BioOne COMPLETE

Diet of Nestling Red-Headed Woodpeckers in South Carolina

Authors: Mark Vukovich, and John C. Kilgo

Source: Southeastern Naturalist, 18(2) : 173-182

Published By: Eagle Hill Institute

URL: https://doi.org/10.1656/058.018.0211

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)

Diet of Nestling Red-headed Woodpeckers in South Carolina

Mark Vukovich[1,*] and John C. Kilgo[1]

Abstract - *Melanerpes erythrocephalus* (Red-headed Woodpecker) has experienced sharp declines in portions of its range. Knowledge of how birds use their nesting habitats, particularly what foods they exploit, may be important in determining causes of population declines, but no modern quantitative study exists on diets of nestling Red-headed Woodpeckers. Our objectives were to identify diets of nestling Red-headed Woodpeckers and quantify variability in food types over time and between roles of males and females in provisioning their young. We conducted observations of nests on the Savannah River Site, SC, from June to September, 2006–2007. We recorded 791 food items fed to nestlings, representing 7 taxa of plants and 18 taxa of animals (16 invertebrate, 2 vertebrate). We assigned food items as either animal matter or soft mast and compared proportions using a binomial mixed model approach. Of the 12 models we tested, 3 received 67% of the cumulative AIC model weight and all included either year or month, indicating annual and monthly variation in foods fed to nestlings. Animal matter composed the majority of Red-headed Woodpecker nestling foods (71.5%), but notably, soft mast was an important component (28.5%). We suggest that future research on Red-headed Woodpeckers consider how the availability of soft mast may or may not limit productivity of this species.

Introduction

Melanerpes erythrocephalus L. (Red-headed Woodpecker) has undergone sharp declines during the past 5 decades across much of its northern and western range (Sauer et al. 2017) and is currently listed as near threatened by the International Union for Conservation of Nature's (IUCN) red list of threatened species (BirdLife International 2017). Reasons for these continuing declines seem to be related to habitat loss (Frei et al. 2015a), lower fecundity along the northern edge of the range (Frei et al. 2015b), and predation from increasing accipiter populations (Koenig et al. 2017). The general nesting habitat associations of Red-headed Woodpeckers are well documented and include declining trees, open understories, low basal-area of trees, and an abundance of dead limbs (Berl et al. 2014, 2015; Kilgo and Vukovich 2014; King et al. 2007). Given the potential role of habitat factors in the decline, understanding how Red-headed Woodpeckers use their nesting habitats, including which food sources they exploit, can be important in determining causes of declines. Knowledge of diets of nestling Red-headed Woodpeckers may reveal relationships to specific habitat characteristics that could be targeted in conservation and management efforts.

Across their range, Red-headed Woodpeckers occupy diverse habitats, resulting in a variable diet (Frei et al. 2015a). However, most information on the diets of Red-headed Woodpeckers comes from a stomach analysis study (ages of birds not

[1]USDA Forest Service, Southern Research Station, PO Box 700, New Ellenton, SC 29809.
[*]Corresponding author - mvukovich@fs.fed.us.

Manuscript Editor: Karl E. Miller

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)

specified) conducted over a century ago (Beal 1911), and nestling diets are known only from a few scattered anecdotal reports (Frei et al. 2015a, but see Bailey 1920 and Venables and Collopy 1989). In addition, parental roles in feeding young are poorly understood; limited data from 2 nests suggested females take a more prominent role (Jackson 1976). No modern study has reported foods of nestling Red-headed Woodpeckers or assessed parental roles during the nesting season. Our objective was to identify diets of nestling Red-headed Woodpeckers and to quantify variability in food types within and between years and parents.

