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Fall movements of Red-headed Woodpeckers in South Carolina

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ABSTRACT. Fall migration of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) can be erratic, with departure rates, directions, and distances varying among populations and individuals. We report fall migration departure dates, rates, and routes, and the size of fall home ranges of 62 radio-tagged Red-headed Woodpeckers in western South Carolina. Rates of fall migration differed among years; all radio-tagged woodpeckers migrated in 2005 (15 of 15), none (0 of 23) migrated in 2006, and 54.2% (13 of 24) migrated in 2007. Of 28 woodpeckers that left their breeding territories, we relocated eight either en route or on their fall home ranges. These woodpeckers migrated short distances (4.3–22.2 km) south along the floodplain forest of a large creek. The variable migration patterns we observed indicate that Red-headed Woodpeckers may best be described as facultative migrants. We determined the home range sizes of 13 woodpeckers in both seasons, regardless of whether they migrated, and fall home ranges were smaller (mean = 1.12 ha) than summer home ranges (mean = 3.23 ha). Fall-winter movements of Red-headed Woodpeckers were concentrated on mast-producing oak (*Quercus* spp.) trees, which may have restricted home range sizes. The partial migration we observed in 2007 suggests that factors other than mast crop variability may also influence migration patterns because woodpeckers that year responded to the same annual mast crop in different ways, with some migrating and some remaining on breeding season home ranges during the fall.

RESUMEN. **Movimientos de *Melanerpes erythrocephalus* durante el otoño en Carolina del Sur**

La migración de *Melanerpes erythrocephalus* durante el otoño puede ser errática entre poblaciones e individuos con variación en las tasa de salida, dirección y distancia. Reportamos fechas, tasa y rutas, y el tamaño de los rangos de hogar de 62 individuos de *Melanerpes erythrocephalus* con radios, en el oeste de Carolina del Sur durante la migración en el otoño. Las tasas de migración durante el otoño variaron entre años, todos los individuos con radios migraron en el 2005 (15 de 15), ninguno migro en el 2006 (0 de 23) y 54.2% migraron en el 2007 (13 de 24). De los 28 carpinteros que dejaron sus territorios reproductivos, localizamos ocho en las rutas o en sus rangos de hogar del otoño. Estos carpinteros migraron cortas distancias (4.3–22.2 km) al sur a lo largo de los bosques inundables localizados a lo largo de grandes arroyos. Los variables patrones de migración observados indican que la mejor forma de describir a *M. erythrocephalus* es como un migrante facultativo. Determinamos el tamaño del rango de hogar de 13 carpinteros en las dos temporadas, sin importar si migraron, los rangos de hogar durante el otoño fueron mas pequeños (promedio = 1.12 ha) que los rangos de hogar durante el verano (promedio = 3.23 ha). Movimientos durante el otoño e invierno de *M. erythrocephalus* se concentraron alrededor de árboles de roble (*Quercus* spp.) produciendo bellotas, los cuales pueden haber restringido el tamaño de los rangos de hogar. La migración parcial que observamos en el 2007 siguieren que factores diferentes a la variabilidad en la cosecha de bellotas pueden estar afectando los patrones de migración, porque los carpinteros ese año respondieron a la misma producción anual de bellotas de diferentes maneras, con algunos migrando y algunos se quedaron en los rangos de hogar reproductivos durante le otoño.

Key words: facultative migration, fall migration, home range, *Melanerpes erythrocephalus*, short-distance migratory movements

The movements and behavior of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) during fall migration are highly erratic, and the frequency, direction, and routes of migration all remain poorly understood (Smith et al. 2000). Smith (1986) characterized Red-headed Woodpecker movements as nomadic, Ingold (1991) considered the species "migratory or semimigratory," and Herkert (1995) categorized them as short-distance migrants. Fall movements by Red-headed Woodpeckers might also be described by terms such as facultative or irruptive migration. Some evidence suggests a semiregular 2- to 4-yr cycle in migratory movements that may follow an east-west axis because areas of

