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Effects of southern flying squirrels *Glaucomys volans* on red-cockaded woodpecker ***Picoides borealis*** reproductive success

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Abstract

Anecdotal data gathered from many populations suggest that southern flying squirrel (SFS, ***Glaucomys volans)*** use of the endangered red-cockaded woodpecker’s (RCW, ***Picoides borealis)*** nest and roost cavities may negatively affect RCW populations. We conducted a controlled experiment to determine the effects of SFSs on RCW reproductive success. During the 1994 and 1995 breeding seasons, SFSs were removed from 30 RCW clusters and 32 clusters served as controls. SFSs were the most frequently encountered occupants of RCW cavities and used 20–33% of RCW cavities in control and treatment clusters over both years. Treatment groups produced significantly more successful nests (2 1 fledgling) than control groups in 1994. In 1995 however, there was no difference in the number of successful nests. In both years, RCW groups nesting in treatment clusters produced significantly more fledglings than groups in control clusters in each of four experimental areas, averaging approximately 0.7 additional fledglings per nesting group. Loss of entire clutches or broods, possibly as a result of predation or abandonment, was a major factor limiting reproduction in control groups in 1994. In contrast, differences in partial brood loss appeared to be the cause of differential fledging success in 1995. Usurpation of RCW roost cavities by SFSs may have placed greater energetic demands on RCWs for cavity defence or thermoregulation, thus reducing energy available for reproduction. Our results show that SFS use of RCW cavities during the breeding season has a significant impact on RCWs and that management of RCW populations should include activities that either minimize SFS populations in RCW clusters or limit access of SFSs to RCW cavities.

INTRODUCTION

The red-cockaded woodpecker (RCW, ***Picoides borealis),*** is a non-migratory, co-operatively breeding species. Once a common resident of open pine woodlands in the southern USA, the RCW is now endangered as a result of old-growth forest destruction and fire suppression (USFWS, 1970, 1985). Approximately 9400 birds remain while only three populations of more than 300 groups now exist (R. Costa, pers. comm.).

RCWs live in family units known as ‘groups’, consisting of a ‘breeding male and female as well as O-5 helpers, which defend a territory containing several nest/roost trees termed a ‘cluster’ (Walters, 1990). Unlike most species of woodpecker that excavate nest cavities in dead trees, RCWs have adapted to the fire-maintained pine forests of the south by constructing their roost and nest cavities in living, fire resistant pines (Ligon, 1970; Short, 1971; Jackson, 1978). RCWs may take more than a year to construct their cavities and, once completed, a cavity may be used for years or decades (Ligon, 1970; Jackson, 1978; Harlow, 1983). RCWs construct resin wells surrounding the cavity entrance, allowing large amounts of sticky resin to coat the tree around the entrance (Ligon, 1970). Cavities are crucial for RCW reproductive success and survival, but their availability is often limited due to a lack of suitable cavity trees and a slow excavation process (Ligon, 1970; Jackson, 1978; Hooper, Robinson & Jackson, 1980; Walters, 1990). Furthermore, many mammals, reptiles, insects and other avian species use RCW cavities (Dennis, 1971; Harlow & Lennartz, 1983; Rudolph, Connor & Turner, 1990; Loeb, 1993). .Southem flying squirrels (SFS, ***Glaucomys volans) are*** one of the most frequent occupants of RCW cavities and are potentially

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the most consequential occupants of RCW cavities. SFSs and RCWs both prefer non-enlarged cavities (Loeb, 1993), suggesting that the potential for interspecific interactions may be great. Therefore, SFS use of RCW cavities may contribute to the decline of RCW populations or impede recovery from endangered status (Lennartz & Heckel, 1987).

Much of the evidence that SFSs affect RCW reproduction is anecdotal (Walters *et* al., 1.988; Ortego, Carrie & Moore, 1995; Richardson & Stockie, 1995) or based on descriptive or observational studies (Harlow & Lennartz, 1983; Lennartz & Heckel, 1987; Conner *et al.*, 1996). The present study tests hypotheses about interactions between SFSs and RCWs and is the first to do so under controlled, experimental conditions. The specific objectives of this study were to: (i) test the effect of SFS removal on RCW reproductive success; and (ii) determine the nature of SFS/RCW interactions by examining differences in various reproductive parameters between control and treatment groups.

