment	1	0.945	0.8	0.3745	1	2.5795	1.86	0.1755
Damage X treatment	2	1.4335	1.21	0.3032	2	0.5103	0.37	0.6932
Error	110	1.1883			114	1.388		
No. of cavities								
Damage	2	16.5596	11.43	0.0001	2	15.8349	9.22	0.0002
Treatment	1	0.8894	0.61	0.4349	1	3.8866	2.26	0.1352
Damage X treatment	2	0.8421	0.58	0.5608	2	0.473	0.28	0.7597
Error	110	1.4483			114	1.7165		
Group size								
Damage	2	2.7107	3.37	0.0379	2	2.8448	3.92	0.0227
Treatment	1	1.9863	2.47	0.1188	1	0.7117	0.98	0.3243
Damage X treatment	2	0.3194	0.4	0.6730	2	0.2202	0.3	0.7390
Error	108	0.8036			109	0.7258		

RCW breeding season (Apr-Jun), once in January-February 1992, and twice in the 1992 RCW breeding season. We considered a cavity or box occupied if it contained animal(s) or egg(s) at the time of inspection. Eggs were identified to species when possible. No cavities or boxes were occupied by species other than RCWs during the winter 1991 check; thus, the winter 1991 data will not be considered.

We collected data on RCW reproductive success during the 1990-92 breeding seasons, using the 1990 data as pretreatment controls, We climbed cavity trees several times to verify nest initiation and count the number of eggs, hatchlings, and young reaching fledgling age. We observed cluster sites for I-2 hours during and after RCWs left their cavities in the morning to determine the number of adults.

We used 2-way ANOVA with an interaction term to test for differences in the number of RCW trees, cavities, and group size, and for differences in clutch size, number of nestlings, and number of fledglings between experimental and control clusters and among damage classes. Least-square means and standard errors were calculated and simultaneous tests between means were used to detect differences among damage classes and between experimental and control groups (SAS Inst. Inc. 1989). Log-likelihood tests of independence (G-tests) or Fisher's Exact tests were used to test for preference or avoidance of nest boxes and cavities, differences in cavity use between control and experimental sites, differences in box use among damage classes and between years, and differences in RCW reproductive performance (nest initiation and successful fledging of young) between control and experimental groups. Fisher's Exact test was used when ≥50% of the cells had expected values <5. Preference for nest boxes versus cavities by species other than RCWs was tested with data from experimental clusters only. Occasionally, a nest box or cavity was used by one species during the first check of the breeding season and another species during the second check. When we analyzed data by species, both instances of use were included in the analysis but were treated as one instance of use when data were grouped. These cases were rare (9 in 1991 and 1 in 1992) and likely had little effect on the results.

RESULTS

Availability of RCW Cavities

In 1991, 116 clusters were included in the study: 61 controls (33 in high damage, 16 in medium damage, and 12 in low damage areas) and 55 experimentals (30 in high, 15 in medium, and 10 in low damage areas). In 1992, 120 clusters were included in the study: 58 controls (31 in high, 17 in medium, and 10 in low damage areas) and 62 experimentals (33 in high, 17 in medium, and 12 in low damage areas). Number of trees and cavities per cluster did not differ significantly between control and experimental clusters in either year but varied significantly among damage classes in both years (Table 1). The interactions between damage class and treatment were not significant (Table 1). In both years, the mean number of trees and cavities per cluster in low damage areas were significantly greater than the mean number of trees and cavities in medium and high damage areas ($P \leq 0.003$; Table 2); the number of trees and cavities in medium and high damage areas did not differ significantly from each other in either year ($P > 0.05$).

We were not able to verify use of cavities by RCWs for roosting. However, we were able to determine group size and assumed that RCWs used cavities for roosting whenever possible (Hooper and Lennartz 1983). Mean group size varied with damage class in 1991 and 1992 but not with treatment or the interaction between treatment and damage class (Table 1). In both years, mean group size was significantly greater in low damage areas than in high and medium damage areas ($P \leq 0.03$; Table 2). Group size did not differ between high and medium damage areas ($P > 0.05$; Table 2). The number of cavities was greater than group size in all damage classes in both years (Table 2).

Use by Potential Cavity Competitors

The most common users of RCW cavities were bluebirds and flying squirrels followed by red-bellied woodpeckers and great-crested flycatchers (Table 3). Cavity use by all species was significantly lower in 1992 than in 1991 ($G = 9.031$, 1 df, $P = 0.003$); 25.2% (86 of 342) of the cavities were used in 1991 whereas only 16.2% (62 of 384) of the cavities were used in 1992. However, the number of clusters in which ≥1 cavity was used by a non-RCW species did not differ between 1991 and 1992 (41.7 vs 49.1%; $G = 1.330$, 1 df, $P = 0.249$).

