



## Can snag creation benefit a primary cavity nester: Response to an experimental pulse in snag abundance

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### ABSTRACT

Thresholds in response by cavity-nesting bird populations to variations in the snag resource are poorly understood. In addition, limited information exists on the value of artificially created snags for cavity-nesting birds. Therefore, uncertainty exists in whether artificially created snags can yield a positive population response among snag-dependent birds. We used an experimental approach to assess the abundance and territory dynamics of a primary cavity nester, the red-headed woodpecker (*Melanerpes erythrocephalus*), in response to three snag density treatments over an 8-year period following treatment installation in 2001. Treatments included snag removal, an unmanipulated control, and a snag pulse (snags experimentally created at 14 times control density). During the first two years post-treatment, abundance of red-headed woodpeckers did not differ among treatments. In 2004, woodpecker abundance in snag pulse plots surpassed that of other treatments and continued to increase until it peaked in 2007 (at nearly 6 times than on control plots), after which it declined but remained greater than on control plots through 2009. Increased woodpecker abundance in high snag density areas was facilitated primarily by a decrease in home range size. Because the red-headed woodpecker is negatively affected by very low snag densities, yet is capable of exploiting pulses in the snag resource by dramatically increasing its abundance, we conclude that snag density regulates populations of this primary cavity nesting species and that snag creation can be an important tool in its conservation.

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### 1. Introduction

Many animal species are dependent on standing dead trees, or snags, for some aspect of their life history. Because the density of snags, particularly those suitable for cavity excavation by large-bodied primary excavators, often is low in managed, short-rotation forests (McComb et al., 1986; Ohmann et al., 1994), interest in the creation of snags by artificial means, variously termed 'morticulture' (Harmon, 2001; Lonsdale et al., 2009) or 'structural enrichment' (Hane et al., 2012; Kroll et al., 2012a) is increasing among forest managers. Snag creation has been suggested as a means to mitigate low snag densities to conserve cavity-dependent birds (Arnett et al., 2010; Brandeis et al., 2002; Bull and Partridge, 1986; Walter and Maguire, 2005). However, because of costs associated with such a program, thorough knowledge of the expected ecosystem response is important (Harmon, 2001). Despite extensive research on cavity nesting birds and snags, many aspects of the relationship between snags and primary cavity excavators remain poorly understood, including thresholds of response to snag densities (Hutto, 2006; Kroll et al., 2012b; Söderström, 2009).

Therefore, a better understanding of the response of primary cavity excavators to pulses in snag availability and the manner in which populations of cavity excavators exploit such resources is needed.

The importance of snags to primary cavity nesters, particularly woodpeckers, is self-evident: these species require snags in which to excavate cavities for nesting. This dependence has been well documented not only through knowledge of species' natural history, but also through studies demonstrating low woodpecker abundance when snags were experimentally removed or occurred in very low densities (Dickson et al., 1983; Hutto and Gallo, 2006; Lohr et al., 2002). Thus, because the availability of snags suitable for cavity excavation may be low in some forests, snags are often considered a limiting resource for woodpeckers (Newton, 1994). However, the ability of woodpeckers to respond to a pulse in snag availability, such as those resulting from insect kills, disease outbreaks, fire or storm damage, or morticulture is less clear. Several workers have shown positive relationships between cavity nesters and snag density (Hutto and Gallo, 2006; McComb et al., 1986; Raphael and White, 1984; Schreiber and deCalesta, 1992; Zarnowitz and Manuwal, 1985), but others have failed to detect such relationships (Gunn and Hagan, 2000; Land et al., 1989; Sedgewick and Knopf, 1986; Spiering and Knight, 2005). Kroll et al. (2012a) determined that degree of use of created snags was dependent on landscape context. These findings suggest that snags

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may not always limit woodpecker abundance, even in managed forests. However, no controlled long-term experiment has examined population response of primary cavity nesters to elevated snag density, and the effects of a pulse of artificially created snags on cavity-nesting bird populations are virtually unknown.

Where positive responses of woodpeckers to snag densities have been shown, the mechanisms that permitted those responses have not been investigated. An increase in woodpecker abundance in response to an increase in snag density may simply be a result of immigrants occupying previously unsuitable (and unoccupied) space. Conversely, if most space already was occupied by woodpecker territories prior to the increase in snag availability, more complex explanations may be necessary to explain the increased density. For example, territorial individuals may be required to reduce their home range size to accommodate the additional territories of contenders (Myers et al., 1979; Pons et al., 2008; Stamps, 1990). Alternatively, these territorial birds may be forced to relax their territorial defensiveness and tolerate a greater degree of spatial overlap with neighbors, thus permitting greater territory packing. For example, Hagan et al. (1996) reported that ovenbird density was greater in new forest fragments as displaced individuals packed into remaining habitat, and they suggested that the reduced pairing success they observed may have resulted from an inability of males to defend territory boundaries. Finally, an increased density of woodpeckers in response to a snag pulse may result from the combination of all three of these potential mechanisms acting together.