Methods

We conducted the study during 2006–2007 on the Savannah River Site (SRS), a 78,000-ha National Environmental Research Park located in Aiken and Barnwell counties, SC, and situated in the Upper Coastal Plain. As a part of a concurrent long-term study on coarse woody debris, our 16 study plots (9.3 ha each) were in upland *Pinus* spp. (pine) forest composed mostly of 40–50-y-old *P. taeda* L. (Loblolly Pine), with scattered 40–100-y-old *Quercus* spp. (oaks), *Carya* spp. (hickories), and *Prunus serotina* L. (Black Cherry). *Andropogon virginicus* L. (Broomsedge), *Liquidambar styraciflua* L. (Sweet Gum), *Sassafras albidum* Nuttall (Sassafras), *Rubus* spp. (blackberry), *Vitis labrusca* L. (Fox Grape), *Vitis rotundifolia* Michaux (Muscadine), and *Vaccinium* spp. (blueberry) typically composed the understories. Prescribed fire was conducted on a 3- to 5-y rotation, and the most recent dormant season burn on our study sites was in 2003.

We captured Red-headed Woodpeckers from May to August 2006–2007 using ground-level and elevated (10–20 m high) mist nets (3 m x 12 m, 3 m x 20 m, and 9 m x 30 m; 38-mm mesh). At cavities, we used a telescoping pole (12 m) with a net attached. We weighed and aged (Pyle 1997) captured birds and banded them with a USGS BRD aluminum band and color bands to facilitate individual identification. Red-headed Woodpeckers cannot be sexed in the hand (Pyle 1997), so we collected breast feathers for DNA-sexing, which was conducted by Avian Biotech International (Tallahassee, FL). See Vukovich and Kilgo (2009) and Kilgo and Vukovich (2012) for additional details on our methodology for capture, banding, sexing, and transmitter attachment. Radio transmitters did not affect the behavior of Red-headed Woodpeckers (Vukovich and Kilgo 2009). We conducted capture and banding under USGS Bird Banding Permit No. 22829 and followed taxon-specific guidelines for the use of wild vertebrates in research (Fair et al. 2010) to ensure animals were treated ethically and humanely.

Our nest observations began 5 June and continued until 5 September because Red-headed Woodpeckers are double-brooded on our study sites. We identified nest locations during surveys and concurrent work (Kilgo and Vukovich 2012, 2014; Vukovich and Kilgo 2009). We attempted to observe each nest during a single 1-h period per month. However, we sometimes obtained multiple observations per nest for a given month, and in such cases, we pooled observation time for the month at that nest. We employed this protocol when observations were interrupted (e.g., by inclement weather) and later resumed or when few other nests were available for

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)

observation. Observation times varied throughout the day from 07:30 to 19:45. We made most of our observations at nests with nestlings ≥2 weeks old due to the relative ease with which prey items can be identified when adults do not actually enter the cavities, as they do when nestlings are young. We acknowledge an inherent bias toward foods delivered to older nestlings. In addition, identification of foods may have been biased toward larger items, which are more visible.

Three observers conducted direct observations of nests using an 88-mm Kowa spotting scope with a 20–60x eyepiece from a distance of 10–20 m, typically from a blind to minimize disturbance. During 2006, M. Vukovich was the sole observer, whereas during 2007, he was assisted by 2 additional observers, whom we trained with a field and classroom demonstration in identifying the common soft mast species (Miller and Miller 2005) and insect orders (Coloeptera, Orthoptera, Lepidoptera, Araneae, Hymenoptera, and Diptera) on our study plots. When a bird arrived at the cavity with food, we identified the parent carrying food (from color band combinations) and recorded the time and identity of the food item to the lowest taxon possible. We only observed nests that had at least 1 marked and sexed adult. Red-headed Woodpeckers are socially monogamous with biparental care (Frei et al. 2015a), so we assumed that unmarked mates were the opposite sex of the marked mate at the nest. Both members of some mated pairs were marked each year (n = 3 in 2006, n = 5 in 2007).