In 1991 damage class had no significant relation to cavity ($G = 3.248$, 2 df, $P = 0.197$) or cluster use ($G = 1.126$, 2 df, $P = 0.569$) although cavity use tended to decrease as damage level increased (Fig. 1). In 1992, cavity use decreased significantly with increasing damage level ($G = 7.525$, 2 df, $P = 0.023$; Fig. 1) as did the number of clusters in which ≥1 cavity was used ($G = 7.884$, 2 df, $P = 0.019$). At least 1 cavity was used in 68.2% of the clusters in low damage areas compared to 34.4% in high damage areas and 38.2% in medium damage areas.

Many species occupied nest boxes during both breeding seasons, the most common being bluebirds and flying squirrels (Table 3). Nuthatches (*Sitta* spp.), tufted titmice, and black rat snakes (*Elaphe* spp.) used the boxes sporadically

Table 2. The number (N) of red-cockaded woodpecker clusters examined in high, medium, and low damage class areas and the mean (±1 SE) number of trees, number of cavities, and group size (adults/cluster) on the Francis Marion National Forest, South Carolina.

Damage class	1991				1992			
	N	No. trees	No. cavities	Group size	N	No. trees	No. cavities	Group size
High	63	2.57 ± 0.23A[a]	2.62 ± 0.05A	1.77 ± 0.11A	64	2.80 ± 0.15A	2.94 ± 0.16A	1.95 ± 0.11A
Medium	31	2.72 ± 0.20A	2.85 ± 0.22A	1.78 ± 0.16A	34	1.95 ± 0.11A	3.00 ± 0.22A	1.94 ± 0.15A
Low	22	3.68 ± 0.23B	4.04 ± 0.26B	2.33 ± 0.19B	22	3.79 ± 0.25B	4.29 ± 0.28B	2.52 ± 0.18B

[a] Means within columns with the same letter are not significantly different ($P > 0.05$).

Table 3. Percent (and no.) of all nest boxes (NB) and red-cockaded woodpecker (RCW) cavities used by non-RCW species on the Francis Marion National Forest, South Carolina during the 1991 and 1992 breeding seasons and during winter 1992. The total number of boxes or cavities examined (*N*) is presented for each season.

	Breeding season 1991		Winter 1992		Breeding season 1992	
Species	NB N = 165	Cavity N = 342	NB N = 170	Cavity N = 409	NB N = 175	Cavity N = 384
Eastern bluebirds	17.6 (29)	10.2 (35)	0.0 (0)	0.0 (0)	17.1 (30)	6.0 (23)
Flying squirrels	6.7 (11)	6.1 (21)	2.4 (4)	0.5 (2)	6.9 (12)	3.6 (14)
Red-bellied woodpeckers	0.0 (0)	2.6 (9)	0.6 (1)	2.0 (8)	0.0 (0)	2.6 (10)
Red-headed woodpeckers	0.0 (0)	0.3 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Downy woodpeckers	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.3 (1)
Northern flickers	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.3 (1)
Great-crested flycatcher	0.0 (0)	4.4 (15)	0.0 (0)	0.0 (0)	2.9 (5)	1.0 (4)
Nuthatch species	2.4 (4)	1.2 (4)	0.6 (1)	0.5 (2)	1.7 (3)	0.3 (1)
Tufted titmice	0.6 (1)	1.2 (4)	0.0 (0)	0.0 (0)	4.0 (7)	1.0 (4)
Screech owls	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.3 (1)
Unidentified birds	1.8 (3)	0.6 (2)	0.6 (1)	0.0 (0)	1.1 (2)	0.5 (2)
Black rat snakes	1.2 (2)	0.3 (1)	0.0 (0)	0.0 (0)	0.6 (1)	0.5 (2)

in both years and great-crested flycatchers only used boxes during 1992. Flying squirrels were the most common nest box occupants during winter 1992 but the winter 1992 occupancy data were low, and they were not analyzed further.

Nest box use did not differ significantly between years with 28.5% of the boxes used in 1991 and 34.3% of the boxes used in 1992 (G = 1.328, 1 df, $P = 0.249$). However, ≥1 box was used in significantly more clusters in 1992 than in 1991 (77.6 vs. 56.4%; G = 5.834, 1 df, $P = 0.016$). Use of nest boxes in relation to damage class was not consistent between years (Fig. 1). In 1991, box use increased with damage class with 13.3% use in low damage areas, 26.7% use in medium damage areas and 34.4% use in high damage areas (G = 5.505, 2 df, $P = 0.064$). In 1992, there was no significant difference in box use among damage classes (G = 1.114, 2 df, $P = 0.573$).