Our objective was to evaluate the degree to which population size of a primary cavity-nester, the red-headed woodpecker (*Melanerpes erythrocephalus*), is limited by snag availability, and in particular, the response of this species to a pulse in snag availability. We chose the red-headed woodpecker as a focal species because they are among the most abundant breeding woodpeckers in mature loblolly pine (*Pinus taeda*) forests on our study area (Lohr et al., 2002), they respond quickly to dying trees (Smith et al., 2000), and they are a Partners In Flight Watch List species (Rich et al., 2004), having declined in the United States and Canada at a rate of 2.7% per year from 1966 to 2011 (Sauer et al., 2012). We examined the response of red-headed woodpecker abundance to various experimentally manipulated levels of snag density, from no snags (snags removed) to baseline levels (control) to a density equivalent to that occurring after a catastrophic event creates a pulse of snags ten times the baseline level, for eight years following treatment. We predicted that woodpecker abundance in snag pulse treatment areas would increase over time as snags decayed and became more suitable and would decrease as snags fell. We predicted that woodpecker abundance would remain constant in control plots and lowest in snag removal plots. From such an outcome, we could conclude that the availability of snags suitable for nesting, or some factor associated with such snags, represents a limiting resource for this primary cavity nester in late-rotation managed pine forests, and that this species is capable of responding to a pulse in the availability of this resource. We also compared home range size and overlap among treatments during the period of peak response and hypothesized that the mechanism allowing elevated abundance would be either smaller home range size or greater overlap on snag pulse treatments than on controls.

## 2. Methods

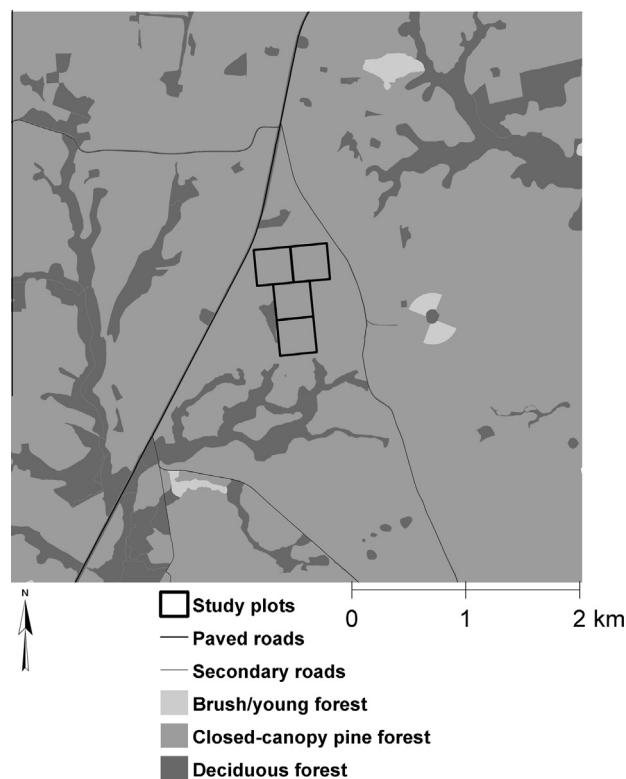
### 2.1. Study area

Our study was conducted on the US Department of Energy's Savannah River Site (SRS), a 78,000-ha National Environmental Research Park in Aiken and Barnwell counties, South Carolina. The

SRS was bounded on the southwest by the Savannah River and was situated in the Upper Coastal Plain and Sandhills physiographic regions. The landscape of the SRS was >90% forested (Fig. 1), with loblolly (*P. taeda*) and longleaf (*Pinus palustris*) pine forests occurring on uplands and deciduous bottomland hardwood forests (dominated by oak, *Quercus* spp., sweetgum, *Liquidambar styraciflua*, red maple, *Acer rubrum*, gum, *Nyssa* spp., and cypress, *Taxodium distichum*) occurring in riparian areas. Our experimental plots were in upland pine forests planted between 1950 and 1953 (48–59 years old during the study) that received prescribed burns at 3–5 year intervals. Forest stands were composed predominantly of loblolly pine, but longleaf pine, slash pine (*Pinus elliottii*), and hardwoods, including oaks, hickories (*Carya* spp.), sweetgum, and black cherry (*Prunus serotina*) also occurred. Midstories were open. Understories were dominated by broomsedge (*Andropogon virginicus*), lespezea (*Lespedeza* spp.), poison oak (*Toxicodendron pubescens*), blackberry (*Rubus* spp.), and wax myrtle (*Myrica cerifera*). Basal area averaged 12.7 m<sup>2</sup>/ha.

### 2.2. Experimental design

To evaluate red-headed woodpecker response to snag abundance, we used experimental plots created for a larger study of the role of coarse woody debris in the ecology of southern pine forests. Treatments included the following: removal (REM), in which all downed wood and snags ≥10 cm in diameter were removed; down woody debris pulse (DWD), in which trees were felled to create 5 times the volume of downed wood as occurred in un-manipulated stands; snag pulse (SNAG), in which trees were killed to increase snag volume and density by about 10-fold over levels that occurred in un-manipulated stands; and un-manipulated control (CON). We used a randomized complete block design in which



**Fig. 1.** Land cover map depicting 25 km<sup>2</sup> surrounding a representative experimental block used to investigate the effect of snag density on red-headed woodpeckers on the Savannah River Site, South Carolina.

the 4 treatments were assigned randomly to 1 of 4 9.3-ha adjacent square plots (305 m × 305 m) within each of 4 replicate stands (blocks) of ≥40 ha in size (4 blocks × 4 plots per block = 16 treatment plots).

