



Factors Affecting Breeding Season Survival of Red-Headed Woodpeckers in South Carolina

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ABSTRACT Red-headed woodpecker (*Melanerpes erythrocephalus*) populations have declined in the United States and Canada over the past 40 years. However, few demographic studies have been published on the species and none have addressed adult survival. During 2006–2007, we estimated survival probabilities of 80 radio-tagged red-headed woodpeckers during the breeding season in mature loblolly pine (*Pinus taeda*) forests in South Carolina. We used known-fate models in Program MARK to estimate survival within and between years and to evaluate the effects of foliar cover (number of available cover patches), snag density treatment (high density vs. low density), and sex and age of woodpeckers. Weekly survival probabilities followed a quadratic time trend, being lowest during mid-summer, which coincided with the late nestling and fledgling period. Avian predation, particularly by Cooper's (*Accipiter cooperii*) and sharp-shinned hawks (*A. striatus*), accounted for 85% of all mortalities. Our best-supported model estimated an 18-week breeding season survival probability of 0.72 (95% CI = 0.54–0.85) and indicated that the number of cover patches interacted with sex of woodpeckers to affect survival; females with few available cover patches had a lower probability of survival than either males or females with more cover patches. At the median number of cover patches available ($n = 6$), breeding season survival of females was 0.82 (95% CI = 0.54–0.94) and of males was 0.60 (95% CI = 0.42–0.76). The number of cover patches available to woodpeckers appeared in all 3 of our top models predicting weekly survival, providing further evidence that woodpecker survival was positively associated with availability of cover. Woodpecker survival was not associated with snag density. Our results suggest that protection of ≥ 0.7 cover patches per ha during vegetation control activities in mature pine forests will benefit survival of this Partners In Flight Watch List species. © 2011 The Wildlife Society.

KEY WORDS accipiter, cover, known-fate models, *Melanerpes erythrocephalus*, mortality, radio telemetry, red-headed woodpecker, snag density, survival.

Red-headed woodpeckers (*Melanerpes erythrocephalus*) occur throughout the east-central United States, south to Texas and north to southern portions of east-central Canada (Smith et al. 2000). Although the species was once common throughout its range, it has declined sharply in the United States and Canada over the past 40 years (National Audubon Society 2008, Sauer et al. 2008), and as a result has been listed as a Partners In Flight Watch List species (Rich et al. 2004). Reasons for the decline of red-headed woodpeckers are unclear but may be related to the loss of suitable habitat. Consequently, most recent research has focused on assessment of habitat requirements (Smith et al. 2000, Rodewald et al. 2005, King et al. 2007). Red-headed woodpeckers use many vegetation types but they typically require areas with a low basal area of trees, sparse to open under- and mid-stories, large snags (standing boles of dead trees), and a high density of dead limbs around the nest (Venables and Collopy 1989, Smith et al. 2000, Rodewald et al. 2005, King et al. 2007). Changes in land-use and forest management, particularly the removal of dead trees and suppression of fire, may be

important factors in the recent population decline (Smith et al. 2000).

Despite their status as a species of high conservation concern, few demographic studies of red-headed woodpeckers have been conducted. Fewer still have documented survival rates of adults (but see Martin 1995) and none have examined factors that affect adult survival. Furthermore, the conspicuous plumage and breeding behavior of red-headed woodpeckers may render them more susceptible to predation during the breeding season than other avian species (Smith et al. 2000). Vukovich and Kilgo (2009a) reported instances of predation by accipiters on red-headed woodpeckers, but the total extent of predation on red-headed woodpeckers during the breeding season is unknown. Efforts to conserve this species may be enhanced by knowledge of its survival patterns and the factors that affect its mortality, particularly if mortality factors can be mitigated through management.

We captured and radio-tagged red-headed woodpeckers on experimental plots in loblolly pine (*Pinus taeda*) forests in South Carolina. Our objectives were to determine survival probability, causes of mortality, and factors affecting survival probability of adult red-headed woodpeckers during the breeding season. Specifically, we examined the potential effects of dense foliar cover and of experimentally

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manipulated snag densities (as an index to cavity abundance and foraging resources) on survival probabilities. We hypothesized that increased foliar cover would provide more effective escape or hiding cover than pine canopy and correlate with increased survival. In addition, we predicted that areas with lower snag density would provide fewer foraging opportunities and roosting cavities, which may reduce survival due to fitness consequences and an increased exposure of woodpeckers to nocturnal predators.

