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RED-COCKADED WOODPECKER ROOST-CAVITY DEFENSE DURING THE NON-BREEDING SEASON

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Abstract.—Endangered Red-cockaded Woodpeckers (*Picoides borealis*) experience high rates of roost cavity usurpation by other species. To better understand why this cooperatively breeding species gets displaced from cavities so often and to provide information useful in decision-making regarding competitor removal programs, we conducted an experimental study of cavity defense. Because a lack of cooperation in cavity defense could explain high usurpation rates, we tested whether Red-cockaded Woodpeckers cooperatively (versus singularly) defend roost cavities of individuals within family groups, and whether group members' defense responses were correlated with intra-group social status. To simulate a cavity usurpation threat, we conducted playback experiments using a mounted male Red-bellied Woodpecker (*Melanerpes carolinus*), a common cavity usurper, in conjunction with taped playback of woodpecker calls and drumming sounds. We did not detect a difference in defense response between sex or social classes. However, only the primary cavity occupant responded to experimental trials at roost cavities, suggesting that Red-cockaded Woodpeckers do not cooperatively defend roost cavities during the post-breeding season. Our finding suggests that cavity usurpation, at least during winter, has not historically been a strong selective factor on group fitness in Red-cockaded Woodpeckers. Therefore, implementation of competitor species control programs may not be warranted based solely on high rates of cavity usurpation without evidence that cavity loss incurs population-level impacts.

The endangered Red-cockaded Woodpecker constructs long-lasting cavities in living pines that they maintain and use for nesting and roosting (Hooper et al. 1982). Other cavity-dwelling species, especially southern flying squirrels (*Glaucomys volans*) and Red-bellied Woodpeckers, commonly usurp Red-cockaded Woodpecker cavities (Jackson 1977, Kappes and Harris 1995, Kappes 2004), but the population-level effects of this interaction remain unclear despite significant attention to the issue (Kappes 1997; findings of negative effects: Franzreb 1997, Laves 1996; findings of no effect: Conner et al. 1996, Mitchell et al. 1999). Despite lack of consensus on whether cavity usurpation contributes to endangerment of the Red-cockaded Woodpecker, removal programs to reduce cavity occupancy rates by other species are increasingly common, particularly during (re) establishment of small populations of woodpeckers (e.g., Franzreb 1997). Flying squirrel (or other species) removal programs are difficult, even in small woodpecker populations, requiring time and labor outside the purview of basic population monitoring programs required by federal law (Kappes 2004). We undertook this study with two goals: (1) to better understand why cavity usurpation rates can be so high in Red-cockaded Woodpeckers, and (2) to produce information useful to managers considering implementation of removal programs to reduce cavity usurpation rates.

The Red-cockaded Woodpecker is a cooperatively breeding species whose groups contain a single breeding pair and up to three helpers, typically males (Lennartz and Harlow 1979, Lennartz et al. 1987, Walters 1990). Despite apparently high levels of cooperation in breeding season activities, observational records provide no evidence that cooperative defense of roost cavities occurs in Red-cockaded Woodpeckers (Ligon 1970, 1971; J. J. Kappes, unpublished data). In other cooperatively breeding bird species (e.g., Acorn Woodpecker *Melanerpes formicivorus* and Florida Scrub Jay *Aphelocom*a *coerulescens*), breeding groups cooperating in aggression can effectively dominate larger-bodied predators or competitors that lone defending birds would find difficult to repel (Mumme and de Queiroz 1985, Francis et al. 1989, Woolfenden and Fitzpatrick 1990). Cooperative defense of a resource implies significance of the resource to inclusive fitness of group members (e.g., Farabaugh et al. 1992, Grinnell 2002). If there is no cooperative defense of roost cavities by Red-cockaded Woodpeckers, this may help explain high cavity usurpation rates in Red-cockaded Woodpecker populations. It could also mean that historical (evolutionary) rates of cavity usurpation were not sufficient to reduce fitness or select for cooperative, and presumably more effective, defense, implying that in established Red-cockaded populations where habitat quality reflects historical conditions, control of cavity usurpers should be of low priority, even if heterospecific occupancy is high. To establish causal inference (James and McCulloch 1995) concerning lack of cooperative defense of roost cavities, we undertook an experimental study of roost-cavity defense in 2 Red-cockaded Woodpecker populations in north-central Florida.

