

## INTERSPECIFIC INTERACTIONS WITH FORAGING RED-CKOKADED WOODPECKERS IN SOUTH-CENTRAL FLORIDA

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**ABSTRACT.**—Interspecific competition for Red-cockaded Woodpecker (*Picoides borealis*) cavities has been well documented and may be one factor contributing to the species' decline. Other forms of interspecific interactions have rarely been documented over most of the species' range and have received little attention. During 806 hours of Red-cockaded Woodpecker foraging observations in south-central Florida we documented 306 interspecific interactions with 19 species. We observed fewer non-foraging interactions (98) than foraging interactions (208). Red-cockaded Woodpeckers lost 70 (71%) of the non-foraging interactions and 177 (85%) of the foraging interactions. Most non-foraging interactions (64%) were with non-woodpecker species, several of which frequently and consistently dominated Red-cockaded Woodpeckers. Together, Eastern Kingbirds (*Tyrannus tyrannus*), Great Crested Flycatchers (*Myiarchus crinitus*), Eastern Bluebirds (*Sialia sialis*), and Pine Warblers (*Dendroica pinus*) won 45 of their 48 (94%) non-foraging interactions with Red-cockaded Woodpeckers. Most foraging interactions (97%) were with other woodpecker species. Red-bellied Woodpeckers (*Melanerpes carolinus*) were involved in 172 (85%) of these interactions, of which they won 168 (98%). We found no relationship between the rate of interactions and the habitats or the local landscape in which these interactions occurred. Red-cockaded Woodpeckers did not appear to move to different and possibly less productive foraging sites after being usurped. In south-central Florida, where hardwood basal areas are relatively low in Red-cockaded Woodpecker habitat, the foraging niche of these two species may overlap to a greater extent than elsewhere in their range. Received 20 July 1998, accepted 5 Feb. 1999.

The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperative breeder restricted to the old growth pine forests of the southeastern United States (Jackson 1971). Despite nearly 30 years of Federal protection, Red-cockaded Woodpecker populations have continued to decline (James 1991). Habitat loss and fragmentation have ultimately been responsible for the species' decline (Lennartz et al. 1983, Conner and Rudolph 1991). Interspecific competition for Red-cockaded Woodpecker nest and roost cavities has been well documented (Jackson 1978, Harlow and Lennartz 1983, Kappes and Harris 1995) and may be one proximate factor contributing to the species' decline (U.S. Fish and Wildlife Service 1985).

Interspecific interactions, other than those involving cavities, have rarely been reported over most of the Red-cockaded Woodpecker's

range (Morse 1970, Nesbitt et al. 1978). Hooper and Lennartz (1981) observed foraging Red-cockaded Woodpeckers from May to March in South Carolina and documented 21 interspecific interactions between Red-cockaded Woodpeckers and one of four woodpecker species or the Brown-headed Nuthatch (*Sitta pusilla*). Only three interactions were related to foraging. Ligon (1970) reported six interactions between Red-cockaded Woodpeckers and Downy (*Picoides pubescens*) and Hairy woodpeckers (*P. villosus*) during 240 hours of observations from May to December in north-central Florida. In contrast, Nesbitt and coworkers (1981) documented 149 interspecific interactions between Red-cockaded Woodpeckers and five woodpecker species during 221 hours of observations from July to October in southwestern Florida. Most interactions involved Red-bellied Woodpeckers (*Melanerpes carolinus*) that often usurped Red-cockaded Woodpeckers from foraging sites. These interactions may have reduced the caloric intake of foraging Red-cockaded Woodpeckers (Nesbitt et al. 1981).

Geographic variation in interactions between species is common (Travis 1996). Explaining this variation may lead to a better understanding of geographical differences in be-

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havior, demography, and habitat selection of potentially interacting species. In this paper we report on interspecific interactions with Red-cockaded Woodpeckers in a small population in south-central Florida.

## METHODS

The Avon Park Air Force Range (AFR) is a 42,900 ha, multiple-use, active military training installation in Polk and Highlands counties, Florida. Dominant native pine communities consist of longleaf (*Pinus palustris*) and south Florida slash pine (*P. elliottii* var. *densa*) and approximately 9,000 ha planted in north Florida slash pine (*P. elliottii* var. *elliottii*). The pine habitats are interspersed with other communities typical of this region such as oak scrub and fresh water marshes. The natural pine habitats support the characteristic bird community for this region (Engstrom 1993), including 21 groups of Red-cockaded Woodpeckers.

