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Parental care in a sexually monomorphic Picid, the Red-headed Woodpecker

Cuidado parental un ave sexualmente monomórfica, el carpintero de cabeza roja

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ABSTRACT. Parental care is energetically costly and is thus shared by parents in many bird species. Little is known about how parental care is shared in pairs of sexually monomorphic species. Red-headed Woodpeckers (*Melanerpes erythrocephalus*) are a sexually monomorphic and socially monogamous species in an almost exclusively dimorphic family (> 99% of species; Picidae). We assessed duration of diurnal incubation and brooding and frequency of nestling provisioning and nest cleaning for individually marked breeding Red-headed Woodpeckers at Fort A.P. Hill, Virginia, USA. Individuals were genetically sexed using DNA from feather samples. In addition to parent sex, we evaluated the influence of nestling characteristics (brood size and nestling age) and exogenous factors (habitat type, date, and maximum daily temperature) on parental care behaviors. We recorded and analyzed video at nests during the incubation and nestling stages. We found that females diurnally incubate more than males and males almost exclusively remove fecal sacs from nests. Using generalized linear mixed models, we found females brood young nestlings more than males, but males are the only parent to enter the cavity when chicks are > 10 days old. We found provisioning peaked during the middle of the nestling period, and provisioning frequency was higher in early summer (before 7 July) compared to late summer. The seasonal reduction in provisioning could be related to resource availability but warrants further study. This division of reproductive roles is common in dimorphic woodpecker species and supports the existence of energetic constraints to successfully fledge altricial offspring.

RESUMEN. El cuidado parental es energéticamente costoso y, por lo tanto, es compartido por los padres en muchas especies de aves. Se sabe poco sobre cómo se comparte el cuidado parental en parejas de especies sexualmente monomórficas. El pájaro carpintero de cabeza roja (*Melanerpes erythrocephalus*) es una especie sexualmente monomórfica y socialmente monógama dentro de una familia casi exclusivamente dimórfica (> 99% de las especies; Picidae). Se evaluó la duración diurna de la incubación y calentamiento de los polluelos y la frecuencia de alimentación de los polluelos y limpieza de los nidos de pájaros carpinteros de cabeza roja marcados individualmente en Fort A.P. Hill, Virginia, EE.UU. Los individuos fueron sexados genéticamente utilizando ADN de muestras de plumas. Además del sexo de los padres, se evaluó la influencia de las características de los pollos (tamaño de la cría y edad de los pollos) y de los factores exógenos (tipo de hábitat, fecha y temperatura máxima diaria) sobre los comportamientos de cuidado por parte de los padres. Se grabó y analizó el vídeo de los nidos durante las fases de incubación y ade polluelos. Encontramos que las hembras durante el día incuban más que los machos y que los machos retiran casi exclusivamente los sacos fecales de los nidos. Utilizando modelos lineales mixtos generalizados, descubrimos que las hembras empollan a los polluelos jóvenes más que los machos, pero los machos son los únicos padres que entran en la cavidad cuando los polluelos tienen más de 10 días. Encontramos que la alimentación alcanzó su punto máximo en la mitad del periodo de polluelos, y la frecuencia de alimentación fue mayor a principios del verano (antes del 7 de julio) en comparación con el final del verano. La reducción estacional en la frecuencia de alimentación podría estar relacionada con la disponibilidad de recursos, pero merece un estudio más profundo. Esta división de los papeles reproductivos es común en las especies de pájaros carpinteros dimórficos y apoya la existencia de restricciones energéticas para que las crías altriciales salgan exitosamente del nido.

Key Words: *brooding; incubation; Melanerpes erythrocephalus; monomorphism; nest cleaning; parental care; provisioning*

INTRODUCTION

Breeding success in socially monogamous pairs of birds is maximized when parental care is coordinated between males and females (Emlen and Oring 1977). Shared parental care is demonstrated by 81% of bird species, yet the care contributed by each sex is rarely equal (Mock and Fujioka 1990, Cockburn 2006). Division of parental care can be influenced by a species' mode of nestling development and whether the sexes are monomorphic. Male parental care is more common in species with altricial young, in which the amount of development and growth required between hatching and fledging is greater than precocial young (Ketterson and Nolan 1994). Also, males of sexually monomorphic species tend to provide a greater proportion of parental care compared to males of dimorphic species (Verner and Willson 1969, Pierotti and Annett 1993, Ketterson and Nolan

1994, Badyaev and Hill 2003). In passerines (Passeriformes; an order of birds with altricial young), male nestling provisioning is common in both monomorphic and dimorphic species, and male incubation is more prevalent in North American monomorphic families than dimorphic families (Verner and Willson 1969, Ketterson and Nolan 1994). However, male care during both the incubation and brooding stages is not common in most dimorphic non-passerine families with altricial young, with an exception of the family Picidae (woodpeckers; Wiebe and Elchuk 2003, Rossmanith et al. 2009, Schroeder et al. 2013).