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greatest abundance of wintering Red-headed Woodpeckers shift longitudinally from year to year (Smith 1986). Further, winter abundance tends to be greater in the central U.S.A. than in the southern U.S.A., suggesting that some birds in southern populations may migrate north during fall (Smith et al. 2000). Much of the annual variation in migratory behavior of Red-headed Woodpeckers is believed to be due to variation in abundance of hard mast crops (Smith 1986, Smith and Scarlett 1987), which may determine whether woodpeckers migrate, how far they migrate, and their routes. Migratory destinations are typically areas with mast-producing trees, particularly oaks (*Quercus* spp.; Smith et al. 2000), and the concentration of movements by woodpeckers in single trees or small patches of trees results in fall-winter territories smaller than breeding territories (Venables and Collopy 1989, Doherty et al. 1996).

Current knowledge of Red-headed Woodpecker fall migratory movements are based largely on anecdotal reports (summarized by Smith et al. 2000). Migratory movements and destinations of a known breeding population of Red-headed Woodpeckers have not been reported. Thus, our objectives were to determine the fall departure dates and rates, the extent of short-distance migratory movements, and fall home range sizes of Red-headed Woodpeckers in a population in South Carolina.

METHODS

Our study was conducted at Savannah River Site (SRS), a 78,000 ha National Environmental Research Park located in Aiken and Barnwell counties, South Carolina (Fig. 1). The SRS was dominated by loblolly (*Pinus taeda*) and longleaf pine (*P. palustris*) forest on the uplands and bottomland hardwood forests along riparian zones, which included the floodplains of the Savannah River and other large streams. Our study plots were in upland pine forest composed mostly of 50- to 60-yr-old loblolly pine, with scattered 40- to 100-yr-old oaks, primarily water (*Quercus nigra*), southern red (*Q. falcata*), and post (*Q. stellata*) oaks, and many standing snags (see Imm and McLeod 2005 for more detail about forest composition of the area). One study plot was in Aiken County and the other in Barnwell County. Study plots were ≥75 m from riparian areas and major roads.

We captured Red-headed Woodpeckers from May to August 2005–2007 using standard ground-level mist nets (38-mm mesh), elevated mist nets, and hoop nets attached to 12 m telescoping poles. Elevated mist nets were suspended from ropes deployed in the midstory and canopy of the forest (Vukovich and Kilgo 2009). We used elevated mist nets and hoop nets primarily to capture woodpeckers at their nest cavities. We banded woodpeckers with USGS aluminum leg bands and color bands to facilitate individual identification, and aged woodpeckers (hatch-year [HY], second-year [SY], and after second-year [ASY]) using plumage characteristics (Pyle 1997). Red-headed Woodpeckers cannot be sexed in the hand (Pyle 1997), so we collected breast feathers for DNA sexing, which was performed by Avian Biotech International (Tallahassee, FL) using polymerase chain reaction (PCR)-based procedures on tissue collected from the calamus of collected feathers (Griffiths et al. 1998).

Captured woodpeckers were fitted with 1.9-g transmitters (BD-2A, 16-wk battery life, Holohil Systems, Ltd., Carp, Ontario, Canada) using a wing-mounted backpack harness. The transmitter-harness package weighed 2.1 g and did not affect woodpecker behavior (Vukovich and Kilgo 2009). We determined fall locations of radio-tagged woodpeckers by homing on foot 2–4 times per week. In summer, we visually confirmed the status of each woodpecker every 48 h if a prior check did not result in a direct visual observation of the woodpecker. We marked locations (± 6 m accuracy) with a handheld GPS unit (Garmin 76, Olathe, KS). We obtained locations of woodpeckers throughout the day. When a signal was lost, we systematically searched the SRS and adjacent areas within ~30 km of the study plots. We acknowledge that we may have misclassified woodpeckers as having migrated when in fact their transmitters failed, potentially biasing our estimates of departure rates upward. However, given the expected battery life of transmitters and our frequent monitoring schedule, we were generally able to determine from signal characteristics when a transmitter was failing and censored it from the data. In addition, among recorded predation events ($N = 19$) in a concurrent study, predators never affected the function of a transmitter (Kilgo and Vukovich 2012). Therefore, we believe that any such bias was unlikely. In 2005, we