To determine the foraging preferences of Red-cockaded Woodpeckers at Avon Park AFR, we observed individuals from 12 groups once a month from April 1995 to March 1996. Red-cockaded Woodpeckers were observed from dawn to dusk whenever possible; observations that ended prior to 13:00 EST were repeated. During a foraging observation period, we recorded the location of the focal individual, its foraging maneuver, and substrate use at 10 minute intervals. Locations were entered into a Geographical Information System (ArcView GIS Version 3.0). We determined home range boundaries and overlaid these boundaries with existing habitat type coverages. From these maps, we calculated the area of each habitat type (13 categories) in each home range and linked individual foraging locations to specific habitat types. These habitat types included pine flatwoods, scrubby flatwoods, oak scrub, sand pine scrub, pine plantation, mixed natural pine and plantation, pine swamp, oak hammock, hardwood forests, cypress, marsh, lake, and human disturbed.

During a subset (806 hours) of the total observation time (1168 hours), we documented all interspecific interactions. We recorded the species, sex (if determinable), type of aggression (aerial chase, tree chase, lunge, usurp, etc.), and the outcome (winner/loser). Individuals that retreated without retaliation were classified as losing. We categorized interactions as foraging or non-foraging interactions. Interactions where the winner examined, or foraged at, the usurped site were categorized as foraging related. All other interactions were categorized as non-foraging. Monthly observation periods varied as did the number of individuals in each group. To avoid observation time and group size biases, we used only those interactions that involved the breeding pair in each cluster and converted those interactions to a rate per hour for all analyses. We used the number of interactions between all individuals to describe the species involved in interspecific interactions with Red-cockaded Woodpeckers, and the number, type and outcome of those interactions.

Because most interactions were instantaneous or no longer than 15–60 s (aerial chases), we assumed interactions between the same individuals were independent if they occurred more than 15 min apart. For interactions that occurred less than 15 min apart, we excluded all but the first interaction as long as the type of interaction (foraging or non-foraging) and habitat were the same. When the type of interaction or habitat differed, we excluded all the interactions, since they could not be aggregated into a single type of interaction. However, if we suspected two different individuals of the other species (e.g., one male and one female) were involved in sequential interactions less than 15 min apart then both observations were considered independent.

To examine whether the frequency of interspecific interactions was habitat specific, we compared the frequency of interactions per habitat type to the expected frequency based on the proportion of time Red-cockaded Woodpeckers foraged in each habitat type. To determine if the frequency of interspecific interactions was related to the local landscape, we compared the frequency of interactions per group to the mean basal area of pines and hardwoods in each Red-cockaded Woodpecker's home range. Given the frequency of foraging interactions between Red-cockaded and Red-bellied woodpeckers, we repeated the above analyses for those interactions.

To determine whether usurpations had a measurable effect on Red-cockaded Woodpecker foraging patterns we performed two analyses. First, we compared the habitats used by Red-cockaded Woodpeckers before and after interactions with Red-bellied Woodpeckers to determine whether the former moved to a different and potentially less productive habitat after an interaction. Second, we compared foraging tree characteristics [dbh (diameter at breast height) and height] and Red-cockaded Woodpecker foraging height before and after usurpations by Red-bellied Woodpeckers to determine whether they moved to different micro-sites after interactions. Male and female Red-cockaded Woodpeckers forage at different locations (Ligon 1970), therefore we analyzed each sex separately. All statistical tests were nonparametric and were performed in the Microsoft Windows 95 operating system using SPSS (version 8.0).

## RESULTS

We observed 306 independent interspecific interactions between 45 color-banded Red-cockaded Woodpeckers and 19 other bird species (Table 1). Interactions involved 26 breeding adult Red-cockaded Woodpeckers (13 ♂, 13 ♀), 10 hatch-year birds (6 ♂, 4 ♀), 6 older helpers (all ♂), and 2 floaters (both ♂). Of the 306 interactions observed, 203 occurred with the breeding Red-cockaded Woodpeckers, 50 with hatch-year birds, 16 with older helpers, and 6 with floaters. Red-cockaded Woodpeck-

TABLE 1. Species observed interacting with Red-cockaded Woodpeckers, the outcome (loser or winner), and the type (foraging or non-foraging) of interaction during 806 hours of foraging observations at the Avon Park Air Force Range, 1995–1996.