We assigned food items as either animal matter (e.g., larvae or adult invertebrate or vertebrate) or soft mast. We did not include in our analysis unknown food items or grit brought to nestlings. We used a binomial mixed model approach in R (R Core Team 2017) using the package lme4 (Bates et al. 2013) to assess effects on our response variable, proportion of animal matter fed to nestlings, calculated for each observational unit (bird within nest). Proportion of plant matter was simply 1 – (proportion of animal matter); thus, this approach addressed both food types. We compared 11 models that included various combinations of year (2006 and 2007), month (June, July, August), and sex of the parent, plus a null model. In each model except the null, we included the random effects of individual birds and nests, which accounted for repeated observations at nests and of individuals. We included year and month to account for yearly and within-breeding season variation in foods. We used differences in Akaike's information criterion adjusted for small samples (ΔAIC_c) and Akaike weights (w_i) to evaluate the strength of evidence among competing models (Burnham and Anderson 2002).

Results

We recorded 95.3 h of observations at 31 Red-headed Woodpecker nests with an overall average of 3.1 h of observation per nest. In 2006, we conducted 18 observations at 15 nests (8 in July, 7 in August, 1 in September) for a total of 26.8 h. We pooled the 1 early September nest with data from August in our analysis. We recorded 26 individual woodpeckers delivering food, 16 of which were marked (n = 6 females, n = 10 males) and 10 of which were unmarked mates (n = 6 females, n = 4 males). In 2007, we conducted 50 observations at 16 nests (12 in June, 13 in July, 25 in August)

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)

for a total of 68.5 h and recorded 29 individual woodpeckers delivering food, 19 of which were marked (n = 7 females, n = 12 males) and 10 of which were unmarked mates (n = 7 females, n = 3 males). We resighted 3 marked birds from 2006 feeding nestlings again in 2007 (n = 2 males, n = 1 female). The 3 resighted birds nested in different snags and had different mates in 2007 than 2006. One nest snag used in 2006 was reused in 2007 but the nest was located in a new cavity.

We recorded 791 food items fed to nestlings (Table 1), representing 7 taxa of plants and 18 taxa of animals (16 invertebrate, 2 vertebrate). Overall parental care

Table 1. Numbers of identified (to lowest taxon possible) and unidentified or unknown foods fed to nestling Red-headed Woodpeckers from June to September 2006 (15 nests) and 2007 (16 nests), Aiken and Barnwell counties, SC.

Taxon	2006	2007
Soft mast		
Prunus serotina L. (Black Cherry)	31	24
Rubus spp.	3	15
Vitis rotundifolia Michaux (Muscadine)	3	
Smilax laurifolia L. (Laurel Greenbrier)		1
Vaccinum spp.	3	15
Vitis spp. (grapes)	-	20
Crataegus spp. (hawthorns)	-	1
Rhus spp.	-	4
Unknown fruits	33	20
Unknown seeds	-	8
Total soft mast	73 (36.1%)	108 (18.3%)
Animal		
Anolis carolinensis Voigt (Green Anole)	-	2
Sceloporus undulatus Bosc and Daudin (Northern Fence Lizard)	-	1
Annelida spp.	1	1
Gryllus spp. (field crickets)	-	61
Dissosteira carolina L. (Carolina Locust)	-	1
Other Orthoptera spp.	9	18
Argiope aurantia Lucas (Golden Garden Spider)	-	4
Araneus spp. (orb-weaving spiders)	-	8
Other Araneidae spp. (spiders)	2	21
Pholcidae spp. (daddy longlegs)	1	2
Blattidae spp. (cockroaches)	9	12
Tettigoniidae sp. (katydid)	-	1
Other Hemiptera sp. (true bug)	-	1
Cicadidae spp.	-	8
Coleoptera spp. (beetles)	4	33
Diptera spp. (true flies)	6	5
Hymenoptera spp. (sawflies, ants, bees, and wasps)	3	16
Lepidoptera spp. (butterfiles and moths)	5	8
Odonata (dragonflies)	-	3
Chilopoda (centipede)	1	-
Unknown winged arthropods	1	40
Unknown arthropods	43	124
Total animal	85 (42.1%)	370 (62.8%)
Total unknown food items	44 (21.8%)	111 (18.8%)