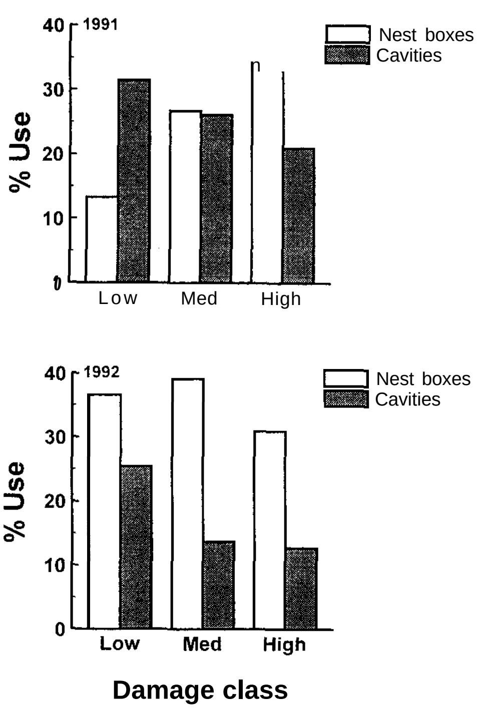

Fig. 1. Percent of nest boxes and red-cockaded woodpecker (RCW) cavities in each damage class that were used by non-RCW species during the 1991 and 1992 RCW breeding seasons on the Francis Marion National Forest, South Carolina.

When data for nest boxes and cavities were combined, there was no significant difference in use among damage classes by all species in 1991 although there appeared to be some differences among damage classes in 1992 (G = 2.630, 2 df, $P = 0.269$ and G = 5.590, 2 df, $P = 0.061$, for 1991 and 1992). In 1992, species other than RCW used 18.3% of the cavities and boxes in high damage areas, 22.2% of the cavities and boxes in medium damage areas, and 29.0% of the cavities and boxes in low damage areas.

We compared nest box use to availability to test for preference or avoidance by non-RCW species (Table 4). In both years, bluebirds significantly preferred nest boxes when data for all damage classes were combined (G = 5.410, 1 df, $P = 0.02$ and G = 19.886, 1 df, $P < 0.001$, for 1991 and 1992) and in high damage areas (G = 3.708, 1 df, $P = 0.05$ and G = 14.886, 1 df, $P < 0.001$ for 1991 and 1992). Nest boxes were used in greater proportion than their availability in low and medium damage areas in both years but this preference was not statistically significant in 1991 (G = 0.135, 1 df, $P = 0.713$

Table 4. Preference (structure use vs. structure availability) of nest boxes and red-cockaded woodpecker (RCW) cavities by bluebirds, flying squirrels and other vertebrate species on the Francis Marion National Forest, South Carolina during the 1991 and 1992 RCW breeding seasons. Only clusters in which both nest boxes and cavities were available were included in the analysis, "Total use" refers to use of both nest boxes and cavities by a species group and "% use in nest boxes" refers to the percentage of cavity and nest box use that occurred in nest boxes.

	Structure availability				Structure use					
	Cavities		Nest boxes		Bluebirds		Flying squirrels		Other species	
Damage Class	No.	%	No.	%	Total use	% use in nest boxes	Total use	% use in nest boxes	Total use	% use in nest boxes
1991										
All clusters	167	50.3	165	49.7	44	65.9*[a]	21	52.4	28	35.7
High damage	80	47.1	90	52.9	24	70.8*	13	76.9	7	71.4
Medium damage	47	51.1	45	48.9	14	64.3	2	0.0	11	36.4
Low damage	40	57.1	30	42.9	6	50.0	6	16.7	10	10.0**
1992										
All clusters	195	52.7	175	47.3	37	81.1***	16	75.0*	33	54.5
High damage	94	50.0	94	50.0	19	89.5***	8	100.0***	9	44.4
Medium damage	56	52.3	51	47.7	13	69.2	4	75.0	11	72.7
Low damage	45	60.0	30	40.0	5	80.0	4	25.0	13	46.2

[a] C-test comparisons of nest box use versus availability: * $P \leq 0.05$. ** $P \leq 0.01$, *** $P \leq 0.001$

and G = 1.577, 1 df, P = 0.209 for low and medium damage areas) although in 1992 the trend was stronger (G = 3.588, 1 df, P = 0.058 and G = 2.806, 1 df, P = 0.094). In 1991, flying squirrels tended to use nest boxes in greater proportion than availability in high damage areas (G = 3.445, 1 df, P = 0.06). Nest boxes were used in proportion to availability in low and medium damage areas and for all damage classes combined (Table 4). In 1992, flying squirrels selected nest boxes over cavities when damage classes were combined (G = 5.321, 1 df, P = 0.02) and in high damage areas (G = 11.446, 1 df, P = 0.001). Although boxes were used in greater proportion than their availability in medium damage areas, this preference was not significant (G = 1.289, 1 df, P = 0.256). No selection or avoidance of nest boxes occurred in low damage areas (G = 0.420, 1 df, P = 0.517).

Because most species other than bluebirds and flying squirrels occurred in low numbers, we combined data for all species other than bluebirds and squirrels (other species). Other species tended to use nest boxes and cavities in proportion to their availability except in low damage areas in 1991 and medium damage areas in 1992. Nest boxes were avoided by other species in low damage areas in 1991 (G = 5.994, 1 df, P = 0.01) and there was a tendency for selection of nest boxes in medium damage areas in 1992 (G = 3.168, 1 df, P = 0.075).