Species	Red-cockaded Woodpecker Loser		Red-cockaded Woodpecker Winner	
	Foraging	Non-foraging	Foraging	Non-foraging
Red-shouldered Hawk	—	1	—	1
Red-bellied Woodpecker	168	6	4	8
Red-headed Woodpecker	—	3	—	—
Northern Flicker	1	—	1	2
Yellow-bellied Sapsucker	—	—	—	2
Downy Woodpecker	2	—	23	11
Hairy Woodpecker	3	—	—	3
Eastern Kingbird	1	14	—	—
Great Crested Flycatcher	—	11	—	—
Florida Scrub-Jay	—	1	—	—
Blue Jay	2	—	—	—
Brown-headed Nuthatch	—	1	1	—
Eastern Bluebird	—	8	—	1
Loggerhead Shrike	—	3	—	—
Northern Mockingbird	—	3	—	—
Pine Warbler	—	12	2	—
Eastern Towhee	—	2	—	—
Red-winged Blackbird	—	4	—	—
Summer Tanager	—	1	—	—
Total # of Interactions	177	70	31	28
Total # of Species	6	14	5	7

ers lost 247 (81%) interactions to 18 species and won 59 (19%) interactions with 9 species (Table 1). Win:loss ratios for Red-cockaded Woodpeckers did not differ between life history stage ( $\chi^2 = 1.23$ ,  $df = 3$ ,  $P > 0.05$ ) or sex ( $\chi^2 = 1.49$ ,  $df = 1$ ,  $P > 0.05$ ).

Interactions between Red-cockaded Woodpeckers and other woodpecker species were most frequent, accounting for 237 (77%) of all interactions. Excluding species with fewer than five observed interactions, five species won more than 85% of their interactions with Red-cockaded Woodpeckers [Eastern Kingbird (*Tyrannus tyrannus*), 100%; Great Crested Flycatcher (*Myiarchus crinitus*), 100%; Red-bellied Woodpecker, 94%; Eastern Bluebird (*Sialia sialis*), 89%; and Pine Warbler (*Dendroica pinus*), 86%; Table 1]. The Downy Woodpecker was the only species Red-cockaded Woodpeckers consistently dominated (34 of 36 encounters).

The rate of interspecific interactions with breeding Red-cockaded Woodpeckers was greatest in June and July. Although interactions varied between months from 0.10 ( $\pm 0.03$  SE) to 0.40 ( $\pm 0.31$ ) interactions per

hour (Fig. 1a), these differences were not significant (Kruskal-Wallis One Way ANOVA:  $\chi^2 = 16.7$ ,  $df = 11$ ,  $P > 0.05$ ).

*Non-foraging interactions.*—Red-cockaded Woodpeckers had 98 non-foraging interactions with 18 species; however, they had only non-foraging interactions with 12 of those species (Table 1). Interactions with Red-headed Woodpeckers (*Melanerpes erythrocephalus*), Eastern Kingbirds, Great Crested Flycatchers, Northern Mockingbirds (*Mimus polyglottos*), and Pine Warblers often involved aerial chases that lasted from 15–60 s. Few of these interactions were initiated by Red-cockaded Woodpeckers. However, in one instance a group of Red-cockaded Woodpeckers mobbed and successfully evicted a Red-shouldered Hawk (*Buteo lineatus*). Of the 98 interactions, Red-cockaded Woodpeckers won 28 and lost 70.

Non-foraging interactions were most frequent during June and July (Fig. 1b) and monthly differences were statistically different (Kruskal-Wallis One Way ANOVA:  $\chi^2 = 23.9$ ,  $df = 11$ ,  $P = 0.013$ ).

