Factors influencing parental care and home range size of a monomorphic species, the Red-headed Woodpecker (Melanerpes erythrocephalus)

L. Abigail Walter
Virginia Commonwealth University

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Factors influencing parental care and home range size in a monomorphic species, the Red-headed Woodpecker (*Melanerpes erythrocephalus*)

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

by

L. ABIGAIL WALTER
B.S., University of Delaware, 2014

Advised by:

LESLEY P. BULLUCK, Ph.D.
Center for Environmental Studies
Virginia Commonwealth University

CATHERINE VIVERETTE, Ph.D.
Center for Environmental Studies
Virginia Commonwealth University

Virginia Commonwealth University
Richmond, Virginia
August, 2019
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ABSTRACT

FACTORS INFLUENCING PARENTAL CARE AND HOME RANGE SIZE IN A MONOMORPHIC SPECIES, THE RED-HEADED WOODPECKER (MELANERPES ERYTHROCEPHALUS)

By L. Abigail Walter, M.S.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

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Major advisors:
Lesley P. Bulluck, Ph.D., Center for Environmental Studies
Catherine Viverette, Ph.D., Center for Environmental Studies

Parental care in animals can be costly and is shared between both parents in many bird species. Not surprisingly, most studies of how parental care is shared between the sexes are in sexually dimorphic species, and much less is known about sexually monomorphic species where sex cannot be determined in the field. This has prevented a full understanding of parental care behaviors – which are intrinsically linked to fitness – in species such as the Red-headed Woodpecker (Melanerpes erythrocephalus) that is experiencing population declines throughout much of its range. In this study we assessed whether Red-headed Woodpecker brooding time, nestling provisioning rates, and nest cleaning rates vary as a function of parent sex, habitat type (savanna and closed canopy forest), brood size, nestling age, temperature and/or date. We recorded and analyzed 128 hours of high-quality video from 21 broods at Fort A.P. Hill, Virginia where this species is relatively abundant. We captured and color-banded Red-headed Woodpeckers, taking breast feather samples for genetic sexing, and determined brood size and chick age of nests using an extendable pole camera. Using generalized linear mixed models, we found the best predictor of nestling provisioning was an interaction between chick age and date; older chicks were fed more frequently in early summer (before 7 July) compared to late summer. The seasonal reduction in provisioning could be related to a reduction in resource availability, but whether or not provisioning in later nests affects nestling survival warrants further study. We found chick age and parent sex to be the
best predictors in brooding models, with females brooding more when chicks are less than 10 days old and males being the only parent to enter the cavity after 10 days. Additionally, males almost exclusively remove fecal sacs from nests, highlighting an observational method to determine sex of breeding adults in the field. Such division of reproductive roles is similar to what is known for dimorphic woodpecker species and likely indicates energetic constraints due to the need for high parental investment from both sexes.

Parental care is inextricably linked with habitat quality and home range size. Parents will travel to obtain the resources necessary to provision their young, and larger home ranges during the demanding nestling provisioning stage may indicate increased effort resulting from fewer available resources near the nest. We estimated home range sizes of 25 breeding adult Red-headed Woodpeckers using PinPoint GPS tags and 95% kernel density estimates (KDEs) with plug-in smoothing factors. We modeled the effects of habitat, sex, nest stage, date, and distance to nearest neighbor on home range estimates. Red-headed Woodpecker males have larger home ranges than females, and late summer home ranges are smaller than those measured before 7 July. More study is needed to determine if sex or date is a stronger factor on home range, given our naive sampling which resulted in more females sampled in late summer and observations that did not continue to the end of the breeding season (late August). Since we found date to be an influential factor to both provisioning rate and home range size, it is possible that seasonal resource changes are an important, unstudied factor related to nationwide declines of this species.
INTRODUCTION

Producing and caring for offspring is a biological imperative associated with significant energetic costs. While parental care in mammals is primarily carried out by females through gestation and lactation, parental care in birds is often shared by both sexes (Emlen and Oring 1977), but is still associated with significant costs. For example, parental care often conflicts with self-care, can increase the risk of predation (Post and Götmark 2006, Kokko and Jennions 2008), and reduce immune function (Hanssen et al. 2005). Time and effort directed toward parental care also leads to fewer additional mating opportunities creating a sexual conflict between parents (Olson et al. 2007). Despite the costs, investment in parental care should result in increased breeding success which is maximized when care is coordinated between sexes in monogamous pairs (Emlen and Oring 1977, Wendeln and Becker 1999, Ringsby et al. 2009, Riechert and Becker 2017).

Social monogamy with biparental care is found in 90% of bird species, though the degree of parental care can still be unequal between the sexes (Lack 1968, Mock and Fujioka 1990). Sexual monomorphism, when the sexes of a species are nearly physically indistinguishable, is associated with monogamy and a higher degree of male parental care compared to dimorphic species (Verner and Willson 1969, Pierotti and Annett 1993, Ketterson and van Nolan 1994, Møller and Birkhead 1994, Badyaev and Hill 2003). In North American passerine birds, incubation is commonly shared between sexes in monomorphic families, and males aid in nestling provisioning for all species of monomorphic passerines where nestlings are altricial and require more parental care (Verner and Willson 1969). Many species are classified as monomorphic even if small differences between the sexes exist (i.e. gulls, blackbirds, and shorebirds). For "truly monomorphic" species, no observable differences occur; males and females cannot be distinguished in the field, making the study of sex-specific parental care especially challenging.

Genetic sexing of individual birds using blood or feathers has made these studies feasible, though there are still many monomorphic species for which little to no sex-specific parental care data exist.
Spatial and temporal variation in resources may influence parental care, especially during the demanding nestling provisioning stage. Breeding pairs preferentially select the highest quality available habitat on the landscape with the most resources to increase survival of offspring. When populations are dense and competition is high, breeding pairs may be relegated to poorer habitat and subsequently experience lower nest success (Weinberg and Roth 1998). Birds nesting in low-quality habitat must travel farther distances to provision young than those in high-quality habitat, resulting in unequal energetic expense for pairs that attempt to provision at equal rates to their high-quality neighbors (Stauss et al. 2005, Tremblay et al. 2005). Temporal changes in food availability such as peaks in insect emergence and fruit ripening often coincide with increased clutch size and number of young fledged (Powell 1983, Safina et al. 1988, Both and Visser 2005, Davis et al. 2005). In addition to habitat and food resources, provisioning rates also vary with brood size and nestling age (Johnstone and Hinde 2006). By including variation in brood size and nestling age in studies of parental care, thresholds can be identified beyond which parents are less able to successfully care for their young. Such information is especially valuable for declining species that may be limited by the availability of high quality habitat. Studies that simultaneously assess how parental care varies across habitat, date, and by sex are rare, especially for sexually monomorphic species.

Parental care and nest success are inextricably linked with habitat quality and home range size (Vickery et al. 1992). As mentioned above, in poor habitat parents tend to require larger territories to acquire enough food to provision nestlings (Stauss et al. 2005, Tremblay et al. 2005). Home range measurements are therefore important to understanding variation in parental care. Techniques for estimating home range size have evolved through time; early studies relied on manual mapping of territories until the advent of radio telemetry using very high frequency (VHF) tags (Anderson 1982, Kenward 1987). Drawbacks to mapping and VHF tags are that observer presence may influence study animal behavior, and only a small number of points is used to estimate home range due to the effort required to collect them (Hebblewhite and Haydon 2010). Large-bodied species can be tracked using satellite transmitters, but this technology is not lightweight enough to be used on small or medium-sized
species. Recently available miniaturized (< 3 g) global positioning system (GPS) tags allow for space-use research on smaller species and collect a large sample of points per individual while also reducing sampling bias by field observers (Hebblewhite and Haydon 2010). More points provide better home range estimates even if the points are moderately autocorrelated, further highlighting the benefits of GPS tags (Reynolds and Laundre 1990, Swihart and Slade 1997, De Solla 2001). Such technology is currently being used for the first time in avian species previously considered to be too small as a way to understand space use and movement with more accuracy. Space use during the demanding nestling stage is especially valuable to assess, as this is when energetic costs are highest and resources are most limiting.

Woodpeckers are a medium-sized, monogamous guild of birds that rely on resources that vary considerably over space and time. Woodpeckers are known for their high degree of shared parental care; males often incubate and provision young, and sexes are often similar in appearance (Gorman 2014). Woodpeckers are considered keystone facilitator species that not only create nest cavities for secondary cavity nesters, but also strip bark from trees which exposes foraging opportunities for other species (Drever and Martin 2010). Likely as a result of this facilitation, woodpeckers are considered indicators of forest avian diversity (Mikusiński et al. 2001). For these reasons, understanding what factors limit woodpecker species during the most demanding life stages can lead to informed conservation practices that benefit a diversity of other species.

In this study we explore factors that may explain variation in parental care and home range size in the Red-headed Woodpecker, a socially monogamous monomorphic species of conservation concern. A literature review revealed that breeding season territory size has been estimated in 24 woodpecker species, and explicitly for males and females in nine woodpecker species (Table 1). Despite extensive study on dimorphic woodpeckers, there is limited knowledge of how monomorphic woodpeckers divide parental care between sexes or whether sexes differ in space use. This research may identify limiting factors for breeding Red-headed Woodpeckers that could inform conservation efforts for this species that has experienced significant declines in portions of its range. Specifically, we:
(1) assessed whether Red-headed Woodpecker brooding time, nestling provisioning rates, and cleaning rates vary as a function of parent sex, habitat, brood size, nestling age, temperature, and/or date, and

(2) determined if breeding Red-headed Woodpecker home range size estimated with GPS tags varies as a function of sex, habitat, distance to nearest neighbor, nestling stage, and/or date.

Study species

Red-headed Woodpeckers (*Melanerpes erythrocephalus*) are a socially monogamous monomorphic bird species of conservation concern. Although most woodpeckers have plumage similarities between sexes, monomorphism is rare; only two of 239 species of woodpecker (Aves:Piciformes:Picidae) are truly monomorphic (Goodwin 1968, Gorman 2014). The Red-headed Woodpecker is an ideal species for studying whether parental care varies between sexes in a largely dimorphic non-passerine clade. Both sexes of the Red-headed Woodpecker incubate, brood, and provision chicks (Jackson 1976a). A recent study by Vukovich and Kilgo (2019) discussed nestling diet of Red-headed Woodpeckers with rich taxonomic detail of prey items. Provisioning results for this species are conflicting and have used small sample sizes, with reports of significant increases in female provisioning with chick age (n = 2 broods, Jackson 1976a) and no difference between sexes (n = 4 broods, Venables and Collopy 1989). Sex was not a significant factor in modern research on Red-headed Woodpecker provisioning rates (Vukovich and Kilgo 2019), but a comprehensive model using date, brood size, and nestling age is still unprecedented for this species. Provisioning rates have been found to be similar between low- and high-quality habitats in Red-headed Woodpeckers (Hudson 2009), but home range has not been compared by habitat type. Breeding season home ranges have been calculated thus far by either antiquated territory mapping techniques (Williams 1977, Venables and Collopy 1989) or by VHF tags (Vukovich and Kilgo 2013).
Red-headed Woodpeckers use a variety of habitat types across the eastern United States during the breeding season, including oak savanna, pine savanna, closed canopy forest, wetlands with snags, and golf courses (Conner 1976, Lochmiller 1979, Brawn 2006, Hudson 2009, Berl et al. 2015, Dallas 2015, Nickley and Bulluck 2019). Red-headed Woodpeckers prefer sites with abundant snags and open understories, but degree of canopy cover and understory composition may differ (Conner 1976, Vierling and Lentile 2006, Kilgo and Vukovich 2014, Nickley and Bulluck 2019). Variation in forest structure can affect the distribution of resources among these habitat types and may therefore influence home range sizes of breeding pairs. Foraging habits of Red-headed Woodpeckers in the summer are primarily focused on flycatching and fruit gathering (Bent 1939), and the availability of flying insects and fruit likely varies between savanna and closed canopy forests (Greenberg et al. 2012).