METHODS

Study area

The Carolina Sandhills National Wildlife Refuge (CSNWR) is located in Chesterfield County, South Carolina and is in a transition zone between the Atlantic Coastal Plain and the Piedmont Plateau physiographic provinces (Myers, Zahner & Jones, 1'986). Approximately 85% of the 18 600 ha refuge is forested in longleaf pine *Pinus palustris* with the remainder :in loblolly *P. taedu,* slash *(P. elliottii)* and pond *(P. serotina)* pine. Deciduous species dominated by oaks *(Quercus* spp.) are common along streams and on lower slopes (R. Ingram, pers. comm.).

Experimental design

The CSNWR was divided into quadrants to reduce potential bias caused by environmental gradients (Hurlbert, 1984). Within, each quadrant, clusters were randomly assigned with equal probability to treatment or control clusters. In clusters designated as treatments ($n = 30$), SFSs were removed from RCW cavity trees as well as from the area surrounding the nest trees (see below). No SFS removal was done in control clusters ($n = 32$). All treatment clusters were: at least 500 m from any other treatment or control clusters. A RCW cavity was defined as any cavity located :in a living pine tree having evidence of resin wells.

SFS removal and observation

All RCW cavities within 500 m of the RCW nest tree in both control and treatment clusters were inspected using a droplight and mirror. In control clusters, all cavity contents were recorded. In treatment clusters, SFSs were removed using a mechanical, pick-up tool (MM Manufacturing, Davis, OK) and all other species found in the cavities were noted but not removed. Furthermore, 16 aluminum Sherman live-traps (7.5 x 9.0 x 25.5 cm) enclosed in wooden trap sleeves were placed horizontally, 1.5 m above ground within each treatment cluster. Traps were arranged in a 4 by 4 grid with 50 m spacing, and located on the nearest pine tree to a grid-point marker. Grids were set up to include the probable nest tree. Trapping was conducted on a g-night open, 5-night closed schedule.

SFS removal was conducted from March to July and was divided into six 2-week periods. SFS removal by Sherman trapping in treatment clusters occurred in every period. SFS removal from RCW cavities in treatment clusters occurred in periods 1, 3 and 5 and SFS observation in control clusters occurred in periods 2, 4 and 6.

RCW reproduction monitoring

All active trees within a cluster were climbed using Swedish climbing ladders and inspected using a mirror and droplight until evidence of a nest was found. Nests were inspected on a regular basis (every 1–5 days) to verify clutch size, initial brood size (and any subsequent partial or total nest loss), fledgling success and total nesting attempts/failures.

Nestlings were removed from cavities at 7-10 days of age using flexible nylon snares (Jackson, 1982), banded with a unique combination of coloured leg bands, and placed back in the cavity following banding. Groups were observed using spotting scopes mounted to gun stocks within 1 week of leaving the nest to verify fledging success. If one or more potential fledglings (observed as nestlings near the expected fledge date) were not located, a second fledge check was conducted. If no fledglings were observed in either fledge check, we continued to monitor the cluster for re-nesting attempts.

To determine group size we observed RCWs during nest tree climbing and nestling banding when group members often congregated in the area of the nest. Group size was also recorded during fledgling observations. These methods allowed groups to be separated into two categories: (i) pairs unassisted by helpers (group size = 2) or (ii) pairs assisted by helpers (group size > 2).

Statistical analyses

Data summary

Start holes (excavations having only an entrance tunnel and no downward depth) were not included in the analyses of SFS use of RCW cavities. Nest initiation dates were estimated by subtracting 11 days for incubation plus 1 day for each egg from a known hatch date, or subtracting 1 day for each egg from the date the last egg was laid. Tests for differences in median nest initiation dates included first attempts only. Groups were considered to have successfully reproduced if they fledged at least one young.

The presence of bark, shredded bark, leaves, or pine needles was designated as nesting or other material. If both an animal species and nesting material were observed, only the animal species was recorded. When eggs were observed and an identifiable adult exited the cavity upon inspection, the species of bird was recorded. Otherwise, eggs or birds were recorded as unknown species and later placed in an 'other bird' category. RCWs were not included in this category.

Hypothesis testing

We used likelihood ratio tests (G-tests: SAS Institute Inc., 1989) to test the null hypotheses that the proportion of cavities used and unused by SFSs were equal in each of three removal periods in both control and treatment clusters in 1995, and that the proportion of RCWs initiating a nest, RCWs successfully nesting, RCW groups with helpers, and form and amount of RCW nest loss was equal between control and treatment clusters. When expected cell values were less than five, we used Fisher's exact test (Sokal & Rohlf, 1995).