We implemented all treatments in 2001 and removed any new wood from REM treatments annually. For DWD and SNAG treatments, we selected for treatment all trees ≥10 cm in diameter at breast height (dbh) within 12 equally spaced, parallel 3.7 × 305-m strips per plot. In DWD plots, treatment trees were felled with a chainsaw. In SNAG plots, trees were killed by chainsaw-girdling. We re-treated with herbicide injection (Pathway®: 5.4% picloram and 20.9% 2,4 D-amine) any trees that did not die within 6 months of the initial girdling. In DWD and SNAG treatments, the trees killed comprised 25% of the pre-treatment basal area of live trees on the plots. In order to keep basal area of live trees, and hence canopy structure, similar among treatments, we thinned and removed 25% of the basal area of live trees in REM and CON treatment plots. All plots received prescribed fire in 2000–2001 prior to treatment implementation and again during March 2003.

### 2.3. Data collection

We conducted annual surveys of all snags within a sample of 0.25-ha subplots (50 m × 50 m) on each treatment plot: 6 on DWD plots, 8 on SNAG plots, and 16 on CON plots. Less sampling intensity was necessary on DWD and SWD than on CON due to the large amount of dead wood generated on those plots (Zarnoch et al., 2013). In 2002, we tagged and measured each snag and in subsequent years added any new snags. Annual measurements on each snag included dbh (cm), height (m), and whether it had fallen since the previous year. Snag data were unavailable for DWD treatment plots in 2009. Herein we included only snags with a dbh of ≥18.4 cm and a height of ≥6.1 m, as data from a concurrent 7-yr study of red-headed woodpecker nest-site selection ( $n = 129$  nests; unpubl.) indicated that only snags (i.e., standing dead tree boles, not limbs) of this size were used for nesting. We summarized snag density at the subplot level.

We surveyed breeding red-headed woodpeckers from 5 May to 27 June 2002–2009 using spot-mapping (Bibby et al., 1992; Robbins, 1970). We surveyed each plot 8 times per year, alternating survey route and plot order (within a block) among visits to eliminate directional or temporal bias. We conducted surveys from approximately 5 min after sunrise until 1000. We traversed plots on transects that followed a 50-m grid, marked at each grid cell corner with re-bar and flagging tape, so that routes passed within 50 m of any location on the plot (see also Lohr et al., 2002). Field datasheets depicted the 50-m grid within each plot to facilitate more precise mapping of bird locations. To delineate woodpecker territories, we developed composite maps for each plot depicting registrations from all eight visits within a year. We considered clusters of ≥3 registrations as 1.0 home range (Robbins, 1970), except when overlapping a plot edge (i.e., within 50 m). We considered edge territories with 1–2 registrations as 0.25 territory and edge territories with 3–4 registrations as 0.50 territory. We considered registrations that did not meet the above criteria as 0.25 territory (i.e., two clustered registrations ≤100 m apart or single registrations ≥100 m from any other registration). Knowledge of the location, provided by a concurrent study (unpubl.), of nearly every red-headed woodpecker nest on the study plots also aided in territory delineation. We assumed that detectability was even among treatments. Because of their bold coloration and highly vocal nature during the breeding season, red-headed woodpeckers are highly visible. In addition, our efforts to maintain uniformity in habitat structure across the treatments (e.g., thinning of the canopy to the same basal area across all treatments) resulted in minimal potential for habitat conditions to affect detectability.

We captured red-headed woodpeckers during the breeding season, May–August, 2006–2007. Red-headed woodpeckers nest through August at SRS, with adults caring for fledglings as late as mid-September (Kilgo and Vukovich, 2012). We captured woodpeckers using ground-level and elevated (10–20 m high) mist nets (3 × 12 m, 3 × 20 m, and 9 × 30 m; 38-mm mesh), and, at cavities, a telescoping pole (12 m) with a hoop net attached (Vukovich and Kilgo, 2009). We weighed and aged (Pyle, 1997) captured woodpeckers and banded them with a USGS BRD aluminum band and color bands to facilitate individual identification. We aged birds in the field as accurately as plumage characteristics permitted, but for analysis we combined all age classes older than second-year (SY) into a single after-second-year (ASY) age class. Because red-headed woodpeckers cannot be sexed in the hand (Pyle, 1997), we collected breast feathers for DNA-sexing (Kilgo and Vukovich, 2012). We dorsally attached a 1.9-g transmitter (16-week battery life, Holohil Systems, Ltd., Carp, ON, Canada) to woodpeckers using a backpack harness, which weighed 2.1 g, an average of 3.1% (range = 2.5–3.6%) of woodpecker body weight, and did not affect behavior of the birds or their ability to use cavities (Vukovich and Kilgo, 2009). Breeding season survival rate of radio-tagged woodpeckers was 0.72 (95% CI: 0.54, 0.85; Kilgo and Vukovich, 2012).

We gave woodpeckers a 24 h acclimation period after capture and radio attachment before entering them in the sample. We located radio-tagged woodpeckers once a day, 4–7 days per week, from May to Aug 2006 and 2007 by homing, using receivers (Telonics, Inc., Mesa, AZ; Advanced Telemetry Systems, Inc., Isanti, MN) with H- or 3-element yagi antennas. We recorded estimated or confirmed locations with a hand-held GPS unit (Garmin International, Inc., Olathe, KS).