STUDY AREA

We conducted the study on the United States Department of Energy's Savannah River Site (SRS), a 78,000-ha National Environmental Research Park in Aiken and Barnwell counties in the Upper Coastal Plain and Sandhills physiographic regions of South Carolina. Our study sites ($n = 4$ forest stands) were 50- to 60-year-old pine forests prescribed-burned at 3- to 5-year intervals. Canopies were dominated by loblolly pine (*Pinus taeda*), with scattered longleaf pine (*P. palustris*), slash pine (*P. elliotii*), and hardwoods, including oaks (*Quercus* spp.), hickories (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), and black cherry (*Prunus serotina*). Midstories were open, with only 11% of the zone between understory and canopy layers occupied by vegetation, primarily saplings of canopy species (J. I. Blake, U.S. Department of Agriculture [USDA] Forest Service, unpublished data). Understories were dominated by broomsedge (*Andropogon virginicus*), lespedeza (*Lespedeza* spp.), poison oak (*Toxicodendron pubescens*), blackberry (*Rubus* spp.), wax myrtle (*Myrica cerifera*), and seedlings of canopy trees. Collectively, the under- and mid-stories were dominated by broadleaf vegetation, which accounted for 80% of the total percent cover of these zones (J. I. Blake, unpublished data). Overstory basal areas averaged 12.7 m²/ha. Red-headed woodpeckers were the most abundant woodpecker on the sites during the breeding season (Lohr et al. 2002).

METHODS

Capture, Sexing, and Aging

We captured red-headed woodpeckers during May–August 2006–2007 using ground-level and elevated (10–20 m high) mist nets (3 m × 12 m, 3 m × 20 m, and 9 m × 30 m; 38-mm mesh), and at cavities using a telescoping pole (12 m) with a net attached. To elevate mist nets, we used 0.64-cm nylon ropes suspended from the tree canopy. We used a fishing rod to place each rope by casting line with an 85-g lead weight over the upper branches of a pine tree. We then removed the weight, attached the fishing line to a rope, and pulled the rope over the limb. With the loops of 1 side of a mist net attached to the rope, we tied the ends of the rope together so that it formed a loop over the limb. We hoisted the net by pulling the loop ropes on either end of the net as if the ropes were on pulleys.

We weighed captured woodpeckers using a Pesola scale (± 0.5 g; Pesola AG, Baar, Switzerland) and banded them with a USGS BRD aluminum band and color bands (Permit No. 22829; U.S. Geological Survey Bird Banding

Laboratory, Laurel, MD) to facilitate individual identification. We aged birds in the field as accurately as possible (Pyle 1997), 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, which was conducted by Avian Biotech International (Tallahassee, FL). We stored feathers at room temperature in a sealed plastic bag and held them no more than 2–3 weeks prior to submission. We dorsally attached a 1.9-g transmitter (16-week battery life; Holohil Systems, Ltd., Carp, Ontario, Canada) to woodpeckers using a backpack harness (Vukovich and Kilgo 2009b). The transmitter-harness package 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 2009b).

Radio Telemetry

We gave woodpeckers a 24-hour acclimation period after capture and radio attachment before entering the sample. We located radio-tagged woodpeckers 4–7 days per week from May–August 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 determined status as alive either by direct observation of radio-tagged woodpeckers or through changes in signal strength or direction. We recorded estimated or confirmed locations with a Global Positioning System unit. We visually confirmed the status of woodpeckers every 48 hours if a prior check did not result in a direct observation of the bird. When we could not detect a radio signal from within a woodpecker's known territory, we searched within a 3.2-km radius of the last known location of the woodpecker. In 2006, we needed an average of 15 days to find missing woodpeckers. In 2007, we found all missing woodpeckers within 24 hours.

We classified the fate (survived, dead, or censored) of each radio-tagged woodpecker at the end of its tracking period. We censored woodpeckers when radio-contact was lost or transmitters slipped off. We confirmed fates of all other woodpeckers as alive or dead. We assigned death as the day the bird disappeared from its territory or the day of the last location it was known to be alive.

We assigned 5 causes of death. We classified deaths as Cooper's hawk (*Accipiter cooperii*) or sharp-shinned hawk (*Accipiter striatus*) predation when we recovered a carcass or transmitter at the nest of 1 of these species. In all such cases, the transmitter antenna had a distinctive sharp kink that was not present on the antennas of other recovered transmitters and at least 1 harness mounting tube was destroyed, indicating that the harness had been forcibly pulled off (see Vukovich and Kilgo 2009a for detailed descriptions of accipiter predation events). We assigned probable raptor predation if the transmitter or carcass was found elevated in a tree or shrub, under a perch with other avian remains present, or was damaged in a manner characteristic of accipiter predation (i.e., carcasses with plucked breast and body feathers and transmitters damaged similar to

those recovered under known accipiter nests). Other raptors observed regularly on the plots included red-shouldered (*Buteo lineatus*) and red-tailed hawks (*B. jamaicensis*) and eastern screech (*Megascops asio*), great horned (*Bubo virginianus*), and barred owls (*Strix varia*). We assigned snake predation when we discovered the transmitter and carcass inside a live snake or found a transmitter in snake feces in a cavity. If we could not attribute cause of death to any of the above factors, we considered it unknown.