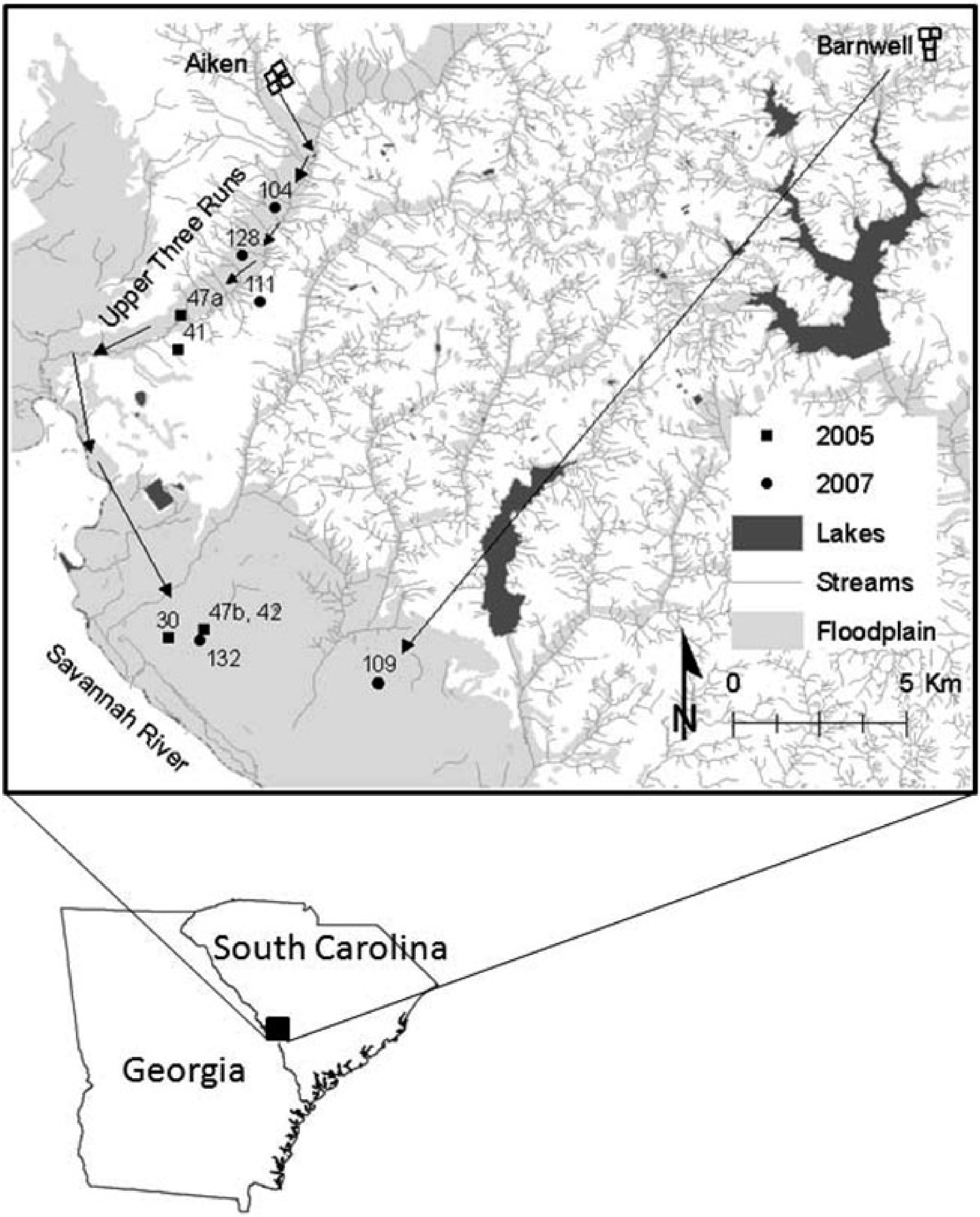

Fig. 1. Possible fall migratory routes (arrows) of nine Red-headed Woodpeckers during 2005–2007 from breeding season home ranges on study plots in upland pine forest (open squares) on the Savannah River Site, Aiken, and Barnwell counties, South Carolina. Locations of fall home ranges are indicated by closed squares (2005) and closed circles (2007). Bird 47 was relocated twice during fall 2005 (47a, 47b).

searched for radio-tagged woodpeckers from a helicopter at an altitude of 610 m along parallel north-south transects. In subsequent years, we searched from a vehicle along forest roads in expanding concentric circles around the bird's home range. We obtained fall locations in the same manner as breeding season locations, and also recorded foraging substrate for woodpeckers that migrated.

Consensus on how to describe the species' migration pattern seems lacking. Considering this point and for consistency, we use simply migration. We classified woodpeckers as migrants if they moved $\geq$ 2 km from their breeding territories to contrast them with those that remained on summer home ranges through the fall. We estimated fall migration departure dates as the midpoint of the period between the last date and time we detected a bird's signal on its summer home range and the first date and time we did not. Our estimates of migration rates are conservative because they are based only on fall movements and some woodpeckers classified as nonmigratory may have migrated during winter after transmitters ceased functioning. To compare migration rates among years, we calculated Clopper–Pearson 95% confidence intervals (Seber 1982) for the proportions of birds that migrated each year and made pair-wise comparisons among years ($\alpha = 0.05$) by evaluating whether CI's overlapped. We used exact Pearson chi-square analyses to determine if migration rates were influenced by sex (2×2) or age (2×3; Proc FREQ; SAS Institute 2008). We used a three-factor analysis of variance (ANOVA; Proc GLM; SAS Institute 2008) to compare departure dates among years and between sexes and age classes.