Effectiveness of Nest Boxes

In 1991, the number of clusters in which ≥1 cavity was used by a species other than RCWs did not differ between experimental and control groups in any damage class or for all damage classes combined (Table 5). However, in high damage areas in 1992 use of control clusters was significantly greater than use of experimental clusters by bluebirds (G = 6.453, 1 df, P = 0.01) and by all species combined (G = 3.774, 1 df, P = 0.05). Use of control clusters by bluebirds and flying squirrels also tended to be greater than use of experimental clusters when all damage classes were combined (Table 5; G = 2.335, 1 df, P = 0.13 and G = 1.850, 1 df, P = 0.17 for bluebirds and flying squirrels).

The number of cavities used by bluebirds, flying squirrels, and other species in 1991 did not differ significantly between control and experimental clusters for any damage class or for all damage classes combined (Table 6). However, when we combined data for all species, we found overall use of cavities in control clusters was greater than in experimental clusters in high damage areas (G = 3.642, 1 df, P = 0.056). In 1992, nest boxes appeared to have a greater influence on cavity use (Table 6). Bluebirds used more cavities in control clusters than in experimental clusters in high damage areas (G = 8.500 1 df, P = 0.004) and for all damage classes combined (G = 4.147, 1 df, P = 0.04). Flying squirrels tended to use more cavities in control than experimental clusters in high damage areas (G = 2.794, 1 df, P = *0.095)* and for all damage classes combined (G = 2.952, 1 df, P = 0.086). When data for all species were combined, significantly more cavities were used in

Table 5. Percent (and no.) of control and experimental (provided with nest boxes) red-cockaded woodpecker (RCW) clusters in which ≥1 RCW cavity was occupied by bluebirds, flying squirrels, other non-RCW species, and all non-RCW species during the RCW breeding season on the Francis Marion National Forest, South Carolina.

	Bluebirds		Flying squirrels		Other species		All species	
Damage class	Control[a]	Exp.[b]	Control	Exp.	Control	Exp.	Control	Exp.
1991								
All	29.5 (18)	27.3 (15)	13.1 (8)	12.7 (7)	22.9 (14)	20.0 (11)	50.8 (31)	47.3 (26)
High	36.4 (12)	23.3 (7)	6.1 (2)	10.0 (3)	18.2 (6)	6.7 (2)	51.5 (17)	40.0 (12)
Medium	18.8 (3)	33.3 (5)	12.5 (2)	6.7 (1)	25.0 (4)	40.0 (6)	43.8 (7)	53.3 (8)
Low	25.0 (3)	30.0 (3)	33.3 (4)	30.0 (3)	33.3 (4)	30.0 (3)	58.3 (7)	60.0 (6)
1992								
All	22.6 (14)	12.1 (7)	14.5 (9)	6.9 (4)	14.5 (9)	20.7 (12)	46.8 (29)	36.2 (21)
High	30.3 (10)	6.5 (2)*	6.1 (2)	0.0 (0)	9.1 (3)	16.1 (5)	45.4 (15)	22.6 (7)*
Medium	11.8 (2)	23.5 (4)	11.8 (2)	5.9 (1)	11.8 (2)	17.6 (3)	29.4 (5)	47.1 (8)
LOW	16.7 (2)	10.0 (1)	41.7 (5)	30.0 (3)	33.3 (4)	40.0 (4)	75.0 (9)	60.0 (6)

[a] There were 61 control clusters in 1991 (33 high damage, 16 medium damage, 12 low damage) and 58 control clusters in 1992 (31 high damage, 17 medium damage, and 10 low damage).

[b] There were 55 experimental clusters in 1991 (30 high damage, 15 medium damage, and 10 low damage) and 62 experimental clusters in 1992 (33 high damage, 17 medium damage, 12 low damage)

* Denotes a significant difference ($P \leq 0.05$) between control and experimental clusters.

control clusters than in experimental clusters in high damage areas (G = 4.907, 1 df, $P = 0.027$).