Biparental care has been observed in socially monogamous and 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

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al. 2013), White-headed Woodpeckers (*Picoides albolarvatus*, Kozma and Kroll 2013), Hairy Woodpeckers (*Leuconotopicus villosus*, Kozma and Kroll 2013), and Lesser Spotted Woodpeckers (*Picoides minor*, Wiktander et al. 2000, Rossmanith et al. 2009). Male woodpeckers sometimes incubate at equal or greater proportions compared to females and almost always incubate and brood nocturnally (Vehrencamp 2000, Pechacek et al. 2005). Both sexes brood offspring diurnally (Wiktander et al. 2000, Rossmanith et al. 2009, Chazarreta et al. 2011). Males also clean the nest of fecal material (Rossmanith et al. 2009, Chazarreta et al. 2011, Kozma and Kroll 2013, Gow et al. 2015, Tremblay et al. 2016) and help females to provision young (Jackson 1976b, Rossmanith et al. 2009, Chazarreta et al. 2011, Loverin et al. 2021). The high proportion of male parental care in woodpeckers could be a result of limitations imposed by nest substrate and cavity availability (Mock and Fujioka 1990), the demanding needs of altricial young (Temrin and Tullberg 1995), and/or certainty of paternity (Møller and Birkhead 1993, Matysioková and Remeš 2013). Woodpeckers face time and energetic constraints in excavating nest cavities and defending them from competitors and predators (Jackson 1976a, Kilham 1977, Ingold 1989). Additional demands for time come after a clutch is laid; offspring in North American species of woodpeckers require anywhere between 35-48 days of care from egg to fledging (Jackson 1976b). During this time, testosterone in male birds and extra-pair copulations are reduced (Michalek and Winkler 2001, Schwagmeyer et al. 2005) and male woodpeckers may provide parental care due to certainty of paternity (Møller and Birkhead 1993, Matysioková and Remeš 2013). Indeed, studies that have assessed paternity in woodpeckers indicate extra-pair young are rare (Haig et al. 1994, Michalek and Winkler 2001, Pechacek et al. 2005, Li et al. 2009, Kellam 2014).

Despite the general understanding that males in monomorphic bird species and dimorphic woodpeckers tend to provide high levels of parental care, little is known about the allocation of parental care between sexes in monomorphic woodpeckers. Woodpeckers are a family of birds in which males and females are similar in appearance but rarely identical—almost all woodpecker species are sexually dimorphic with regard to size or due to small plumage differences. The Lewis's Woodpecker (*Melanerpes lewis*) and Red-headed Woodpecker (*Melanerpes erythrocephalus*) are the only two species (comprising < 1%) of woodpeckers that are truly monomorphic (Table A1.1). The term "monomorphism" has been used to describe both monochromatic species with slight differences in plumage and monochromatic species with size dimorphism. However, "truly monomorphic" species exhibit no observable differences between males and females; sex cannot be determined using either physiological measurements, plumage characteristics, or even the presence of a brood patch. Sometimes, monomorphic woodpeckers will even exhibit reverse mounting behavior (Kilham 1977, Vierling et al. 2020). Genetic sexing of individual birds using biosamples has made studying and quantifying behaviors in sexually monomorphic species more feasible (Morinha et al. 2012) but has yet to be used to quantify allocation of parental care in either of the truly monomorphic woodpecker species. Quantifying the allocation of parental care in previously under-studied sexually monomorphic species adds valuable insight to our understanding of the evolution of shared parental care and sexual

monomorphism in birds. Further, such research expands our understanding of monomorphic species' natural history and allows for comparison to the significant body of research on parental care behaviors in dimorphic birds.

In this study, we assess whether males and females share parental care equally in a truly monomorphic species, the Red-headed Woodpecker—a socially monogamous bird of conservation concern (Frei et al. 2020, U.S. Fish and Wildlife Service 2021). We hypothesize that males and females will contribute relatively equally to diurnal parental care duties and exhibit similar allocation of effort as seen in dimorphic woodpeckers. Specifically, we predict that male and female Red-headed Woodpeckers will contribute equally to diurnal incubation, brooding, and provisioning. We expect males to be the primary parent to clean the nest of nestling fecal material, consistent with other woodpecker species. In addition to parent sex, we also assess whether nestling characteristics (chick age and brood size) as well as exogenous factors (temperature, date, and habitat type) influence parental care behaviors (brooding and provisioning). We predict there will be no difference in provisioning based on exogenous factors, but provisioning rates will increase as brood size and chick age increase. We also predict brooding durations will be reduced when temperatures are higher and as brood size increases and chick age increases. We acknowledge that other sex-specific parental care contributions occur, but are not assessed in this study, such as egg laying, cavity excavation, nocturnal incubation, and nocturnal brooding. We assume that nocturnal incubation and brooding carried out by male woodpeckers is no more energetically expensive than roosting alone, and therefore would not be expected to influence diurnal activities. To conduct our study, we quantify parental care behaviors of individually marked and genetically sexed Red-headed Woodpeckers using video recordings focused on the outside of nest cavities and model whether variation in these parental care behaviors is explained by parent sex, nestling characteristics, and exogenous factors.

METHODS

Study site
We conducted this study at Fort A.P. Hill (38.0718°N, 77.3274° W), a 31000 ha military installation in Caroline County, Virginia, USA. The army base is a mostly natural landscape composed of a complex mosaic of oak savanna, pine savanna, wetland, and closed-canopy forest. Savannas and forests have been managed for decades through prescribed fire and timber harvesting practices.

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") to study Red-headed Woodpeckers. These sites 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 breeding Red-headed Woodpeckers (Nickley and Bulluck 2019). Habitats were classified as savanna or closed-canopy based on 2016 National Agriculture Imagery Program (NAIP) aerial imagery. 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).

Banding methods
We captured and banded woodpeckers from February to May in 2016, and April to July in 2017 and 2018, using either canopy mist nets or a pole net. Mist nets were elevated with a rope pulley system on living trees adjacent to nest snags to target individuals as they approached or departed nest cavities (Kilgo and Vukovich 2012). The pole net was placed over a nest cavity entrance at dawn. Captured woodpeckers were color-banded with a unique combination of three colors and one U.S. Fish and Wildlife Service aluminum band (Permit No. 23486; U.S. Geological Survey Bird Banding Laboratory, Laurel, Maryland, USA). We recorded body mass and standard body measurements. We collected three breast feathers for genetic sexing by Animal Genetics (Tallahassee, Florida, USA). The sex of banded woodpeckers was unknown to researchers until all field data were collected to eliminate any potential for bias.