### 2.4. Home range analysis

Although we targeted only one member of each breeding pair for capture, when we caught both male and female, we randomly selected only one for inclusion in analyses. We calculated kernel home range estimates using all available radio locations from each woodpecker (mean = 35; range = 20–53), except that when we obtained multiple locations at the nest cavity we included that point only once. We used an information-theoretic model-selection approach (Horne and Garton, 2006a) in Program Animal Space Use 1.3 Beta (Horne and Garton, 2007) to determine for each woodpecker whether the adaptive or fixed kernel provided the most parsimonious kernel estimate. We assessed the relative support for each kernel estimator using the likelihood cross-validation criterion (CVC), and chose the estimator whose model produced the lowest CVC value. We then used the likelihood-cross-validation (CVh) smoothing factor calculated in Animal Space Use 1.3 Beta to delineate 70% kernel home ranges in the Home Range Tools extension (Rodgers and Carr, 1998) of ArcView 3.2 (ESRI, Redlands, CA). We chose the CVh smoothing factor because it performs better than the least-squares cross-validation smoothing factor when sample sizes are <50 points (Horne and Garton, 2006b). We selected the 70% contour because outer contours (>80%) are supported by the least amount of data and are therefore less reliable, whereas inner contours provide more robust representations of space use (Seaman et al., 1999). Börger et al. (2006) recommended 50–90% contours and Seaman et al. (1999) recommended contours ≤80%, particularly for numerical analyses comparing home range sizes and measures of overlap between populations. We felt that the 70% contour simultaneously provided the accuracy of the inner contours while minimizing the error of imputing woodpecker use to area beyond home range boundaries (particularly important in the context of home range overlap), and thus

most appropriately represented actual woodpecker home range boundaries.

Home ranges of some woodpeckers overlapped treatment plot boundaries. To compare home range sizes between treatments, we assigned individual breeding woodpeckers to the treatment occupied by  $\geq 75\%$  of their home range. To determine proportional occupation among treatments, we used the clipping tool in ArcMap 9.2 to clip home ranges along plot boundaries. We then divided the area of the clipped section by the area of the whole home range to determine whether to include individuals in the analysis. We excluded from analysis any woodpecker with  $\leq 75\%$  of its home range within a single treatment.

To compare home range overlap between treatments, we calculated two measures of overlap: the percent area overlap (Kernohan et al., 2001) and the utilization distribution overlap index (UDOI; Fieberg and Kochanny, 2005). The UDOI typically ranges from zero (no overlap) to 1 (100% overlap of normally distributed utilization distributions), though it can exceed 1. We determined overlap indices only for our treatment-assigned woodpeckers, but we included as potential neighbors in the overlap analyses all SY or older radio-tagged woodpeckers regardless of treatment assignment and breeding status because SY and older birds represented potential competitors for breeding territory space. We considered two woodpeckers neighbors if there were no other territories between them and if the distance between them was within the activity radius (distance between nest cavity and home range boundary) of the bird with the smaller home range (Pechacek, 2004). To determine percent area overlap between neighbors, we used the clipping tool in ArcMap 9.2 to clip shared portions of overlapping home ranges. Because we did not know home ranges of all neighbors of all focal woodpeckers, we standardized overlap on a per neighbor basis. For each woodpecker, we summed its area of overlap with all its neighbors and divided by the number of neighbors, including those with which it did not overlap, to get area of overlap per neighbor. We then divided this figure by the woodpecker's total home range area and multiplied by 100 to get the percent of each woodpecker's home range shared per neighbor. To calculate UDOI, we imported the utilization distribution determined by Animal Space Use into ArcMap 9.2 and performed computations using the raster calculator. For woodpeckers with multiple neighbors, we summed UDOIs and divided by the number of neighbors to obtain per neighbor UDOI.

## 2.5. Statistical analysis

We had no a priori reason to believe that red-headed woodpeckers would respond to the DWD treatment, as they did not respond to the removal of DWD in an earlier study on our plots (Lohr et al., 2002). Although they forage on the ground, red-headed woodpeckers do not typically forage on downed logs (Smith et al., 2000). Therefore, after verifying that estimated snag densities did not differ between DWD and CON treatments (difference in least squares means = 0.810 [95% CI: -1.838, 3.458];  $F_{1,3} = 0.95$ ;  $p = 0.402$ ), we considered the DWD treatment as a second control, designating original controls as CON1 and DWD as CON2.

We compared snag density among treatments using a randomized block repeated measures design with block, block\*treatment, subplot(block\*treatment), and block\*treatment\*year as random factors, treatment as the fixed factor, and year as the repeated measures factor (Proc MIXED; SAS Inst., 2004). We tested treatment using block\*treatment as the error term, and we tested year and year\*treatment using block\*treatment\*year as the error term. We used the Kenward–Roger method for denominator degrees of freedom (SAS Inst., 2004). We did not include the REM treatment in the comparison of snag densities between treatments because snag

density in REM plots was zero. When the year by treatment interaction term was significant, we compared snag density between treatments separately for each year by contrasting the mean of CON1 and CON2 (designated as CON) against SNAG (Proc MIXED; SAS Inst., 2004). We present parameter estimates for CON1 and CON2 as well as their mean value CON. We used a Bonferroni correction for the number of pairwise contrasts to control experiment-wise error rate at alpha = 0.05. We compared red-headed woodpecker density among treatments using the same model structure, except that the REM treatment was included and the model did not include the subplot(block\*treatment) term because we did not subsample treatment plots for woodpecker density.

The uneven distribution of telemetered birds among blocks and treatments precluded use of our design model to compare home range size and overlap indices between treatments. Therefore, we compared these variables between treatments (SNAG and CON) using a linear model (Proc GLM; SAS Inst., 2004), with year and sex as additional factors, as well as all interactions, such that model structure was [response = treatment + year + sex + treatment\*year + treatment\*sex + year\*sex + treatment\*year\*sex]. We recognize that this approach considered individual birds, rather than plots, as experimental units and that individual birds on the same plot were not statistically independent. Consequently, these results must be viewed as exploratory rather than confirmatory. We arcsine transformed percent overlap data for statistical analysis. We present least squares means  $\pm$  standard error, except for back-transformed percent data, which we present as least squares means with 95% confidence intervals.