We used t-tests (SAS Institute Inc., 1989) to test the null hypothesis that mean number of SFS captures in Sherman live traps were equal between periods when SFSs were concurrently removed from cavities and periods when they were not being removed. We used two-way analysis of variance (ANOVA: SAS Institute Inc., 1989) with an interaction term to test for differences in reproductive measures between control and treatment groups within quadrants. To check the validity of the equal variance assumption for r-tests and ANOVA, we employed equal variance tests (F-tests) for comparing two or more population variances (Hartley, 1950).

Relatively small sample sizes did not permit us to conduct all analyses within quadrants. However, the effect of quadrant was not significant during preliminary ANOVA analyses, indicating that reproductive success was not dependent on the quadrant in which clusters were located. Therefore, we pooled data over quadrants when testing for equal proportions of control and treatment clusters in fledgling success classes. For all statistical tests, we used a significance level of $P \leq 0.05$ to reject null hypotheses; means $\pm$ 1 SE are presented.

RESULTS

RCW cavity contents

We inspected 416 and 437 individual RCW cavities in 1994 and 1995, respectively. In both years, nesting material was the most frequently encountered cavity content, and SFSs were the most frequently encountered vertebrate species (Table 1). Nesting material was also found in many cavities containing SFSs. SFSs used 24.9% (55 out of 221) of control group cavities and 23.6% (46 out of 195) of treatment group cavities in 1994, and 33.2% (82 out of 247) of control group cavities and 20.5% (39 out of 190) of treatment group cavities in 1995. In 1994 and 1995, all (100%) observations of RCWs and most (77.2 and 83.7%) observations of SFSs in cavities occurred in normal-sized cavities.

Table 1. Contents of red-cockaded woodpecker cavities on the Carolina Sandhills National Refuge inspected 2-3 times in March-July, 1994 and 1995

Cavity contents	1994 (n = 950)	1995 (n = 1273)
Empty	396	595
Nesting or other Material†	191	263
Southern flying squirrel (*Glaucomys volans*)	161	215
Red-cockaded woodpecker (*Picoides borealis*)	79	81
Eastern screech owl (*Otus asio*)	33	21
Other birds (not RCW, screech owl)‡	44	35
Invertebrates (*Hymenoptera, Coleoptera, Formicidae*)	22	30
Water	19	27
Squirrels (*Sciurus* spp.)	2	4
Snakes (*Elaphe* spp.)	3	2

n is the total number of inspections.
† Includes bark, shredded bark, leaves, pine needles and grass.
‡ Other birds (or their eggs) included eastern bluebird (*Sialis sialia*), great crested flycatcher (*Myiarchus crinitus*), red-bellied woodpecker (*Melanerpes carolinensis*), wood duck' (*Aix sponsa*), northern flicker (*Colaptes auratus*), barred owl (*Strix varia*), European starling (*Sturnus vulgaris*), red-headedwoodpecker (*M. erythrocephalus*), and American kestrel (*Falco sparverius*).

Effects of removal on SFS use of RCW cavities

We captured 86 and 261 SFSs in Sherman traps during 20 384 and 22 208 trap-nights in 1994 and 1995, respectively. The number of cavities containing SFSs and the number of SFSs encountered during successive cavity removal or inspection periods declined in treatment clusters but remained constant in control clusters in 1995 (Table 2). The number of RCW cavities with at least one SFS in treatment clusters was dependent on the period in which removal took place (G = 6.974, d.f. = 2, $P = 0.031$), but was independent of period in control clusters (G = 1.349, d.f. = 2, $P = 0.509$). Furthermore, the mean number of SFSs captured in Sherman trap grids per 1000 trap-nights was significantly less during periods when SFS removal from cavities was also occurring (8.47 ($\pm$ 0.94)) than in periods without cavity removal (16.63 ($\pm$ 0.18); $t = -3.99$, d.f. = 4, $P = 0.008$). Because three complete cycles of removal and observation in treatment and control clusters were not conducted in 1994 similar analyses of SFS abundance were not performed.