*Foraging interactions.*—Red-cockaded

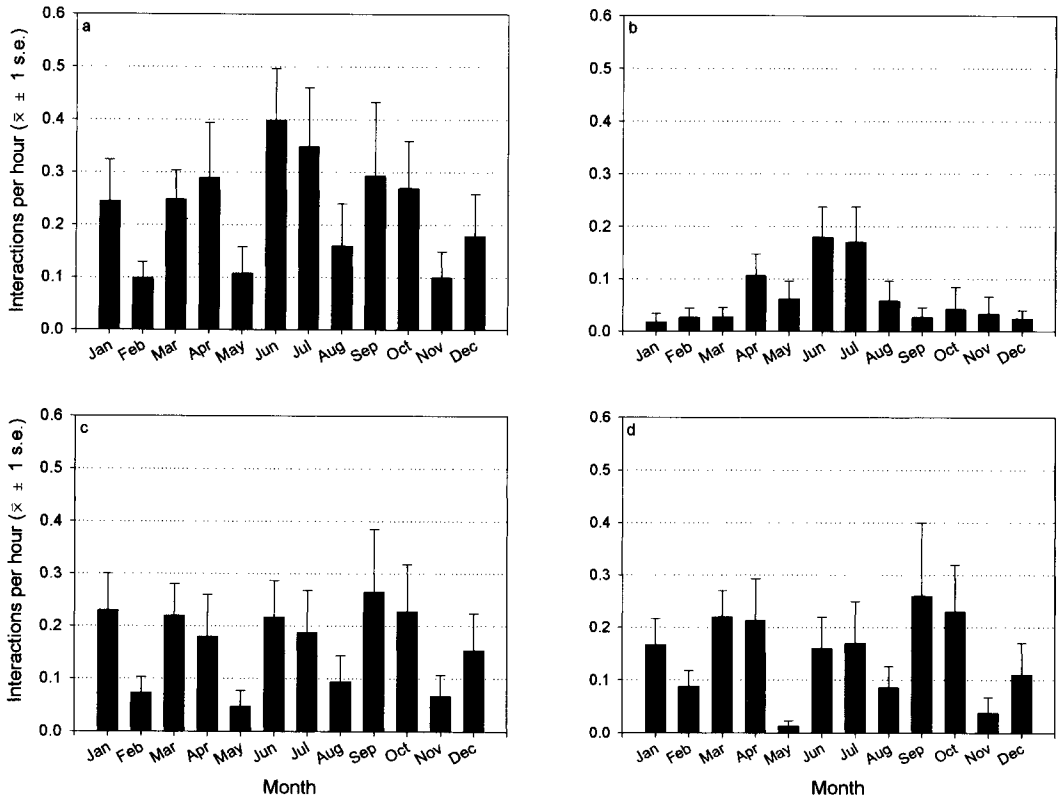


FIG. 1. Interspecific interactions ( $\bar{x} \pm 1$  SE for each month) observed per hour with breeding adult Red-cockaded Woodpeckers at Avon Park Air Force Range, in south-central Florida, 1995–1996: (a) all interactions, (b) non-foraging interactions, (c) foraging interactions, and (d) all interactions with Red-bellied Woodpeckers.

Woodpeckers had 208 foraging interactions with eight species. With six of these species they had both foraging and non-foraging interactions, but foraging interactions were more frequent than non-foraging interactions (Table 1). Most foraging interactions were between Red-cockaded Woodpeckers and other woodpeckers (202 of 208, 97%), but interactions with Blue Jays (*Cyanocitta cristata*), Eastern Kingbirds, Brown-headed Nuthatches, and Pine Warblers also were observed. Red-cockaded Woodpeckers lost most (177 of 208, 85.1%) foraging interactions; however, 74% of the 31 interactions they won were with Downy Woodpeckers. Red-cockaded Woodpeckers lost a greater percentage of foraging interactions (85.1%) than they did non-foraging interactions (71.4%;  $\chi^2 = 7.14$ ,  $df = 1$ ,  $P = 0.008$ ). None of the foraging interactions were initiated by Red-cockaded Woodpeckers, except for those with Downy Woodpeckers.

Downy Woodpeckers frequently foraged near Red-cockaded Woodpeckers and often were aggressively chased and their foraging locations usurped. The rate of foraging interactions with breeding Red-cockaded Woodpeckers did not vary monthly (Kruskal-Wallis One Way ANOVA:  $\chi^2 = 14.2$ ,  $df = 11$ ,  $P = 0.22$ ; Fig. 1c).

*Red-bellied Woodpeckers.*—Most interspecific interactions occurred between Red-cockaded and Red-bellied woodpeckers (186 of 306, 61%). Of the 186 interactions between Red-cockaded and Red-bellied woodpeckers, the latter won 174 (94%). Red-bellied Woodpeckers successfully usurped foraging Red-cockaded Woodpeckers in all but 4 of 168 foraging interactions. Red-bellied Woodpeckers frequently foraged within sight of Red-cockaded Woodpeckers but usurped them only after the Red-cockaded Woodpecker had found food. We also observed Red-bellied Wood-

TABLE 2. Variation in habitat characteristics and the rate ( $\bar{x} \pm 1$  SE) of all interspecific interactions (per hour of observation), foraging and non-foraging interactions, and interactions with Red-bellied Woodpeckers, with breeding Red-cockaded Woodpeckers from different groups at the Avon Park Air Force Range, 1995–1996.