RCW Reproductive Success

Only groups with ≥2 adult RCWs were included in the analyses of reproductive performance ($N = 71$, 93, and 98 for 1990, 1991, 1992). In 1990, before the introduction of nest boxes, there were no significant differences between control and experimental clusters in the number of groups that nested ($G = 1.022$, 1 df, $P = 0.312$) or fledged ≥1 young (G = 0.312, 1 df, $P = 0.576$). Further, among groups which nested, there was no significant difference between controls and experimentals in the number of groups that fledged ≥1 young (G = 0.082, 1 df, $P = 0.775$). However, in 1991 and 1992, several differences in reproductive performance were observed between experimental and control groups (Fig. 2). In 1991 significantly more experimental than control groups successfully initiated a nest (G = 3.575, 1 df, $P = 0.059$) and fledged ≥1 young (G = 9.410, 1 df, $P = 0.002$). Further, of those groups that nested, significantly more experimental than control groups fledged ≥1 young (G = 5.863, 1 df, $P = 0.015$). In 1992 there was no difference in the number of control and experimental groups that nested (Fig. 2; G = 0.212, 1 df, $P = 0.645$) but among all groups, and only those that nest-

Table 6. Percent (and no.) of red-cockaded woodpecker (RCW) cavities in control and experimental (provided with nest boxes) clusters on the Francis Marion National Forest, South Carolina that were occupied by bluebirds, flying squirrels, other non-RCW species, and all non-RCW species.

	Bluebirds		Flying squirrels		Other species		All species	
Damage class	Control[a]	Exp[b]	Control	Exp	Control	Exp	Control	Exp.
1991								
All	11.4 (20)	9.0 (15)	6.3 (11)	6.0 (10)	10.3 (18)	9.6 (16)	26.4 (48)	22.8 (38)
High	16.5 (14)	8.8 (7)	3.5 (3)	3.8 (3)	8.2 (7)	2.5 (2)	27.1 (23)	15.0 (12)*
Medium	7.3 (3)	10.6 (5)	7.3 (3)	4.3 (2)	12.2 (5)	12.8 (6)	26.8 (11)	25.5 (12)
LOW	6.1 (3)	7.5 (3)	10.2 (5)	10.0 (4)	12.2 (6)	17.5 (8)	28.6 (14)	35.0 (14)
1992								
All	8.5 (16)	4.6 (7)*	5.3 (10)	2.1 (4)	5.8 (11)	7.7 (15)	19.0 (36)	13.3 (26)
High	12.8 (12)	1.2 (1)*	2.1 (2)	0.0 (0)	3.2 (3)	5.3 (5)	18.1 (17)	7.4 (7)*
Medium	4.3 (2)	7.3 (4)	4.4 (2)	1.8 (1)	4.4 (2)	5.4 (3)	13.0 (6)	14.3 (8)
LOW	4.1 (2)	2.2 (1)	12.2 (6)	6.7 (3)	12.5 (6)	15.6 (7)	26.5 (13)	24.4 (11)

[a] There were 175 cavities examined in control clusters in 1991 (8.5 in high damage, 41 in medium damage, and 49 in low damage clusters) and 189 cavities examined in control clusters in 1992 (94 in high damage, 46 in medium damage, and 49 in low damage clusters).

[b] There were 16i cavities examined in experimental clusters in 1991 (80 in high damage, 47 in medium damage and 40 in low damage clusters) and 195 cavities examined in 1992 (94 in high damage. 56 in medium damage, and 45 in low damage clusters)

* Denotes a significant difference ($P \leq 0.05$) between control and experimental clusters.

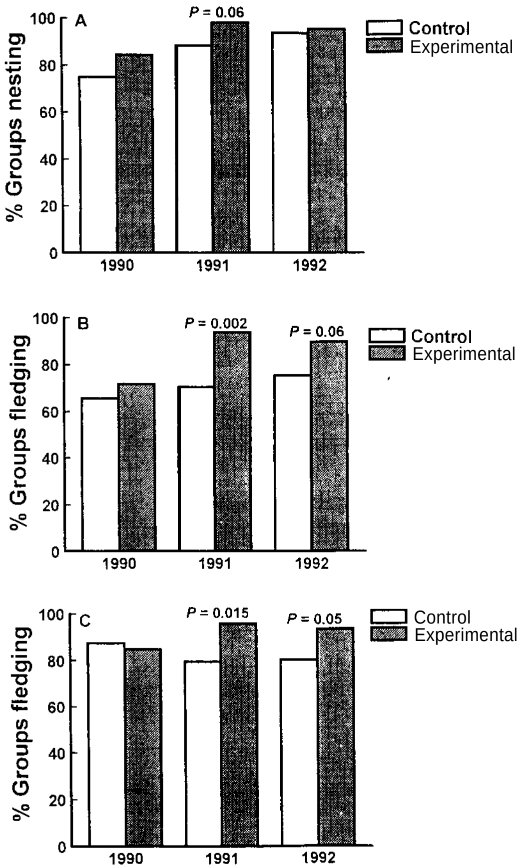

Fig. 2. A) Percent of red-cockaded woodpecker (RCW) groups with ≥2 adults that nested, B) percent of RCW groups with ≥2 adults that fledged ≥1 young, and C) percent of only those RCW groups that nested that fledged ≥1 young.

ed, more experimental groups fledged ≥1 young (G = 3.576, 1 df, P = *0.059* and G = 3.734, 1 df, P = 0.05). The number of groups with helpers did not differ significantly between control and experimental groups in any year (G = 1.104, 1 df, P = *0.293*, G = 0.001, 1 df, P = *0.974*, and G = 0.047, 1 df, P = 0.828 for 1990, 1991, and 1992).