Between 1994 and 1995, the number of SFSs per inspection at the beginning of the RCW nesting season dropped 21.0 and 27.1% in control and treatment clusters, respectively (Table 2). However, the decrease in SFSs per inspection between the beginning of the 1994 and 1995 nesting seasons was not statistically significant among control (Wilcoxon $Z = -0.492$, $P = 0.623$) or treatment cavities (Wilcoxon $Z = -0.617$, $P = 0.538$).

Effects of SFSs on RCW reproduction

Removal of SFSs had no effect on RCW nest initiation dates. Among nesting groups, the median nest initiation dates for first attempts were 23 and 26 April for control groups and 25 and 22 April for treatment groups in 1994

Table 2. Southern flying squirrels (*SFSs*) observed in red-cockaded woodpecker (RCW) cavities over the RCW breeding season in treatment and control clusters in 1994 and 1995

Year	Cluster Type/period	Number of inspections	Cavities with ≥ 1 SFS	Number of SFS	SFS per inspection	% change in SFS per inspection
1994						
	Control					
	Period 2	204	41	94	0.461	*
	Period 4	218	41	102	0.468	1.5
	Treatment					
	Period 1	209	32	74	0.354	*
	Period 3	187	29	62	0.332	-6.2
1995						
	Control			84		
	Period 2	231	57	87	0.364	*
	Period 4	243	50		0.358	-1.7
	Period 6	242	51	81	0.335	-8.0
	Treatment					
	Period 1	178	24	46	0.258	*
	Period 3	189	22	39	0.206	-20.2
	Period 5	190	11	15	0.079	-69.4

Squirrels were removed when encountered in treatment clusters.

and 1995, respectively and did not differ significantly between control and treatment groups in 1994 ($Z = -0.29$, $P = 0.766$) or 1995 ($Z = 0.97$, $P = 0.333$). SFS removal also had no effect on a RCW group's ability to initiate a nest. All control groups that had at least one male and one female attempted to nest in 1994 (26) and 1995 (26), while all treatment groups with a pair nested in 1994 (28) and all but one (26) nested in 1995. There was no difference in the proportion of nesting in control (11 out of 26) or treatment groups (11 out of 28) with at least one helper in 1994 ($G = 0.051$, d.f. = 2, $P = 0.821$), but in 1995, a higher proportion of treatment groups (13 out of 26) had helpers than did control groups (6 out of 26; $G = 4.137$, d.f. = 2, $P = 0.042$).

The proportion of groups that produced at least one fledgling was significantly greater in treatment (25 out of 28) than control groups (17 out of 26) in 1994 ($G = 4.599$, d.f. = 2, $P = 0.032$). However, there was no difference in the proportion of nesting in treatment (24 out of 26) or control groups (23 out of 26) that produced at least one fledgling in 1995 (Fisher's one-tailed exact test, $P = 0.500$). Except for egg production in 1994, nesting treatment groups laid more eggs, hatched more nestlings and fledged more young than control groups in 1994 and 1995 (Table 3). The quadrant x cluster interaction terms in the ANOVA comparing RCW reproductive success between control and treatment groups were not significant (P values > 0.200), indicating that differences in reproductive parameters between treatment and control groups were consistent among all four quadrants in both years. Therefore, we removed the interaction term from the ANOVA. Mean fledgling production within quadrants in 1994 and mean egg and fledgling production within quadrants in 1995 were significantly different between control and treatment groups (Table 4). The greater number of fledglings produced by treatment groups averaged over all groups was 0.81 and 0.58 fledglings in 1994 and 1995, respectively (Table 3).

Although the number of fledglings produced per final nest attempt was greater in treatment groups than in control groups in 1994, the number of fledglings produced per successful group did not differ ($F = 2.43$, d.f. = 1, $P = 0.128$). In contrast, treatment groups produced significantly more young per nesting group and per successful group in 1995 ($F = 10.55$, d.f. = 1, $P = 0.002$). The number of fledglings produced per successful group was 2.28 (± 0.14) and 2.42 (± 0.13) in treatment clusters and 1.88 (± 0.17) and 1.87 (± 0.13) in control clusters in 1994 and 1995, respectively.