We delineated territories of radio-tagged woodpeckers using the 95% fixed kernel estimator with least squared cross-validation (Seaman and Powell 1996). We used ArcMap 9.3 and ArcView 3.2 (ESRI, Redlands, CA) with Animal Movements extension (Hooge and Eichenlaub 1997) for home range delineation. We included woodpeckers in the fall home-range analysis only when we had $\geq$ 11 locations (mean = 13.5; range = 11–16). We acknowledge that the kernel estimator is sensitive to small sample sizes of relocations (Seaman et al. 1999), but our sample was limited by the duration of the period between migration and transmitter battery failure, combined with the need to maintain temporal independence between observations. We attempted to control for this potential bias by limiting the range in number of points per bird. To compare summer and fall home ranges of individual birds with a sufficient number of locations to compute both, we used the same number of locations to delineate each bird's summer and fall home range. Because the number of available locations per bird was more limited during fall, we randomly selected a subset of summer locations for each bird.

Mean duration of the monitoring period for home range size determination was 50 d per bird during summer (range = 30–84 d) and 56 d per bird during fall (range = 44–76 d). Summer home ranges included locations determined from 15 June to either 15 September or migration, whichever came first. We selected 15 September as the cutoff because we observed nestlings in cavities through August and adults caring for fledglings through mid-September. In addition, we never observed radio-tagged woodpeckers making postbreeding or exploratory movements prior to migration and this time period falls within the known migratory period of the species (Smith et al. 2000); all birds remained in summer home ranges either until they migrated or through the fall if they did not migrate. For woodpeckers that remained on summer home ranges during fall, we delineated fall home ranges using locations obtained from 15 September to 30 November because, after 15 September, we frequently observed woodpeckers foraging in and among oak trees and carrying acorns, which was characteristic fall behavior.