Despite differences in the number of groups that successfully nested and fledged young after the addition of nest boxes, control and experimental groups showed few differences in mean clutch size, number of hatchlings, or number of fledglings (Table 7). Before the addition of nest boxes, there were no significant differences between control and experimental groups in the number of eggs, hatchlings, or fledglings ($P >$ 0.18). After the addition of nest boxes in experimental clusters, the number eggs, hatchlings, and fledglings still did not differ between control and experimental clusters in either 1991 ($P > 0.29$) or 1992 ($P >$ 0.08). However in 1990, before the addition of nest boxes in experimental clusters. damage class had a significant effect on the number of eggs, hatchlings, and fledglings (F = 4.50, 2, 51 df, P = 0.0158; F = 4.49, 2, 51 df, P = 0.0159; and F = 3.23, 2, 51 df, P = 0.0476). Clutch size, number of hatchlings, and number of fledglings were all significantly lower ($P \leq$ 0.05) in high damage areas than in medium and low damage areas which did not differ significantly from each other. Damage class was not a significant factor affecting reproductive parameters in 1991 or 1992 although the interaction term for the number of fledglings in 1991 was significant (F = 3.87, 2, 81 df, $P = 0.0249$). In low damage areas, the number of fledglings was significantly greater (P = 0.0471) in experimental groups but in medium damage areas, the number of fledglings tended to be greater in control groups (P = 0.1139; Table 7).

To further test the effect of cavity use by other species on RCW reproductive performance, we examined the relation between RCW reproductive success and the presence or absence of other species in cavities and nest boxes. In 1991, RCW groups were less likely to initiate a nest (G = 4.431, 1 df, P = 0.035) and fledge ≥1 young (G = 2.972, 1 df, P = 0.085) when ≥1 cavity was occupied by another species. In 1992, RCW groups were also less likely to initiate a nest if ≥ 1 cavity was occupied by another species (G = 6.565, 1 df, P = 0.059), but there was no effect on fledging success (G= 0.447, 1 df, P = 0.504). In contrast, occupation of ≥1 nest box had no effect on nest initiation in 1991 or 1992 (G = 1.286, 1 df, P = 0.257 and G = 0.831, 1 df, P = 0.362 for 1991 and 1992) or on fledging success (≥ 1 young fledged) in 1991 or 1992 (G = 0.504, 1 df, P = 0.478 and G = 1.450, 1 df, P = *0.229* for 1991 and 1992). However, for groups that nested, clutch size, number of hatchlings, and number of fledglings did not differ significantly between clusters in which ≥1 cavity was occupied and in which no cavities were occupied.

DISCUSSION

Interspecific competition occurs when 2 or more species use a resource in limited supply and use by one species decreases the fitness of members of the other species (Begon et al. 1986). Because cavities are a critical limiting re-

Table 7. Mean (and 1 SE) number of eggs, hatchlings, and nestlings produced by red-cockaded woodpecker groups that attempted to nest by damage class and treatment (with or without nest boxes in the cluster) on the Francis Marion National Forest, South Carolina. Nest boxes were placed in experimental treatments in December, 1990 so comparisons of 1990 control and experimental groups represent pretreatment controls.

Damage class	No nesting groups		Eggs		Hatchlings		Fledglings	
	Control	Exp	Control	Exp	Control	Exp.	Control	Exp
1990								
All	24	33	3.3 (0.1)	3.5 (0.1)	1.x (0.2)	2.1 (0.2)	1.4 (0.2)	1.6 (0.2)
High	10	15	3.0 (0.2)	3.1 (0.1)	1.4 (0.3)	1.5 (0.2)	1.0 (0.3)	1.3 (0.2)
Medium	8	9	3.3 (0.2)	3.6 (0.2)	2.1 (0.3)	2.2 (0.3)	1.6 (0.3)	1.7 (0.3)
LOW	6	9	3.5 (0.2)	3.7 (0.2)	1.8 (0.4)	2.6 (0.3)	1.5 (0.3)	2.0 (0.3)
1991								
All	38	46	3.3 (0.1)	3.5 (0.1)	2.0 (0.2)	2.2 (0.2)	1.6 (0.1)	1.7 (0.1)
High	17	24	3.2 (0.2)	3.3 (0.1)	1.6 (0.2)	2.1 (0.2)	1.4 (0.2)	1.8 (0.2)
Medium	11	12	3.3 (0.2)	3.4 (0.2)	2.4 (0.3)	1.9 (0.3)	2.2 (0.2)	1.5 (0.2)
Low	10	10	3.4 (0.2)	3.7 (0.2)	2.0 (0.3)	2.7 (0.3)	1.3 (0.3)	1.9 (0.3)
1992								
All	46	45	3.2 (0.1)	3.5 (0.1)	1.9 (0.2)	2.2 (0.2)	1.5 (0.1)	1.8 (0.1)
High	23	23	3.3 (0.1)	3.4 (0.1)	1.8 (0.2)	2.0 (0.2)	1.4 (0.2)	1.6 (0.2)
Medium	12	14	3.4 (0.2)	3.5 (0.2)	2.1 (0.3)	2.0 (0.2)	1.7 (0.2)	1.7 (0.2)
LOW	11	8	2.9 (0.2)	3.5 (0.2)	1.7 (0.3)	2.6 (0.3)	1.4 (0.2)	2.0 (0.3)