The proportion of groups experiencing total nest loss on their final nesting attempt was significantly greater in control groups (34.6%) than in treatment groups (10.7%) in 1994 (Table 5: $G = 4.599$, d.f. = 1, $P = 0.032$). However, the proportion of groups experiencing total nest losses in control (7.7%) and treatment groups (7.7%) did not differ in 1995 (Table 5: Fisher's one-tailed exact test, $P = 0.500$). The proportion of groups experiencing partial nest loss did not differ between control and treatment groups in 1994 (Table 5: $G = 2.145$, d.f. = 1, $P = 0.143$) or 1995 (Fisher's exact test, $P = 0.500$). Within groups that experienced partial nest loss, control groups lost 46.7 and 43.4% of the eggs or nestlings they produced that were not lost to total nest loss in 1994 and 1995 respectively, and treatment groups lost 38.6 and 32.6% of their eggs or nestlings (Table 5). The amount of partial loss in groups experiencing partial nest loss was not statistically different between control and treatment groups in 1994 (Table 5: $G = 0.943$, d.f.= 1, $P = 0.331$) or 1995 ($G = 2.029$, d.f. = 1, $P = 0.154$).

Distinctly different patterns of re-nesting were observed between control and treatment groups. Among first nesting attempts, 10 control and six treatment groups had total losses in 1994. Of these, two control (20.0%) and four treatment groups (66.7%) re-nested. One out of the two re-nests in control groups and three out of the four re-nests among treatment groups were successful. In 1995, six first nesting attempts by control

Table 3. Reproductive success parameter estimates of nesting red-cockaded woodpecker groups in control and treatment clusters within quadrants in 1994 and 1995

		1994				1995			
		Control		Treatment		Control		Treatment	
Quadrant	Reproduction parametef	*n*	$\bar{X}$ (± SE)	n	$\bar{X}$ (± SE)	*n*	$\bar{X}$ (± SE)	*n*	X (± SE)
1	Eggs	6	3.33 (± 0.33)	7	3.14 (± 0.26)	6	3.50 (± 0.22)	7	3.29 (± 0.18)
	Nestlings	6	2.33 (± 0.42)	7	2.57 (± 0.37)	6	2.67 ± 0.33	7	2.43 (± 0.43)
	Fledglings	6	1.33 (± 0.33)	7	2.29 (± 0.18)	6	1.50 ± 0.22	7	2.14 (± 0.40)
2	Eggs	7	3.71 (± 0.47)	8	3.75 (± 0.16)	7	3.29 (± 0.29)	8	3.75 (± 0.25)
	Nestlings	7	2.57 (± 0.53)	9	3.11 (± 0.31)	7	2.43 (± 0.37)	8	2.63 (± 0.26)
	Fledglings	7	0.71 (± 0.47)	9	2.00 (± 0.37)	7	1.86 (± 0.26)	8	2.25 (± 0.25)
3	Eggs	4	3.75 (± 0.25)	7	3.00 (± 0.38)	6	2.83 (± 0.17)	7	3.57 (± 0.20)
	Nestlings	4	2.25 (± 0.63)	7	2.43 (± 0.48)	6	1.67 (± 0.56)	7	2.86 (± 0.14)
	Fledglings	4	1.50 (± 0.65)	7	1.71 (± 0.52)	6	1.33 (± 0.42)	7	2.29 (± 0.18)
4	Eggs	9	3.44 (± 0.24)	5	3.80 (± 0.20)	7	3.40 (± 0.20)	4	3.75 (± 0.25)
	Nestlings	9	2.22 (± 0.47)	5	3.00 (± 0.32)	7	2.43 (± 0.43)	4	2.25 (± 0.85)
	Fledglings	9	1.44 (± 0.34)	5	2.20 (± 0.20)	7	1.86 (± 0.40)	4	2.25 (± 0.85)
All	Eggs	26	3.54 (± 0.17)	27	3.41 (± 0.14)	26	3.27 (± 0.12)	26	3.58 (310.18)
	Nestlings	26	2.35 (± 0.24)	28	2.79 (± 0.19)	26	2.31 (± 0.21)	26	2.58 (± 0.19)
	Fledglings	26	1.23 (± 0.21)	28	2.04 (± 0.18)	26	1.65 (± 0.17)	26	2.23 (± 0.18)

The values given are the mean (± SE).