Habitat Variables

To evaluate whether snag abundance affected woodpecker survival, we used experimental plots created for a larger study of the role of coarse woody debris in the ecology of southern pine forests. Snag treatments included low and high snag density. Snag numbers in plots with low snag density ($n = 8$ plots) were unmanipulated. In plots with high snag density ($n = 4$ plots), snag volume was increased 10-fold over that in unmanipulated plots. The square treatment plots were 9.3 ha and were located in 4 separate forest stands, each with 1 high density and 2 low density adjacent plots. Snag treatments were implemented in 2001 by chainsaw-girdling of all trees within 20 equally spaced 3.7-m wide strips per plot. Any trees that did not die within 6 months of initial girdling were re-treated with herbicide injection. All created snags had decayed sufficiently by 2004 as to be actively used for cavity excavation by red-headed woodpeckers for nesting and roosting. During 2006–2007, the combined (pine and hardwood) density of snags ≥ 18.4 cm in diameter at breast height and ≥ 6 m in height (the minimum size used by red-headed woodpeckers for cavity excavation; J. Kilgo and M. Vukovich, USDA Forest Service, unpublished data) averaged 5.6 ± 0.6 (SE) snags/ha on low snag density plots and 29.6 ± 3.5 snags/ha on high snag density plots. Live trees in low snag density treatment plots were thinned and removed in 2001 at a rate equivalent to the number of trees killed in high snag density treatment plots. Thus, basal area and size distribution of live trees, and hence canopy and stand structure, was similar between treatments.

We assigned each radio-tagged woodpecker to either low or high snag density treatment based on the type of treatment plot in which its nest snag was located. Because telemetry data indicated that woodpeckers concentrated much of their activity in the immediate vicinity of the nest (J. Kilgo and M. Vukovich, unpublished data), we felt that habitat conditions at the nest snag were the most appropriate criteria for categorizing territories by treatment type. We determined nest snags by observation of nesting behavior (frequent diurnal use of the cavity, delivery of food to nestlings). If a woodpecker's nest location was not determined, we assigned the bird to the treatment on which $\geq 75\%$ of its territory was located; any woodpecker whose nest-snag location was unknown and who had $\leq 75\%$ of its territory on 1 treatment or the other was dropped from analysis. We assigned treatments by this process for 6 birds that lacked nest snags. We delineated territory boundaries as the 95% minimum convex polygon (MCP) of all available locations per bird ($\bar{x} = 27$, range = 3–51) using Home

Range Extension (Rodgers and Carr 1998) in ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA). We felt the MCP more accurately characterized territory boundaries because it did not impute woodpecker use to areas beyond the peripheral points, as do probabilistic contouring estimators. Territories were tightly packed on our plots and boundaries were vigorously defended. Thus, territory boundaries effectively constituted barriers to movement. In such cases, Kernohan et al. (2001) observed that non-contouring estimators such as MCPs are appropriate because they better conform to the barrier. In addition, territories generally were compact in shape rather than elongate or irregular.

To evaluate whether foliar cover affected woodpecker survival, we determined the number of cover patches available to each woodpecker. We defined cover to include dense canopy or sub-canopy hardwood crowns that were ≥ 5 m in height, width, and depth and consisted of either individual or multiple stems. We also included dense patches of young pine trees (5- to 15-yr old) with a combined crown ≥ 5 m in height, width, and depth. Number of cover patches available was assessed based on the largest woodpecker territory we measured (11.4 ha; 95% MCP) and thus included the amount of area in which we expected most woodpeckers would seek cover. We tallied the number of cover patches within 191 m (the radius of an 11.4-ha circle) of the territory center using a handheld rangefinder to verify distance to each patch.

Survival Analysis

We conducted known-fate modeling in Program MARK (White and Burnham 1999), which allows the staggered entry of animals into analysis (Pollock et al. 1989), to estimate survival probability and to examine the influence of factors potentially affecting survival. We used an information theoretic approach to draw inference regarding a priori hypotheses about potential influences on survival probabilities (Burnham and Anderson 2002). We defined the breeding season as the 18-week period starting in early May and ending early September (2 May–4 Sep). The latest date we observed a nestling in a nest in either year was August 30, and although a few late pairs still cared for fledglings as late as mid-September, this time period encompassed the majority of red-headed woodpecker breeding activity in South Carolina (Smith et al. 2000; J. Kilgo and M. Vukovich, unpublished data). Our analysis involved 2 steps. First, we assigned woodpeckers to 2 groups based on calendar year (2006 and 2007) and estimated temporal effects on survival by comparing models in which survival varied by week in an unspecified manner (t), varied linearly through time (T), varied quadratically through time (TT), varied by year, or varied differently among weeks between years ($yr \times t$). The product of the weekly survival probability estimates produced under the $S(t)$ model was equivalent to the staggered-entry Kaplan–Meier estimate (when based on weekly intervals) for the season (Kaplan and Meier 1958, Pollock et al. 1989); we present these estimates for comparative purposes with other survival research. We then

established a set of 9 a priori candidate models based on red-headed woodpecker biology and habitat characteristics to estimate potential effects on survival probabilities (Burnham and Anderson 2002). Each of these models included the most appropriate time trend variable identified in the previous step and the additive effect of the biological and/or habitat variable of interest. We hypothesized that snag treatment and number of available cover patches would influence survival probabilities either individually or in various combinations with sex and age of woodpeckers. Thus, the 9 variables we evaluated included: sex; age; sex \times age; snag treatment; snag treatment \times sex; snag treatment \times age; number of cover patches; number of cover patches \times sex; and number of cover patches \times age. Model definitions and names followed the conventions of Lebreton et al. (1992) and White and Burnham (1999).