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)

was variable between years, with males delivering 60% of items (122 of 202) and females delivering 40% (80 of 202) in 2006, whereas females delivered 55% of items (326 of 589) and males delivered 45% (263 of 589) in 2007. Of the 791 food items, 155 (19.6%) could not be identified. The proportions of prey items we could not identify were similar between years (44 of 202 in 2006 [21.8%]; 111 of 589 in 2007 [18.8%]). We were able to identify 636 food items as either soft mast (181 of 636 [28.5%]) or animal matter (455 of 636 [71.5%]). Adults fed more animal matter than soft mast to nestlings in both years (2006: 85 of 158 items [54%]; 2007: 370 of 479 [77%]). Nestlings were fed twice as much soft mast in 2006 (n = 73 of 202; 36.1%) compared to 2007 (108 of 589; 18.3%;).

Three models had ΔAIC_c values <2.0 and received 67% of the cumulative AIC model weight (Table 2). All 3 top models included either year or month, indicating annual and monthly variation in foods fed to nestlings (Table 2, Fig. 1). Support for models that included the sex term were weak (Table 2).

Discussion

We found Red-headed Woodpecker nestling diets were diverse and included a variety of animal and soft mast species. Orthopterans, particularly *Gryllus* spp. (field crickets), were the most frequent component of nestling diets, but we identified 15 other taxa of invertebrates, as well as 2 species of vertebrates. Notably, Red-headed Woodpeckers fed nestlings a high proportion of soft mast (28.5%). Although this figure fell within the range reported for nestlings of other species of Melanerpine woodpeckers (Koenig et al. 2008: 14–42%; Martindale 1983: 24%; Schroeder et al. 2013: 20.5%), it was somewhat higher than that reported

Table 2. Model selection results, ranked by change in Akaike's information criterion (ΔAIC_c) and Akaike weight (w_i), used to evaluate differences in foods fed to nestling Red-headed Woodpeckers from June to September 2006–2007 in Aiken and Barnwell counties, South Carolina.

Model	df	AIC_c	ΔAIC_c	w_i
(Bird[A])+(Nest[B])+Year[C]+Month[D]	6	668.1	0.0	0.33
(Bird)+(Nest)+Year	4	669.2	1.1	0.19
(Bird)+(Nest)+Year*Month	7	669.7	1.6	0.15
(Bird)+(Nest)+Year+Sex[E]	5	670.4	2.3	0.11
(Bird)+(Nest)+Year*Month+Sex	8	671.0	2.9	0.08
(Bird)+(Nest)+Month	5	671.4	3.2	0.07
(Bird)+(Nest)+Sex+Month	6	672.5	4.3	0.04
(Bird)+(Nest)+Year+Sex*Month	9	673.3	5.2	0.02
(Bird)+(Nest)	3	675.1	6.9	0.01
(Bird)+(Nest)+Sex	4	676.0	7.9	0.01
(Bird)+(Nest)+Sex*Month	8	676.4	8.3	0.01
(.)	1	761.7	93.6	>0.001

[A]Individual bird, used to test for random effects.
[B]Individual nest, used to test for random effects.
[C]2006 and 2007, used to determine yearly differences.
[D]Month of the year, used to determine monthly food differences.
[E]Sex of the parent that fed nestling food, used for differences between parents.

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)

for what were most likely adult Red-headed Woodpeckers during summer (mean 20.7% for August and September; Beal 1911). Presumably Red-headed Woodpecker nestling development is not slowed by such a high content of fruit in their diet, and they possess digestive tracts adapted to absorb amino acids (Levey and Martinez del Rio 2001, Weathers et al. 1990). Given its apparent importance, the role of soft mast in Red-headed Woodpecker nesting ecology, particularly single-