Monitoring nests
We monitored nests from mid-April through early August in 2017 and 2018. From April through May we searched for new nest snags (dead trees with a nest cavity) and re-visited previously active nest snags to ascertain if they were still in use. After identifying active nests in 2017, we checked nests by observing 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 checked nest contents with a cavity inspection camera (IBWO.org, Little Rock, Arkansas, USA) on an extendable 15 m Crain CMR Series Measuring Rod (SECO Manufacturing, Redding, California, USA). We did not check active nests with cavity entrances beyond the limits (> 15 m) of our extendable pole. The cavity camera allowed us to collect data on the nest stage, number of eggs, brood size, chick age, and nest fate with more certainty than our previous observation methods. Before inserting the cavity inspection camera into a nest cavity, we knocked on the snag to flush potentially incubating woodpeckers. We monitored active nests an average of once every 6 days (SD ± 1.83), depending on access to training areas.

We determined the age of chicks using hatch day when possible. When hatch day was not known, we estimated chick age by 1) using a known fledge date (n = 2 where fledging was observed), assuming the nestling period was 26 days (Frei et al. 2020), or 2) comparing cavity camera images of the chicks with an unknown age to cavity camera images of chicks with a known hatch date. Images taken from nest cavities were used to determine and describe developmental milestones such as eye opening, pinfeather emergence, feather development, and additional behaviors that have not yet been published at length for this species (Figs. A2.1-9).

Recording parental care behavior observations
We placed FS400 Flash Memory camcorders (Canon, Ota City, Tokyo, Japan) on tripods within 10 m of nest snags to record parental care behaviors at the nest. Cameras were focused on the

nest cavity entrance and recorded video on fair weather days anywhere between 06:35-15:15 from May to 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 identified by their color band combination, and 3) nests in videos during the nestling stage contained a known number of chicks with known age. We identified and timestamped adult woodpecker behaviors at the nest using BORIS (Behavioral Observation Research Interactive Software, Friard and Gamba 2016). We associated behaviors with a woodpecker's unique color band combination or by name for each unbanded mate, with the assumption 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 utility poles for cavities in Illinois (Atterberry-Jones and Peer 2010). For analysis, we included the following four parental care behaviors in the ethogram: incubating eggs (in-cavity for > 3 min), brooding (in-cavity for > 1 min and not followed by a cleaning event), feeding chicks (delivering a food item to the nest), and nest cleaning (removal of fecal material or soiled wood chips from the nest). Incubation and brooding had duration times while feeding chicks and nest cleaning were point events.

Parental care analyses
We recorded incubation length for each parent during videos of nests with eggs. For nests with chicks, we recorded brooding length, the number of provisioning visits, and the number of cleaning events for each parent. To test for differences in incubation duration between sexes, we used a paired Student's t-test. We used a Wilcoxon signed-rank test to compare nest cleaning rates between sexes because the data were not normal.

To analyze brooding durations and provisioning counts, we ran generalized linear mixed models (GLMMs) using R package *glmmTMB* (Brooks et al. 2017). To determine the best distribution to use for our models, we compared model fit (AIC) for the brooding models using a non-zero-inflated Gaussian error distribution, a zero-inflated distribution, and a truncated binomial hurdle model. A hurdle model accounts for a 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). Likewise, for the provisioning models (count data) that contained many zeros, we compared model fit using a zero-inflated negative binomial distribution to a Poisson error distribution. For both brooding and provisioning analyses, video length was used as an offset in the models to account for variable recording time among samples (Foster and Bravington 2013).

To model brooding duration and provisioning rate, we compared models that included parent sex, nestling characteristics (chick age and brood size), and exogenous factors (temperature or date and habitat type). Descriptions of models and their associated variables can be found in Table 1. For nestling characteristics, we first assessed whether a linear or quadratic association with chick age was a better predictor of these parental care behaviors. We considered a quadratic effect of chick age because we expected brooding duration and provisioning to vary in a nonlinear fashion as chicks developed. The nestling characteristics of chick age and

Table 1. Description of models compared in our assessment of Red-headed Woodpecker (*Melanerpes erythrocephalus*) brooding and provisioning at Fort A.P. Hill, Virginia, USA. Maximum temperature was used in brooding models and date was included in provisioning models. [†]Model only included in provisioning models, not brooding models

Model	Variables Included
Null model	Random effects of woodpecker ID and brood ID (included in all models)
Time of day and nestling characteristics	Video start time + chick age + brood size (included in all models except null)
Parent sex	Sex
Exogenous factors	Habitat + (temperature (T_{max}) OR date)
Parent sex and exogenous factors	Sex + habitat + (temperature (T_{max}) OR date)
Parent sex - chick age interaction	Sex × chick age
Date - chick age interaction[†]	Date × chick age
Global with parent sex - chick age interaction	Sex × chick age + habitat + (temperature (T_{max}) OR date)
Global with date - chick age interaction[†]	Date × chick age + habitat + (temperature (T_{max}) OR date)