We compared fall home range sizes among years and between sexes, age classes, and habitats of woodpeckers using a four-factor ANOVA (Proc GLM; SAS Institute 2008). Due to limited sample size for this analysis and because SY birds in our study population seldom bred, we combined HY and SY into an immature age class. Habitats included upland pine (for woodpeckers that remained on their summer territories on our upland pine study sites) and bottomland hardwood forest (for woodpeckers that migrated from summer territories). We used a paired t-test to compare breeding and fall home range sizes of woodpeckers with a sufficient number of locations to determine both, and we include both woodpeckers that migrated and woodpeckers that did not. All means are reported ± SE.

RESULTS

Migration rates. From 2005 to 2007, we radio-tagged 62 Red-headed Woodpeckers, four of which we recaptured and monitored during multiple years (1 bird for 3 yr, 3 birds for 2 yr). Fall migration rates of radio-tagged Red-headed Woodpeckers with breeding season territories ($N = 62$) differed among years. All radio-tagged woodpeckers migrated in 2005 (15 of 15; 95% CI = 0.78–1.0; $N = 7$ males, 7 females, 1 unknown sex; $N = 12$ ASY, 3 SY). None (0 of 23; 95% CI = 0–0.15; $N = 11$ males, 12 females; $N = 17$ ASY, 4 SY, 2 HY) migrated in 2006; all remained on summer territories until 27 November when all transmitters had stopped working. In 2007, 54.2% (13 of 24; 95% CI = 32.8–74.5%) of radio-tagged woodpeckers migrated from summer home ranges. Migration rates in 2007 did not differ either between the sexes (8 males and 5 females migrated; 5 males and 6 females did not; $\chi^2_1 = 0.6$, $P = 0.68$) or among age classes (9 ASY, 3 SY, and 1 HY birds migrated; 7 ASY, 2 SY, and 2 HY birds did not; $\chi^2_2 = 0.6$, $P = 0.85$).

Departure dates. Mean departure date for woodpeckers that migrated ($N = 28$) was 22 September (range = 11 September–5 October). We excluded from departure date analysis three woodpeckers that migrated, including one randomly from a radio-tagged pair to ensure independence, one because its sex was unknown, and one because it was the only HY bird that migrated. Departure dates did not differ between 2005 ($N = 14$) and 2007 ($N = 13$; $F_{1,20} = 0.2$, $P = 0.63$) so we removed year from the model. Departure dates did not differ between sexes ($N = 12$ females and 13 males; $F_{1,22} = 0.01$, $P = 0.98$) or age classes ($N = 19$ ASY and 6 SY birds; $F_{1,22} = 0.1$, $P = 0.82$).

Migratory movements. We were unable to relocate 20 of 28 radio-tagged woodpeckers after they migrated. Thus, 71% of woodpeckers likely migrated >30 km. We relocated eight woodpeckers after they migrated, including three in 2005 (1 ASY male and 2 ASY females) and five in 2007 (1 ASY male, 2 ASY females, 1 SY male, and 1 HY male). In addition, in 2005, we observed an ASY male with a failed transmitter near his radio-tagged mate (ASY female) on her postmigration fall home range. Thus, we relocated nine woodpeckers after migration. Mean date of relocating woodpeckers after migrating was 12 October (range = 30 September–8 November), and mean elapsed time between departure from summer territories and relocation on fall territories was 13.8 d (range = 1–32 d). We tracked woodpeckers in their fall territories for an average of 50.4 ± 3.6 d.

Median distance of short-distance (<30 km) migratory movements was 16.6 km (range = 16.4–22.2 km) for females ($N = 4$) and 6.7 km (range = 4.3–16.7 km) for males ($N = 5$). Fall home ranges were all in bottomland hardwood forests composed primarily of laurel (*Q. laurifolia*), water, white (*Q. alba*), southern red, and cherrybark oaks (*Q. pagoda*), and loblolly pine, water tupelo (*Nyssa aquatica*), and bald cypress (*Taxodium distichum*) that ranged in age from 50 to 150 years. All observations of radio-tagged birds in these areas ($N = 62$) were in either laurel or water oak trees.