Over 90% of the Red-headed Woodpecker historic population was lost in the early 1900s, largely due to anthropogenic induced loss of American beech (*Fagus grandifolia*) forests which have historically provided this species with abundant hard mast (Beal 1911, Whitney 1996). Modern day Red-headed Woodpecker declines are caused by a combination of changes in land management, fire suppression, loss of small farms, dead tree removal, competition with invasive European starlings (*Sturnus vulgaris*) for nest cavities, and predation by *Accipiter* spp. (Ingold 1989, Peterjohn 1989, Kilgo and Vukovich 2012, Kilgo and Vukovich 2014, Frei et al. 2017, Koenig et al. 2017). Populations declined more than 67% range-wide from 1970 to today (Rosenberg et al. 2016), but are increasing in some areas (i.e., 1.2% per year in Virginia, Sauer et al. 2017). Understanding what aspects of Virginia habitat contributes to successful parental care may help us to better manage Red-headed Woodpecker populations elsewhere.

**Study area**

The study took place at Fort A.P. Hill, a 31,000-ha military installation in Caroline County, Virginia, USA. Habitat at the army base is a complex mosaic of oak savanna, pine savanna, wetlands, and closed-canopy forests. Savanna habitats have been maintained for decades through active management practices including prescribed fire and timber harvesting.
Due to limitations of shared use with military personnel, we chose several focal areas (delineated and referred to by the U.S. Army as “training areas” or “recreation areas”) to study Red-headed Woodpeckers. These sites (training areas [hereafter referred to as TAs] 5A, 5B, 18C and Travis Lake recreation area, Figure 1) were chosen based on the locations of known nests found during the 2016 summer field season, and because they had a mix of open and closed canopy forests occupied by Red-headed Woodpeckers during the breeding season (Nickley and Bulluck 2019). Habitats were classified as being savanna or closed canopy based on 2016 National Agriculture Imagery Program (NAIP) aerial imagery (Nickley and Bulluck 2019). Polygons were drawn around areas that were visually determined to be open or closed forest, with a 70% canopy cover threshold to determine habitat type, and vegetation surveys were used to ground-truth the layers (Nickley and Bulluck 2019).

Information on vegetation composition in closed canopy and savanna habitat types can be found in Nickley and Bulluck (2019). There are additional fruiting plants within our TAs of note: wild grapes, including summer grape (Vitis aestivalis) and a southern variety of graybark grape (V. cinerea var. floridana); huckleberries (Gaylussacia frondosa, G. baccata), blueberries (Vaccinium pallidum), blackberries (Rubus spp.), deerberry (Vaccinium stamineum), black cherry (Prunus serotina), devil's walkingstick (Aralia spinosa), winged sumac (Rhus copallinum), sassafras (Sassafras albidum), spicebush (Lindera benzoin), elderberry (Sambucus canadensis), serviceberry (Amelanchier spp.), possumhaw viburnum (Viburnum nudum), flowering dogwood (Cornus florida), Virginia creeper (Parthenocissus quinquefolia), autumn olive (Elaeagnus umbellata), Chinese privet (Ligustrum sinense), hackberry (Celtis occidentalis), black gum (Nyssa sylvatica), American holly (Ilex opaca), poison ivy (Toxicodendron radicans var. radicans) and poison sumac (Toxicodendron vernix). Near wetlands, highbush blueberries are more common (Vaccinium formosum, V. fuscatum, and V. × marianum).
METHODS

Monitoring nests

Collection of data on breeding Red-headed Woodpeckers took place from mid-April through early August in 2017 and 2018. From April–May, we searched for new nest snags and re-visited previously active nest snags found during point count surveys to ascertain if they were still in use (Nickley and Bulluck 2019). After discovering nests in 2017, we observed parental behavior at the nest cavity for a maximum of 30 min using binoculars. Nests were deemed to have eggs when adults traded incubation shifts or when adults entered the cavity for at least 3 min (Jackson 1976b, Nickley and Bulluck 2019). Nests were categorized as containing chicks when parents started bringing food items to the nest (Jackson 1976b). Starting in July 2017 and throughout all of the 2018 season, we used a cavity inspection camera (IBWO) on an extendable 15 m measuring pole (Crain CMR Series) with a wireless monitor. The cavity camera allowed us to collect data on nest stage, chick age, number of eggs, brood size, and nest fate with more certainty than our previous observation methods. Before inserting a camera into a nest cavity, we knocked on the snag to flush potentially incubating woodpeckers. We were unable to check some nests because the cavity entrances were too high (> 15 m) to access. We monitored active nests every 2–7 days, depending on access to TAs. After finding nests empty when chicks were > 25 days old, we conducted fledge checks for a maximum of 30 min to search for fledglings around the nest snag. Nests still active after 8 August were not included in fledge success analyses.

We determined age of chicks using known hatch day when available. When hatch day was not known, we estimated chick age using cavity camera images and known fledge dates, assuming that the nestling period was 26 days (Frei et al. 2017). Images taken from nest cavities were used to determine and describe developmental milestones such as eye opening, pinfeather emergence, feather developments, and additional chick behaviors which have not yet been published at length for this species (Appendix A).
Recording parental behavior observations

We placed video cameras (Canon FS400) on tripods within 10 m of nest snags to record parental behavior at the nest. Cameras were focused on the nest cavity entrance and recorded woodpecker activity between 0715–1515 from May–August in 2017 and 2018. Because we were interested in sex-specific parental care behavior, we only included videos in our analysis if: 1) at least one adult was color banded and genetically sexed, 2) banded individuals could be clearly identified by their color band combination and 3) the nest contained a known number of chicks with known age. We scored adult woodpecker behaviors at the nest using BORIS (Behavioral Observation Research Interactive Software, Friard and Gamba 2016). We associated behaviors with a woodpecker’s color band combination (see banding methods below) or a unique identifier for each unbanded mate of a banded adult, and assumed that no additional birds were providing parental care. Cooperative breeding was not observed in our system, and has only been reported in two nests in a high-density nesting site reliant on telephone poles for cavities in Illinois (Atterberry-Jones and Peer 2010). For analysis, we included the following three parental care behaviors: feeding chicks (delivering a food item to the nest), cleaning nest (removal of fecal material from the nest), and brooding (in-cavity for > 1 min and not followed by a cleaning event). Only brooding had a duration time, while feeding chicks and cleaning nest were point events. We also determined the identity of prey items provisioned to chicks under broad classifications of either fruit, arthropod, or unidentified (item obscured, parent moved too fast, or video quality was poor).

Parental care analyses

We recorded number of cleaning events, number of provisioning visits, and brooding length for each parent in each video. To test for differences between sexes in nest cleaning we ran a Wilcoxon signed rank test. To analyze provisioning counts and brooding durations, we used R package glmmTMB to run generalized linear mixed models (GLMMs, Brooks et al. 2017).

To model provisioning rate, we included chick age (days) and brood size in all models because these factors are known to be important (Wright and Cuthill 1990, Rossmanith et al. 2009). Since
provisioning visits were count data and contained numerous zeros, we compared our simple model with chick age and brood size using a zero-inflated negative binomial distribution to the same model with a Poisson error distribution using AIC; we determined the zero-inflated negative binomial to fit the data best. Ordinal date, habitat (closed canopy and savanna), and sex were included as additional fixed effects of interest. We standardized ordinal date to a z distribution to facilitate model convergence. We checked correlation between chick age and date, and included the following interactions: chick age × parent sex; chick age × date; and chick age × habitat. We expected chick age to be the most important factor driving provisioning rate, and were interested to see if sexes responded to this increased demand differently, or if date or habitat affected a parents’ ability to provide resources to nestlings as they developed. We also included a quadratic effect of chick age because parental care may level off or decline after some peak age where nestling demand is greatest. Lastly, woodpecker ID and brood ID were included in provisioning models as random effects because some woodpeckers had more than one nesting attempt and we recorded parental care at the same nest on different days during the nestling period.

To model brooding duration, we used the same simple base model as provisioning with chick age and brood size being included in all models. We compared how this base model performed using a non-zero-inflated Gaussian error distribution, a zero-inflated distribution, and a truncated binomial hurdle model. A hurdle model accounts for high frequency of true zero observations in the data by first fitting a binomial response (i.e., the nest is brooded or not) and then models the remaining non-zero values separately (Lambert 1992, Martin et al. 2005). The hurdle model fit the data best based on AIC model comparisons. We included the same fixed effects as in the provisioning models except that we replaced ordinal date with maximum daily temperature (T \text{max}) because we expected temperature to better estimate brooding. Maximum daily temperatures were obtained from the National Oceanic and Atmospheric Administration (NOAA) Global Historical Climatology Network - Daily dataset (Menne et al. 2012a, Menne et al. 2012b) from the station in Corbin, VA (38.2022°N, -77.3747°W) located 8.4 km from our focal TAs. We also included the following interactions: chick age × parent sex; chick age × brood size; chick age × T \text{max}. We expected brooding duration to decrease with chick age, brood size, and T \text{max}, and
were interested to see if sexes differed in how they adjusted their brooding time as chicks matured. We included a quadratic effect of chick age because we expected brooding to decrease in a nonlinear fashion as chicks mature.

For both provisioning and brooding analyses, length of video was used as an offset in the models to account for variable recording time among video samples (Foster and Bravington 2013). Models were compared using AIC, top models were chosen based on the lowest ΔAIC value, and models with ΔAIC < 2.0 were considered equally supported. However, these equally supported models were typically nested iterations of the top model so we identified which parameters were most important in these nested models by assessing β estimates and p-values. Predictions for brooding time and provisioning rate were generated from the top performing models and then plotted using R package stats::predict. Predicted provisioning counts were adjusted using each sample’s video length and brood size to calculate provisioning visits per chick per hour. Brooding durations were adjusted using only video length to determine brooding minutes per hour.