Study Design

We tested two hypotheses: whether breeding groups cooperatively defend roost cavities during the post-breeding season and, if not, whether a Red-cockaded Woodpecker's defense response at its own cavity correlates with its sex or social status. We simulated a cavity usurpation threat using a combination of taped-call playbacks with presentations of a male Red-bellied Woodpecker taxidermy mount at selected Red-cockaded Woodpecker roost cavities. If breeding groups cooperatively defend their roost cavities against usurpation we predicted that the breeding groups would collectively respond to our experimental usurpation with aggressive behavior regardless of whose cavity was threatened. Alternatively, if Red-cockaded Woodpeckers do not cooperate in roost-cavity defense, we predicted only the individual whose cavity was directly threatened would respond aggressively, and the level of response would reflect the bird's social status.

In cooperatively breeding species an individual's dominance status, determined by sex and social rank within the breeding group, can influence their level of aggressiveness in resource defense (e.g., Florida Scrub Jay; Francis et al. 1989). In Red-cockaded Woodpecker breeding groups, the breeding male roosts in the group's nesting cavity (Ligon 1970) which is, therefore, the most important to the group's breeding success. Since territory ownership is paternally inherited (Walters 1990), we reasoned that breeding males should defend their roost cavities most aggressively. Conversely, the breeding female is typically the last to acquire a cavity, is often forced by group males to roost outside of a cavity at night when there are insufficient cavities (Hooper and Lennartz 1983, Doerr et al. 1989, Rudolph et al. 1990, Carrie et al. 1998), and is evicted from the breeding cluster by the helper male when he inherits the territory (Lennartz et al. 1987). Therefore, in comparing responses by the target birds (the adult Red-cockaded Woodpecker whose cavity was directly threatened) in our experiments, we predicted that breeding males would be more aggressive than helper males who, in turn, would be more aggressive than breeding females.

STUDY AREA AND METHODS

We conducted playback experiments at two sites in north-central Florida: Goethe State Forest (Levy County, FL) and Camp Blanding Training Site (Clay County, FL). At the time of the study, Goethe State Forest supported 30 active breeding groups on 20,213 ha of forest, while Camp Blanding Training Site supported 14 active breeding groups on 22,742 ha of forest. Both sites contain pine flatwoods and sandhills dominated by longleaf pine (*Pinus palustris*). As part of an ongoing intensive monitoring program (Kappes 2004), all individual Red-cockaded Woodpeckers at both sites were uniquely identifiable from a distance, as all had been captured (as nestlings) and fitted with numbered aluminum leg bands and unique combinations of colored plastic bands. The monitoring program included identification of every individual bird's roosting cavity via regular (bi-weekly) roost checks conducted prior to and throughout this study. Roost checks involved observations of marked individuals going to roost in the evening and nighttime cavity observations using video cameras (Kappes 2004). These intensive monitoring activities provided us precise information on where "target" birds were roosting.

We designed three trial types—experimental treatments, references, and roosting observations—applied during the post-breeding months of July and August (1999 and 2001). Trial types were further identified to sex and age class: breeding males (BM), breeding females (BF), and helper males (HM). To detect differences in aggression among trial types, we relied on behaviors that others have identified, described, and used in the same context (Ligon 1970, Walters 1990, Bowman et al. 1999), including, the number (per min) of vocalizations, perch-to-perch hops, and strikes (using bill or body) on the model, and closest approach distances to the model (treatment and reference trials only). Some behaviors not chosen *a priori* were only observed during roost observations, including hitching and pecking on trunks (basic foraging behavior for this species; Ligon 1970), resin well maintenance (pecking around the cavity entrance to generate resin flow; Rudolph et al. 1990), and entering the cavity (going to roost). Treatment trials were conducted in both years but due to the limited number of breeding groups available in each year, reference trials were only conducted in 1999 and roosting observations were only conducted in 2001.