Areas used by these birds may have been reached by following riparian courses downstream (generally south) from summer territories (Fig. 1). We relocated one woodpecker (bird 47) in a riparian area while en route between summer and fall areas (Fig. 1). Another woodpecker (bird 109) crossed watersheds to reach its fall home range (Fig. 1). One area of the Savannah River floodplain was used by woodpeckers in both 2005 and 2007 (birds 30, 42, 47, and 132; Fig. 1).

Among two breeding pairs of woodpeckers where both sexes had transmitters and at least one member migrated, neither pair was relocated together after migrating; in one case, both migrated, but only the male was relocated and, in the other case, the female migrated and the male remained on its summer home range. However, on one occasion, we observed a banded male (bird 42) <20 m from his radio-tagged mate (bird 47) on her fall home range (Fig. 1).

Fall territories. For woodpeckers where we measured home range size in both seasons, fall ranges (mean = 1.12 ± 0.52 ha) were smaller than summer ranges (mean = 3.23 ± 0.88 ha; $N = 13$; $t_{12} = 2.2$, $P = 0.054$). Overall, mean fall home range size was 1.10 ± 0.37 ha ($N = 18$). We detected no yearly (2005 = 0.25 ± 0.13 ha, $N = 3$; 2006 = 1.56 ± 0.82 ha, $N = 8$; 2007 = 0.93 ± 0.18 ha; $N = 7$; $F_{2,17} = 0.7$, $P = 0.51$) or age-related (ASY = 1.18 ± 0.56 ha, $N = 12$; immatures = 0.92 ± 0.20 ha, $N = 6$; $F_{1,17} = 0.2$, $P = 0.63$) differences in home range size so we dropped year and age from the model. Fall home range size did not differ between the sexes (males = 0.83 ± 0.18 ha, $N = 10$; females = 1.42 ± 0.83 ha, $N = 8$; $F_{1,15} = 0.9$, $P = 0.36$) or between habitats (upland pine = 1.30 ± 0.51 ha, $N = 13$; bottomland hardwood = 0.57 ± 0.22 ha, $N = 5$; $F_{1,15} = 1.0$, $P = 0.32$).

DISCUSSION

During our study, we observed the full range of migratory responses by Red-headed Woodpeckers, with all radio-tagged birds migrating from breeding ranges in 2005, none migrating in 2006, and partial migration (54%) in 2007. In addition, the presence or absence of Red-headed Woodpeckers on our study plots during the winters of 2002–2005 (J. C. Kilgo and M. A. Vukovich, unpubl. data) may provide insight into whether the woodpeckers migrated during previous years (2001–2004). These data suggest complete migration may have occurred in 2002 because no Red-headed Woodpeckers were detected during eight visits to our 16 9.3 ha plots during winter 2003, though they were abundant during the breeding season. No more than partial migration may have occurred in 2001, 2003, and 2004 because Red-headed Woodpeckers were present (at least 20 individuals detected) during each winter following those years (2002, 2004, and 2005). These data cannot be viewed as conclusive evidence of migration because movement into and out of plots between summer and winter almost certainly occurred. However, we believe that the data are at least suggestive of broad patterns. If so, then during the 7-yr period from 2001 to 2007, complete migration may have occurred in two years, at least partial migration in four years, and no migration in one year. Similarly, Smith (1986) reported an erratic 2- to 4-yr cycle in Red-headed Woodpecker migration using range-wide Christmas Bird Count data to infer migratory patterns from areas of winter concentrations.

All nine Red-headed Woodpeckers we relocated moved south or southwest from breeding areas to their fall-winter territories. Smith et al. (2000) suggested that some southern populations may migrate north during fall, citing observations of birds flying north during fall in Florida and Alabama and a winter recovery in Tennessee of a bird banded during summer in Florida. Factors determining migration direction of birds in our study are unclear. Some individuals from our Aiken study site apparently used the Upper Three Runs creek floodplain, either stopping en route or following the floodplain to the larger Savannah River floodplain. Red-headed Woodpeckers have been observed following water courses during migration and stopping when they encountered good mast crops (Graber and Graber 1977, Smith 1986, Robbins and Easterla 1992). Conversely, one of our radio-tagged birds crossed watersheds during migration, but still traveled southwest to the Savannah River floodplain. Whatever the determining factor, our findings suggest that when Red-headed Woodpeckers in the SRS migrate during fall, many do so in a southerly direction.