brood size were included in all models, except for the null model, because these factors are well known to influence parental care in birds (Wiktander et al. 2000, Rossmanith et al. 2009, Musgrove and Wiebe 2014). All models included random effects of woodpecker ID and brood ID because some woodpeckers had more than one nesting attempt and we sometimes recorded parental care at the same nest on different days during the nestling period. For exogenous factors, we included temperature, date, and habitat type as predictors of parental care behaviors. We used date as a predictor in provisioning models. For brooding duration models, we used maximum daily temperature (T_{max}) as a predictor instead of date because we expected T_{max} to be a better estimate of brooding time and these two variables were correlated ($P <$ 0.001, $t = 5.0$, df = 86). Moreover, we chose to use T_{max} rather than minimum daily temperature (T_{min}) because our videos were recorded during the warmer half of the day, and because we found T_{max} and T_{min} were significantly positively correlated during both the incubation period ($P < 0.001$, $\rho = 0.7$) and nestling period ($P < 0.001$, $\rho = 0.5$) using the Spearman rank correlation test. 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, Virginia, USA (38.2022°N, -77.3747°W) located 8.4 km from our study site. We used habitat type, classified as closed-canopy or savanna, as the second exogenous factor in both brooding and provisioning models. Habitat was included because vegetation characteristics could cause differences in food availability and/or competitors and influence the time budget of parents and their ability to care for their young. Video start time was included in brooding and provisioning models to account for temporal effects on behavior. We assessed a chick age × parent sex interaction for both provisioning rate and brooding duration because we were interested in whether sexes differed in how they adjusted their allocation of effort as chicks matured. Lastly, we assessed a chick age × date interaction for provisioning because we suspected chicks may be fed more earlier in the season than later in the season (when it may be drier and hotter, leading to lower food availability).

Models were ranked using AIC$_c$, top models were chosen based on the lowest ΔAIC$_c$ value, and models with ΔAIC$_c$ < 2.0 were considered equally supported. Predictions for brooding time and provisioning rate were generated from the top-performing models and then plotted using *stats::predict* in R (R Core Team 2021). Brooding durations were adjusted using video length to determine

brooding min per hr. Provisioning counts were adjusted using each sample's video length and brood size to calculate provisioning visits per chick per hr. We tested for overdispersion and correct model specification by running diagnostic tests on the scaled residuals using the DHARMa package in R (Hartig 2019). All analyses were conducted in R 4.0.5 (R Core Team 2021).

RESULTS

Nest monitoring and chick development
We monitored a total of 74 Red-headed Woodpecker nesting attempts (broods) in 48 nest cavities; 14 were in closed-canopy forest and 34 in savanna. Out of 35 individual banded woodpeckers, five were seen in both years. Three of those five had a new mate. We observed that two of the five woodpeckers moved to new nest snags in the second year, 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 female mate. In 2017, we monitored 39 broods of 24 pairs; in 2018 we monitored 35 broods of 26 pairs. We checked 24 (61.5%) of the 2017 broods and 28 (80.0%) of the 2018 broods with a cavity inspection camera. Broods that were not checked with a cavity inspection camera either fledged before we obtained the camera (in 2017) or were too high for the extendable pole. Out of all nests monitored ($N = 74$ broods), we had nest contents information for 52 (70.2%). Of 13 failed broods, eight (61.5%) failed during the egg stage and five (38.5%) during the chick stage. The cause of these failures is not known. Although we found fewer nests in closed-canopy forest, on average there were more eggs and chicks in closed-canopy nests than in savanna nests (Table 2). Early and late summer broods showed no difference in clutch size (Table 3). We regularly observed two or more brooding attempts by pairs in a breeding season, which is not uncommon (Ingold 1987, Venables and Collopy 1989).

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 observed hatch date 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 five chicks in a nest, but this was shortly after hatching, and brood reduction (number of nestlings decreasing between nest checks) was common (44.4% of broods reduced). Mean brood size was 2.3 chicks (SD = 0.8, $N = 36$). Based on our ethogram, the oldest chicks that an adult "brooded" (in-cavity > 1 min and not followed by a cleaning event) were a

Table 2. Summary of brood data collected from Red-headed Woodpecker (*Melanerpes erythrocephalus*) nests (N = 48 broods, 33 of which were found during incubation) during the 2017 and 2018 breeding seasons at Fort A.P. Hill, Virginia, USA. Values in parentheses are one standard deviation. Hatch proportion is the proportion of eggs that hatched. Proportion chicks fledged is the number of fledges from all the nests divided by the total number of chicks in all the nests. Proportion eggs fledged is the number of fledges from all the nests divided by the total number of eggs in all the nests. Fledged broods are broods that fledged chicks. In-progress broods were nests that still contained chicks at the conclusion of our field season in early August. Failed broods are the number of broods that had prematurely disappeared, and we assumed depredated eggs or chicks. Uncertain fate is a category used for 2 broods with chick age data too incomplete to determine if the nestlings fledged or failed. Total broods are the total number of broods found per habitat. [†]These nests were not included in any video analyses.

Metric	Closed canopy	Savanna	Mann-Whitney U test
Maximum # eggs	4.4 (± 0.8), *N* = 11	3.7 (± 0.8), *N* = 22	*P* = 0.04, *U* = 172
Maximum # chicks	2.8 (± 0.4), *N* = 9	2.2 (± 0.8), *N* = 24	*P* = 0.04, *U* = 153
# Fledged chicks	2.3 (± 0.6), *N* = 3	2.1 (± 0.8), *N* = 9	-
Hatch proportion	68% (± 21.0), *N* = 7	55% (± 21), *N* = 14	-
Proportion chicks fledged	89% (± 19), *N* = 3	83% (± 20), *N* = 9	-
Proportion eggs fledged	53% (± 18), *N* = 3	50% (± 30), *N* = 5	-
Fledged broods	3 (21.4%)	14 (41.2%)	-
In progress broods	7 (50.0%)	11 (32.4%)	-
Failed broods	3 (21.4%)	8 (23.5%)	-
Uncertain fate[†]	1 (7.1%)	1 (2.9%)	-
Total broods	14	34	-

pair of 19-day-old nestlings, by a male, for a duration of 6.3 min. 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 that chicks 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 previously reported nestling periods of 27 days (Bent 1939) and 29 days (Yohannes 2017).