RCW group	Pine basal area (m <sup>2</sup> /ha)	Hardwood basal area (m <sup>2</sup> /ha)	All interactions	Foraging interactions	Non-foraging interactions	Red-bellied Woodpecker interactions
1	8.13	0.0	0.16 ± 0.09	0.11 ± 0.07	0.05 ± 0.04	0.10 ± 0.06
2	12.44	0.0	0.19 ± 0.05	0.15 ± 0.05	0.04 ± 0.04	0.11 ± 0.04
3	8.97	0.0	0.20 ± 0.06	0.17 ± 0.01	0.04 ± 0.02	0.14 ± 0.06
5	6.6	0.28	0.20 ± 0.06	0.15 ± 0.01	0.06 ± 0.03	0.14 ± 0.06
7	7.49	0.07	0.10 ± 0.05	0.06 ± 0.03	0.04 ± 0.04	0.04 ± 0.02
8	9.28	0.04	0.10 ± 0.06	0.04 ± 0.02	0.06 ± 0.06	0.04 ± 0.02
15	11.34	0.03	0.42 ± 0.09	0.27 ± 0.09	0.15 ± 0.05	0.22 ± 0.09
19	9.18	0.46	0.22 ± 0.07	0.18 ± 0.07	0.04 ± 0.02	0.15 ± 0.05
21	10.25	0.44	0.17 ± 0.11	0.11 ± 0.07	0.05 ± 0.04	0.11 ± 0.07
23	6.55	0.01	0.42 ± 0.15	0.34 ± 0.13	0.08 ± 0.03	0.35 ± 0.14
31	12.15	0.86	0.22 ± 0.09	0.16 ± 0.08	0.07 ± 0.03	0.13 ± 0.07
33	12.33	0.0	0.34 ± 0.09	0.24 ± 0.07	0.09 ± 0.04	0.22 ± 0.02

peckers following Red-cockaded Woodpeckers as they foraged between different pine stands. Red-cockaded Woodpeckers won only 12 interactions with Red-bellied Woodpeckers: 4 foraging interactions and 10 non-foraging interactions.

The rate of interactions between Red-bellied Woodpeckers and breeding Red-cockaded Woodpeckers varied monthly (Kruskal-Wallis One Way ANOVA:  $\chi^2 = 19.3$ ,  $df = 11$ ,  $P = 0.055$ ; Fig. 1d); however, no consistent pattern was evident. The rate of interactions did not differ between the breeding and non-breeding season (Mann-Whitney  $U$ -test:  $Z = -0.59$ ,  $P > 0.05$ ). No sex-related difference existed in the rate of interactions between Red-cockaded and Red-bellied woodpeckers ( $\chi^2 = 5.13$ ,  $df = 1$ ,  $P > 0.05$ ).

**Habitat relationships.**—Red-cockaded Woodpeckers foraged predominately (93.8% of observation time) in pine flatwood, scrubby flatwood, and pine plantation habitats (Bowman et al. 1998, unpubl. data). The frequency of foraging and non-foraging interactions did not differ from the relative frequency of habitats used by foraging Red-cockaded Woodpeckers ( $\chi^2 = 4.74$  and  $2.18$ ,  $df = 4$  and  $2$ , respectively,  $P > 0.05$ ). We also found no significant correlations between the rate of interactions and the area of any of the 13 habitat types in Red-cockaded Woodpecker home ranges (Pearson correlations: all  $P > 0.05$ ). Pine basal area in home ranges varied from

6.6 to 12.4 m<sup>2</sup> per ha, and hardwood basal area varied from 0.0 to 0.44 m<sup>2</sup> per ha (Table 2); however, neither the total number of interactions nor foraging or non-foraging interactions were correlated with the basal area of pines or hardwoods within each home range.

Interactions with Red-bellied Woodpeckers in different habitat types did not differ from the relative frequency of habitats used by Red-cockaded Woodpeckers ( $\chi^2 = 0.18$ ,  $df = 3$ ,  $P > 0.05$ ). However, the rate of these interactions was positively correlated with the percentage of each home range comprised of pine plantation (Spearman rank correlation:  $r = 0.62$ ,  $P < 0.05$ ). No significant correlations existed between the rate of interactions and the area of any of the other 12 habitat types or the pine or hardwood basal area in Red-cockaded Woodpecker home ranges (Spearman rank correlation: all  $P > 0.05$ ).