We used Akaike's Information Criterion adjusted for small sample size (AIC_c) for model selection, and considered our most plausible models to be those that were both ≤ 2.0 AIC_c units from the best approximating model and did not include any uninformative parameters (Burnham and Anderson 2002, Arnold 2010). We used Akaike weights (w_i) to evaluate the strength of evidence among competing models (Burnham and Anderson 2002). The global model ($S(\text{yr} \times t)$) was a saturated model and assessment of the goodness-of-fit of this model was not possible.

We believe our study met the following assumptions required for our analysis: radio-tagged birds were representative of the population; survival was independent among individuals; censoring of birds for which signals were lost was independent of the fate of those birds; and radio transmitters did not affect survival (Winterstein et al. 2001). Most breeding pairs (≥ 1 member) of red-headed woodpeckers ($>80\%$) and many non-breeding individuals (approx. 40%) on our experimental plots (which were representative of mature pine forests at SRS) were represented in our sample, based on territory-mapping we conducted concurrently (J. Kilgo and M. Vukovich, unpublished data). We attempted to minimize dependence among individuals in the sample by targeting only 1 member of each breeding pair during capture, although our sample includes both members of 5 pairs. In addition, although Atterberry-Jones and Peer (2010) suggested that a low level of cooperative breeding may occur in red-headed woodpeckers, thus potentially compromising independence if both a helper and a breeder were included in the sample, we saw no evidence of cooperative breeding in our population during 96 hours spent observing 32 nests (J. C. Kilgo and M. A. Vukovich, unpublished data) and countless hours radio-tracking and observing 128 woodpeckers. Among our censored birds (4), the fates of only 2 were unknown, and we do not believe that the failure of these 2 transmitters was associated with the potential death of the woodpeckers. Our transmitters survived known woodpecker mortality events inflicted by ≥ 3 species of predator and ≥ 1 unknown agent, despite occasionally sustaining external damage, whereas 2 transmitters failed on birds known to be alive. We believe that transmitters did not affect survival because they affected neither the ability of woodpeckers to

enter and exit cavities, nor the amount of time engaged in behaviors such as preening or feeding that might have distracted woodpeckers from vigilance and predisposed them to predation (Vukovich and Kilgo 2009b). However, Vukovich and Kilgo (2009b) did not assess direct effects of transmitters on woodpecker mortality, and we acknowledge that transmitters may have rendered woodpeckers more vulnerable to predation, thus biasing our survival estimates low. Therefore, considering body mass as an index to the percent of body mass that transmitters occupied, we included in our candidate set of survival models 3 that evaluated effects of woodpecker mass (mass alone and mass interacting with both sex and age). These models allowed us to assess whether smaller woodpeckers (whose transmitters accounted for a greater percentage of their body mass) survived at a lesser rate than larger woodpeckers, both in general and within age and sex classes, as such a relationship would suggest negative transmitter effects.

RESULTS

Radio-Marked Woodpeckers

We captured and radio-tracked 80 red-headed woodpeckers in 2006 ($n = 41$: 24 M [3 SY, 21 ASY], 17 F [5 SY, 12 ASY]) and 2007 ($n = 39$: 22 M [11 SY, 11 ASY], 17 F [8 SY, 9 ASY]). Only 3 woodpeckers did not breed (1 SY M and 1 ASY M in 2006, 1 SY F in 2007). Two woodpeckers were censored in 2006 when we lost contact with their transmitters, and 2 were censored in 2007, 1 when its transmitter slipped off and the other when its transmitter failed. The latter was re-captured 9 weeks later and re-entered the at-risk sample. Mean mass of woodpeckers was 68.5 ± 0.7 g (SE; range = 56.0–94.5 g). Males averaged 70.4 ± 0.6 g and females averaged 65.9 ± 1.2 g.

Sources of Mortality

Twenty woodpeckers died during the study ($n = 11$ in 2006; $n = 9$ in 2007). Avian predation (Cooper's hawk, sharp-shinned hawk, and probable raptor predation combined) was the primary cause of mortality among woodpeckers for both years (17 of 20; 85%). Accipiters killed 12 (60%) woodpeckers (6 of 11 mortalities in 2006 and 6 of 9 mortalities in 2007): Cooper's hawks killed 7 woodpeckers (5 in 2006, 2 in 2007) and sharp-shinned hawks killed 5 woodpeckers (1 in 2006, 4 in 2007). Cause of death for 5 woodpeckers (3 in 2006, 2 in 2007) was probable raptor predation. Gray rat snakes (*Elaphe obsoleta*) killed 2 woodpeckers (1 in 2006, 1 in 2007). We could not determine the cause of death for 1 woodpecker in 2006.