We modeled amount of fruit and arthropod prey brought to nestlings using GLMMs. We tested the best distribution for each prey type before running models, determining the best distribution and the top model using ΔAIC scores. We included brood size and chick age in all models before including fixed effects: habitat, date, parent sex, and quadratic chick age. The same interactions from provisioning models were incorporated into fruit and arthropod models. Video length was used as an offset in these prey models. We did not use the random effect for woodpecker ID in brooding models, fruit models, or arthropod models because it limited the ability of these models to converge.

Bandung and GPS tagging

We captured and banded woodpeckers from January 2016–August 2018, using either canopy mist nets or a pole net placed over a cavity entrance. Mist nets were elevated with a rope pulley system on living trees adjacent to nest snags in order to target individuals as they approached or departed nest cavities. Captured woodpeckers were color-banded with a combination of three colors and one USFWS
aluminum band ( Permit No. 23486; U.S. Geological Survey Bird Banding Laboratory, Laurel, MD). We recorded body mass, standard body measurements, and attempted to age birds according to criteria in Pyle and Howell (1995). We also collected three crown feathers for feather reflectance analysis (to be investigated at a later date) and three breast feathers for genetic sexing by Animal Genetics, Inc. (Tallahassee, FL). Sex of banded woodpeckers was blinded from researchers until all field data were collected to eliminate any potential for bias.

To estimate home ranges, we attached Lotek PinPoint 50 (2.9 g) or PinPoint 10 (1.9 g) GPS units to individual birds using backpack harnesses with materials and dimensions similar to Vukovich and Kilgo (2009); we did not deploy units ≥ 5% body mass on any woodpecker (Caccamise and Hedin 1985, Hooge 1991). Upon recapture and removal of the GPS unit, we recorded each woodpecker’s body mass again and compared mean mass change for tagged birds against untagged birds using an unpaired Welch’s two-sample t-test to determine if tags had a negative effect. To further assess the potential negative impact of GPS tags, we compared provisioning rates between tagged and untagged birds using an unpaired Mann-Whitney U test.

Home range analysis

In the 2017 breeding season, GPS tags were scheduled to gather locations (fix points), from 0600–2030 in 30-min (PinPoint 50 tags) and 1-hr (PinPoint 10 tags) intervals. Batteries were expected to last 10 days with this fix schedule, which we determined was ideal to both gather enough points for home range estimation and allow enough time to deploy units on multiple woodpeckers. We standardized the schedule to attempt a fix every 30 min for both tag types in 2018 after an adjustment to the fix window allowed enhanced battery conservation.

Our GPS units automatically calculated horizontal dilution of precision (HDOP), a dimensionless number, using geometry of satellites in space relative to each unit (El-Rabbany 2002). We used HDOP values to remove fixes with high location error (LE), since HDOP is correlated with LE. HDOP values increase when satellites are physically blocked from communicating with GPS units (i.e. in dense forests,
canyons, ravines, Frair et al. 2010), are caused by having too few satellites in the sky, and when satellites are located too close together (Langley 1999, El-Rabbany 2002). Removing fixes from datasets to reduce LE using HDOP is a technique that has been used before with lightweight GPS tags (Recio et al. 2011). It is also useful to remove points with a low satellite number, since fixes with < 5 satellites have high HDOP and LE (Recio et al. 2011). We removed fixes with > 2 HDOP or fixes with less than 6 satellites based on estimates from test data. Our test data was generated by deploying GPS units at known locations in savanna and closed canopy forests at Fort A.P. Hill in November 2017 and 2018. We calculated Euclidean distance from each tag’s known location to its GPS fixes to determine mean LE. We used combinations of HDOP and the number of satellites to retain the greatest number of fixes while maintaining the lowest mean LE. We retained 38.6% of fixes using < 2 HDOP and ≥ 6 satellites, with mean LE of 30.2 m (SD ± 39.7). In the test data, we did remove more fixes from closed canopy habitat (66.1%) than savanna (42.4%). However, LE was not significantly different between the two habitats after the data was filtered to remove fixes with > 2 HDOP or fixes with less than 6 satellites (p = 0.5, U = 13,100).

We calculated 95% fixed kernel home range size (Seaman and Powell 1996) in R using package KernSmooth (Deng and Wickham 2011, Wand 2015). Minimum convex polygon (MCP) is known to over-estimate home range size, so using kernel density estimates is recommended (Franzreb 2006, Walter et al. 2011). Home ranges were estimated individually with the plug-in smoothing method (hp, Fieberg 2014). Although most woodpecker home range studies use the fixed kernel least squares cross-validation (LSCV) smoothing method (Elchuk and Wiebe 2003, Franzreb 2006, Vukovich and Kilgo 2013, Ojeda and Chazarreta 2014), LSCV may not be the most appropriate method for analyzing GPS data (Walter et al. 2011). The LSCV method does not perform well when fixes are identical or discretized (Hemson et al. 2005, Walter et al. 2011). Discretization of data comes from GPS units truncating fixes when calculating locations, eliminating trailing decimal points so fixes are arranged in a grid pattern (Walter et al. 2011). Aspects of woodpecker behavior such as their use of the same roost cavities, nest cavities, and flycatching branches result in many clustered and identical fixes. The plug-in method for bandwidth selection is more
accurate for truncated GPS data, and has been used in other woodpecker space-use analyses to increase accuracy of home range estimates with VHF tags (Lorenz et al. 2015, Tomasevic and Marzluff 2018). We determined that models that handle autocorrelation such as Brownian bridge movement models (BBMM) were not the best choice for our data specifically because Red-headed Woodpeckers occupy small areas and because exploratory movements were not of interest (Walter et al. 2011). While kernel density estimates (KDEs) require data that are not spatially autocorrelated, under these circumstances, KDE $h_{pi}$ is suggested over BBMM, especially since KDE $h_{pi}$ and BBMM home range estimates are often comparable (Walter et al. 2011).

We modeled 95% KDE home range estimates using general linear models (GLMs) with a Gaussian distribution to determine influence of sex, habitat, date, nearest neighbor distance, and nest stage on home range size. Chick age and brood size was not available for all nests with GPS tagged birds, so we categorized nests as containing 1) eggs, 2) young chicks (< 13 days old), or 3) old chicks (≥ 13 days old).

All analyses were conducted in program R, version 3.5.2 (R Core Team 2018).

RESULTS

Nest monitoring and chick development

We monitored a total of 74 Red-headed Woodpecker nesting attempts (broods). In 2017, we monitored 39 broods of 24 pairs; in 2018 we monitored 35 broods of 26 pairs. We checked 23 (58.9%) of the 2017 broods with the cavity camera and 28 (80.0%) of 2018 broods. Broods that were not checked with a camera either fledged before we obtained it (in 2017) or were too high for the extendable pole. We regularly observed two or more brooding attempts by pairs in a breeding season.

Only a few studies (Bent 1939, Short 1982, Yohannes 2017) have reported nest contents for this species, so we present our observations here to contribute to the understanding of this species’ basic biology. The first egg of the 2018 breeding season was observed on 15 May and the earliest hatch date was observed on 31 May. The latest hatch date observed was 27 July 2018, though our field season did
not extend beyond 8 August and later hatch dates are possible. Clutch size ranged from 3–6 eggs, with an average of 4.0 (SD = 0.9, n = 33). We observed up to 5 chicks in a nest, but this was shortly after hatching, and brood reduction was common (44.4% of broods had the number of nestlings decrease from hatching to fledging). Mean brood size was 2.3 chicks (SD = 0.8, n = 36). The oldest that an adult would brood was for day 19 nestlings. Using our best nest check data (all from 2018, in which we observed the first egg laid and checked nests frequently until chicks were near fledge age), we observed chicks to remained in the nest an average of ~31 days before fledging (SD = 3.0, n = 6). The oldest chick observed in a nest was 36 days old, longer than published nestling periods of 27 days (Bent 1939) and 29 days (Yohannes 2017).

Out of all nests monitored (n = 74 broods), we had nest contents information for 52 (70.2%) checked with a camera. Of 13 failed broods, 8 (61.5%) failed during the egg stage and 5 (38.5%) during the chick stage. The cause of these failures is not known. We positively confirmed fledging for many more nests in the 2016 (n = 21) and 2017 (n = 3) breeding seasons despite similar fledge check efforts in all years; in 2018, the presence of fledglings was confirmed at only one nest. Although we found fewer nests in closed canopy habitat, on average there were more eggs and chicks in closed canopy than savanna (Table 2). Early and late summer broods showed no difference in clutch size (Table 3).

Based on a sample of 14 broods that were checked regularly, we observed pinfeathers starting to emerge at 7 days after hatching for a single-chick nest, but for nests with 2–3 chicks pinfeathers emerged around day 10. Eyes began to open as slits by day 11–12 and were fully open by day 15. Chicks were seen clinging to the cavity walls as early as day 12. Downy feathers covered the nestlings by day 16, but feather tracts were still visible on chicks’ crowns and scapulars. By day 18, feather tracts were no longer visible (Appendix A). Chicks were seen with their heads out of cavity entrances starting at day 16. Chicks were often seen aggressively begging for food with half of their bodies out of the cavity entrance for about a week before fledging.

We recorded two chicks fledging on video, an occurrence not previously described (Frei et al. 2017). In one fledge event, the chick was recorded calling with chattering “rrr rrr” contact calls (Short
1982) and its head out of the nest cavity for 5 min before flying out of the nest. In the second instance, the chick was calling with chattering sounds and high begging “chee-chee” calls (Short 1982) as well as pecking at small fungi surrounding the cavity before fledging. Both fledglings had a downward trajectory. Siblings in both nests emerged with their head out once the others had fledged. Recordings of both fledge events are available via Cornell Laboratory of Ornithology Macaulay Library (http://macaulaylibrary.org, ML488612, ML488613).

**Parental care**

To assess rates of parental care during the nestling stage, we used 128 hrs of high-quality video from 21 broods in 18 nest cavities (10 broods in 2017 and 11 in 2018) to generate provisioning counts, cleaning counts, and brooding durations for each parent woodpecker (n = 35). Videos ranged from 41–243 min in length (n = 88), with a mean duration of 174 min per brood (SD ± 51.8). Recall that we recorded behavior at the same nest on different days (n = 15 broods) and therefore have a larger sample of videos than actual nests monitored; brood ID was included as a random effect in our models to account for pseudoreplication. Chick age and date were not correlated (τ = -0.04, p = 0.7, z = -0.4). Parental care did not differ between years when compared with Mann–Whitney U tests; specifically, provisioning rates (p = 0.56, U = 1030), brooding duration (p = 0.99, U = 961.5), and cleaning rates (p = 0.72, U = 920) were not different, so we pooled data from both years. A total of 1650 parental care observations were recorded and four (0.2%) observations were excluded from analysis because the identity of the parent was unknown. Seven (33.3%) broods were in closed canopy forest and 14 (66.6%) were in savanna habitat. Out of 35 individual banded woodpeckers, five were seen in both years and three had a new mate. We observed that two woodpeckers moved to new nest snags in 2018, both with a new mate. Additionally, only two nest snags were re-used in our footage; one by the same pair, and another by the same male with a new mate.