Trial Protocol.—Treatment trials involved presentations of a male Red-bellied Woodpecker taxidermy mount and taped-call playback of Red-bellied Woodpecker vocalizations to elicit aggressive responses. Previous studies have demonstrated the effectiveness and appropriateness of model presentations/playbacks of competitor or predator species in generating aggressive responses in various bird species (e.g., Chandler and Rose 1988, Pearson and Rohwer 2000, Radford and Blakey 2000). We assumed that experiments using a Red-bellied Woodpecker mount and playback would be an adequate stimulus for eliciting group and/or individual aggressive defense responses, defined by extreme values of our response behaviors (i.e., high numbers of hops, strikes, and vocalizations, and close approaches, etc.). However, given the critical nature of this assumption, we also tested for it in our design by using two forms of controls: reference trials and procedural controls.

Reference trials consisted of presentations of a white piece of paper (crumpled to approximate the dimensions of a Red-bellied Woodpecker) and background noise from a blank tape. Reference trials would likely not elicit aggression but would disturb the birds, as in neophobic responses (Greenberg 1989). By comparing behavioral responses during the reference and treatment trials, we could determine whether the Red-bellied Woodpecker mount elicited an aggressive response or solely a disturbance behavior.

In addition to treatment and reference trials, we also conducted procedural controls to identify and qualitatively describe potential observer effects on response behaviors deriving from experimental set-up of treatment and reference trials. Procedural controls consisted of un-manipulated observations of roosting behavior, conducted during the winter of 2001. To make these observations, the observer positioned himself 15 m from the target roost tree and, without setting up a playback or attaching any object to the cavity tree, recorded target bird behaviors during the brief period when they return and enter their cavities to roost for the evening.

In treatment and reference trials the model (Red-bellied Woodpecker mount or piece of paper, respectively) was fastened 1 cm below the cavity entrance. A portable stereo speaker ($16 \times 12.5 \times 6.5$ cm) was positioned 30 cm below the cavity and masked with pine bark. During treatment trials a 24-s sequence of Red-bellied Woodpecker *chee-wuck* vocalizations (Kilham 1961) and drumming (recorded from a commercial CD; Cornell Laboratory of Ornithology & Interactive Audio 1992) was broadcast from the speaker once per min for 3 min. In reference trials, background noise from a blank tape was broadcast from the speaker. The observer, partially concealed by vegetation, was positioned 15 m from the tree and controlled the speaker using a tape player and extension cord.

For all trial types (treatment, reference, and roosting observations), one group member was tested per night prior to roost time when Red-cockaded Woodpeckers typically return to their cluster as a group (ca. 20-30 min before sunset). When the target Red-cockaded Woodpecker came within 30 m of its cavity, a trial was started and lasted 3 min. During treatment and reference trials, we recorded the target bird's vocalization rate, perch-to-perch hops, drums, strikes, and the closest approach distance to the mount (or piece of paper). Of these behaviors only vocalizations and perch-to-perch hops were exhibited during roosting observations of target birds. If other adult Red-cockaded Woodpeckers (secondary Red-cockaded Woodpeckers) approached within 30 m, only their closest approach distance and number of strikes on the mount (treatment trials only) were recorded.