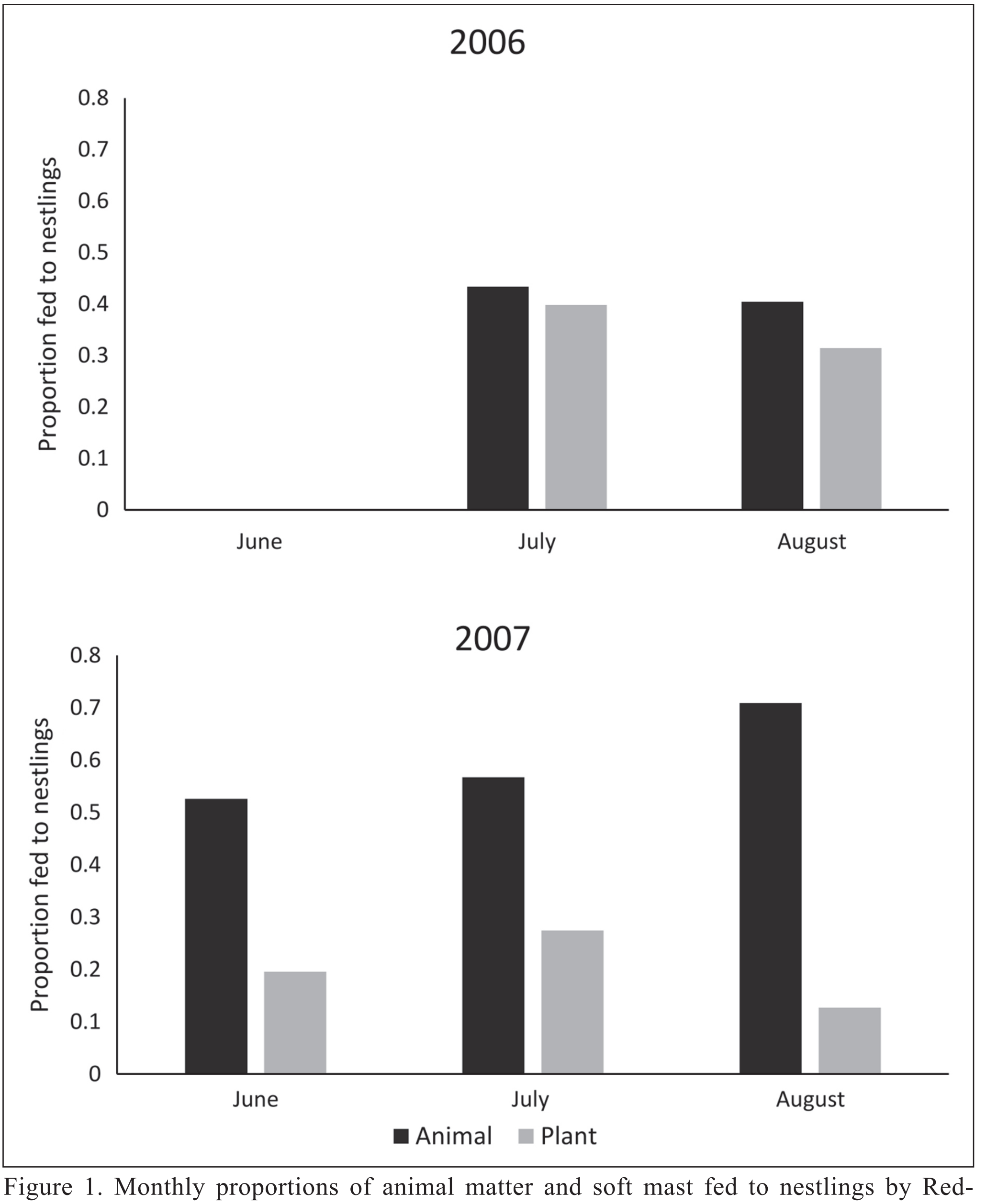

Figure 1. Monthly proportions of animal matter and soft mast fed to nestlings by Red-headed Woodpeckers in 2006 and 2007, Aiken and Barnwell counties, SC. Unknown food items are not shown in graph so proportions do not sum to 1 within months.

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)

brooded populations in northern latitudes with shorter growing seasons, warrants further investigation.