The mean provisioning rate across all nests was 4.8 (SD ± 3.8) visits per hr, and 2.4 (SD ± 1.7) visits per chick per hr. There were seven nest videos where one adult out of the pair did not provision,
with a similar average length (177 min ± 43.5 SD) to the total sample – in five cases the female did not provision, and five cases were in savanna habitat. There was no effect of GPS tags on provisioning rate when comparing GPS-tagged woodpeckers to those that never wore a tag (p = 0.17, U = 179, Figure 2).

In the provisioning models, the zero-inflated negative binomial distribution had a better fit than negative binomial (ΔAIC = 27.2) or Poisson error distribution (ΔAIC = 103.0). Provisioning rate differed significantly as a function of the number of chicks in the nest so brood size was included as a fixed effect in all models. Models with a quadratic term for chick age performed better than models without it (ΔAIC = 7.5), indicating that provisioning peaked in the middle of the nestling stage. Our highest ranking provisioning model included chick age² × date, a linear effect for chick age, and accounted for brood size (Table 4). The interaction chick age² × date was significant (Table 5), with more provisioning throughout the entire nestling stage in early summer and a decrease in provisioning for older nestlings in late summer (Figure 3). Other models that performed similarly (ΔAIC < 2.0) were variations of this best model, adding habitat (ΔAIC = 1.0) or parent sex (ΔAIC = 1.9, Table 4). Although parent sex was not a significant factor for provisioning in the top model, we did find variation in the proportion of provisioning by each sex at the brood level that was not associated with nestling age (Figure 4).

Out of all prey items brought to chicks (n = 1307), 11.2% were fruit, 55.2% were arthropods, and 33.7% were unidentified. We identified blueberries/huckleberries (Vaccinium spp. and Gaylussacia spp.) and blackberries (Rubus spp.) as the only fruits gathered by adult woodpeckers. Arthropods were identified to order when possible, but 88% were not classifiable below phylum due to video quality. We observed Insecta orders Blattodea, Coleoptera, Diptera, Hymenoptera, Lepidoptera, Odonata, Orthoptera and Arachnida:Araneae. We compared Poisson, negative binomial, and zero-inflated negative binomial distributions for each prey type, and found negative binomial to have a better fit for fruit items and zero-inflated negative binomial to fit best for arthropods. We tested fruit models for overdispersion since this was the only model set using count data without a zero-inflated distribution (Gardner et al. 1995), and found they were not overdispersed (p = 0.15 to 0.75). The best-fitting model for fruit provisioning included an interaction between habitat × date, accounting for sex, brood size, and chick age (Table 5,
Table 6, Figure 5). More fruit was provisioned to nests by males in closed canopy habitats. Arthropod prey were best modeled by chick age and brood size (Table 5, Table 7, Figure 6) where more arthropods were delivered in larger and older broods. Arthropods composed a larger proportion of nestling diet than fruit in both habitat types (Figure 7).

In the brooding models, the negative binomial hurdle distribution had a better fit than the Poisson hurdle (ΔAIC = 25.3), zero-inflated Gaussian (ΔAIC = 31.2) or Gaussian (ΔAIC = 176.4) distributions. The best fitting conditional model for brooding included chick age × sex and brood size (Figure 8). The interaction of chick age and sex was not significant (p = 0.16). One other brooding model has ΔAIC < 2, but was an iteration of the top model including habitat as a fixed effect (ΔAIC > 2, Table 8). Since date was correlated with maximum daily temperature (p < 0.001, t = 5.0, df = 86), we never used both factors in the same model.

Males cleaned the nest (mean = 1.4 ± 0.21 SE) significantly more often than females (mean = 0.2 ± 0.08 SE, p < 0.001, z = -4.32, V = 38, Figure 9).

**Home range size**

We GPS tagged 35 RHWO; 23 woodpeckers in 2017 and 12 in 2018. We retrieved 19 (83%) in 2017; one unit was later retrieved in 2018. We retrieved 7 (58%) of those deployed in 2018. Our capture technique depended on woodpeckers attending an active nest; so we were unable to retrieve units after nest predation, chicks fledging, or when access to TAs was limited due to troop activities. Additionally, some GPS units were not retrieved because they fell off, likely due to a new harness material (silicone tubing) tried in 2018. Compared with non-tagged birds, those with GPS tags did not lose significantly more mass between captures (p = 0.55, t = 0.60, df = 35, Figure 10). GPS units collected points over 2–14 days (mean = 7.3, SD ± 2.8, df = 25) during the incubation (n = 6) and nestling (n = 19) stages. After filtering out points based on HDOP and the number of satellites, tags gathered an average of 109 (SD ± 52.4) points per woodpecker; fewer GPS fixes were acquired in closed canopy forest (mean = 70, SD ± 33.0) compared to savanna (mean = 128, SD ± 49.9, p = 0.002, t = -3.5, df = 20).
We included 25 woodpeckers in the home range analysis, all with > 30 points (Worton 1987, Seaman et al. 1999). For one RHWO whose eggs hatched during its GPS tag deployment, we classified the nest as incubating. Six woodpeckers were in the incubation stage during deployment. The number of fixes was not correlated with 95% KDE home range size ($p = 0.56, t = -0.59, \text{ Adj } r^2 = -0.03$). Our estimates of Red-headed Woodpecker 95% fixed KDE $h_{pi}$ home ranges were 2.7 ha on average (SD ± 1.1, range = 1.2 – 4.9 ha). The top two models for home range size included sex and date as a predictor; these models performed similarly (Table 9). Home range was larger for males (mean = 3.1 ha, SD ± 0.8, n = 10) compared to females (mean = 2.4 ha, SD ± 1.1, n = 15, Figure 11a) and smaller in late summer (mean = 2.5 ha, SD ± 1.1, n = 15, Figure 11b) compared to early summer (3.0 ha, SD ± 1.0, n = 10), although neither sex nor date were significant. By chance, we deployed more GPS tags in late summer on females (11/15, 73.3%), and more females were tagged in savanna (11/17, 64.7%). We did not calculate percentage overlap, but found it to be visually apparent that breeding pair home ranges overlap and have the nest snag located in the center of the core area (Figure 12).

**DISCUSSION**

This thesis is the first study to assess a comprehensive suite of sex-specific parental care behaviors in genetically sexed Red-headed Woodpeckers. Sex-specific differences in monomorphic woodpeckers have been understudied; especially considering monomorphic species represent less than 1% of the largely dimorphic Picidae family. We found that males almost exclusively clean the nest of waste, males provision fruit to chicks at a significantly higher rate than females, females brood almost exclusively, and males are more likely to enter the cavity for visits longer than a minute when nestlings are greater than 10 days old. Additionally, we found that provisioning rates remain high throughout the nestling stage in the early breeding season but decline later, suggesting that food availability may be lower for late broods. Moreover, this study is the first to estimate home range size in this species using GPS tags. We found that male Red-headed Woodpeckers have larger average home ranges than females, and that home ranges are larger before 7 July and smaller after this date. However, temporal differences
may be confounded by sex-specific differences in home range due to naive tagging of individuals (i.e., sex was not known at the time of capture and more females were tagged later in the season).

Parental care behaviors

Our findings show that mean Red-headed Woodpecker nestling provisioning rate is not different between the sexes, which is consistent with dimorphic woodpeckers. Four studies have investigated provisioning rates in Red-headed Woodpeckers: two had a small sample size (n = 2 broods, Jackson 1976a; n = 4 broods with data, Venables and Collopy 1989), one found no difference between provisioning rate in golf course and non-golf course habitat and did not assess differences between sexes (Hudson 2009), and a recent study focusing on nestling diet included fewer individual woodpeckers but more broods than our study (n = 26 individuals, 31 broods, Vukovich and Kilgo 2019). The evolution of a monogamous social structure of woodpeckers and other cavity-nesting birds is likely the result of several factors, including limitations imposed by nest substrate and cavity availability (Mock and Fujioka 1990). As such, woodpeckers generally maximize parental care in an effort to increase fitness and maintain a mate rather than seek extra-pair copulations (Pechacek et al. 2005). Shared nestling provisioning between parents have been observed in dimorphic woodpecker species, including Northern Flickers (Colaptes auratus, Wiebe and Elchuk 2003), Golden-fronted Woodpeckers (Melanerpes aurifrons, Schroeder et al. 2013), Ladder-backed Woodpeckers (Dryobates scalaris, Schroeder et al. 2013), and Lesser Spotted Woodpeckers (Picoides minor, Rossmanith et al. 2009). Bi-parental care increases fledge success (Pechacek et al. 2005) and this factor is likely one of the main reasons for monogamy in woodpeckers, although many other factors are known to contribute (Klug 2018).

Although sharing parental care in woodpecker pairs has been widely documented, investigation of individual variation in parental care has been reported in only a small proportion of studies. In Lesser Spotted Woodpeckers, a species that is sometimes polyandrous, males provision nestlings more reliably than females and females will even abandon nests with a small number of nestlings (Rossmanith et al. 2009). High paternal investment of males in monogamous woodpecker nests may stem from lower...
survival rates of females (Wiktander et al. 2000, Kilgo and Vukovich 2012). Increased male involvement in monogamous woodpecker pairs may also be related to increased certainty of paternity (Michalek and Winkler 2001). We found that the ratio of male:female nestling provisioning was rarely 50:50 and varied among broods in Red-headed Woodpeckers (Figure 4). This is common in many dimorphic species and is likely related to individual quality or other environmental factors. We collected crown feathers from all banded woodpeckers and have measured carotenoid content and overall brightness and plan to assess whether individual provisioning rate is related to feather ornamentation.

We found that provisioning rate is explained by an interaction between chick age and date. Provisioning increases with chick age in early summer, but declines after for older nestlings in late summer (after July 7). Temporal variation in provisioning rates may indicate that there are pulses in prey availability such that nestling growth and survival are limited at times when food is less available. Late summer nests may have less food resources available to support the energetic demands of growing and developing nestlings. Although our sample of late summer broods is small, clutch size and the number of chicks per brood was similar between early and late summer broods (Table 3), which is consistent with a Mississippi population (Ingold 1989). However, survival of nestlings has been shown to be greater for nests with earlier clutch initiation dates (Yohannes 2017) and late summer nests can be less likely to fledge chicks (Ingold 1989). It is possible that temporal variation in food availability leads to reduced provisioning and decreased nestling survival in Red-headed Woodpeckers and that this is more likely in late summer broods.

Red-headed Woodpeckers are opportunistic foragers and notorious omnivores (Bent 1939); their diet during the breeding season is varied and consists of fruits in addition to terrestrial and aerial arthropods and occasional vertebrates (Beal 1911, Nauman 1932, Venables and Collopy 1989, Vukovich and Kilgo 2019). When analyzing prey items provisioned to chicks, we were able to model two main categories: arthropods and fruit. Arthropod provisioning increased with chick age, which was consistent with overall provisioning. Arthropods are an important component in this species’ diet; Red-headed Woodpecker populations increase after periodical cicada emergences (Magicicada spp., Koenig and
Peaks in arthropod emergence vary throughout the breeding season (Stagliano et al. 1998), and it is likely that this variation in abundance corresponds to provisioning rates in Red-headed Woodpeckers. Further, arthropods have higher protein content compared with fruits and are therefore most likely to meet the energetic demands of growing and developing nestlings (Morton 1973, Koenig et al. 2008). Since arthropods are important for developing offspring, it is not surprising that a monogamous pair would invest equal effort to providing this resource.