## 3. Results

### 3.1. Snag treatments

During 2002–2009 across all plots, we tallied 2639 snags that fit the criteria for nesting red-headed woodpeckers. Our treatment was effective at increasing snag densities on SNAG plots. We compared snag density between SNAG and CON treatments separately for each year (Table 1) because there was an interaction between treatment and year (the treatment effect varied by year;  $F_{12,44.5} = 9.75$ ,  $p < 0.001$ ). Snag density was greater on SNAG than on CON during every year (Fig. 2). During the first year post-treatment (2002), only about one-third of the girdled trees had died by the time we measured snags and snag density on SNAG was 13.13 snags/ha (SE = 2.18). By the second year post-treatment (2003) all girdled trees had died and snag density was 40.50 snags/ha (SE = 1.78), about 14 times that on CON (2.96 snags/ha; SE = 1.32; Fig. 2). This difference between actual

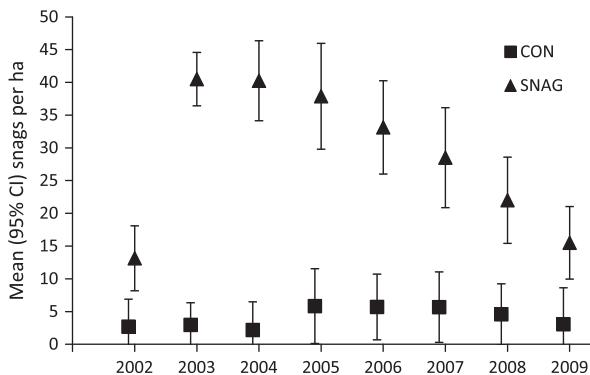
**Table 1**

Parameter estimates and test statistics from models comparing snag density among treatments (CON1 and CON2 = controls, SNAG = snag pulse treatment) at the Savannah River Site, South Carolina, 2002–2009.

Year	Intercept	Treatment			F	df	P
		CON1	CON2	SNAG <sup>a</sup>			
2002	13.13	-11.19	-9.69	0	8.9	2, 6	0.016
2003	40.50	-38.75	-36.33	0	198.5	2, 3.8	<0.001
2004	40.25	-38.73	-37.42	0	67.5	2, 8.6	<0.001
2005	37.88	-32.38	-31.71	0	27.0	2, 8.8	<0.001
2006	33.13	-27.06	-27.79	0	25.5	2, 8.6	<0.001
2007	28.50	-23.00	-22.67	0	15.4	2, 8.7	0.001
2008	22.00	-17.50	-17.33	0	12.0	2, 8.8	0.003
2009	15.50	-12.44	NA <sup>b</sup>	0	15.8	1, 5.5	0.009

<sup>a</sup> Parameter estimate for SNAG is zero because this parameter was the baseline for the model and is therefore equivalent to the intercept.

<sup>b</sup> Data for CON2 were not available for 2009.



**Fig. 2.** Least square mean estimates (95% CI) of snag density on control (CON, representing the mean of CON1 and CON2) and snag treatment plots (SNAG) on the Savannah River Site, South Carolina, 2002–2009. Snag removal treatment is not shown because the number of snags was zero.

(14-fold) and planned (10-fold) rate of increase was attributable to differences between SNAG and CON in the size distribution of snags, with SNAG having fewer snags in smaller diameter classes (and thus proportionally more snags in the larger classes), combined with the fact that we considered only larger snags ( $\geq 18.4$  cm in dbh and  $\geq 6.1$  m tall) in calculating the 14-fold rate of increase whereas the 10-fold rate of increase was based on all snags  $\geq 10$  cm in dbh and any height.

The experimentally created snags began to fall in 2004, annually decreasing the magnitude of the difference between SNAG and CON. By 2009, snag density on SNAG had decreased by 74% to an average of 15.50 snags/ha (SE = 2.27), only 5 times the density on CON in that year (3.06 snags/ha; SE = 2.16; Fig. 2) or 4 times the long-term mean density on CON, 2002–2009, of 3.96 snags/ha.

### 3.2. Woodpecker density

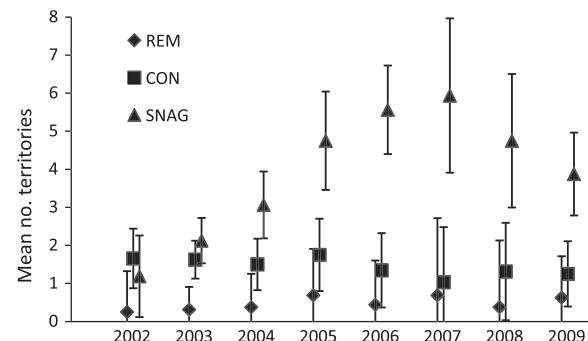
We tallied 231.75 red-headed woodpecker breeding territories from 2002 to 2009 on our experimental plots. Because there was an effect of the year  $\times$  treatment interaction on woodpecker density ( $F_{21,93} = 1.85$ ,  $p = 0.024$ ), we compared density among treatments separately for each year (Table 2). Although woodpecker density was lower on REM than CON in every year, this difference was significant only during 2003 (Fig. 3). Beginning in 2004 and continuing through 2009, density on SNAG was greater than REM and CON, but REM and CON did not differ (Fig. 3). The number of woodpecker territories on SNAG peaked in 2007, 6 years post-treatment, and declined thereafter (Fig. 3).