Our top 6 models included various combinations of annual and monthly effects, indicating temporal variation in types of food fed to nestlings. The monthly fluctuations we observed in food resources fed to nestlings were likely a natural result of plant phenology. Other studies on woodpeckers have reported within-breeding season variation in foods fed to nestlings (Pechacek and Kristin 2004, Rossmanith et al. 2007), but little evidence exists in the literature to indicate that nestling woodpecker diets vary annually. Diets of nestling *Leuconotopicus borealis* Viellot (Red-cockaded Woodpecker) showed little year-to-year variation (Hanula et al. 2000). We suspect the annual variation we observed reflected temporal variation in relative availability of food types, particularly soft mast. For example, the total number of soft mast items observed was comparable between years even though observation time in 2006 was less than half that in 2007, suggesting production and availability of soft mast may have been greater in 2006. Annual variability in soft mast production in mature Loblolly Pine forests on the Savannah River Site can be substantial (Greenberg et al. 2012, McCarty et al. 2002). Factors that may have affected availability of soft mast include late spring freezes, which would reduce production of soft mast, and time since prescribed fire, after which there is a slow decline in production of soft mast in the annual understory (Lashley et al. 2015). Our study sites were burned during the winter of 2003, 3–4 years prior to our study, which was within the time-frame of a slow decline in soft mast observed by Lashley et al. (2015). However, the annual difference we observed in soft mast fed to nestlings seemed to suggest more substantial changes in availability of soft mast, consistent with large annual fluctuations in production that occur irrespective of fire (Greenberg et al. 2012). Similarly, we detected a sharp increase of animal matter fed to nestlings in August 2007, particularly Orthopterans (*Gryllus* spp.), relative to August 2006. Orthopteran populations are known to fluctuate seasonally (Veazey et al. 1976) and can compose up to 21% of adult Red-headed Woodpecker diets in August (Beal 1911). As with soft mast, time since fire may affect arthropod assemblages, with Orthopteran biomass increasing with time since fire (Chitwood et al. 2017). Whether differences we observed between years were related to time since prescribed fire remains unclear, but such potential fire effects warrant additional study.

We detected weak evidence for a difference between the sexes in what was fed to nestlings, with males generally feeding nestlings more soft mast in both years and females consistently feeding nestlings more animal matter. It remains unclear whether these apparent differences are important in the development of nestlings, with the food types from each parent combining to form a more nutritionally complete diet. Nevertheless, the weak support of the models with sex indicates parents overlapped in the types of foods they fed nestlings. Although Jackson (1976) found that female Red-headed Woodpeckers conducted 75% of the feedings after 12 d, our observations of overall parental effort between years indicate no clear and consistent dominant role in feeding by either sex, as both parents were capable of

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)

adequately provisioning nestlings. However, we observed a single parent (a female) that continued to feed an older nestling that successfully fledged at least 7 d after the other parent was depredated (Kilgo and Vukovich 2012; M. Vukovich and J.C. Kilgo, unpubl. data).

We suggest that future research on Red-headed Woodpeckers consider how availability of food resources may or may not limit productivity of this species. In particular, the importance of soft-mast–producing plants is often overlooked by ecologists (McCarty et al. 2002, Perry et al. 1999), and Red-headed Woodpeckers typically occupy disturbed areas with fruiting plants, shrubs, and trees during the breeding season (Frei et al. 2015a). The phenology of Red-headed Woodpecker's nesting cycle (April–September), which is later than most woodpeckers (Frei et al. 2015a) may even be linked to the availability of soft mast. The foods we identified indicate that Red-headed Woodpeckers often forage on or near the ground and within the understory during the nesting season, so fruit counts and arthropod sampling could easily be conducted at ground level (Cooper and Whitmore 1990, Lashley et al. 2014). Additionally, such sampling need not be extensive, since core areas of home ranges that encircle nest snags of Red-headed Woodpeckers are relatively small (Kilgo and Vukovich 2014). More detailed habitat studies tied to nestling diets and nest success could improve criteria for determining suitable habitat thresholds and possibly increase our understanding of regional declines in Red-headed Woodpeckers.