Although not as high quality nutritionally, fruit can provide a source of water, micronutrients, carotenoids, and sugars to nestling birds (Herrera 1982, Breitwisch et al. 1984). We found that fruit provisioning varied significantly as a function of date, habitat, and sex. Fruit provisioning rate was greatest for nestlings in early summer (prior to July 7), in closed canopy habitat, and males provisioned significantly more fruit than females. Similar to arthropods, we expect that huckleberry, blueberry, and blackberry fruits were provisioned during times of greatest availability when berries were ripe and most abundant. However, woodpecker fruit consumption was highest when fruit availability was lowest in Brazil (Mikich 2002). Fruit resources could be of special importance for nestlings by providing water in summer months (Debussche et al. 1987), or could provide nutritional balance (Bairlein 1996), especially since the sugar to protein ratio of fleshy fruits is higher for plant species that fruit in early summer (Stapanian 1982). These factors may help explain why we did not find higher fruit provisioning in savanna habitat despite the fact that open habitats tend to produce more fruit due to increased sun exposure (Greenberg et al. 2012).

Our findings for prey item analyses yielded similar nestling diet proportions to Vukovich and Kilgo (2019), but we observed a smaller proportion of fruit. Fruits identified at the Savannah River Site included more species than we observed, although many of the species listed were also present at Fort A.P. Hill. We may not have observed some common fruits, such as wild grapes (Vitus spp.) and wild cherry (Prunus serotina) identified by Vukovich and Kilgo (2019), in our recordings because they fruit later in the summer – beyond our observation period that ended 8 August (Stiles 1980, Stapanian 1982).
Sex-specific foraging niche partitioning has not previously been observed in Red-headed Woodpeckers, but our finding that fruit delivery rates differed between the sexes may indicate that adults search for food in different places. Other woodpecker species are known to have sex-specific foraging niche partitioning; this phenomenon has been documented in Hispaniolan Woodpeckers (*Melanerpes striatus*, Wallace 1974), Puerto Rican Woodpeckers (*Melanerpes portoricensis*, Wallace 1974), Downy Woodpeckers (*Dryobates pubescens*, Peters and Grubb 1983), and Middle Spotted Woodpeckers (*Dendrocopos medius*, Pasinelli 2000). Despite earlier research on foraging behavior in Red-headed Woodpeckers (Reller 1972, Williams 1975, Venables and Collopy 1989), more observational study using banded and sexed individuals is warranted to determine if sex-specific foraging niche partitioning occurs in this species.

Brooding duration of nestlings was best predicted by sex and chick age; brooding duration is greatest for nestlings less than 10 days old and is primarily done by females, after which only males enter the cavity for relatively short visits. The decline in brooding with chick age is a well-known phenomenon associated with the emergence of feathers and the ability of older nestlings to independently thermoregulate (Dawson and Evans 1957). It is possible that males may enter the nest cavity during the latter half of the nestling period to search for fecal sacs; males were observed to spend more time entering nest cavities in Black-backed Woodpeckers (*Picoides arcticus*, Tremblay et al. 2016) and Northern Flickers (Wiebe and Elchuk 2003) as well, although the reason why is still not understood.

Nest sanitation is thought to benefit nestlings by reducing the abundance of harmful microbes and parasites (Gow et al. 2015). We found nest cleaning was done almost exclusively by males in our study. This finding is consistent with earlier research that used behavioral-based sexing (Venables and Collopy 1989) but also observed Red-headed Woodpecker males cleaned nests more than females (n = 2 broods with data). The pattern of males cleaning more than females is apparent in many woodpecker species (Rossmanith et al. 2009, Gow et al. 2015, Tremblay et al. 2016, Chazarreta et al. 2011), which is unusual compared with other avian taxa where male parents exclusively clean nests in only 1.3% of species (Ibáñez-Álamo et al. 2017). Males may almost exclusively clean the nest as compensation for females
being the primary diurnal brooding parent. Such division of labor between the sexes may be explained by the energetic constraints hypothesis proposed by Burke et al. (2015) where the female is assumed to be in relatively poor condition after spending so much time brooding in the day without being able to forage, and therefore allocates more time to foraging in the later nestling stage while the male takes care of nest sanitation.

The separation of reproductive roles is an effective strategy for monogamous pairs to successfully raise offspring (Ketterson and van Nolan 1994). However, spending time on parental care contributes to the sexual conflict in breeding pairs by reducing opportunities for extra-pair copulations (EPC, Olson et al. 2007). Studies that have assessed paternity in woodpeckers indicate EPC are rare (Li et al. 2009, Kellam 2014). Some reasoning for this is that sexual conflict is weaker in species with altricial young, which demand more care than precocial young (Temrin and Tullberg 1995). Male and female woodpeckers must invest significant energy in parental care to raise their altricial young, limiting opportunities for EPC. This level of nest attention increases nestling survival (Mock and Fujioka 1990, Pechacek et al. 2005). Red-headed Woodpeckers divide parental care so that males are responsible for excavation, provisioning, nocturnal brooding, and nest cleaning whereas females contribute to egg laying, provisioning, and diurnal brooding. This results in similar energy expense by both sexes. Even in polyandrous woodpeckers, females that significantly reduce parental care in the late nestling stage provide equal or greater care in the early period (Rossmanith et al. 2009). As such, patterns in social and genetic monogamy in Red-headed Woodpeckers are likely a result of sexual conflict and energy constraints, limiting the ability of a single parent to successfully care for chicks.

**Home range size**

Our study found Red-headed Woodpeckers have an average breeding home range 95% KDE h_{pi} of 2.7 ha. Red-headed Woodpecker home ranges are much smaller than other genera in the United States, with the exception of sapsuckers (Genus *Sphyrapicus*, Table 1). North American woodpecker home ranges span from the estimate of nearly 500 ha in large-bodied Pileated Woodpeckers (*Dryocopus*
*pileatus*, Bull and Holthausen 1993) to 4.9 ha in the small Downy Woodpecker (Twomey 1945). Even among woodpeckers of similar size to Red-headed Woodpeckers, home range size can vary significantly; breeding Northern Flickers have a much larger home range (25 ha, Elchuk and Wiebe 2003) than Red-bellied Woodpeckers (3.1 ha, *Melanerpes carolinus*, Williams 1977). These differences are likely driven by diet (Wiebe and Moore 2017, Miller et al. 2019). The diverse diet of Red-headed Woodpeckers may enable them to have smaller territories than other species of woodpecker (Frei et al. 2017) as they are able to acquire all necessary resources in a smaller area compared with a specialist that has to travel farther distances to find enough of a single resource.

Most existing data on Red-headed Woodpecker home range sizes are based on pre-telemetry estimation methods and focus on winter territories (Kilham 1958, MacRoberts 1975, Moskovits 1978, Williams and Batzli 1979, Doherty et al. 1996). Some breeding season estimates of home range size do exist for Red-headed Woodpeckers. In Florida pine savanna habitat, breeding season home ranges are estimated to be 5.7 ha per pair via territory mapping calculations (Venables and Collopy 1989). Vukovich and Kilgo (2013) deployed VHF tags on RHWO, and estimated 95% KDE_{LSCV} breeding season home ranges to be 3.23 ha in South Carolina pine savanna. The difference in home range estimates between our study and Vukovich and Kilgo (2013) is not great (< 1 ha) and is likely due to the length of tracking in our studies. Vukovich and Kilgo (2013) deployed units for several weeks while the current study deployed GPS tags for less than two weeks. While this is the most likely reason for our smaller home range estimates, other factors could be resource availability, habitat type, differences in tag accuracy, or the effect of smoothing factor on KDE.

We found Red-headed Woodpecker males have larger home ranges than females. Reasons for this difference may be attributable to several aspects of individual behavior. Males are the primary parent that cleans nests of fecal material, and they may travel far distances to distribute chick waste. In passerines, fecal sacs are carried further from the nest as species body size increases (Guigueno and Sealy 2012), however there is a paucity of information on where fecal sacs are dropped in relation to a nest or within a territory. Foraging niche partitioning may also influence home range size; higher rates of fruit
provisioning by males may require further movements to gather berries that may be patchily distributed. Although it is possible that males may be more territorial than females, and therefore serve as primary defenders of the home range against neighbors, there is little evidence to support this; males and females have been observed to be equally aggressive (Nichols and Jackson 1987).

We found home range size is larger in early summer (prior to 7 July). This does not fit our expectation that smaller home ranges would be observed during the time of highest provisioning, which was in early summer. One possible explanation for this is that the cost of foraging farther from the nest is greater later in the breeding season when air temperatures are high and the risk of thermoregulatory stress increases (Weathers 1981). It is difficult to know from our data whether sex or date (season) is a more important factor in home range size as these are confounded in this study. Sex was not known at the time of capture, and by chance we tagged more females in late summer. Future research tracking more individuals may reveal clearer differences between sexes, habitats and seasons.

We did not see a difference in home range size as a function of habitat type. However, we only classified a territory as either savanna or closed canopy based on the location of the nest snag. In most cases, the home range encompassed more than one habitat type, and woodpeckers may benefit from access to the variety of resources present in more heterogeneous cover types. Red-headed Woodpeckers choose nest snag location primarily as a result of what snags are available, and will nest in less-preferred closed canopy habitat when snags are abundant (Nickley and Bulluck 2019). We intend to use our home range estimates in future analyses to assess variation in home range size as a function of forest cover and habitat heterogeneity. In addition to open savanna and closed canopy forests, wetlands are also abundant at Fort A.P. Hill and are used by Red-headed Woodpeckers. We expect that birds occupying landscapes with more cover types will have smaller home ranges than birds occupying landscapes with more homogeneous landscapes.

Red-headed Woodpeckers have been found to decrease territory size in areas of high snag density to accommodate increased conspecific abundance (Kilgo and Vukovich 2014). However, we did not find home range size at Fort A.P. Hill to differ as a function of distance to nearest nesting neighbor. Many of
our GPS tagged woodpeckers were in areas with high nest density, partly because Red-headed Woodpeckers tend to breed in areas with high snag density. This resulted in a small sample size of isolated individuals with large nearest nesting neighbor distance values. As such, our models did not have a lot of variation in nearest neighbor distances (range = 21.6 – 363.1 m) to determine if it may be a meaningful factor influencing home range size.