Data Analysis.—To determine if birds responded aggressively to treatment trials, data from the three social classes (BM, BF, and HM) were combined to compare vocalizations, hops, and approach distances between reference and treatment trials using Mann-Whitney *U*-tests (SPSS © v. 9.0). To ascertain observer effects on Red-cockaded Woodpecker roosting behavior, we compared behaviors exhibited during roosting observations and treatment trials. We tested the cooperative defense hypothesis by comparing the approach distances and strikes of target Red-cockaded Woodpeckers with secondary respondents at treatment cavities (Mann-Whitney *U*-test). To test the social class hypothesis, we only compared the behavioral responses of the cavity owners (not the secondary respondents; Kruskal-Wallis Median Tests; SPSS © v. 9.0). If the overall P was ≤ 0.20 for any response variable, pairwise post-hoc Tukey Median Tests were conducted among the three treatment categories (BM, BF, HM). In order to satisfy requirements of our permit to experiment on an endangered species (R. Costa, pers. comm.)

and minimize disturbance, only one target bird per group was tested; and this limited our maximum sample size to the number of groups at both sites in any given season. Because of sample size constraints we used $P \leq 0.20$ to warrant pairwise comparisons. This was deemed satisfactory in that it allowed us to minimize type II error, which favors identification of potentially important factors (Shrader-Frechette and McCoy 1994, Zar 1999).

RESULTS

Forty-nine trials were conducted at cavities being used by single breeding males (BM), breeding females (BF), or helper males (HM); 29 trials in 1999 (14 treatments: 5 BM, 5 BF, and 4 HM; and 15 references: 5 each of BM, BF, and HM), and another 20 trials in 2001 (10 treatments: 5 BM and 5 BF; and 10 roosting observations: 5 BM and 5 BF). Group size varied by year and trial type (3-4 Red-cockaded Woodpeckers: 1999 HM and 2001 BM and BF trials; 2 Red-cockaded Woodpeckers: 1999 BM and BF trials). Sample size was constrained by the number of Red-cockaded Woodpecker groups in both sites with the detailed information on group structure and cavity use we needed; all available breeding groups at both sites were used in each year.

Controls.—During roosting observations, half of the target birds (3 BM and 2 BF) entered their cavities before the end of the 3-min sampling period; therefore, statistical comparison of response behaviors between roosting observations and treatment trials was not appropriate. While visible, birds were hitching, pecking, and/or maintaining resin wells—typical maintenance behaviors not observed during treatment trials. Vocalizations and perch to perch hops were infrequent during roosting observations.

When comparing reference and treatment trials, we found no difference in vocalization rates, but birds hopped more and approached closer in treatment trials (Mann-Whitney *U*-test; Table 1). Six individuals struck the Red-bellied Woodpecker mount (3BM, 2 BF, and 1 HM) and no birds struck the reference (Table 1). Drumming was never observed.

Social Status.—In non-parametric analyses of treatment trials (Kruskal-Wallis Median Test with a post-hoc Tukey Median Test) we found significant differences in vocalization rates and perch-to-perch hops among sex and social classes, but no difference in approach distances (Table 2; no pairwise comparisons were made). The small number of individuals striking the Red-bellied Woodpecker mount precluded statistical analysis of this behavior (Table 2).

Cooperative Defense.—In nine experimental trials (1999: 2 BM, 2 BF; 2001: 4 BF, 1 BM) a second, and sometimes a third, adult Red-cockaded Woodpecker approached within 30 m of the target tree. Although there were only 4 experimental trials with helper males, no