Acknowledgments

We thank K. Legleu and K. Nayda, who served as observers; K. Frier for assistance in the field; J. Blake and K. Wright for logistical support; M. Conroy for statistical advice; and L. Bulluck, J. O'Keefe, and 2 anonymous reviewers for reviewing the manuscript. Funding was provided by the US Department of Energy–Savannah River Operations Office through the USDA Forest Service Savannah River under Interagency Agreement No. DE-AI09-00SR22188 and by the USDA Forest Service Southern Research Station.

Literature Cited

Bailey, F.M. 1920. The Red-headed Woodpecker. Pp. 169–172, *In* T.G. Pearson (Ed.). Portraits and Habitats of Our Birds. National Association Audubon Society, New York, NY.

Bates, D., B. Bolkder, B. Maechler, and S. Walker. 2013. Lme4: Linear mixed-effect using Eigen and S4. R package, version 1.1-15. Available online at http:/CRAN.R-project.org/package=lme4. Accessed 6 February 2018.

Beal, F.E.L. 1911. Food of the woodpeckers of the United States. US Department of Agriculture Biological Survey Bulletin 37, Washington, DC.

Berl, J.L., J.W. Edwards, J.S. Bolsinger, and T.E. Katzner. 2014. Survival of Red-headed Woodpeckers' (*Melanerpes erythrocephalus*) nests in northern New York. The Wilson Journal of Ornithology 126:700–707.

Berl, J.L., J.W. Edwards, and J.S. Bolsinger. 2015. Scale-dependent and multi-metric nest habitat thresholds for Red-headed Woodpeckers at the northern periphery of their range. Condor 117:203–216.

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)

BirdLife International 2017. *Melanerpes erthrocephalus* (amended version of 2016 assessement). The IUCN red list of threatened species 2017: e.T22680810A118537463. Available online at http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T22680810A118537463.en. Accessed 5 November 2018.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd Edition. Springer-Verlag, New York, NY. 488 pp.

Chitwood, M.C., M.A. Lashley, B.L. Sherrill, C. Sorenson, C.S. DePerno, and C.E. Moorman. 2017. Macroarthropod response to time-since-fire in the Longleaf Pine ecosystem. Forest Ecology and Management 391:390–395.

Cooper, R.J., and R.C. Whitmore. 1990. Arthropod sampling methods in ornithology. Studies in Avian Biology 13:29–37.

Fair, J., E. Paul, and J. Jones (Eds.). 2010. Guidelines on the use of wild birds in research. Ornithological Council, Washington, DC.

Frei, B., K.G. Smith, J.H. Withgott, and P.G. Rodewald. 2015a. Red-headed Woodpecker (*Melanerpes erythrocephalus*). *In* P.G. Rodewald (Ed.). The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY. Available online at https://doi.org/10.2173/bna.rehwoo.02.1. Accessed 8 March 2018.

Frei, B., J.W. Fyles, J.L. Berl, J.W. Edwards, and J.J. Nocera. 2015b. Low fecundity of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) at the northern edge of the range. Wilson Journal of Ornithology 127:639–645.

Greenberg, C.H., D.J. Levey, C. Kwit, J.P. McCarty, S.F. Pearson, S. Sargent, and J. Kilgo. 2012. Long-term patterns of fruit production in five forest types of the South Carolina Upper Coastal Plain. Journal of Wildlife Management 76:1036–1046.

Hanula, J.L., D. Lipscomb, K.E. Franzreb, and S.C. Loeb. 2000. Diet of nestling Red-cockaded Woodpeckers at three locations. Journal of Field Ornithology 71:126–134.

Jackson, J.A. 1976. A comparison of some aspects of the breeding ecology of Red-headed and Red-bellied woodpeckers in Kansas. Condor 78:67–76.

Kilgo, J.C., and M. Vukovich. 2012. Factors affecting breeding season survival of Red-headed Woodpeckers in South Carolina. Journal of Wildlife Management 76:328–335.