This study likely provides the best estimates of home range size for Red-headed Woodpeckers to date because GPS tags collect multiple unbiased locations per day, providing a larger sample size of accurate spatial points than is possible with VHF tags. Humans must record locations by tracking VHF-tagged birds, and it would take several months to obtain the number of points acquired by a GPS tag in just a few days or weeks. However, obtaining locations from a narrow time window may not be the best representation because home ranges may expand and contract at different stages of the nesting cycle. Most of our tags were deployed during the nestling stage and we did not find that home range size varied as a function of chick age. GPS tags can be formatted to collect fewer points per day over a longer time frame to cover a larger portion of the nesting cycle, but the risk of not retrieving the device increases as nests fail and/or fledge and birds move away from the nest tree. We noted Red-headed Woodpeckers would hide behind trunks and branches when humans or other perceived predators were near; thus, using GPS tags for a species such as the Red-headed Woodpecker that changes its normal activities in the presence of researchers is therefore optimal to collect unbiased data.

Conservation implications

Our findings that late summer broods receive fewer feeding visits and that parents have smaller home ranges during this time may highlight a potential factor related to this species’ nationwide declines. A large-scale study on aerial insect abundance in regions across the United States over time could provide groundwork for understanding the relationship of insects to Red-headed Woodpecker population changes. Aerial insectivorous birds are declining in North America, but woodpeckers are not included in studies about this trend (Nebel et al. 2010, Michel et al. 2016). To assess fledgling survival, it is of conservation
importance to quantify fledgling dispersal distances and compare juvenile survival based on nest initiation
date and habitat type, especially as these factors may be related to provisioning and subsequent
development of fledglings. We also recommend an assessment of foraging niche partitioning between
sexes and survival of adults in these niches to determine if landscape changes have contributed to
increased depredation of females (Kilgo and Vukovich 2012).

Going forward, we believe a broader investigation is warranted that includes breeding, foraging,
and parental care behavior study of Lewis’s Woodpecker, the only other monomorphic woodpecker
species in the world. Lewis’s Woodpeckers are aerial insectivores with similar life history patterns to
Red-headed Woodpeckers with populations that have declined at similar rates, with a 72% loss since 1970
(Goodwin 1968, Bock et al. 1971, Rosenberg et al. 2016). Both face similar pressures by human
development, but Lewis’s Woodpecker populations are estimated to be 20 times smaller than Red-headed
populations and are therefore at an even greater risk (Rosenberg et al. 2016). These closely-related
species are very similar genetically, sharing more than 95% base pairs (Navarro-Sigüenza et al. 2017). As
such, understanding population declines in Red-headed Woodpeckers may inform conservation practices
of Lewis’s Woodpeckers, especially if declines are determined to be a result of habitat changes (Kilgo
and Vukovich 2012, Koenig et al. 2017) or insect abundance (Nebel et al. 2010, Koenig et al. 2011, Rota
et al. 2015).
LITERATURE CITED


Walter, W. D., J. W. Fischer, S. Baruch-Mordo, and K. C. VerCauteren (2011). What is the proper method to delineate home range of an animal using today’s advanced GPS telemetry systems: The


Figure 1. Map of Fort A.P. Hill, Virginia with points showing focal training areas (TAs) for RHWO nests that were recorded on video. Habitat was hand-digitized based on 2016 NAIP aerial imagery by Ben Nickley. Layers for TAs, streams, and ponds were provided by Fort A.P. Hill Fish & Wildlife.
Table 1. Breeding woodpecker mean home range sizes, including but not limited to species of the United States. Woodpeckers in the U.S. with no available home range data include: Arizona Woodpecker (*Dryobates arizonicus*), gilded flicker (*Colaptes chrysoides*), and Ladder-backed Woodpecker (*Dryobates scalaris*). The method for data collection in each study is noted as either very high frequency (VHF) or territory mapping (map). If the authors compared male and female home ranges, the result was noted as equal (=) or greater than (>). Details of estimation methods were described to the extent that authors provided information. Some home ranges were reported by breeding pairs instead of individuals. Outliers for Pileated Woodpecker (1,464 ha, Bull and Holthausen 1993) and Red-headed Woodpecker (2.7 ha in a pastured woodlot, Williams 1977) were excluded from estimated home range means (marked with *) in this table. All home ranges were estimated during the breeding season except for two (marked with v) which also included months during the post-breeding season. General trends in this table show that home ranges of woodpeckers in genus *Melanerpes* (mean = 6.0 ha, n = 8) are comparable to sapsuckers (*Sphyrapicus*, mean = 7.3 ha, n = 4) and much smaller than other woodpeckers (121.0 ha, n = 19).

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Data</th>
<th>Home range (ha)</th>
<th>Sexes</th>
<th>Estimation method</th>
<th>Contour</th>
<th>Author(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern Flicker</td>
<td><em>Colaptes auratus</em></td>
<td>VHF</td>
<td>25.0</td>
<td>M = F</td>
<td>Fixed KDE, 95%</td>
<td>LSCV</td>
<td>Elchuk and Wiebe 2003</td>
</tr>
<tr>
<td>White-headed Woodpecker</td>
<td><em>Dryobates albolarvatus</em></td>
<td>VHF</td>
<td>225.4</td>
<td>na</td>
<td>MCP</td>
<td>na</td>
<td>Dixon 1995</td>
</tr>
<tr>
<td></td>
<td></td>
<td>VHF</td>
<td>75.7</td>
<td>na</td>
<td>Adaptive KDE, 85%</td>
<td>na</td>
<td>Dixon 1995</td>
</tr>
<tr>
<td></td>
<td></td>
<td>VHF</td>
<td>124.9</td>
<td>M = F</td>
<td>Fixed KDE</td>
<td>LSCV</td>
<td>Lorenz et al. 2015</td>
</tr>
<tr>
<td>Red-cockaded Woodpecker</td>
<td><em>Dryobates borealis</em></td>
<td>VHF</td>
<td>74.0</td>
<td>na</td>
<td>Minimum area</td>
<td>na</td>
<td>Porter and Labisky 1986</td>
</tr>
<tr>
<td></td>
<td></td>
<td>VHF</td>
<td>56.9</td>
<td>M = F</td>
<td>Fixed KDE, 95%</td>
<td>LSCV</td>
<td>Franzreb 2006</td>
</tr>
<tr>
<td>Nuttall's Woodpecker</td>
<td><em>Dryobates nuttallii</em></td>
<td>map</td>
<td>~ 65</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>Miller and Bock 1972, Lowther et al. 2018</td>
</tr>
<tr>
<td>Downy Woodpecker</td>
<td><em>Dryobates pubescens</em></td>
<td>map</td>
<td>4.9</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>Twomey 1945</td>
</tr>
<tr>
<td>Hairy Woodpecker</td>
<td><em>Dryobates villosus</em></td>
<td>VHF</td>
<td>64.4</td>
<td>M = F</td>
<td>Fixed KDE, 95%</td>
<td>na</td>
<td>Ripper et al. 2007</td>
</tr>
<tr>
<td>Black Woodpecker</td>
<td><em>Dryocopus martius</em></td>
<td>VHF</td>
<td>232.8</td>
<td>na</td>
<td>KDE, 95%</td>
<td>na</td>
<td>Bocca et al. 2007</td>
</tr>
<tr>
<td>Pileated Woodpecker</td>
<td><em>Dryocopus pileatus</em></td>
<td>VHF</td>
<td>489.0 * v</td>
<td>M = F</td>
<td>MCP</td>
<td>na</td>
<td>Bull and Holthausen 1993</td>
</tr>
<tr>
<td>Middle Spotted Woodpecker</td>
<td><em>Leiopicus medius</em></td>
<td>VHF</td>
<td>7.2</td>
<td>M = F</td>
<td>MCP</td>
<td>na</td>
<td>Pasinelli et al. 2001</td>
</tr>
<tr>
<td>Golden-fronted Woodpecker</td>
<td><em>Melanerpes aurifrons</em></td>
<td>map</td>
<td>17.4 per pair</td>
<td>na</td>
<td>Minimum area</td>
<td>na</td>
<td>Husak 2000</td>
</tr>
<tr>
<td>Red-bellied Woodpecker</td>
<td><em>Melanerpes carolinus</em></td>
<td>map</td>
<td>3.1</td>
<td>na</td>
<td>Planimeter</td>
<td>na</td>
<td>Williams 1977</td>
</tr>
<tr>
<td>Species</td>
<td>Scientific Name</td>
<td>Method</td>
<td>Density</td>
<td>Sex Ratio</td>
<td>Estimation</td>
<td>Reference</td>
<td></td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-----------------------</td>
<td>--------</td>
<td>---------</td>
<td>-----------</td>
<td>------------</td>
<td>-------------------------</td>
<td></td>
</tr>
<tr>
<td>Red-headed Woodpecker</td>
<td><em>Melanerpes erythrocephalus</em></td>
<td>map</td>
<td>0.72 *</td>
<td>na</td>
<td>Planimeter</td>
<td>na</td>
<td>Williams 1977</td>
</tr>
<tr>
<td></td>
<td></td>
<td>map</td>
<td>5.7 per pair</td>
<td>na</td>
<td>Minimum area</td>
<td>na</td>
<td>Venables and Collopy 1989</td>
</tr>
<tr>
<td></td>
<td></td>
<td>VHF</td>
<td>3.2 v</td>
<td>na</td>
<td>Fixed KDE</td>
<td>LSCV</td>
<td>Vukovich and Kilgo 2013</td>
</tr>
<tr>
<td>Acorn Woodpecker</td>
<td><em>Melanerpes formicivorus</em></td>
<td>VHF</td>
<td>5.2</td>
<td>M &gt; F</td>
<td>MCP</td>
<td>na</td>
<td>Hooge 1995</td>
</tr>
<tr>
<td>Lewis's Woodpecker</td>
<td><em>Melanerpes lewis</em></td>
<td>na</td>
<td>6.1 per pair</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>Thomas et al. 1979</td>
</tr>
<tr>
<td>Gila Woodpecker</td>
<td><em>Melanerpes uropygialis</em></td>
<td>map</td>
<td>6.3 per pair</td>
<td>na</td>
<td>Planimeter</td>
<td>na</td>
<td>Hensley 1954</td>
</tr>
<tr>
<td>Black-backed Woodpecker</td>
<td><em>Picoides arcticus</em></td>
<td>VHF</td>
<td>204.0</td>
<td>na</td>
<td>MCP</td>
<td>na</td>
<td>Tremblay et al. 2009</td>
</tr>
<tr>
<td></td>
<td></td>
<td>VHF</td>
<td>89.0</td>
<td>na</td>
<td>BBMM, 95%</td>
<td>na</td>
<td>Tremblay et al. 2009</td>
</tr>
<tr>
<td>American Three-toed Woodpecker</td>
<td><em>Picoides dorsalis</em></td>
<td>VHF</td>
<td>59.6</td>
<td>M = F</td>
<td>Adaptive KDE</td>
<td>na</td>
<td>Pechacek and d'Oleire-Oltmanns 2004</td>
</tr>
<tr>
<td>Grey-headed Woodpecker</td>
<td><em>Picus canus</em></td>
<td>VHF</td>
<td>73.3</td>
<td>na</td>
<td>MCP</td>
<td>na</td>
<td>Rolstad and Rolstad 1995</td>
</tr>
<tr>
<td>Green Woodpecker</td>
<td><em>Picus viridis</em></td>
<td>VHF</td>
<td>98.0</td>
<td>na</td>
<td>MCP</td>
<td>na</td>
<td>Rolstad et al. 2000</td>
</tr>
<tr>
<td>Red-naped Sapsucker</td>
<td><em>Sphyrapicus nuchalis</em></td>
<td>VHF</td>
<td>13.2</td>
<td>M = F</td>
<td>MCP</td>
<td>na</td>
<td>Walters 1996</td>
</tr>
<tr>
<td>Red-breasted Sapsucker</td>
<td><em>Sphyrapicus ruber</em></td>
<td>VHF</td>
<td>5.9</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>Manning and Shepard 1999</td>
</tr>
<tr>
<td>Williamson's Sapsucker</td>
<td><em>Sphyrapicus thyroideus</em></td>
<td>map</td>
<td>6.8</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>Crockett 1975</td>
</tr>
<tr>
<td>Yellow-bellied Sapsucker</td>
<td><em>Sphyrapicus varius</em></td>
<td>map</td>
<td>3.1</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>Rushmore 1969</td>
</tr>
</tbody>
</table>
**Table 2.** Summary of brood data collected from Red-headed Woodpecker nests (n = 52 broods) in two focal habitat types in 2017 and 2018 breeding seasons at Fort AP Hill, Caroline County, Virginia. Nests in wetland habitat (n = 4) are not included in this table. In progress broods were nests that still contained chicks at the conclusion of our field season. Values in parentheses are one standard deviation.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Closed canopy</th>
<th>Savanna</th>
<th>Mann-Whitney U test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum # eggs</td>
<td>4.4 (± 0.8), n = 11</td>
<td>3.7 (± 0.8), n = 22</td>
<td>p = 0.04, U = 172</td>
</tr>
<tr>
<td>Maximum # chicks</td>
<td>2.8 (± 0.4), n = 9</td>
<td>2.2 (± 0.8), n = 24</td>
<td>p = 0.04, U = 153</td>
</tr>
<tr>
<td># Fledged chicks</td>
<td>2.3 (± 0.6), n = 3</td>
<td>2.1 (± 0.8), n = 9</td>
<td>-</td>
</tr>
<tr>
<td>Hatch proportion</td>
<td>68% (± 21.0), n = 7</td>
<td>55% (± 21), n = 14</td>
<td>-</td>
</tr>
<tr>
<td>Proportion chicks fledged</td>
<td>89% (± 19), n = 3</td>
<td>83% (± 20), n = 9</td>
<td>-</td>
</tr>
<tr>
<td>Proportion eggs fledged</td>
<td>53% (± 18), n = 3</td>
<td>50% (± 30), n = 5</td>
<td>-</td>
</tr>
<tr>
<td>Fledged broods</td>
<td>3 (21.4%)</td>
<td>14 (41.2%)</td>
<td>-</td>
</tr>
<tr>
<td>In progress broods</td>
<td>7 (50.0%)</td>
<td>11 (32.4%)</td>
<td>-</td>
</tr>
<tr>
<td>Failed broods</td>
<td>3 (21.4%)</td>
<td>8 (23.5%)</td>
<td>-</td>
</tr>
<tr>
<td>Uncertain fate</td>
<td>1 (7.1%)</td>
<td>1 (2.9%)</td>
<td>-</td>
</tr>
<tr>
<td>Total broods</td>
<td>14</td>
<td>34</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 3. Summary of data from Red-headed Woodpecker nests collected during early (before 7 July) and late (after 7 July) summer in 2017 and 2018 breeding seasons. Data on fledging rate was excluded because we were not able to observe the conclusion of the nesting period for late summer broods. Values are mean ± SD.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Early summer</th>
<th>Late summer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum # eggs</td>
<td>3.9 (± 0.9), n = 24</td>
<td>3.9 (± 0.8), n = 11</td>
</tr>
<tr>
<td>Maximum # chicks</td>
<td>2.4 (± 0.8), n = 30</td>
<td>2.4 (± 0.9), n = 5</td>
</tr>
<tr>
<td>Hatch proportion</td>
<td>58.0% (± 21), n = 18</td>
<td>64% (± 21), n = 4</td>
</tr>
<tr>
<td>(# eggs hatched / clutch size)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
**Figure 2.** A box plot of provisioning rate between GPS tagged (n = 11) and control Red-headed Woodpeckers (n = 14, p = 0.17, U = 179), showing no significant difference.
Table 4. Summary of the top ten models of provisioning (counts) by breeding Red-headed Woodpeckers at Fort A.P. Hill, Virginia, including: fixed effects in each model, log likelihood (logLik), AIC, AIC differences compared with the top performing model (ΔAIC), and Akaike weights. The base model, which included only chick age and brood size, was not among the top ten models.