source among hole nesting birds (von Haartman 1957, 1971; Short 1979; Nilsson 1984, 1986), intense interspecific competition may occur when cavities are limited (Garcia 1983, Minot and Perrins 1986, Weitzel 1988; Ingold 1989, 1994; Barba and Delgado 1990). Cavities also may be limiting for some arboreal mammals (Barkalow and Soots 1965, Burger 1969, Weigl 1978) and thus, there is the potential for competition between birds and mammals.

As a limiting resource decreases, intensity of competition for the resource is expected to increase. Hurricane Hugo greatly reduced the number of available cavities on the Francis Marion National Forest for all cavity nesting species, not just RCWs. On the Santee Experimental Forest in the center of the Francis Marion, the volume of standing timber was reduced from 178 m^3/ha to 24 m^3/ha with the larger size classes most heavily damaged (Hook et al. 1991); trees within the large size classes are the most likely to contain cavities (Rosenberg et al. 1988, Sabin 1991). Although the storm created an abundance of snags, cavities usually are not excavated until snags are 5-6 years of age (Sabin 1991). Therefore, the remaining RCW cavities, the newly created artificial cavities, and the nest boxes we installed were probably highly valuable resources for many of the cavity nesting species on the Francis Marion.

Our results indicate that interspecific competition for RCW cavities occurred during the study. When the number of cavities for all species was increased in experimental clusters through the addition of nest boxes, there was a significant increase in RCW nest initiation rates in 1991 and in both years there was a significant increase in fledgling success among all groups and among nesting groups. Both control and experimental groups were less likely to nest if ≥1 cavity was occupied by another species. Further, in 1990 when no nest boxes were in any clusters, reproductive performance was significantly lower in high damage areas than in medium and low damage areas. Addition of nest boxes eliminated differences among groups in the various damage classes, possibly due to lower use of cavities by other species.

Despite differences in reproductive performance between control and experimental groups after the addition of nest boxes, mean clutch size, brood size, and number of fledglings did not vary with treatment for those groups that nested. These data suggest that the major effect of competitors was prevention of nesting or destruction of whole clutches or broods. A similar phenomenon occurs in RCW populations in the Sandhills of North Carolina (LaBranche and Walters 1994). The presence of helpers in breeding groups may be an important factor affecting reproductive success (Lennartz et al. 1987, Walters 1990). In our study however, control and experimental groups were just as likely to have helpers indicating that the differences in reproductive performance were not due to the presence or absence of helpers.

Our sample was too small to test whether nesting and fledging success varied with damage class. Despite the addition of artificial cavities, the mean number of RCW cavities per cluster was lower in high and medium damage areas than in low damage areas (Table 2). Therefore, we expected competition for cavities to be greater in high and medium damage areas. Our expectations were met only partially. Both bluebirds and flying squirrels clearly preferred nest boxes over cavities in high damage areas, and boxes were most effective in reducing cavity use by other species in high damage areas suggesting that demand for cavities was most intense in these areas. However, although in 1991 box use was higher in high damage areas, cavity use and use of nest boxes and cavities combined tended to be greater in low damage areas (Fig. 1), perhaps reflecting greater mortality of all species in high damage areas during the hurricane or subsequent movement to low damage areas for food and other resources. Therefore, although cavities may have been in greater demand in high and medium damage areas, other factors may have reduced overall cavity use in these areas.

Previous studies of RCW cavity use have shown that flying squirrels (Dennis 1971, Harlow and Lennartz 1983, Rudolph et al. 1990, Loeb 1993) or red-bellied woodpeckers (Jackson 1978, Kappes 1993) are the most common cavity occupants. In contrast, we found that bluebirds were the most important occupant of RCW cavities followed by flying squirrels, red-bellied woodpeckers, and (in 1991) great crested flycatchers. Bluebirds occupied 36.5–38.0% of the cavities and 50.0–58.0% of the nest boxes occupied by non-RCW species. The only other study to report that bluebirds were important RCW cavity occupants was also conducted on the Francis Marion National Forest (Harlow and Lennartz 1983). Bluebirds prefer relatively open areas such as clearcuts, wooded pastures, or pine stands with sparse understories (Kibler 1969, Willner et al. 1983, Munro and Rounds 1985, Allen and Sweeney 1990). Pre-Hugo management practices on the Francis Marion were highly favorable for RCWs (Hooper et al. 1991*b*) and included frequent burning of the understory and maintenance of relatively open stands of mature pine sawtimber. These practices also provided suitable habitat for bluebirds. Post-Hugo conditions were probably even more favorable for bluebirds. As other forested areas that are being managed for RCW recovery approach the mature stands and sparse midstories that characterized the Francis Marion National Forest, bluebirds may become more common in RCW clusters and competition between RCWs and bluebirds may increase. Bluebirds' strong preference for nest boxes over RCW cavities in experimental clusters and their decreased use of RCW cavities in 1992 in experimental clusters suggests that nest boxes may be effective in decreasing cavity competition between bluebirds and RCWs in forests where bluebirds are common.