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 (Fig. A2.4, Fig. A2.5). Eyes began to open as slits by day 11-12 and were fully open by day 16 (Fig. A2.5, Fig. A2.6). Chicks were seen clinging to the cavity walls as early as day 11 (Fig. A2.5). Downy feathers covered the nestlings by day 16, but feather tracts were still visible on chicks' crowns and scapulars (Fig. A2.6). By day 18, feather tracts were no longer visible (Fig. A2.7). Chicks were seen with their heads out of cavity entrances starting on day 16. Chicks were often seen aggressively begging for food out of the cavity entrance for ~1 wk before fledging.

We recorded two chicks fledging from separate nests on video. In one fledge event, the chick was recorded calling with chattering "*rrr rrr*" contact calls (Short 1982, Jackson 1976a) 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. A sibling in each nest emerged with a head out of the cavity entrance once the fledglings had departed. Recordings of both fledge events are available via Cornell Laboratory of Ornithology Macaulay Library (https://search.macaulaylibrary.org/catalog?assetId=ML488612,%20ML488613).
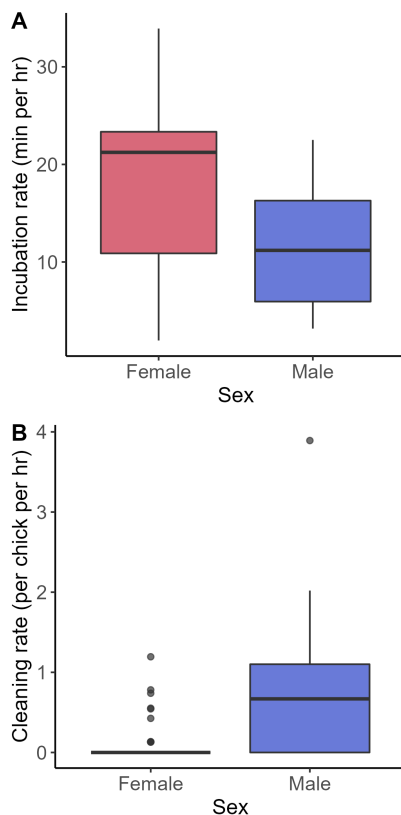
Parental care

To assess diurnal incubation rates, we used 35 total hr of video across 10 broods with eggs in nine different nest cavities (7 broods in 2017, 3 broods in 2018, 1 cavity re-used in 2018). We assessed incubation duration for each parent woodpecker (*N* = 20) from videos ranging 120-237 min in length (mean = 190 ± 50.5 SD). We retained 135 incubation events (duration > 3 min) and excluded one because the parent was unidentifiable. Females incubated at longer intervals (8.3 min ± 5.9 SD, *N* = 74) than males (6.9 min ± 3.9 SD, *N* = 61). Incubation durations were summed for each parent in each video, then converted to a rate (min per hr) by dividing by the video length. The diurnal incubation rate by females was about twice as long as males, on average, although this was not statistically significant (*P* = 0.07, *t* = 2.0, df = 10, Fig. 1a).

To assess rates of parental care during the nestling stage, we used 128 total hr of high-quality video across 21 broods in 18 different nest cavities (10 broods in 2017 and 11 in 2018) to quantify brooding rates, provisioning counts, and cleaning counts for each parent woodpecker (*N* = 35). Videos ranged from 41-243 min in length (*N* = 88), with a mean duration of 174 min (SD ± 51.8). A total of 1650 parental care observations were recorded and 4 (0.2%) observations were excluded from analysis because the parent was unidentifiable. We analyzed a total of 115 brooding events, 1307 provisioning events, and 224 cleaning events. We also counted 214 events categorized as "visits" in which a parent entered the nest cavity, did not stay inside longer than 1 min, and did not leave with a fecal sac. Chick age and date were not correlated (τ = -0.04, *P* = 0.6, *z* = -0.6). Parental care did not differ between years; specifically, brooding rates (*P* = 0.86, *U* = 941.5), provisioning rates (*P* = 0.56, *U* = 1030), and cleaning rates (*P* = 0.46, *U* = 877) were not different, so we pooled data from both years. Males cleaned the nest (mean = 0.72 ± 0.12 SE) at a rate (per chick per hr) significantly higher than females (mean = 0.11 ± 0.04 SE, *P* < 0.001, *z* = -4.32, V = 38, Fig. 1b).

Table 3. Summary of Red-headed Woodpecker (*Melanerpes erythrocephalus*) nesting data collected during early summer (before 7 July) and late summer (after 7 July) in the 2017 and 2018 breeding seasons Fort A.P. Hill, Virginia, USA. We split the season using 7 July, which is the median date between the mean fledge date of the first broods (3 July ± 6.9 SD, N = 9) and 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). 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.