<table>
<thead>
<tr>
<th>Model factors</th>
<th>logLik</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>chick age$^2 \times$ date + brood size + chick age</td>
<td>-277.0</td>
<td>574.0</td>
<td>0.0</td>
<td>0.184</td>
</tr>
<tr>
<td>chick age$^2 \times$ date + brood size + chick age + habitat</td>
<td>-276.5</td>
<td>575.0</td>
<td>1.0</td>
<td>0.113</td>
</tr>
<tr>
<td>chick age$ \times$ date + brood size + chick age$^2$</td>
<td>-277.7</td>
<td>575.3</td>
<td>1.3</td>
<td>0.094</td>
</tr>
<tr>
<td>chick age$^2 \times$ date + brood size + chick age + sex</td>
<td>-276.9</td>
<td>575.9</td>
<td>1.9</td>
<td>0.072</td>
</tr>
<tr>
<td>chick age$ \times$ date + brood size + chick age$^3$ + habitat</td>
<td>-277.1</td>
<td>576.1</td>
<td>2.1</td>
<td>0.063</td>
</tr>
<tr>
<td>chick age$^2 \times$ sex + brood size + chick age + habitat</td>
<td>-277.3</td>
<td>576.6</td>
<td>2.6</td>
<td>0.051</td>
</tr>
<tr>
<td>chick age$^2 \times$ sex + brood size + chick age + date</td>
<td>-277.3</td>
<td>576.6</td>
<td>2.6</td>
<td>0.051</td>
</tr>
<tr>
<td>chick age$^2 \times$ date + brood size + chick age + habitat + sex</td>
<td>-276.4</td>
<td>576.8</td>
<td>2.8</td>
<td>0.044</td>
</tr>
<tr>
<td>chick age$^2 \times$ sex + brood size + chick age + habitat + date</td>
<td>-276.5</td>
<td>577.1</td>
<td>3.1</td>
<td>0.040</td>
</tr>
<tr>
<td>chick age$ \times$ date + brood size + chick age + sex</td>
<td>-277.6</td>
<td>577.2</td>
<td>3.2</td>
<td>0.037</td>
</tr>
</tbody>
</table>
Table 5. Beta estimates, 95% confidence intervals, and p-values for factors used in the top performing models for overall provisioning, provisioning of fruit, and arthropods brought to nestlings by Red-headed Woodpeckers from 2017 – 2018.

<table>
<thead>
<tr>
<th>Response</th>
<th>Variable</th>
<th>β</th>
<th>95% CI</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Provisioning</td>
<td>chick age² × date</td>
<td>-0.001</td>
<td>-0.001, -0.0002</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>brood size</td>
<td>0.504</td>
<td>0.321, 0.687</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>chick age</td>
<td>0.107</td>
<td>0.053, 0.162</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Fruit</td>
<td>habitat (savanna) × date</td>
<td>-0.630</td>
<td>-1.240, -0.021</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>brood size</td>
<td>0.460</td>
<td>0.040, 0.879</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>chick age</td>
<td>0.075</td>
<td>0.035, 0.115</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>sex (male)</td>
<td>0.501</td>
<td>-0.010, 1.011</td>
<td>0.05</td>
</tr>
<tr>
<td>Arthropods</td>
<td>chick age</td>
<td>0.016</td>
<td>-0.004, 0.037</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>brood size</td>
<td>0.464</td>
<td>0.255, 0.673</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Figure 3. Predicted Red-headed Woodpecker provisioning rate from the top performing model that included an interaction between chick age and date. To display this result, we split the season into before and after the date of 7 July, which is after the mean fledge date of the first broods (3 July ± 6.9 SD, n = 9) and prior to the mean first egg date of the second broods (11 July ± 6.8 SD, n = 5), to represent early summer (before 7 July) and late summer (after 7 July).
Figure 4. Variation in Red-headed Woodpecker male and female provisioning proportions by brood ID for all pairs at Fort A.P. Hill, VA. Sex was not an important factor to predict brood level provisioning rate despite variation among individual pairs. Some important notes about the woodpeckers at these nests include: 1) the female at NB18C4 in 2018 was observed on video visiting the nest, but did not participate in any parental care activities, 2) in 2018, the first and second broods of Timber were raised by the same pair, 3) at 18CA2, the male found a new female in 2018, and 4) the female at Catfish in 2017 moved to the Noisy nest in 2018 and paired with a new mate.
**Table 6.** Summary of the top ten models for fruit (counts) delivered by breeding Red-headed Woodpeckers at Fort A.P. Hill, Virginia, including: fixed effects used in each model, log likelihood (logLik), AIC, AIC differences (ΔAIC), and Akaike weights. The base model, which included just chick age and brood size, was not among the top ten models.

<table>
<thead>
<tr>
<th>Model factors</th>
<th>logLik</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>date × habitat + chick age + brood size + sex</td>
<td>-112.7</td>
<td>263.4</td>
<td>0.0</td>
<td>0.232</td>
</tr>
<tr>
<td>date × habitat + chick age² + chick age + brood size + sex</td>
<td>-122.5</td>
<td>265.0</td>
<td>1.6</td>
<td>0.106</td>
</tr>
<tr>
<td>date × habitat + chick age + brood size</td>
<td>-124.5</td>
<td>265.0</td>
<td>1.6</td>
<td>0.104</td>
</tr>
<tr>
<td>chick age + brood size + date + habitat + sex</td>
<td>-124.7</td>
<td>265.5</td>
<td>2.1</td>
<td>0.082</td>
</tr>
<tr>
<td>date × chick age + brood size + habitat + sex</td>
<td>-123.8</td>
<td>265.5</td>
<td>2.1</td>
<td>0.081</td>
</tr>
<tr>
<td>date × habitat + chick age² + chick age + brood size</td>
<td>-124.2</td>
<td>266.4</td>
<td>3.0</td>
<td>0.051</td>
</tr>
<tr>
<td>date × chick age² + chick age + brood size + habitat + sex</td>
<td>-123.2</td>
<td>266.5</td>
<td>3.1</td>
<td>0.050</td>
</tr>
<tr>
<td>chick age² + chick age + brood size + date + habitat + sex</td>
<td>-124.3</td>
<td>266.6</td>
<td>3.2</td>
<td>0.046</td>
</tr>
<tr>
<td>date × chick age + chick age² + brood size + habitat + sex</td>
<td>-123.5</td>
<td>267.1</td>
<td>3.6</td>
<td>0.037</td>
</tr>
<tr>
<td>chick age × habitat + brood size + date + sex</td>
<td>-124.6</td>
<td>267.3</td>
<td>3.9</td>
<td>0.033</td>
</tr>
</tbody>
</table>
Figure 5. a) The predicted rate of fruit provisioning by Red-headed Woodpecker parents over the course of the breeding season and across two different habitats from the top performing model. b) A violin plot showing a significant difference in fruit provisioning rates between sexes (p = 0.05, z = -1.95, V = 239).
Table 7. Summary of the top ten GLMMs for arthropod prey (counts) delivered by breeding Red-headed Woodpeckers at Fort A.P. Hill, Virginia, including: fixed effects used in each model, log likelihood (logLik), AIC, AIC differences (ΔAIC), and Akaike weights.