Survival

Seasonal (18 weeks) survival probabilities of red-headed woodpeckers did not differ between the breeding seasons of 2006 (0.64 ± 0.09 ; 95% CI = 0.45–0.79) and 2007 (0.68 ± 0.09 ; 95% CI = 0.48–0.83) and the year effect model ($S(\text{yr})$) received essentially no support from the data ($\Delta\text{AIC}_c = 15.02$, $w_i = 0.000$). Weekly survival probabilities varied from 0.93 (± 0.03) to 1.00 ($\pm <0.001$; Fig. 1), with a decline during the middle of the season and an increase at the end; more woodpeckers died during June

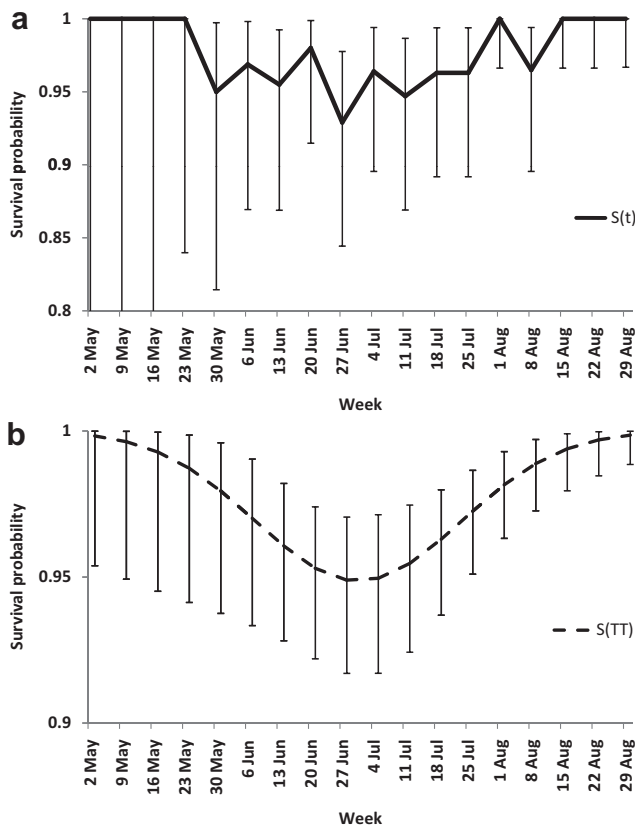


Figure 1. Weekly survival probabilities (a) estimated with model $S(t)$ where survival was allowed to vary by week and (b) modeled with a quadratic time trend, $S(TT)$, for red-headed woodpeckers during the breeding season in pine forests of Aiken and Barnwell counties, South Carolina, USA, 2006–2007. Error bars indicate 95% profile likelihood confidence intervals. We truncated the Y-axis in panel (a) at 0.8 to better illustrate detail; lower 95% confidence intervals for 2 May, 9 May, and 16 May were 0.53, 0.53, and 0.68, respectively.

($n = 6$) and July ($n = 12$) than during May ($n = 0$) and August ($n = 2$). The best model describing temporal trends in survival rate was the quadratic time trend model ($S(TT)$; Table 1, Fig. 1), which explained the pattern in weekly survival probabilities using fewer parameters than $S(t)$. Quadratic time trend, therefore, was included as an additive effect in all models assessing effects of biological and habitat covariates.

In addition to the quadratic time trend variable, the best-supported biological and habitat model (Tables 1 and 2) indicated that survival was associated with the sex of woodpeckers interacting with the number of available cover patches. Assuming an even sex ratio and the median number of cover patches (6), this model estimated seasonal survival at 0.72 (95% CI = 0.54–0.85). Survival probability for females under this model was 0.82 (95% CI = 0.54–0.94) and for males was 0.60 (95% CI = 0.42–0.76), but survival of females was more strongly affected (positively) by number of patches than that of males (Fig. 2a). Although 3 models met our criteria for consideration as the best competing models, the best-supported model ($w_i = 0.503$) was more than twice as plausible as the second- ($w_i = 0.204$) and third-best models ($w_i = 0.200$). Further, the number of available cover patches appeared in all 3 of these models, indicating that our data provided considerable evidence that this variable was associated with survival probability, whether alone or in concert with other factors. Although the interaction of age and number of available cover patches in association with survival was not the best-supported model, this model did receive some support from our data (Table 1), with survival of SY birds more strongly associated with number of patches than that of ASY birds (Fig. 2b). Cumulative seasonal survival probability, irrespective of covariate effects (from model $S(t)$) was 0.66 (SE = 0.06; 95% CI = 0.52–0.77).

We found no evidence for an association between snag treatment and survival probability. The ΔAIC_c value of the best model that included snag treatment, $S(TT + \text{snag treatment})$ was 7.12, and the confidence interval for the regression coefficient of the snag treatment variable overlapped 0 ($\beta = 0.539$, SE = 0.457, 95% CI = -0.356 – 1.436). Models relating woodpecker survival to body mass also received little support from our data; the best model that included mass had a ΔAIC_c value of 8.05 and was 56 times less plausible than our top model.

DISCUSSION

This research provides the first direct measure of survival probabilities and the first information on cause-specific mortality for the red-headed woodpecker, a Partners In Flight Watchlist species. The breeding season survival rate (0.72) of

Table 1. Model selection results used to estimate breeding-season survival probabilities (S) of radio-tagged red-headed woodpeckers in pine forests of Aiken and Barnwell counties, South Carolina, USA, 2006–2007. We present only those models receiving 0.95 of the cumulative Akaike's Information Criterion (AIC_c) weight.