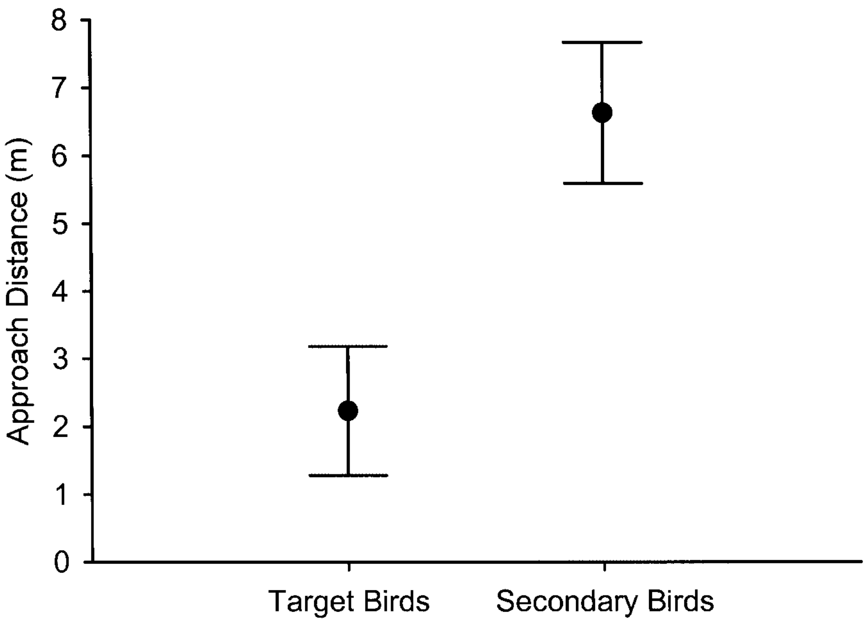

Figure 1. Mean (± 1 SE) approach distances of target Red-cockaded Woodpeckers for those receiving treatment trials involving presentations of the Red-bellied Woodpecker taxidermal mount and taped-call playback of vocalizations at his/her roost cavity versus other birds in the target bird's social group (secondary birds) that came within detection distance of the playback occurring at the target bird's roost cavity. Approach distances are summarized for N = 9 target and N = 12 secondary birds.

breeding adults responded (i.e., approached within 30 m) to threats at the young birds' cavities. In none of the 9 trials with secondary respondents did the secondary respondent strike the mount. All secondary respondents were significantly farther from the Red-bellied Woodpecker mount than the cavity owner (Mann-Whitney *U*-test: Z = -2.475, P = 0.01; Fig. 1). They did not exhibit behaviors that would suggest cooperative defense behaviors, but rather behaviors more similar to those observed during roosting observations. Secondary birds either went to roost in their own cavities, left the immediate area, or spent time pecking and hitching on nearby trees. One HM chased the BF being tested.

Discussion

Did treatment trials elicit aggression?—If observer effects during treatment trials inhibited Red-cockaded Woodpecker aggression, we should have obtained similar responses in treatment and roosting observations. However, whereas behaviors exhibited in treatment trials

Table 1. Comparison of mean behavioral responses of Red-cockaded Woodpeckers in treatment versus reference trials (social classes combined).

	Mean ± 1 SE		
Behavior	Combined treatment trials	Combined reference trials	Mann-Whitney U-test
Vocalizations/3 min	45.58 ± 7.75	49.00 ± 10.57	$P = 0.697$
Hops/3 min	2.63 ± 0.56	1.27 ± 0.27	$P = 0.160$
Approach Distance (m)	3.32 ± 0.82	6.55 ± 1.64	$P = 0.056$
Strikes/3 min	2.58 ± 1.55	0 ± 0	N/A[1]

[1]Unable to conduct statistical analysis because of insufficient sample size.

matched behaviors reported as aggressive defense behaviors for this species (Ligon 1970, 1971; Hooper et al. 1982; J. M. Davis and J. J. Kappes, personal observation), behaviors observed during roosting observations reflected natural maintenance behaviors. We conclude that if there were any observer effects on responses during any trials, they were strongly masked in treatment trials by aggressive responses to the mount.

Distinctive behavioral differences between treatment and reference trials were also observed, suggesting that aggression toward simulated usurpation did occur, over and above any neophobia generated by experimental conditions. Physical strikes on the mount and close approach distances observed during treatment trials, but not in reference trials, reflect behaviors we have witnessed in interactions between Red-bellied and Red-cockaded woodpeckers (J. M. Davis and J. J. Kappes, personal observation; Table 1). Similar to other studies demonstrating that playback and models can generate aggressive responses in birds (e.g., Chandler and Rose 1988, Pearson and Rohwer 2000, Radford and Blakey 2000), we conclude that treatment trials in this study adequately mimicked a cavity usurpation threat.