<table>
<thead>
<tr>
<th>Model factors</th>
<th>logLik</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>chick age + brood size [base model]</td>
<td>-255.9</td>
<td>523.7</td>
<td>0.0</td>
<td>0.140</td>
</tr>
<tr>
<td>chick age + brood size + date</td>
<td>-255.1</td>
<td>524.2</td>
<td>0.5</td>
<td>0.110</td>
</tr>
<tr>
<td>chick age \times date + brood size</td>
<td>-254.4</td>
<td>524.8</td>
<td>1.1</td>
<td>0.081</td>
</tr>
<tr>
<td>chick age^2 \times date + brood size + chick age</td>
<td>-253.5</td>
<td>525.1</td>
<td>1.3</td>
<td>0.071</td>
</tr>
<tr>
<td>chick age^2 + chick age + brood size + date</td>
<td>-254.7</td>
<td>525.3</td>
<td>1.6</td>
<td>0.064</td>
</tr>
<tr>
<td>chick age^2 + chick age + brood size</td>
<td>-255.7</td>
<td>525.4</td>
<td>1.7</td>
<td>0.061</td>
</tr>
<tr>
<td>chick age + brood size + date + habitat</td>
<td>-254.9</td>
<td>525.8</td>
<td>2.0</td>
<td>0.051</td>
</tr>
<tr>
<td>chick age + brood size + date + sex</td>
<td>-254.9</td>
<td>525.8</td>
<td>2.0</td>
<td>0.051</td>
</tr>
<tr>
<td>chick age \times date + brood size + chick age^2</td>
<td>-254.0</td>
<td>526.0</td>
<td>2.3</td>
<td>0.045</td>
</tr>
<tr>
<td>chick age \times date + brood size + habitat</td>
<td>-254.2</td>
<td>526.3</td>
<td>2.6</td>
<td>0.038</td>
</tr>
</tbody>
</table>
Figure 6. Red-headed Woodpecker predicted arthropod provisioning per hour as a function of chick age and brood size from the top performing model.
Figure 7. Red-headed Woodpecker parental provisioning rates by prey item and habitat type (closed canopy and savanna) at Fort A.P. Hill, VA.
Table 8. An AIC comparison of the top ten models for brooding duration by breeding Red-headed Woodpeckers at Fort A.P. Hill, Virginia, including: fixed effects used in each model, log likelihood (logLik), AIC, AIC differences (ΔAIC), and Akaike weights.

<table>
<thead>
<tr>
<th>Model factors</th>
<th>logLik</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>chick age × sex + brood size</td>
<td>-110.4</td>
<td>246.8</td>
<td>0.0</td>
<td>0.428</td>
</tr>
<tr>
<td>chick age × sex + brood size + habitat</td>
<td>-109.3</td>
<td>248.5</td>
<td>1.8</td>
<td>0.176</td>
</tr>
<tr>
<td>chick age × sex + brood size + habitat + $T_{max}$</td>
<td>-107.6</td>
<td>249.2</td>
<td>2.4</td>
<td>0.128</td>
</tr>
<tr>
<td>chick age × sex + brood size + $T_{max}$</td>
<td>-109.8</td>
<td>249.6</td>
<td>2.8</td>
<td>0.104</td>
</tr>
<tr>
<td>chick age + brood size + sex</td>
<td>-114.1</td>
<td>250.3</td>
<td>3.5</td>
<td>0.074</td>
</tr>
<tr>
<td>chick age + brood size + sex + habitat</td>
<td>-112.9</td>
<td>251.9</td>
<td>5.1</td>
<td>0.033</td>
</tr>
<tr>
<td><strong>chick age + brood size [base model]</strong></td>
<td><strong>-117.3</strong></td>
<td><strong>252.5</strong></td>
<td><strong>5.8</strong></td>
<td><strong>0.024</strong></td>
</tr>
<tr>
<td>chick age + brood size + $T_{max}$ + sex</td>
<td>-113.7</td>
<td>253.4</td>
<td>6.7</td>
<td>0.015</td>
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<tr>
<td>chick age + brood size + $T_{max}$ + sex + habitat</td>
<td>-114.8</td>
<td>255.6</td>
<td>8.8</td>
<td>0.005</td>
</tr>
<tr>
<td>chick age + brood size + $T_{max}$ + brood size</td>
<td>-116.9</td>
<td>255.7</td>
<td>9.0</td>
<td>0.005</td>
</tr>
</tbody>
</table>
Figure 8. Predicted nestling brooding durations by adult Red-headed Woodpeckers as a function of chick age from the top performing model. Females brood nestlings more than males when chicks are young, but then stop brooding around day 10. Males continue to brood for short periods when chicks are older than 10 days.

Figure 9. Nest cleaning rates for male and female Red-headed Woodpeckers at Fort A.P. Hill, Virginia. Males have higher nest cleaning rates than females (p < 0.001, z = -4.32, V = 38).
Figure 10. Mass change (g per day) for GPS tagged vs. control breeding Red-headed Woodpeckers at Fort A.P. Hill, Virginia. There is no significant effect of GPS tags on mass change (p = 0.55, df = 35, t = 0.59).
Figure 11. a) Home range estimates of 95% KDE $h_{pi}$ for breeding female and male Red-headed Woodpeckers at Fort A.P. Hill, Virginia. b) Red-headed Woodpecker adult home range estimates (95% KDE $h_{pi}$) in early (before 7 July) and late (after 7 July) summer.
Table 9. An AIC comparison of models for 95% kernel home range estimates of breeding Red-headed Woodpeckers at Fort A.P. Hill, Virginia, including: the fixed effects used in each model, log likelihood (logLik), AIC, AIC differences (ΔAIC), and Akaike weights. Also included for each model factor are a beta estimate (β), 95% confidence interval, and p-value.

<table>
<thead>
<tr>
<th>Model factors</th>
<th>logLik</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Weight</th>
<th>β</th>
<th>95% CI</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>date</td>
<td>-34.9</td>
<td>75.9</td>
<td>0.0</td>
<td>0.336</td>
<td>-0.36</td>
<td>-0.76, 0.05</td>
<td>0.10</td>
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<tr>
<td>sex</td>
<td>-34.9</td>
<td>75.8</td>
<td>0.0</td>
<td>0.341</td>
<td>0.72</td>
<td>-0.10, 1.53</td>
<td>0.10</td>
</tr>
<tr>
<td>nearest neighbor distance</td>
<td>-35.6</td>
<td>77.3</td>
<td>1.4</td>
<td>0.167</td>
<td>0.26</td>
<td>-0.16, 0.68</td>
<td>0.23</td>
</tr>
<tr>
<td>habitat (savanna)</td>
<td>-36.0</td>
<td>78.1</td>
<td>2.2</td>
<td>0.111</td>
<td>-0.39</td>
<td>-1.28, 0.51</td>
<td>0.41</td>
</tr>
<tr>
<td>nest stage</td>
<td>-36.0</td>
<td>79.9</td>
<td>4.1</td>
<td>0.045</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>old chicks</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.27</td>
<td>-0.88, 1.42</td>
<td>0.65</td>
</tr>
<tr>
<td>young chicks</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-0.20</td>
<td>-1.28, 0.88</td>
<td>0.72</td>
</tr>
</tbody>
</table>
Figure 12. Home ranges displaying 95% (solid lines) and 50% (dotted lines) kernel density estimates of 5 Red-headed Woodpeckers at 3 nests during the 2017 breeding season in the Travis Lake recreation area. Nest snag locations are represented by triangles. SRGG is the only unpaired woodpecker; GOSY and YSOG make up a pair, as do RYSG and SUOB (sex of each indicated by symbols in legend). Northing and easting units are in UTMs.
APPENDIX A

Photographs of Red-headed Woodpecker chicks taken during the 2017 and 2018 breeding seasons at Fort A.P. Hill, Caroline County, Virginia. Photos were taken with a cavity inspection camera (IBWO) on an extendable 15 m measuring pole (Crain CMR Series) with a wireless color monitor. All photos are from nests with known hatch dates, and differences in speed of development may be due to brood size or hatching asynchrony.

**Image 2.** Red-headed Woodpecker chicks aged approximately 1 day.

**Image 3.** Chicks age 6 days, eyes still closed with no feather emergence.
Image 4. A single chick, aged 7 days, with emerging pinfeathers.

Image 5. Chicks aged 11 days with emerging pinfeathers. Eyes are beginning to open and chicks are beginning to cling to cavity walls.
Image 6. Chicks aged day 16 with feathers covering most of their body, but bare feather tracts still visible on head and scapulars.

Image 7. Day 18 chicks, clinging higher on the cavity walls with feathers fully covering their bodies and the gape flange (enlarged corners of beak) is virtually disappeared.
Image 8. Day 21, feathers are well-developed, pattern on primaries and secondaries visible.

Image 9. Day 28, chicks are fully developed.
Lynn (Abby) Abigail Walter was born on April 1, 1992 in Newark, Delaware. She graduated from the University of Delaware with a B.S. in Wildlife Conservation, a B.S. in Ecology, and minor in Marine Studies in December 2014. Abby’s passion for birds started while volunteering at Ashland Nature Center Hawk Watch in Hockessin, DE, which eventually led her to study ornithology abroad in Costa Rica. She began her first wildlife field position with researchers at the University of Delaware on the FRAME (Forest Fragments in Managed Ecosystems) project. Abby continued this research to complete an undergraduate thesis investigating the seasonal effects of vegetation cover and food availability on white-footed deer mouse nest box occupancy in urban forest fragments under the guidance of Dr. Jake Bowman. Abby took her first position after graduation in Charlestown, RI contributing to Piping Plover and shorebird conservation with the U.S. Fish and Wildlife Service. Her nest position was also with the USFWS, but in Crawfordville, FL where she helped to relocate Red-cockaded Woodpeckers from Apalachicola National Forest to St. Marks National Wildlife Refuge. Abby has been working with Red-headed Woodpeckers at Fort A.P. Hill since January 2016 and plans to pursue a career in conservation after the completion of her Master’s degree.