Metric	Early summer	Late summer
Maximum # eggs	3.9 (± 0.9), *N* = 24	3.9 (± 0.8), *N* = 11
Maximum # chicks	2.4 (± 0.8), *N* = 30	2.4 (± 0.9), *N* = 5
Hatch proportion (# eggs hatched per clutch size)	58.0% (± 21), *N* = 18	64.0% (± 21), *N* = 4

Fig. 1. Red-headed Woodpecker (*Melanerpes erythrocephalus*) male and female diurnal incubation rates and nest cleaning rates from video recordings collected between sunrise and 15:15 at Fort A.P. Hill, Virginia, USA in 2017 and 2018. A) Females incubate more than males, although this was not statistically significant. B) Males clean the nest of fecal material significantly more than females.
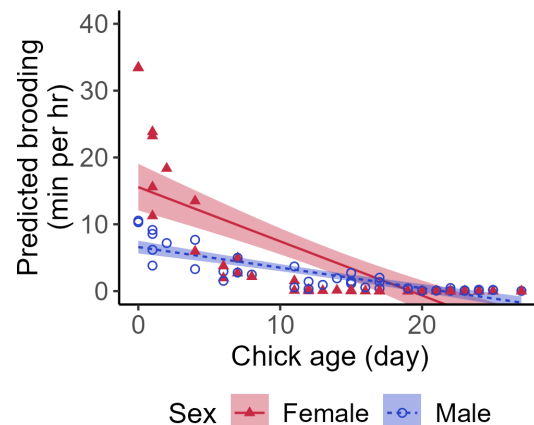

intervals (7.3 min ± 6.0 SD, N = 62) than males (4.3 min ± 2.9 SD, N = 53) and had a maximum diurnal brooding length (30.2 min) twice as long as males (15.1 min). Nestling characteristics and exogenous factors were not supported as important predictors of brooding.

Table 4. An AIC$_c$ comparison for seven models of brooding duration by breeding Red-headed Woodpeckers (*Melanerpes erythrocephalus*) at Fort A.P. Hill, Virginia, USA. See Table 1 for description of variables included in each model. [†]The number of parameters in the model [‡]AIC$_c$ value = 332.2

Model	df[†]	logLik	ΔAIC$_c$	weight
Parent sex - chick age interaction[‡]	17	-144.7	0.0	0.827
Parent sex	15	-150.2	4.8	0.077
Global with parent sex - chick age interaction	21	-140.8	5.4	0.055
Time of day and nestling characteristics	13	-153.9	6.5	0.032
Parent sex and exogenous factors	19	-146.4	9.7	0.007
Exogenous factors	17	-150.3	11.0	0.003
Null model	7	-180.8	44.9	0.000

Fig. 2. Predicted nestling brooding durations by adult Red-headed Woodpeckers (*Melanerpes erythrocephalus*) 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. The regression line includes 95% confidence intervals.

In the brooding models, the negative binomial hurdle distribution had a better fit than the zero-inflated Gaussian (ΔAIC = 72.1), Poisson hurdle (ΔAIC = 207.1), or Gaussian (ΔAIC = 382.1) distributions. The best-fitting model for brooding included an interaction between parent sex and chick age (Table 4, Fig. 2). Females brood nestlings significantly more than males when chicks are young (< 10 days), but males continue to brood older chicks for short periods. Females brooded diurnally at longer

The mean provisioning rate per parent, across all broods and chick ages, was 4.8 (SD ± 3.8) visits per hr and 2.4 (SD ± 1.7) visits per chick per hr. Assuming chicks were provisioned equally, each chick was fed an average of 4.8 times (SD ± 2.7) per hour with the combined effort of both parents. There were seven videos in which one adult in the pair did not provision (these videos had a similar average length, 177 min ± 43.5 SD). In five of the seven cases, the female did not provision, and five of the seven were in savanna habitat.

In the provisioning models, the zero-inflated negative binomial distribution had a better fit than the negative binomial (ΔAIC = 27.2) and Poisson error distribution (ΔAIC = 103.0). Provisioning models with a quadratic term for chick age (i.e., when chick age was squared) performed better than models with a linear effect of chick age (ΔAIC = 7.5). Our highest-ranking provisioning model included a date by chick age interaction (Table 5, Table 6). This model suggests that Red-headed Woodpeckers provision slightly more in early summer (before July 7) compared to late summer (Fig. 3a) and that the highest rates of provisioning are in the middle of the nestling stage. In addition, brood size was an important factor in predicting provisioning rates (Fig. 3b); larger broods are provisioned more than smaller broods.

Table 5. An AIC_c comparison for nine models of provisioning (counts) by breeding Red-headed Woodpeckers (*Melanerpes erythrocephalus*) at Fort A.P. Hill, Virginia, USA. See Table 1 for description of variables included in each model. [†]The number of parameters in the model [‡]AIC_c value = 579.3

Model	df[†]	logLik	ΔAIC$_c$	weight
Date - chick age interaction[‡]	12	-275.6	0.0	0.605
Exogenous factors	11	-278.7	3.7	0.097
Time of day and nestling characteristics	9	-281.5	4.0	0.084
Global with date - chick age interaction	14	-274.9	4.2	0.072
Global with parent sex - chick age interaction	14	-275.3	5.1	0.047
Parent sex - chick age interaction	12	-278.2	5.3	0.043
Parent sex and exogenous factors	12	-278.6	6.2	0.028
Parent sex	10	-281.4	6.4	0.025
Null model	5	-303.7	39.0	0.000

Although parent sex was not included in the top provisioning model, we did find variation in the proportion of provisioning by each sex at the brood level (Fig. A3.1). We did a post-hoc analysis to see if we could explain the variation in the proportion of provisioning events done by females and found that none of our measured covariates (habitat, time of day, number of chicks, date, chick age, video length, or distance to nearest breeding pair) were significant predictors.