Table 2. Comparison of median behavioral responses of Red-cockaded Woodpeckers responding to treatment trials (BM = breeding males; BF = breeding females; HM = helper males).

	Median (Minimum, Maximum)[1]			
Behavior	BM	BF	HM	Kruskal-Wallis Median Test
Vocalizations/3 min	[a,b]59 (9, 133)	[a]32 (0, 85)	[b]35.5 (1, 143)	$P = 0.079$
Hops/3 min	[c,d]3.5 (1, 10)	[c]0.5 (0, 3)	[d]3.5 (1, 9)	$P = 0.045$
Approach Distance (m)	2.5 (0, 15)	3.5 (0, 10)	0.55 (0, 2.4)	$P = 0.497$
Strikes/3 min	1 (1, 13)	22 (9, 35)	3 (3,3)	N/A[2]

[1]Tukey Median Tests, shared letters indicate significant differences; a, b, c = ($P = 0.05$, q = 3.79); d = ($P = 0.10$, q = 3.03).

[2]Unable to conduct statistical analysis because of insufficient sample size.

Lack of Cooperative Defense of Roost Cavities.—The highly significant difference in approach distance ($P = 0.01$) between target and secondary birds (Fig. 1), lack of aggression toward the Red-bellied Woodpecker mount by secondary birds, and infrequent occurrence of secondary birds in treatment trials all support the hypothesis that during the post-breeding season, Red-cockaded Woodpeckers do not cooperate in defense toward potential roost cavity usurpers. Red-cockaded woodpeckers are generally aggressive toward Red-bellied Woodpeckers when encountered during foraging (Ligon 1970, Bowman et al. 1999, J. M. Davis and J. J. Kappes, personal observation). And in the breeding season (1999) we witnessed cooperative defense of an active Red-cockaded Woodpecker nest cavity containing nestlings (J. J. Kappes, personal observation). In this encounter, all group members (BM, BF, and HM) immediately responded to the presence of a male Red-bellied Woodpecker at, and inside, the nest cavity with close approaches and repeated strikes on the intruder. If Red-cockaded Woodpeckers ever cooperatively defend roost cavities during the post-breeding season, we would have expected at least one secondary respondent to react aggressively during our trials. Our experimental results support opportunistic observations of roost-cavity defense (Ligon 1970, 1971) and suggest that despite cooperative breeding nest defense and general aggression toward cavity usurping species, Red-cockaded Woodpeckers do not cooperatively defend roost cavities during the post-breeding season.

Aggression and Dominance Status.—The responses of target birds at their own cavities did not clearly support our hypothesis regarding strength of response ordered by social class. Breeding males did hop and vocalize more than both breeding females and helper males (Table 2), but approach distances were the same for all 3 classes. One individual of each sex/social class struck the model during trials, indicating that all birds were capable of the most extreme form of individual aggression toward a usurper (Table 1). In light of the lack of group defense, this last finding of relatively equal defense of roost cavity across social classes underscores the importance of roost cavities as an individual, rather than collective, resource for members of Red-cockaded Woodpecker groups during the post-breeding season.