**Table 2**

Parameter estimates and test statistics from models comparing number of red-headed woodpecker territories per plot among treatments (REM = snag removal, CON = control, SNAG = snag pulse treatment) at the Savannah River Site, South Carolina, 2002–2009. Numerator and denominator degrees of freedom for all tests were 3 and 9, respectively.

Year	Intercept	Treatment				F	P
		REM	CON1	CON2	SNAG <sup>a</sup>		
2002	1.19	-0.94	0.50	0.44	0	2.1	0.171
2003	2.13	-1.81	-0.44	-0.56	0	14.5	<0.001
2004	3.06	-2.69	-1.56	-1.56	0	10.0	0.003
2005	4.75	-4.06	-3.00	-3.00	0	10.2	0.003
2006	5.56	-5.13	-4.00	-4.44	0	34.1	<0.001
2007	5.94	-5.25	-4.56	-5.25	0	8.14	0.006
2008	4.75	-4.38	-2.88	-4.00	0	7.0	0.010
2009	3.88	-3.25	-2.38	-3.25	0	12.2	0.002

<sup>a</sup> Parameter estimate for SNAG is zero because this parameter was the baseline for the model and is therefore equivalent to the intercept.



**Fig. 3.** Least square mean estimates (95% CI) of number of red-headed woodpecker territories per 9.3-ha plot on snag removal (REM), control (CON, representing the mean of CON1 and CON2), and snag pulse (SNAG) treatments on the Savannah River Site, South Carolina, 2002–2009.

### 3.3. Radio-tagged sample

We captured 93 woodpeckers, 91 of which we radio-tagged, during 2006–2007. After eliminating hatch year woodpeckers ( $n = 6$ ), woodpeckers with  $<20$  locations (due to natural mortality, transmitter failure, loss of contact, or dispersal,  $n = 26$ ), and woodpeckers with a mate already in the sample ( $n = 3$ ), we analyzed home ranges of 56 woodpeckers. Among these 56 woodpeckers, 4 did not nest and the territories of 21 were  $\leq 75\%$  on either SNAG or CON treatments. Thus, our sample of focal woodpeckers for comparison of home range size and overlap among treatments consisted of 31 woodpeckers: 15 on SNAG and 16 on CON. Of those 31 woodpeckers, 11 were captured in 2006 and 20 in 2007. Eighteen were male and 13 were female. However, we considered as potential neighbors to the 31 focal woodpeckers all 56 woodpeckers for which we delineated home ranges. The adaptive kernel estimator was more appropriate for 22 and fixed kernel for 9 of our 31 focal woodpeckers. Only one woodpecker used REM ( $\geq 75\%$  of home range area), so we compared home range size and overlap only between SNAG and CON.

### 3.4. Home range size and overlap

Home range sizes of our 31 focal birds ranged from 0.43 to 4.39 ha. Home range size differed between treatments, being smaller on SNAG (0.97 ha; SE = 0.23;  $n = 15$ ) than on CON (2.01 ha; SE = 0.19;  $n = 16$ ; Table 3 and Fig. 4).

Woodpeckers on SNAG plots had more neighbors (3.6; SE = 0.37) than woodpeckers on CON (1.5; SE = 0.33;  $t_{29} = -4.30$ ;  $p < 0.001$ ). Percent overlap per neighbor ranged from 0% to 39.0% and differed between years, being greater in 2007 (3.57%; 95% CI: 3.37, 6.94%) than in 2006 (0.39%; 95% CI: -0.06, 0.33%; Table 3). Percent overlap per neighbor on SNAG was 3.11% (95% CI: 2.71, 5.82%) and on CON was 0.56% (95% CI: 0.31, 0.87%; Fig. 4). UDOI per neighbor averaged 0.009 and ranged from 0.000 to 0.072 and was not affected by any variable in our model (Table 3).