Although we found that most (20 of 28, 71%) radio-tagged Red-headed Woodpeckers that migrated apparently left the SRS area, eight birds moved <30 km to winter in nearby oak-dominated forests. Thus, although Smith et al. (2000) suggested that no population of Red-headed Woodpeckers was truly resident to an area, some individuals in a population may be resident to local areas (i.e., encompassing a radius of <30 km). After leaving breeding territories, such individuals move only short distances and then return to the same breeding areas the following spring; other birds in the same population migrated greater distances than we were able to quantify. More long-term study of known marked populations is needed to ascertain the proportions of local populations that are resident.

Red-headed Woodpeckers in our study varied in the persistence of their pair bonds during and after migration, with one pair maintaining their bond throughout the year and others severing bonds prior to or during fall migration. Hall (1983) suggested that small groups of migrating Red-headed Woodpeckers might be family groups, but Moskovits (1978) reported that family groups break up during fall as individuals seek areas with hard mast. In 2005, we relocated a marked pair of woodpeckers together in the same tree in the Savannah River floodplain after they had migrated, suggesting that they may have migrated together. These two birds also returned to their same nest snag the following summer. Similarly, Ingold (1991, pers. comm.) reported two banded Red-headed Woodpecker pairs returning after migrating to nest in the same snag in consecutive years. However, we marked three pairs during 2005 and 2006 and only one female remained in the area the following year. In 2007, we tracked both members of two pairs that apparently separated, with one bird migrating (once the male and once the female) and the other remaining on its breeding territory. Although these five pair bonds may have persisted in subsequent years (if any of the first three pairs moved from our study area, but remained together and if the migrating member of the second two pairs returned in 2008 after our study was completed), these observations suggest that Red-headed Woodpecker pair bonds are often severed, at least temporarily.

Fall home ranges of Red-headed Woodpeckers in our study were smaller than summer home ranges. Although previous studies of home range sizes of wintering Red-headed Woodpeckers (Kilham 1958, MacRoberts 1975, Moskovits 1978, Williams and Batzli 1979, Doherty et al. 1996) did not involve the use of radio telemetry, the territory sizes calculated were similar to those in our study (0.04–1.2 ha). In Florida, Venables and Collopy (1989) reported that summer territories were larger (3.1–8.5 ha) than nearby winter territories (0.5–0.6 ha). Woodpeckers that migrated to bottomland sites in our study frequently remained in the same small cluster of trees for the duration of our monitoring period.

The variability in migration rates and distances that we observed among years and among individuals within years, together with the known erratic nature of migration by Red-headed Woodpeckers (Smith 1986, Smith et al. 2000), is consistent with a facultative migration strategy. Newton (2011) described facultative migration as optional, occurring in response to food and weather conditions at the time, with distance traveled variable between individuals and years at the population level. Red-headed Woodpeckers are known to be dependent on oak mast during fall and winter, and acorn crops may exhibit extreme annual variability (Sork et al. 1993). However, temporal and spatial variation in hard mast crops and weather alone may not explain the within-population variability in migratory patterns we observed (i.e., some migrating and some not, and migrating birds moving variable distances) because all individuals in the population were exposed to the same general food and weather conditions. The extent to which social factors such as population density, dominance status, and nesting success might interact with food and weather to influence migration patterns remain unclear. For example, migratory movements of facultative migrants like Great Spotted Woodpeckers (*Dendrocops major*) are partially dependent on population density as well as cone crops (Lindén et al. 2011). Additional information is needed on how mast crops and other factors determine Red-headed Woodpecker migration patterns.

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