Model description	No. parameters	AIC_c	AIC_c weight	ΔAIC_c^a
$S(TT + \text{numberpat} \times \text{sex})^b$	6	172.28	0.501	0.00
$S(TT + \text{numberpat} \times \text{age})^c$	6	174.09	0.203	1.81
$S(TT + \text{numberpat})$	4	174.12	0.200	1.84
$S(TT)$	3	178.75	0.020	6.47
$S(TT + \text{sex} + \text{age} + \text{snagtrt} + \text{numberpat} + \text{mass})^d$	8	179.37	0.014	7.09
$S(TT + \text{snagtrt})$	4	179.39	0.014	7.12

^a ΔAIC_c , difference between AIC_c of a model and the best performing model.

^b TT = quadratic time trend. Numberpat = number of cover patches available to each woodpecker.

^c Age = woodpecker age class (second year or after second year).

^d Snagtrt = low (unmanipulated) or high (10-fold increase) density experimental snag treatment used by each woodpecker. Mass = woodpecker body mass at capture.

Table 2. Parameter estimates (β), standard errors, odds ratios, and 95% confidence intervals of odds ratios for the predictor variables in the top model hypothesized to affect survival of radio-tagged red-headed woodpeckers in pine forests of Aiken and Barnwell counties, South Carolina, USA, 2006–2007.

Variable ^a	β	SE	Odds ratio	95% CI
T	−0.876	0.508	0.416	0.154–1.129
TT	0.046	0.024	1.047	1.000–1.097
Numberpat	0.624	0.219	1.866	1.213–2.869
Sex	2.435	1.240	11.416	1.003–130.061
Numberpat \times sex	−0.562	0.253	0.570	0.347–0.936

^a T indicates linear time trend; TT indicates quadratic time trend; Numberpat indicates number of cover patches available to each woodpecker.

red-headed woodpeckers at our study sites in pine forests of the South Carolina Coastal Plain was comparable to previously reported indirect measures of red-headed woodpecker annual survival. Martin (1995) cited unpublished data from D. Ingold to report an annual survival rate of 0.62. Although survival patterns of this species outside the breeding season are unknown, Doherty et al. (1996) reported that only 1 of 14 (7%) red-headed woodpeckers observed through winter in Ohio died, suggesting that overwintering mortality may be low. Thus, depending on mortality rates during migration, a breeding season survival rate of 0.72 conceivably may not

decline much lower during the remainder of the year than the 0.62 level reported for red-headed woodpeckers by Martin (1995) or the 0.56 level reported as the average annual survival rate among all North American woodpeckers combined (Wiebe 2006).

Probability of survival was positively associated with the number of cover patches available to woodpeckers. All of our top 3 models included this variable, either alone or in interaction with sex or age of woodpeckers. Because the model including number of available cover patches alone received some support from our data, cover apparently was important to some degree to all woodpeckers, regardless of age or sex, though females, and to a lesser extent SY birds, apparently benefitted more from cover patches than males and ASY birds. An effect of cover on survival in birds has long been assumed (Stoddard 1931) and this assumption has formed the basis of an extensive body of work on avian behaviors ranging from space and habitat use to flocking and vigilance (Pulliam and Mills 1977, Lima et al. 1987). However, few studies have actually demonstrated an association between cover and survival probabilities of adult birds (but see Watts 1990, Williams et al. 2000). The exact mechanism underlying this relationship in red-headed woodpeckers is unclear, because little information is available in the literature regarding how this species evades predators. Members of Picidae generally dodge avian predators by hitching around the tree on which they are feeding when attacked (Lima 1993). However, red-headed woodpeckers spend more time than most woodpeckers on the ground foraging, particularly during the breeding season, and more time on the wing flycatching and interacting with conspecifics (Smith et al. 2000). These behaviors may increase the chance that red-headed woodpeckers will not be on a tree when attacked and thus cannot simply move to the other side. In such cases, they presumably make use of any dense cover available as they flee the predator. In addition, we frequently observed red-headed woodpeckers hiding in broadleaf foliage to escape detection by human observers, suggesting that they may also hide in cover when an avian predator is present. Additional research is needed to better understand the manner in which red-headed woodpeckers evade predators and use cover.

Survival probabilities of red-headed woodpeckers on our plots were unrelated to snag density. We hypothesized that the high density of snags on our treatment plots would result in an abundance of cavities available for roosting, precluding the need for woodpeckers to roost in the open at night, which in turn would minimize the risk of nocturnal predation and thereby increase survival. Two factors may explain the lack of an effect of snag density. First, most mortality resulted from diurnal avian predators, against which cavities presumably would provide no protection. We attributed 25% of mortalities (5 of 20) to unknown raptors that conceivably could have been nocturnally hunting owls, and we suspect that some of those deaths were attributable to accipiters. Second, adult females and SY birds of both sexes (i.e., most birds that were not incubating or brooding at night) often roosted in the open and always in the canopy of a live pine tree, despite the availability of both unoccupied cavities and snags where