Kilgo, J.C., and M.A. Vukovich. 2014. Can snag creation benefit a primary cavity nester: Response to an experimental pulse in snag abundance. Biological Conservation 171:21–28.

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.

Koenig, W.D., D.J. Schaefer, S. Mambelli, and T.E. Dawson. 2008. Acorns, insects, and the diets of adult versus nestling Acorn Woodpeckers. Journal of Field Ornithology 79:280–285.

Koenig, W.D., E.L. Walters, and P.G. Rodewald. 2017. Testing alternative hypotheses for the cause of population declines. Condor 119:143–154.

Lashley, M.A., J.R. Thompson, M.C. Chitwood, C.S. DePerno, and C.E. Moorman. 2014. Evaluation of methods to estimate understory fruit biomass. PloS One 9:e96898. DOI:10.1371/journal.pone.0096898.

Lashley, M.A., M.C. Chitwood, C.A. Harper, C.S. DePerno, and C.E. Moorman. 2015. Variability in fire prescriptions to promote wildlife foods in the Longleaf Pine ecosystem. Fire Ecology 11:62–79. DOI:10.4996/fireecology.1103062.

Levey, D.J., and C. Martinez del Rio. 2001. It takes guts (and more) to eat fruit: Lessons from avian nutritional ecology. Auk 118:819–831.

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)

Martindale, S. 1983. Foraging patterns of nesting Gila Woodpeckers. Ecology 64:888–898.

McCarty, J.P., D.J. Levey, C.H. Greenberg, and S. Sargent. 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. Forest Ecology and Management 164:277–291.

Miller J.H., and K.V. Miller. 2005. Forest Plants of the Southeast and their Wildlife Uses. University of Georgia Press, Athens, GA. 464 pp.

Pechacek, P., and A. Kristin. 2004 Comparative diets of adult and young Three-toed Woodpeckers in a European alpine forest community. Journal of Wildlife Management 68:683–693.

Perry, R.W., R.E. Thill, D.G. Peitz, and P.A. Tappe. 1999. Effects of different silvicultural systems on initial soft mast production. Wildlife Society Bulletin 27:915–923.

Pyle, P. 1997. Identification guide to North American Birds, Part 1. Slant Creek Press, Bolinas, CA. 732 pp.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://www.R-project.org/. Accessed 29 November 2017.

Rossmanith, E., K. Höntsch, N. Blaum, and F. Jeltsch. 2007. Reproductive success and nestling diet in the Lesser Spotted Woodpecker (*Picoides minor*): The early bird gets the caterpillar. Journal of Ornithology 148:323–332.

Sauer, J.R., D.K. Niven, J.E. Hines, D.J. Ziolkowski Jr., K.L. Pardieck, J.E. Fallon, and W.A. Link. 2017. The North American Breeding Bird Survey, Results and Analysis 1966–2015. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD. Available online at https://www.mbr–pwrc.usgs.gov/bbs/. Accessed 6 November 2018.

Schroeder, E.L., C.W. Boal, and S.N. Glasscock. 2013. Nestling diets and provisioning rates of sympatric Golden-fronted and Ladder-backed Woodpeckers. The Wilson Journal of Ornithology 125:188–192.

Veazey, J.N., C.A. Kay, T.J. Walker, and W.H. Whitcomb. 1976. Seasonal abundance, sex ratio, and macroptery of field crickets in northern Florida. Annals of the Entomology Society of America. 69:374–380.

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, FL.

Vukovich, M., and J.C. Kilgo. 2009. Effects of radio transmitters on the behavior of Red-headed Woodpeckers. Journal of Field Ornithology 80:308–313.

Weathers, W.W., W.D. Koenig, and M.T. Stanback. 1990. Breeding energetics and thermal ecology of the Acorn Woodpecker in central coastal California. Condor 92:341–359.

Downloaded From: https://bioone.org/journals/Southeastern-Naturalist on 06 Jun 2019
Terms of Use: https://bioone.org/terms-of-use Access provided by United States Department of Agriculture National Agricultural Library (NAL)