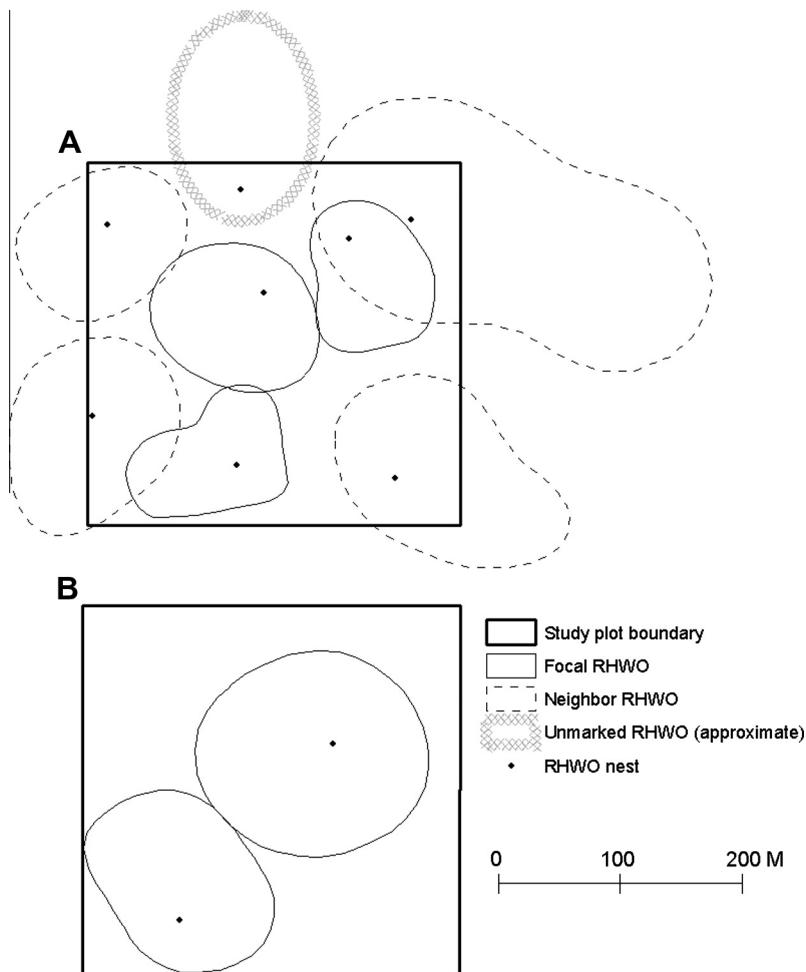
## 4. Discussion

The abundance of red-headed woodpeckers responded dramatically to the experimental pulse in snag density, with peak abundance on snag plots increasing nearly 6-fold over that on control plots. This response, coupled with the reduced abundance on our snag removal plots reported for an earlier phase of the study (1997–1999; Lohr et al., 2002) and during 2003 of this study, demonstrates that red-headed woodpecker populations in managed pine forests are regulated by the availability of suitable snags. In

**Table 3**

Parameter estimates and test statistics from models comparing home range size, percent home range overlap, and the utilization distribution overlap index (UDOI) of red-headed woodpeckers among snag density treatments, sexes, and years at the Savannah River Site, South Carolina, 2006–2007. Numerator and denominator degrees of freedom for all tests were 1 and 23, respectively.

Parameter	Response variable								
	Home range size			Percent overlap			UDOI		
	Estimate	F	P	Estimate	F	P	Estimate	F	P
Intercept	1.02 (0.29)			14.10 (3.23)			0.15 (0.01)		
Treatment	1.10 (0.41)	12.1	0.002	−4.64 (4.57)	3.2	0.089	−0.01 (0.01)	0.0	0.867
Sex	−0.10 (0.43)	1.1	0.314	−1.86 (4.79)	1.8	0.189	0.00 (0.01)	0.2	0.644
Yr	0.10 (0.51)	0.6	0.462	0.20 (5.60)	4.9	0.037	−0.01 (0.01)	2.0	0.168
Treatment*sex	−0.55 (0.67)	0.2	0.682	0.13 (7.37)	1.2	0.286	0.03 (0.02)	1.0	0.323
Treatment*yr	0.11 (0.72)	0.5	0.494	−9.66 (7.91)	0.2	0.700	0.01 (0.02)	0.1	0.804
Sex*yr	−0.17 (0.93)	0.1	0.819	−12.44 (10.32)	0.7	0.426	−0.01 (0.03)	0.8	0.383
Treatment*sex*yr	0.61 (1.19)	0.3	0.613	14.17 (13.20)	1.2	0.294	−0.02 (0.03)	0.4	0.562



**Fig. 4.** Home ranges (70% fixed and adaptive kernel) of red-headed woodpeckers (RHWO) on representative (A) snag and (B) control plots at the Savannah River Site, South Carolina, 2006. Focal RHWO home ranges were at least 75% within treatment plot boundaries and were used in comparison of home range size and overlap among treatments. Neighbor RHWO home ranges were <75% within treatment plot boundaries and therefore were not included in these comparisons but were considered potential neighbors in calculating home range overlap. The approximate boundary of the unmarked RHWO home range is included to show that the space was occupied, as evidenced by spot-mapping surveys, but the home range boundary was unknown.

habitat conditions that are otherwise suitable, when snags are scarce, red-headed woodpecker abundance will be low, whereas when snags are abundant, red-headed woodpeckers are capable of exploiting that resource by increasing their abundance. Several studies have shown positive relationships between primary cavity nesters and snags (Hutto and Gallo, 2006; McComb et al., 1986; Raphael and White, 1984), but only in response to catastrophic, stand-replacement fire has such a large response been documented

(Murphy and Lehnhausen, 1998). Zarnowitz and Manuwal (1985) reported a 5-fold difference in cavity nester abundance between plots with low and high snag densities in managed forests in northwestern Washington, but this included primary and secondary cavity nesters combined.

Red-headed woodpeckers responded rapidly to the snag pulse. After the creation of snags in 2001, abundance increased steadily for 6 years and peaked in 2007, after which it began a gradual