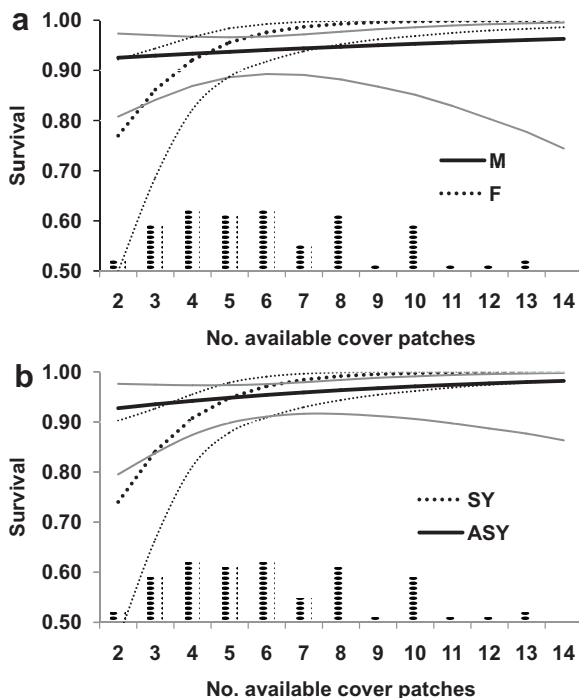


Figure 2. Effects of number of available cover patches on point estimates of survival of (a) male and female and (b) second year (SY) and after second year (ASY) red-headed woodpeckers during the breeding season in pine forests of Aiken and Barnwell counties, South Carolina, USA, 2006–2007. Lighter lines indicate 95% confidence intervals. Stacked dots indicate sample size of woodpeckers at each number of cover patches. We estimated survival while holding time constant at the median interval (week 10). Range in number of cover patches shown is mean (6.84) \pm 2 standard deviations, except on lower end because value was outside of actual range of data and was therefore truncated.

cavities could have been excavated (Vukovich and Kilgo 2009b, J. Kilgo and M. Vukovich, unpublished data). If these birds chose to roost in the open, either cavities provided little protection or nocturnal predation was of minimal importance. In either case, abundant snags and cavities would play no role in limiting mortality.

Avian predation, primarily by accipiters, was the greatest source of mortality to red-headed woodpeckers during the breeding season, and this pattern was evident during both years. Due to their relative rarity in the Southeast, the effects of sharp-shinned hawks on red-headed woodpecker populations in the region, although locally intense, may be minimal. In contrast, predation by Cooper's hawks, whose breeding range more closely coincides with that of red-headed woodpeckers and some of whose populations have increased during the past 30–40 years (Bednarz et al. 1990, Titus and Fuller 1990, Sauer et al. 2008), could represent a limiting source of mortality for some red-headed woodpecker populations, particularly when sharp-shinned hawks are also present. In addition, most mortality occurred during June and July, encompassing the peak of the nestling and fledgling period for red-headed woodpeckers in South Carolina (Smith et al. 2000; J. Kilgo and M. Vukovich, unpublished data). June and July also coincides with the late nestling and fledgling stages of accipiter nesting (Bildstein and Meyer 2000, Rosenfield and Bielefeldt 2006, Vukovich and Kilgo 2009a) when prey demand increases. Intensive predation at this time may have negative consequences not just on adult woodpecker survival but potentially on reproductive success as well.

Our assessment of woodpecker body mass as a potential predictor of survival probability provided partial evaluation of whether radio transmitters might have affected survival probability of our sample birds. Our data provided no support for any model that included the effect of woodpecker mass on survival probability, indicating that even the smallest individuals, for which our transmitters accounted for the greatest proportion of their body weight, were no less likely to survive than larger birds. Although we acknowledge that transmitters may have increased mortality risk and biased our survival estimate low, based on the lack of relationship with body mass, combined with the lack of any effect of transmitters on the behavior of our birds (Vukovich and Kilgo 2009b), we believe our survival estimate is accurate for our study population.

MANAGEMENT IMPLICATIONS

Red-headed woodpeckers are associated with the habitat conditions that historically occurred across broad expanses of fire-maintained longleaf pine forest. The current distribution of this forest type is largely restricted to areas managed either for the endangered red-cockaded woodpecker (*Picoides borealis*) or for northern bobwhite (*Colinus virginianus*). Under management programs for these 2 species, prescribed fire, chemical, or mechanical treatments are used to control encroaching midstory vegetation and to maintain open understory and sparse midstory conditions. However, depending on the intensity of vegetation control

efforts and silvicultural practices, some areas contain little remaining cover at any level. Our findings suggest that such conditions were associated with considerably lower survival of red-headed woodpeckers, particularly females and SY birds, and that survival was highest for birds that had at least 8 cover patches in their territories (0.7/ha). When considering only SY birds, the highest survival probabilities were associated with at least 14 cover patches. Therefore, in areas managed for red-cockaded woodpeckers or northern bobwhite, managers should consider leaving some patches of relatively dense vegetation during vegetation control activities to provide habitat for red-headed woodpeckers.