Red-cockaded Woodpeckers moved to a new habitat type following only 5 of 120 (4%) usurpations by Red-bellied Woodpeckers for which we had data. No significant difference existed in the dbh or height of the trees used by foraging Red-cockaded Woodpeckers (male or female) before and after usurpation (Kruskal-Wallis One Way ANOVAs: all  $P > 0.05$ ), nor did any differences exist in the height at which Red-cockaded Woodpeckers (male or female) foraged before and after usurpation (Kruskal-Wallis One Way ANOVAs: all  $P > 0.05$ ).

## DISCUSSION

Thirty-two percent of interspecific interactions were not related to foraging. Non-foraging interactions were highly seasonal, occurring during the breeding season for most species. Many of these interactions may have been related to nest and/or fledgling defense as many occurred near nests or young of the species interacting with Red-cockaded Woodpeckers. Although these interactions were seasonal and relatively infrequent in our population, other forms of non-foraging interactions (e.g., cavity competition) could play an important role in the dynamics of Red-cockaded Woodpecker populations (Kappes and Harris 1995).

Most interspecific interactions were related to foraging and occurred between Red-cockaded and Red-bellied woodpeckers. Red-cockaded Woodpeckers lost virtually all foraging interactions with Red-bellied Woodpeckers. Red-cockaded Woodpeckers interacted frequently with Downy Woodpeckers, winning most encounters. Therefore, the latter interactions likely had no deleterious impacts on Red-cockaded Woodpeckers.

Habitat use, foraging behavior, and diet of Red-cockaded and Red-bellied woodpeckers appear to be dissimilar. Red-bellied Woodpeckers use most habitats occurring within their range (Sprunt 1954, Breitwisch 1977 and references within) but may prefer hardwood habitats (Short 1982, Root 1988). In Florida, their use of tree species for foraging is diverse and varies by habitat type (Breitwisch 1977). Red-bellied Woodpeckers spend 20–69% of their foraging time on dead trees (Williams 1975, Breitwisch 1977, Williams and Batzli 1979). In contrast, Red-cockaded Woodpeckers forage almost exclusively on living pines (Hooper and Lennartz 1981) in relatively open pine forests.

In south Florida pine habitat, Breitwisch (1977) observed foraging Red-bellied Woodpeckers gleaning and probing (80%) but rarely excavating (10%). At Avon Park AFR, foraging Red-cockaded Woodpeckers used surface probes (54%) most frequently, excavated frequently (40%), and rarely gleaned (4%; Bowman et al. 1998, unpubl. data).

Little dietary overlap appears to exist between Red-cockaded and Red-bellied wood-

peckers (Beal 1911). Red-bellied Woodpecker stomachs ( $n = 271$ ) contained 31% animal matter, of which 6% was ants; Red-cockaded Woodpecker stomachs ( $n = 76$ ) contained 81% animal matter, of which 56% was ants. Both species consumed a similar percentage of beetles (~10%); however, little overlap existed in the remaining fraction of animal matter.

Niche overlap between these two species appears to be low, even in south Florida, yet interactions between Red-bellied and Red-cockaded woodpeckers appear to be higher here than elsewhere in their ranges. It is possible that these interactions are simply overlooked elsewhere, especially if they are more frequent outside of the breeding season. If so, and these interactions have deleterious impacts on Red-cockaded Woodpeckers, then they should be examined more closely elsewhere. However, geographical variation in interspecific competition may be real and be caused by variation in population densities of the species (Thompson 1988), indirect effects as species assemblages change, the productivity or vegetation composition of habitats (Travis 1996) or some interaction of these factors.

Data on the density of Red-bellied Woodpeckers across their range are not available; in general they appear as abundant in Florida as elsewhere in the southeastern coastal plain (Bock and Lepthien 1975, Root 1988, Price et al. 1995). At Avon Park AFR, the density of Red-cockaded Woodpeckers is low compared to populations outside of peninsular Florida (Bowman et al. 1998, unpubl. data). Data on the regional variation in density of both Red-cockaded and Red-bellied woodpeckers are needed to determine whether differences in density contribute to variations in interspecific interactions.

Indirect effects related to the presence of other species may have contributed to the high rate of observed interactions. At Avon Park AFR, five species of woodpeckers and the Brown-headed Nuthatch are sympatric with Red-cockaded Woodpeckers; however, many of these species are sympatric in pine habitats outside of peninsular Florida. The abundance and diversity of species utilizing similar resources in different habitats may contribute to

variation in the rate of interspecific interactions.