decline that continued through the last two years of our monitoring, though it remained more than three times higher than on control plots. During the first two years post-treatment, woodpecker abundance on plots where snag density was increased did not differ from that on control plots. Red-headed woodpeckers are relatively weak excavators for woodpeckers (Ingold, 1994; Jackson, 1976), and snags likely had not decayed sufficiently for cavity excavation during the first two years. However, by 2004, three years post-treatment, the decay state of snags had reached a threshold in suitability, as nesting abundance on snag plots had surpassed that on control plots. Other workers have reported similar increases in woodpecker use of snags as a function of snag age (Arnett et al., 2010; Brandeis et al., 2002; Moorman et al., 1999), but none have reported such a rapid and extensive response in use by primary cavity nesters. Although first cavities have been reported as early as two (Bull and Partridge, 1986) and three (Hallett et al., 2001) years after treatment in conifers in the Pacific Northwest, US, most research there indicates that at least five years must elapse before snags are suitable for cavity excavation (Walter and Maguire, 2005). Many factors affect decay rates, including tree species, size, and cause of death (Conner and Saenz, 2005; Moorman et al., 1999; Parish et al., 2010), but pine snags in southeastern North America may decay at a faster rate than in the Pacific Northwest, as evidenced by the more rapid use by woodpeckers that we observed. In addition, snags in our plots did not persist as long as those in the northwestern US. For example, the half-life (i.e., time until 50% of snags have fallen) of large created snags on our plots was 6 years (Zarnoch et al., 2013), whereas that of natural ponderosa pine (*P. ponderosa*) snags was 12–17 years (Dunn and Bailey, 2012). Thus, loblolly pine snags in southern forests become suitable for cavity excavation sooner after tree death but do not persist as long as snags in other regions.

Red-headed Woodpeckers on plots where snag density was increased reduced their home range sizes in the face of pressure from conspecifics contending for the abundant snag resources. Territory size regulation in birds has been the subject of extensive research (Adams, 2001), and considerable evidence indicates that both abundant resources and the pressure from conspecifics attracted by those resources can be important in explaining reduced territory sizes (Both and Visser, 2000; Myers et al., 1979; Pons et al., 2008; Sillett et al., 2004). Elevated resource levels to which woodpeckers on our plot may have responded include snags and potentially food. Conclusive evaluation of this alternative would have required examination of home ranges size at low bird density and high snag density (e.g., experimental removal of birds from high density plots). However, we believe that contender pressure was the proximate cause of the reduction in home range size rather than increased snag or food resources for the following reasons. Regarding food resources, red-headed woodpeckers are considered more generalist in their foraging behavior than other eastern woodpeckers, spending more time sallying for insects (Leonard and Heath, 2010) and foraging on the ground (Smith et al., 2000; Willson, 1970), and their diets contain very few wood-boring beetle larvae (Martin et al., 1951). Although they forage on recently dead trees, by 2004 when we first detected an increased abundance of woodpeckers, the created snags had been dead approximately three years, long enough to have lost most of their bark and dried out. At this point in the decay process, relatively few arthropods remain (Howden and Vogt, 1951), particularly those on which red-headed woodpeckers forage. In addition, no differences were detected between our plots where snag density was increased and control plots in either ground- (Ulyshen and Hanula, 2009) or bark-dwelling arthropod abundance (J.L. Hanula, unpubl. data). Regarding snag resources, a pair of woodpeckers conceivably requires no more than two snags in their home range: one for the nest cavity and one for roosting by whichever member of the pair

is not incubating, typically the female, although non-incubating birds frequently roosted outside of cavities (Vukovich and Kilgo, 2009). Hence, the availability of abundant snags within a home range offers no clear benefit for essential life history processes like feeding and nesting, and thus we see no reason why home range size should be smaller directly in response to snag abundance alone.

Regardless of whether red-headed woodpeckers reduced home range size in response to the abundant snag resource or to pressure from contenders for those snags, this reduction was the primary mechanism that facilitated the increase in woodpecker abundance. The minimal overlap we observed, even on plots with increased snag density where small home ranges were tightly packed, highlights the highly territorial nature of this species; individuals seem to have little tolerance for incursion into their home ranges by neighbors. Home range size, on the other hand, is flexible, presumably to some low threshold below which sufficient resources cannot be secured. The presence of many unused snags within each home range suggests that this threshold may have been reached on our plots, and that the availability of resources other than snags limited further reduction in home range size. If so, the red-headed woodpecker abundance we observed may represent the maximum attainable for the species.

Our study reveals that the creation of large snags ( $\geq 18.4$  cm in dbh and  $\geq 6.1$  m in height) by girdling or herbicide injection can increase local population size of a primary cavity nester, the red-headed woodpecker, and that the beneficial effects can persist at least 6 years. In addition, populations of secondary cavity nesting birds likely benefitted from the many cavities created by red-headed woodpeckers. However, beneficial effects of snag creation likely will be limited if other habitat conditions are not suitable. Nesting habitat for red-headed woodpeckers is typified by open mid and understories with little vertical structure, so creation of snags in dense forest may offer little benefit. Likewise, landscape context may affect the degree of use of created snags; creating snags in forest stands extensively surrounded by stands in which snags are a limiting resource likely will maximize their use relative to doing so in habitat already containing abundant snags (Kroll et al., 2012a). In addition, provision of snags could have detrimental effects on populations if they create ecological sinks. For example, high concentrations of these conspicuous woodpeckers may attract avian predators, conceivably resulting in greater mortality, or the increased social pressure associated with high woodpecker densities may negatively affect reproduction (e.g., through greater energy expenditures for territorial defense). Survival of adult woodpeckers was not affected by our snag pulse treatment (Kilgo and Vukovich, 2012), but we did not evaluate effects on reproductive success. Although Hane et al. (2012) reported that avian nesting success on plots with a high density of created snags was no different than on low density plots in Oregon, additional research is needed to better elucidate potential limitations to snag creation as a management tool for woodpecker conservation. Nevertheless, we conclude that red-headed woodpecker populations can respond dramatically to an increase in snag availability. Therefore, we recommend the creation of large snags at densities as great as 10–14 times that of baseline levels for conservation of red-headed woodpeckers and other cavity-nesting birds.

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