Table 4. Results of ANOVA comparing reproductive success of nesting red-cockaded woodpecker groups in control and treatment clusters within quadrants in 1994 and 1995

	1994				1995			
Source of variation	d.f.	MSE	*F*	Pr > *F*	d.f.	MSE	*F*	*Pr>F*
Eggs								
Quadrant	3	0.750	1.17	0.330	3	0.343	0.98	0.409
Cluster type	1	0.122	0.19	0.664	1	1.414	4.04	0.050
Nestlings								
Quadrant	3	0.740	0.58	0.630	3	0.163	0.15	0.930
Cluster type	1	2.646	2.08	0.156	1	0.884	0.81	0.373
Fledglings								
Quadrant	3	0.700	0.67	0.577	3	0.247	0.31	0.820
Cluster type	1	9.554	9.09	0.004	1	4.559	5.67	0.021

Significant effects are in bold.
MSE, mean squared error; Pr, probability.

Table 5. Amount of partial (PNL) and total (TNL) nest loss in control and treatment groups in 1994 and 1995

Year	Treatment	Total eggs produced	No. nests	No. nests with PNL[†]	No. of eggs with TNL	No. of eggs or nestlings lost to PNL	No. of eggs or nestlings lost to TNL
		92					
1994	Control	92	26	18	9	28	32
	Treatment		28	24	3	34	4
					2		
1995	Control	85	26	22	2	33	9
	Treatment	93	26	21		28	7

Losses are reported for final nesting attempts
† A group losing part of brood and then all of the remainder at a later date is in both PNL and TNL categories.

groups failed while only two first attempts by treatment groups failed. Of these failures, five control and zero treatment groups attempted to re-nest. Four out of the five control re-nests were successful in 1995.

DISCUSSION

Our results indicate that SFS use of RCW cavities and clusters negatively affected RCW reproduction at CSNWR. SFSs were the most common vertebrate occupants of RCW cavities and were most commonly found in non-enlarged cavities, those used by RCWs (Table 1). Furthermore, bark, shredded bark, leaves, or pine needles, uncommon nesting material of RCWs, was the most frequently encountered cavity content. Removal of SFSs from treatment clusters resulted, in significantly more fledglings in both years than in control clusters where no SFSs were removed. Reproductive success of treatment groups surpassed control groups in all four quadrants in both years (Table 4).

Many other investigations have also found SFSs to be common RCW cavity occupants (Dennis, 1971; Jackson, 1978; Harlow & Lennartz, 1983; Rudolph *et* al., 1990; Kappes, 1993; Loeb, 1993; Richardson & Stockie, 1995). Use of cavities by SFSs in this study cannot directly be compared to occupancy rates from other studies because the number of inspections of each cavity and the manner in which cavity occupancy was defined differed between studies. However, the cavity occupancy rate of RCW cavities by SFSs in control groups (24.9 and 33.5% in 1994 and 1995, respectively) are similar to rates from Texas (21.9%: Rudolph et *al.*, 1990), South Carolina (25%: Dennis, 1971) and Georgia (10.5–21.0%: Loeb, 1993). In contrast to studies that associated RCW nest failures with the presence of rat snakes (Lennartz & Heckel, 1987; Richardson & Stockie, 1995), the infrequency with which rat snakes were observed in our study suggests that they are not important to RCW reproduction at CSNWR.

Although several investigators (e.g. Jackson, 1978; Lennartz & Heckel, 1987; Loeb, 1993; Montague *et* al., 1995; Richardson & Stockie, 1995) have suggested that SFSs have a negative impact on RCW, our study is the first to provide experimental evidence of the impact of SFSs. The success of the experiment was dependent on effective reduction of SFS numbers in treatment clusters. Although SFS removal was conducted intensively, complete removal is impossible to verify. However, removal efforts resulted in a significant decline in the use of RCW cavities by SFSs over time indicating that the treatment affected local SFS numbers. Furthermore, significantly fewer SFSs *were* captured in Sherman traps during periods in which both Sherman trapping and cavity removal occurred, than in periods in which only Sherman trapping was carried out.

Differences in reproductive parameters between control and treatment groups suggest mechanisms by which SFS removal affects RCW fitness. SFSs could affect RCW reproduction in several ways including preventing nest initiation, delaying nest initiation, causing RCWs to excavate new nests, thus expending energy that would otherwise be available for reproduction, and causing partial or total nest loss. We found no evidence that SFSs prevented or delayed nest initiation or caused RCWs to switch nest cavities (Laves, 1996). In contrast, our data suggest that SFSs affect RCW reproductive success by causing partial and total nest loss.