Differences in pine forests between south-central Florida and more temperate forests may have contributed to the relatively high rates of interactions with Red-bellied Woodpeckers. In southern Florida, most Red-cockaded Woodpeckers occur in mesic and hydric flatwoods. These habitats have lower hardwood basal area than do more temperate pine communities (Beever and Dryden 1992, pers. obs.). Elsewhere, Red-bellied Woodpeckers' preference for hardwoods may minimize their foraging overlap with Red-cockaded Woodpeckers, but we know little about habitat-specific foraging strategies of either species. Although hardwood basal area varied among the 12 Red-cockaded Woodpecker home ranges, overall, basal area was low and was not correlated with the frequency of Red-bellied Woodpecker interactions.

All Red-cockaded Woodpecker populations in peninsular Florida support fewer than 50 groups (Cox et al. 1995). In peninsular Florida, Red-cockaded Woodpeckers have larger home ranges (Nesbitt et al. 1981; DeLotelle et al. 1983; Bowman et al. 1998, unpubl. data) and produce fewer fledglings (Jansen and Patterson 1983; DeLotelle and Epting 1992; Bowman et al. 1998, unpubl. data) than other populations. These characteristics suggest that these populations may occupy relatively poor quality habitat; however, few correlations exist between various measures of Red-cockaded Woodpecker demography and habitat characteristics (Beyer et al. 1996; Bowman et al. 1998, unpubl. data). Although these results do not suggest a deleterious effect of interspecific competition, the relatively high rates we documented bear further investigation, especially where these interactions have not been reported. Aggressive interaction between species is not sufficient to demonstrate competition, but interspecific competition may contribute to variation in the abundance and reproductive potential of species. It is possible that some synergistic interaction of habitat and community structure, such as competition, may be related to regional differences in Red-cockaded Woodpecker demography.

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#### LITERATURE CITED

- BEAL, F. E. L. 1911. Food of the woodpeckers of the United States. U.S. Dept. Agric. Biol. Surv. Bull., 37:1-64.
- BEEVER, J. W. AND K. A. DRYDEN. 1992. Red-cockaded Woodpeckers and hydric slash pine flatwoods. Trans. N. Am. Wildl. Nat. Res. Conf. 57:693-700.
- BEYER, D. E., R. COSTA, R. G. HOOPER, AND C. A. HESS. 1996. Habitat quality and reproduction of Red-cockaded Woodpecker groups in Florida. J. Wildl. Manage. 60:826-835.
- BOCK, C. E. AND L. W. LEPTHIEN. 1975. A Christmas count analysis of woodpecker abundance in the United States. Wilson Bull. 87:355-366.
- BOWMAN, R., D. L. LEONARD, JR., L. K. BACKUS, P. M. BARBER, A. R. MAINS, L. M. RICHMAN, AND D. SWAN. 1998. Demography and habitat characteristics of the Red-cockaded Woodpecker (*Picoides borealis*) at the Avon Park Air Force Range: Final Report, 1994-1998. Department of Defense, Avon Park, Florida.
- BREITWISCH, R. J. 1977. The ecology and behavior of the Red-bellied Woodpecker, *Centurus carolinus* (Linnaeus) (Aves: Picidae), in south Florida. M.Sc. thesis, Univ. of Miami, Miami, Florida.
- CONNOR, R. N. AND D. C. RUDOLPH. 1991. Forest habitat loss, fragmentation, and Red-cockaded Woodpecker populations. Wilson Bull. 103:446-457.
- COX, J., W. W. BAKER, AND D. WOOD. 1995. Status, distribution, and conservation of the Red-cockaded Woodpecker in Florida: a 1992 update. Pp. 475-464 in Red-cockaded Woodpecker: recovery, ecology, and management (D. L. Kulhavy, R. G. Hooper, and R. Costa, Eds.). College of Forestry, Stephen F. Austin State Univ., Nacogdoches, Texas.
- DELOTELLE, R. S. AND R. J. EPTING. 1992. Reproduction of the Red-cockaded Woodpecker in central Florida. Wilson Bull. 104:285-294.
- DELOTELLE, R. S., J. R. NEWMAN, AND A. E. JERAULD. 1983. Habitat use by Red-cockaded Woodpeckers in central Florida. Pp. 59-67 in Proceedings of the Red-cockaded Woodpecker symposium II (D.A. Wood, Ed.). Florida Game and Fresh Water Fish Comm., Tallahassee.
- ENGSTROM, R. T. 1993. Characteristic mammals and birds of longleaf pine forests. Proc. Tall Timbers Fire Ecol. Conf. 18:127-138.
- HARLOW, R. F. AND M. R. LENNARTZ. 1983. Interspecific competition for Red-cockaded Woodpecker cavities during the nesting season in South Carolina. Pp. 41-43 in Red-cockaded Woodpecker symposium II (D. A. Wood, Ed.). Florida Game and Fresh Water Fish Comm., Tallahassee.