Use of cavities and nest boxes by flying squirrels was lower than expected. Only 3.6–6.1% of the cavities and 6.7-6.9% of the nest boxes were used by flying squirrels during the RCW breeding season, compared to cavity occupancy of 19.1% on the Francis Marion in 1976-80, 10.5-21.0% in central Georgia (Loeb 1993), about 25% in coastal South Carolina (Dennis 1971) and 21.9% in eastern Texas (Rudolph et al. 1990). Several factors related to the effects of Hurricane Hugo may have contributed to lower cavity use by flying squirrels including mortality during the storm and greatly reduced supplies of acorns, the major food item for flying squirrels throughout the year (Harlow and Doyle 1990). Flying squirrels are highly dependent on cavities (Weigl 1978) and their limited supply may have also resulted in lower flying squirrel populations. Further, the greatly reduced stem densities may have forced squirrels to travel greater distances on the ground, increasing travel costs and predation risks. The high demand for cavities by RCWs and other species also may explain the relatively low use of cavities by flying squirrels during this study. Flying squirrel use of RCW cavities in Florida is greatest in clusters where the RCW demands are lowest and empty cavities are regularly available (Kappes 1993). Finally, the high use of cavities and nest boxes by bluebirds also may have decreased flying squirrel use of these structures.

The low use of cavities and nest boxes by flying squirrels during winter contrasts with previous studies that have found nest box use to be highest in winter (Goertz et al. 1975, Stojeba 1978, Sawyer and Rose 1985). However, southern flying squirrel use of RCW cavities at the Savannah River Site in the Upper Coastal Plain of South Carolina also decreases in the winter (Lotter 1997). Low use of RCW cavities and nest boxes in winter was likely due to seasonal changes in habitat use. During fall and winter flying squirrels in South Carolina preferentially use pine stands with a dense hardwood midstory and avoid pine stands with little or no hardwood midstory although no selection occurs during the spring and summer (Heiterer 1994). During the 1991 RCW breeding season, flying squirrels showed no overall preference or avoidance of nest boxes although there was a tendency to prefer boxes over cavities in high damage areas. In 1992, flying squirrels significantly preferred boxes over cavities, particularly in high damage areas, suggesting that nest boxes may be effective in deterring flying squirrels from RCW cavities. However, because of relatively low use of cavities by flying squirrels during this study, our results are inconclusive and further studies are warranted.

Red-bellied woodpeckers also may have been an important competitor for RCW cavities. In Florida, red-bellied woodpeckers are the most important RCW cavity competitor and outside roosting by RCWs is related directly to cavity use by red-bellied woodpeckers (Kappes 1993). Because we limited our observations to daylight hours, we may have underestimated red-bellied woodpecker use of RCW cavities. Nevertheless, because we only observed 1 red-bellied woodpecker in a nest box, snag retention may be the most effective method for reducing competition from red-bellied woodpeckers (Kappes 1993).

MANAGEMENT IMPLICATIONS

The effects of cavity use by other species on RCW populations often have been questioned. Although the circumstances of this study may have been extreme (severe resource limitation after a catastrophic event), the unique conditions provided an excellent setting for studying competitive interactions. Further, because competitive effects on rare species are difficult to measure (Schoener 1983), an experimental approach is more likely to detect competitive interactions, if they exist, than a purely observational/correlative approach. Our experimental approach showed that use of RCW cavities by other species decreases RCW reproductive performance. We believe that an experimental approach may be a more effective and efficient way to determine the presence of competitive interactions for RCW cavities and the addition of nest boxes is one technique that can be used effectively in experimental studies of RCW cavity competition.

Nest boxes also may be an effective management tool. Although nest boxes had limited success in reducing RCW cavity use by other species, their presence was correlated with increased nesting and fledging rates. Concerns that the presence of nest boxes in RCW clusters may attract other species to the area and increase competitive pressures on RCWs were not substantiated by our study. In addition to better reproductive performance in experimental areas, we found no difference in reproductive performance between groups in clusters in which ≥1 box was occupied and groups in clusters in which no boxes were occupied. Therefore, even if nest boxes attract other species to the area, use of the boxes by these species has no apparent negative effect on RCWs.

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