Differential reproductive success by control and treatment groups was primarily a result of total nest losses in 1994 and partial nest losses in 1995. In 1994, the proportion of groups experiencing total nest loss on their final nesting attempt was greater in control than treatment groups, while partial nest loss did not differ between control and treatment groups. Conversely, in 1995 there was no difference between control and treatment groups in the proportion of groups experiencing total nest loss or partial nest loss (Table 5). Furthermore, among nesting groups in 1994, there was a significant difference in the number of fledglings produced by control and treatment groups but successful control and treatment groups produced equal numbers of fledglings (Table 4). Therefore, most of the differences in fledging success in 1994 were due to total nest loss. In contrast, in 1995 there was a difference in fledging success between successful control and treatment groups in addition to differences in fledging success between control and treatment nesting groups. This suggests that partial nest loss was the primary cause of overall differential success in 1995. These results provide further evidence that SFSs affected reproductive success by causing total nest loss in 1994 and partial nest loss in 1995.

Interactions that result in total and partial nest losses are probably quite different, suggesting that SFSs and RCWs may interact in several ways. Greater total nest losses in control groups in 1994 suggest that predation or cavity usurpation resulting in desertion may have been important interactions. Several other studies have implicated predation by SFSs as being responsible for total nest losses (Lennartz & Heckel, 1987; LaBranche & Walters, 1994; Ortego *et al.*, 1995; Richardson & Stockie, 1995). Lennartz & Heckel (1987) found SFSs in cavities that had contained RCW eggs or nestlings within the previous week. We inspected nest cavities twice a week throughout the breeding season, but observed no instances of SFS occupancy in nests that failed in either year of the study. However, failure to detect SFSs in nest cavities that had recently lost their contents does not exclude the possibility that SFSs caused the loss.

Although the means by which SFSs could cause total nest loss through predation or inducing nest desertion are conceptually straightforward, the mechanisms that cause partial nest loss are not. It is likely that most SFS/RCW interactions occur at dusk, night or dawn. Breeding males incubate eggs and brood young at night. Even if SFSs do not evict a nesting male RCW (Rudolph *et al.,* 1990), they may keep him from fully incubating eggs, resulting in lower hatching success. Further, SFSs may disrupt roosting breeding females and helpers. RCWs that expend energy defending their cavities from SFSs or roost outside their cavity may have less time and energy to devote to brooding or provisioning nestlings resulting in lower fledging rates.

Our results indicate that there are two mechanisms, total and partial nest loss, by which SFSs may affect RCW reproduction. However, the reasons why total nest loss should be more important in 1994 and partial loss more important in 1995 are not clear. One potential explanation for differing mechanisms between years is differential SFS abundance. Although there was no statistical difference between years in SFS abundance in RCW cavities, the number of SFSs encountered per cavity inspection during the first observation period of each year decreased for both control and treatment clusters. Relatively higher abundances of SFSs could lead to higher predation rates and relatively higher rates, of total nest loss in 1994. Once a nest incurs total loss, the amount of partial loss it might have sustained cannot be measured. Thus, the detrimental actions of SFSs that cause partial losses could have taken place in 1994 but were not detected. Conversely, in 1995, lower numbers of SFSs in cavities may have resulted in lower total nest losses and differential partial nest loss was detected. However, the abundance of SFSs in Sherman traps increased from 1994 to 1995. Because estimates of SFS abundance differ depending on trapping method, SFS relative abundance cannot conclusively explain the differing mechanisms for the effect of SFSs on RCWs.

That SFSs affect the number of helpers present in a RCW group provides a further mechanism for the effect of SFSs on RCW reproduction. Male fledglings generally follow one of two life-history strategies: (i) become a helper, or (ii) disperse to search for a breeding vacancy (Walters, 1990). Females generally disperse. Therefore, the additional fledglings produced by treatment groups in 1994 (with a reduction of SFSs) may have increased the number of male fledglings that became helpers in 1995. RCW pairs that are assisted by helpers generally fledge more offspring than unassisted pairs (Ligon et *al.*, 1986; Lennartz, Hooper & Harlow, 1987; Manor, 1990; Walters, 1990; Neal *et* al., 1993). Thus, SFS removal may increase reproduction both directly, by increasing fledgling production in the year of removal, and indirectly, by causing an increase in group size in subsequent years. In the years following this study an even greater compounded increase in the proportion of RCW groups having helpers may result.