- HOOPER, R. G. AND M. R. LENNARTZ. 1981. Foraging behavior of the Red-cockaded Woodpecker in South Carolina. *Auk* 98:321-334.
- JACKSON, J. A. 1971. The evolution, taxonomy, distribution, past populations and current status of the Red-cockaded Woodpecker. Pp. 4-29 in *The ecology and management of the Red-cockaded Woodpecker* (R. L. Thompson, Ed.). Bur. Sport Fish. Wildl., U.S. Dept. of Interior, and Tall Timbers Research Station, Tallahassee, Florida.
- JACKSON, J. A. 1978. Competition for cavities and Red-cockaded Woodpecker management. Pp. 103-112 in *Endangered birds: management techniques for threatened species* (S. A. Temple, Ed.). Univ. of Wisconsin Press, Madison.
- JAMES, F. C. 1991. Signs of trouble in the largest remaining population of Red-cockaded Woodpeckers. *Auk* 108:419-423.
- JANSEN, D. K. AND G. A. PATTERSON. 1983. Late nesting and low reproductive success of Red-cockaded Woodpeckers in the Big Cypress National Preserve, Florida, in 1983. Pp. 99 in *Red-cockaded Woodpecker symposium II* (D. A. Wood, Ed.). Florida Game and Fresh Water Fish Comm., Tallahassee.
- KAPPES, J., JR. AND L. D. HARRIS. 1995. Interspecific competition for Red-cockaded Woodpecker cavities in Apalachicola National Forest. Pp. 389-393 in *Red-cockaded Woodpecker: recovery, ecology, and management* (D. L. Kulhavy, R. G. Hooper, and R. Costa, Eds.). College of Forestry, Stephen F. Austin State Univ., Nacogdoches, Texas.
- LENNARTZ, M. R., P. H. GEISSLER, R. F. HARLOW, R. C. LONG, K. M. CHITWOOD, AND J. A. JACKSON. 1983. Status of the Red-cockaded Woodpecker on federal lands in the south. Pp. 7-12 in *Red-cockaded Woodpecker Symposium II* (D. A. Wood, Ed.). Florida Game Fresh Water Fish Comm., Tallahassee.
- LIGON, J. D. 1970. Behavior and breeding biology of the Red-cockaded Woodpecker. *Auk* 87:255-278.
- MORSE, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecology* 40:119-168.
- NESBITT, S. A., D. T. GILBERT, AND D. B. BARBOUR. 1978. Red-cockaded Woodpecker fall movements in a Florida flatwood community. *Auk* 95:145-151.
- NESBITT, S. A., B. A. HARRIS, A. E. JERAULD, AND C. B. BROWNSMITH. 1981. Report of the investigation of Red-cockaded Woodpeckers in Charlotte County. Florida Game and Fresh Water Fish Comm., Tallahassee.
- PRICE, J., S. DROEGE, AND A. PRICE. 1995. The summer atlas of North American birds. Academic Press, San Diego, California.
- ROOT, T. 1988. Atlas of wintering North American birds. Univ. of Chicago Press, Chicago, Illinois.
- SHORT, L. L. 1982. Woodpeckers of the world. Delaware Museum of Natural History, Greenville.
- SPRUNT, A., JR. 1954. Florida bird life. Coward-McCann, Inc., New York.
- THOMPSON, J. N. 1988. Variation in interspecific interactions. *Annu. Rev. Ecol. Syst.* 19:65-87.
- TRAVIS, J. 1996. The significance of geographic variation in species interactions. *Am. Nat.* 148:S1-S8.
- U.S. FISH AND WILDLIFE SERVICE. 1985. Red-cockaded Woodpecker recovery plan. U.S. Fish and Wildlife Service, Atlanta, Georgia.
- WILLIAMS, J. B. 1975. Habitat utilization by four species of woodpeckers in a central Illinois woodland. *Am. Midl. Nat.* 93:354-367.
- WILLIAMS, J. B. AND G. O. BATZLI. 1979. Interference competition and niche shifts in the bark-foraging guild in central Illinois. *Wilson Bull.* 91:400-411.