We found no evidence of overdispersion or model misspecification for brooding or provisioning models based on residual plots and diagnostic tests in the DHARMa package (dispersion test $P = 0.432$ for best performing brooding model; $P = 0.72$ for the best performing provisioning model).
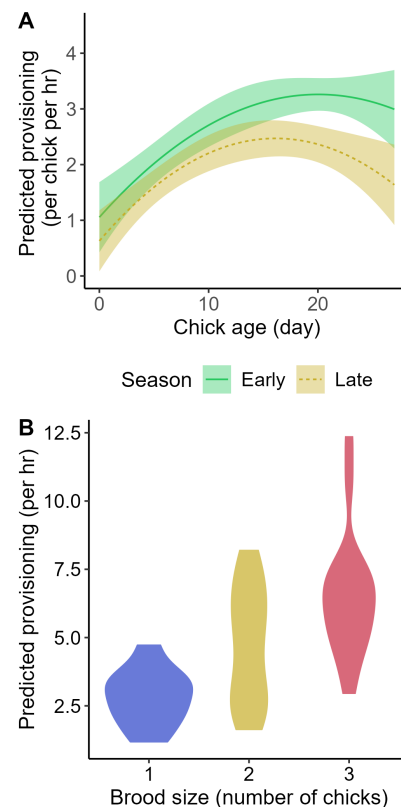
DISCUSSION
Through video observations of color-banded Red-headed Woodpeckers at the nest, we found diurnal parental care behaviors are shared relatively equally between the sexes of this truly monomorphic species. Specifically, females diurnally incubate

Table 6. Beta estimates, 95% confidence intervals, and p-values for fixed effects used in the top-performing models for overall provisioning and brooding of breeding Red-headed Woodpeckers (*Melanerpes erythrocephalus*) at Fort A.P. Hill, Virginia, USA in 2017 and 2018.

Response	Variable	β	95% CI	p
Brooding [conditional model]	Parent sex	-1.046	-1.645, -0.448	<0.001
	Chick age	-0.206	-0.318, -0.095	<0.001
	Video start time	0.014	-0.232, 0.260	0.912
	Brood size	-0.271	-0.705, 0.164	0.222
	Parent sex x chick age	0.134	0.015, 0.253	0.027
Provisioning	Chick age	0.119	0.064, 0.173	<0.001
	Chick age^2	-0.003	-0.005, -0.001	0.001
	Date	-0.067	-0.364, 0.231	0.661
	Video start time	0.087	-0.018, 0.192	0.105
	Brood size	0.542	0.354, 0.730	<0.001
	Date x chick age^2	-0.002	-0.004, 0.000	0.108

Fig. 3. Predicted Red-headed Woodpecker (*Melanerpes erythrocephalus*) provisioning rates from the top-performing model. Values reported are provisioning rates of just one parent. A) Older chicks are provisioned more frequently than younger chicks, and provisioning frequency is lower in "late summer" (after 7 July) compared to "early summer" (before 7 July). The shaded area behind the curve represents 95% SE. B) Violin plots show nests with larger broods are provisioned more frequently. Their shape reflects how data are distributed, with wider areas indicating more values at that rate of provisioning.

and brood young nestlings more than males; we did not find incubation to be significantly greater, although brooding was. Males almost exclusively clean the nest of fecal material, and provisioning rates are equal between the sexes. These results align with what is known about sexually dimorphic woodpecker species. Such consistency between dimorphic and monomorphic species suggests that biparental care is likely more linked to the life history of woodpeckers than to plumage. Male care is critical for reproductive success in woodpeckers due to their role in excavating nest cavities and nocturnally incubating and brooding.

We observed Red-headed Woodpecker females diurnally brood nestlings significantly more and incubate eggs negligibly more than males. Incubation and brooding are considered to have relatively low energy requirements, which could be why females are able to contribute so much time to these activities after laying eggs (Williams 1996). While females brood and incubate, males may be assisting the nest in other ways, such as by defending their territory and nest cavity from diurnal nest predators, cavity usurpers, and other pairs of Red-headed Woodpeckers (Reller 1972, Kilham 1977, Berl et al. 2013). We did not observe more than the occasional European Starling (*Sternus vulgaris*) at our study site, but often witnessed Red-headed Woodpecker intraspecific aggression. Red-headed Woodpeckers are highly dependent on nest snag availability, which may be clustered across the landscape, and can result in overlapping territories (Kilham 1977, Kilgo and Vukovich 2014). Kilham (1977) noted that males are the primary defender during such agonistic interactions.

The most important factors we found to be associated with brooding rates for Red-headed Woodpeckers are parent sex and chick age. We did not find the exogenous factors of habitat type nor T_{max} to influence brooding rates, though these covariates were coarse and biased in relation to the time of day we recorded video, which we discuss in more detail below. We expected higher daily temperatures would reduce required brooding time because Red-headed Woodpecker nests are typically in standing dead trees or in dead limbs of living trees in open areas (Frei et al. 2020), thereby receiving more sunlight that could increase the internal nest temperature. However, T_{max} may have had a minimal impact on cavity temperatures. Tree diameter is one of the strongest factors affecting the maximum and the stability of internal cavity temperature (Wiebe 2001); larger trees insulate nest cavities from temperature fluctuations better than smaller trees. Red-headed Woodpeckers may prefer the use of large (i.e., greater diameter) dead trees for nest cavities (Nickley and Bulluck 2019) partly for this reason. We found females brood chicks during the day until they are ~10 days old, at which point nestlings start to grow pinfeathers and are better able to thermoregulate (Dawson and Evans 1957). Ten days after hatching, males almost exclusively enter the cavity for "brooding" events. Our ethogram classified any time a parent entered the cavity for > 1 min and did not leave with a fecal sac during the nestling stage to be a brooding event. However, cavity entries during the later nestling stage have also been observed in male Black-backed Woodpeckers (*Picoides arcticus*, Tremblay et al. 2016) and Northern Flickers (Wiebe and Elchuk 2003), and it is thought that rather than brooding, males are likely stimulating nestling defecation and/or adding fresh wood chips by excavating inside the cavity (Backhouse 2005, Chazarreta et al. 2011, Tremblay et al. 2016). This is also likely

for our observed "brooding" events by males later in the nestling period.