Many previous observations and investigations of SFSs and RCWs provide evidence for decreased RCW reproductive success as a result of SFSs. RCW nest failures as a result of cavity occupancy by other species have been documented throughout the RCW's range (Harlow & Lennartz, 1983; Lennartz & Heckel, 1987; Walters *et* al., 1988; LaBranche & Walters, 1994; Ortego *et* al., 1995; Richardson & Stockie, 1995). Lennartz & Heckel (1987) also observed a greater number of nesting attempts by RCWs in the Piedmont relative to the Coastal Plain, presumably a result of high nest predation. Furthermore, the reduced female survival of Piedmont RCWs may have been a result of increased energetic demands associated with rnore numerous re-nesting attempts. In the Sandhills of North Carolina, SFSs were observed in active cavities more frequently during a year in which a comparatively large proportion of RCW groups failed to nest (Walters *et al., 1988).* Evidence of the effect of SFSs on the turnover rate of RCW cavities has also been documented. Loeb & Stevens (1995) found that 50.4% (111) of nest attempts occurred in a different nest cavity than was used the previous year and suggested that 22 of these attempts were in a different cavity as a result of SFS occupancy.

One recent investigation (Conner *et al.*, 1996), which examined the effects of SFSs on RCW reproduction in eastern Texas concluded that SFSs have no negative effects on RCWs. We believe that there are several explanations for our differing conclusions. First, the two study populations in eastern Texas and eastern South Carolina are at extreme ends of the SFS distribution in the USA and the relative abundance, or behaviour of SFSs in these areas could vary greatly. Second, the lack of statistical significance in their study is not surprising given their small sample sizes and resultant low power of their experiment. Observational and correlative studies are less likely than experimental studies to detect the effects of one species on another especially when one of the species is'rare or endangered (Schoener, 1983).

Groups that had SFSs removed from their clusters produced approximately 0.7 more fledglings than groups in which no removal occurred. Therefore, a RCW population having 100 breeding pairs could produce an additional 70 fledglings per year in the absence of SFSs. If these groups produce an average of 1.5 fledglings per group without SFS removal (150 fledglings per year), the additional 70 fledglings would represent a reproductive increase of almost 50%. However, producing additional fledglings alone will not necessarily benefit RCWs at the population level. RCW population growth is best measured by the number of groups rather than number of individuals (Walters, 1991). Unless suitable habitat exists for recruitment of new groups, additional fledglings will provide few population benefits. Walters (1991) and Heppel, Walters & Crowder (1994) suggest that efforts to improve reproduction have little potential to promote population recovery. These efforts increase group size but not number of reproducing groups. If new sites become available, the additional young produced in the absence of SFSs would be potential colonizers of these sites. For example, Copeyon, Walters & Carter (199 1) induced RCWs to occupy recruitment stands and form new groups in areas that had been unoccupied for over 15 years by stocking them with artificially constructed cavities. Furthermore, increased fledgling production may help buffer small populations from extirpation due to stochastic demographic and environmental events (Gilpin & Soulé, 1986).

The problem of controlling overabundant native species to protect threatened, endangered or rare species is an emerging issue in conservation biology (Garrott, White & White, 1993; Goodrich & Buskirk, 1995). The data presented here show SFS removal has a positive effect on RCW reproductive success. However, SFS removal may not be appropriate in many RCW populations. In addition to the high monetary cost (four full-time employees removed SFSs in 30 RCW clusters during each season of this study) alternative methods may be as effective and less detrimental to the community. Goodrich & Buskirk (1995) present a decision model to help determine when and how to control abundant native species. This model can easily be applied to the RCW/SFS situation. For example, in the case of very small and/or declining populations where the loss of a few nests or individuals will put the population at risk of extirpation, removal of SFSs from cavities and clusters may be necessary. However, in cases where the population is not at immediate risk, other methods such as squirrel excluder devices (Montague *et al.*, 1995; Loeb, 1996) or nest boxes (Loeb & Hooper, 1997) may adequately reduce SFS use of RCW cavities. Many of the techniques employed by RCW managers (e.g. translocation, artificial cavity construction, control of antagonistic species) are stop-gap measures employed to treat proximate causes of decline (Temple, 1986). Ultimately, habitat management (e.g. long rotations, prescribed burning, midstory control) that fosters RCW population growth and the establishment of viable populations will be the best protection for RCWs.

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