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LITERATURE CITED

- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178.
- Atterberry-Jones, M. R., and B. D. Peer. 2010. Cooperative breeding by red-headed woodpeckers. *Wilson Journal of Ornithology* 122:160–162.
- Bednarz, J. C., D. Klem, Jr., L. J. Goodrich, and S. E. Senner. 1990. Migration counts of raptors at Hawk Mountain, Pennsylvania, as indicators of population trends, 1934–1986. *Auk* 107:96–109.
- Bildstein, K. L., and K. Meyer. 2000. Sharp-shinned Hawk (*Accipiter striatus*). Account 482 in A. Poole and F. Gill, editors. *The birds of North America*. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. 2nd edition. Springer-Verlag, New York, New York, USA.
- Doherty, P. F. Jr., T. C. Grubb, Jr., and C. L. Bronson. 1996. Territories and caching-related behaviors of red-headed woodpeckers wintering in a beech grove. *Wilson Bulletin* 108:740–747.
- Kaplan, E. L., and P. Meier. 1958. Nonparametric observations from incomplete observations. *Journal of the American Statistical Association* 53:457–481.
- Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 in J. J. Millspaugh and J. M. Marzluff, editors. *Radio tracking and animal populations*. Academic Press, San Diego, California, USA.
- King, R. S., K. E. Brashear, and M. Reiman. 2007. Red-headed woodpecker nest-habitat thresholds in restored savannas. *Journal of Wildlife Management* 71:30–35.
- Lebreton, J., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lima, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bulletin* 105: 1–47.
- Lima, S. L., K. L. Wiebe, and L. M. Dill. 1987. Protective cover and the use of space by finches: is closer better? *Oikos* 50:225–230.
- Lohr, S. M., S. A. Gauthreaux, and J. C. Kilgo. 2002. Importance of coarse woody debris to avian communities in loblolly pine forests. *Conservation Biology* 16:767–777.

- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- National Audubon Society. 2008. The Christmas Bird Count historical results. National Audubon Society, Ivyland, PA. <<http://www.audubon.org/bird/cbc>>. Accessed 25 Jun 2009.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- Pulliam, H. R., and G. S. Mills. 1977. The use of space by wintering sparrows. *Ecology* 58:1393–1399.
- Pyle, P. 1997. Identification guide to North American birds Part 1. Slant Creek Press, Bolinas, California, USA.
- Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Inigo-Elias, J. A. Kennedy, A. M. Martell, A. O. Panjabi, D. N. Pashley, K. V. Rosenberg, C. M. Rustay, J. S. Wendt, and T. C. Will. 2004. Partners in Flight North American landbird conservation plan. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Rodewald, P. D., M. J. Santiago, and A. D. Rodewald. 2005. Habitat use of breeding red-headed woodpeckers on golf courses in Ohio. *Wildlife Society Bulletin* 33:448–453.
- Rodgers, A. R., and A. P. Carr. 1998. HRE: the home range extension for ArcViewTM: user's manual. Beta test version 0.9, July 1998. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem, Research, Thunder Bay, Ontario, Canada.
- Rosenfield, R. N., and J. Bielefeldt. 2006. Cooper's Hawk (*Accipiter cooperii*) Account 75 in A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2008. The North American Breeding Bird Survey, results and analysis 1966–2007. United States Geological Survey. <<http://www/bwr-usgs.gov/bbs/bbs.html>>. Accessed 25 Jun 2009.
- Smith, K. G., J. H. Withgott, and P. G. Rodewald. 2000. Red-headed Woodpecker (*Melanerpes erythrocephalus*). Account 518 in A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.
- Stoddard, H. L. 1931. The bobwhite quail: its habits, preservation, and increase. Charles Scribner's Sons, New York, New York, USA.
- Titus, K., and K. M. Fuller. 1990. Recent trends in counts of migrant hawks from northeastern North America. *Journal of Wildlife Management* 54:463–470.
- Venables, A., and M. W. Collopy. 1989. Seasonal foraging and habitat requirements of red-headed woodpeckers in north-central Florida. Nongame Wildlife Program Final Report Project No. GFC-84-006, Florida Game and Freshwater Fish Commission, Tallahassee, Florida, USA.
- Vukovich, M. A., and J. C. Kilgo. 2009a. Notes on breeding sharp-shinned hawks and Cooper's hawks in Barnwell County. South Carolina. *Southeastern Naturalist* 8:547–552.
- Vukovich, M. A., and J. C. Kilgo. 2009b. Effects of radio transmitters on the behavior of red-headed woodpeckers. *Journal of Field Ornithology* 80:308–313.
- Watts, B. D. 1990. Cover use and predator-related mortality in song and savannah sparrows. *Auk* 107:775–778.
- Wiebe, K. L. 2006. A review of adult survival rates in woodpeckers. *Annales Zoologica Fennici* 43:112–117.
- Williams, C. K., R. S. Lutz, R. D. Applegate, and D. H. Rusch. 2000. Habitat use and survival of northern bobwhite (*Colinus virginianus*) in cropland and rangeland ecosystems during the hunting season. *Canadian Journal of Zoology* 78:1562–1566.
- White, G. C., and K. P. Burnham. 1999. Program MARK—survival estimation from populations of marked animals. *Bird Study* 46(supplement):S120–S139.
- Winterstein, S. R., K. H. Pollock, and C. M. Bunck. 2001. Analysis of survival data from radiotelemetry studies. Pages 351–380 in J. J. Millsbaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

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