Management Implications.—Our results suggest that during most of the year, when not engaged in nesting activity, cavity defense is a singular pursuit for Red-cockaded Woodpeckers and, therefore, unlikely to be effective in most usurpation attempts made by squirrels and larger-bodied birds seeking roost cavities. High rates of cavity occupation by usurpers may be explained, in part, by our finding of lack of cooperative cavity defense. In our study populations, flying squirrels occupied up to a mean of 87% of cavities per cluster (cavities belonging to one group of Red-cockaded Woodpeckers) and Red-bellied Woodpeckers occupied up to a mean of 77% of cavities per cluster (Kappes 2004). Elusive evidence for negative population-level effects of such high rates of cavity occupancy by usurpers on woodpecker reproductive success (Franzerb 1997, Laves 1996, Conner et al. 1996, Mitchell et al. 1999, Kappes 2004) calls into question whether the interaction can even be described as competitive in nature (Kappes 1997). Given that social animals cooperate to gain inclusive fitness (Woolfenden and Fitzpatrick 1990, Farabaugh et al. 1992), all evidence suggests that displacement of individual Red-cockaded Woodpeckers from roost cavities does not represent an historically important threat to fecundity or individual survival (Taylor and Irwin 2000). Depending on whether cavity occupation rates by heterospecifics are representative of historical (evolutionary) rates, the justification for implementation of cavity usurper control programs in managed Red-cockaded Woodpecker populations should not be based on usurpation rates alone. If current usurpation rates are similar to historical rates then control programs targeting flying squirrels or Red-bellied Woodpeckers may be unwarranted. These three species have co-evolved together and there can be unintended negative indirect effects of manipulating these species' relative abundances (Kappes 2004). The observation of frequent usurpation by itself, without indications of compromised survival or reproduction of Red-cockaded Woodpeckers, should be taken as insufficient to implement a control program. Under conditions where habitat characteristics are approaching historic qualities (see James et al. 2001) and Red-cockaded Woodpecker populations are stable and reproducing, this caution may be especially valid. In contrast, control of cavity usurpation has proven to be effective in enhancing the success of population reintroduction (e.g., Franzerb 1997).

Under the scenario that current usurpation rates may greatly exceed historic rates, selection for better defense of cavities may now be significant, but Red-cockaded Woodpeckers may not have had sufficient time to respond to this selection pressure with better cavity defense tactics. In this case, our finding of weak cavity defense by Red-cockaded Woodpeckers would represent yet another case of a behavior that is maladaptive in human-altered environments (Battin 2004). Across the species' range, the quality of remaining Red-cockaded Woodpecker habitat is lower than it historically was; for example, high quality foraging habitat is rare (Walters et al. 2002). Habitat degradation from the perspective of Red-cockaded Woodpeckers may favor their cavity usurpers (Conner and Rudolph 1989, Everhart et al. 1993, Kappes and Harris 1995)—and population increases of flying squirrels and Red-bellied Woodpeckers may be elevating cavity occupancy rates to historically unprecedented levels. In this case, high levels of cavity usurpation throughout the year could be a significant factor in the Red-cockaded Woodpecker's current or future endangerment, lending greater justification to broader implementation of control programs to reduce cavity usurpation rates.

As in all ecological problems, multiple factors are at work defining the status of Red-cockaded Woodpeckers (James et al. 2001), and multiple factors must be addressed in the species' restoration and protection. For example Walters et al. (2002) recommend integrated habitat management to simultaneously restore both high quality breeding and foraging habitat, since their characteristics are essentially the same. We suggest that analyses be undertaken to determine the effects of habitat restoration on the abundance and activity of southern flying squirrels and Red-bellied Woodpeckers at Red-cockaded Woodpecker cavities. If they decline as habitat quality increases, then control programs might be more important as a management tool in protecting Red-cockaded Woodpecker populations until habitat quality is upgraded throughout the species' range. If, however, current rates of cavity occupation by other species reflect historic rates and do not diminish as restoration proceeds, then control of usurpation via removal programs may be wasted effort. This is because both the birds' cavity defense behaviors (this study) and evaluations of the effects of usurpation suggest no strong negative effects in established populations. The most effective long-term solution to both the uncertainty and the potential harm of cavity usurpation in Red-cockaded Woodpecker management, and to habitat degradation, is likely to be integrated and vigorous habitat restoration (James et al. 2001, Walters et al. 2002).

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