Males remove fecal material from the nest more than females in many woodpecker species (Wozniak and Mazgajski 2003, Rossmanith et al. 2009, Chazarreta et al. 2011, Kozma and Kroll 2013, Gow et al. 2015, Tremblay et al. 2016). Our result that Red-headed Woodpecker males were the primary nest cleaners is consistent with research in other woodpecker species as well as one study on Red-headed Woodpeckers that used behavioral-based sexing (Venables and Collopy 1989, $N = 2$ broods). It is not clear why males would be the primary nest cleaners in woodpeckers, but Wozniak and Mazgajski (2003) suggested the color of soiled material inside the cavity may trigger a response in males to remove fecal material and add wood chips to keep it clean. Hormones such as corticosterone can influence rates of nest cleaning, but whether levels of these hormones differ between the sexes in Red-headed Woodpeckers is unknown (Gow et al. 2015). However, one explanation may be that because males nocturnally brood nestlings (Vehrencamp 2000, Pechacek et al. 2005, Chazarreta et al. 2011), they are simply attempting to reduce their own exposure to infection, parasites, and/or predation (Ibáñez-Álamo et al. 2014, Azcárate-García et al. 2019). In addition, males may allocate more effort to clean the nest to compensate for females' effort toward egg laying, diurnal incubation, and diurnal brooding of young nestlings. We found males cleaned the nest once every 1.4 hr on average, but females only once every 9.1 hr. Because males were 6.5 times more likely than females to clean the nest of fecal material and soiled wood chips, future studies on marked populations of Red-headed Woodpeckers may be able to use nest cleaning rates as a reliable way to infer parent sex without genetically sexing individuals.

As we predicted, Red-headed Woodpecker provisioning rate varies with the developmental stage of nestlings, peaking around 15 days post-hatching. Provisioning remained relatively high from day 15 until fledging for observations we recorded in the early season, but later in the nestling season, provisioning declined after day 15 post-hatching. Loverin (2021) also found a peak in provisioning of Black-backed Woodpeckers at day 16 of the nestling period and in earlier nests compared with later nests. The decline we observed in provisioning after day 15 in the late season, but not the early season, can be explained by two alternative hypotheses. One is that the availability of food declines as the nesting season progresses, and the other is that larger food items are available later in the season, allowing for fewer provisioning trips to provide the same level of nutrition. We were not able to identify food items nor animal taxon for a large enough portion of parental provisioning trips to include food type or size in our analyses. We are therefore unable to test these two alternative hypotheses to explain the decline in provisioning in later season nests.

Though we did not explicitly include prey type or size in our analyses, we can speak generally about the types of food items brought to nestlings by Red-headed Woodpecker parents in our study system and compared with another recent study. We observed Red-headed Woodpeckers foraging for and provisioning nestlings with insects and arachnids from a variety of taxonomic orders as well as blackberries (*Rubus spp.*), blueberries (*Vaccinium pallidum*), and huckleberries (*Gaylussacia frondosa, G. baccata*).

Vukovich and Kilgo (2019) have described Red-headed Woodpecker nestling diet in detail and reported a decrease in the proportion of plant matter fed to nestlings in South Carolina at the end of the breeding season. However, the fruiting species we saw being fed to nestlings at Fort A.P. Hill flower early and produce fruit throughout the summer, suggesting no issue with abundance (Stiles 1980, Pavlovic et al. 2011, Gallinat et al. 2018). Red-headed Woodpeckers are excellent flycatchers that depend on aerial insects to supplement their summer diet of ground-dwelling and arboreal insects and fruit (Conner 1979); it is possible that aerial insect declines across North America (Sánchez-Bayo and Wyckhuys 2019) could be a limiting factor to late-season provisioning. Further study is needed to quantify soft mast production and insect abundance near Red-headed Woodpecker nests to determine if our observed reduction in late-season provisioning rates is common and if so, whether it is a function of food availability or differences in prey type or size.

Although the mean provisioning rate was not different between Red-headed Woodpecker males and females across all observed nests, the ratio of male-to-female provisioning varied quite a bit among broods. In some broods the male was the primary provider while the female was the primary provider in others. This may simply be due to our videos capturing a snapshot in time (a few hours in a day); in other words, this observed variation may be due to chance. In an effort to elucidate if individual variation among broods was random, we conducted a post-hoc analysis. We assessed whether the variation in the proportion of female parental care could be explained by any of our measured covariates but did not find any to show a significant relationship, suggesting this among-brood variation could be due to chance and a product of our short video observations.

There are several limitations to our study that are worthy of mention and provide context for our results. Our primary goal was to quantify how parental care was shared between the sexes in this monomorphic woodpecker. Therefore, our other explanatory variables are quite coarse and do not provide conclusive evidence on the impact of habitat and/or temperature on parental care. We encourage future studies of Red-headed Woodpecker provisioning, and parental care in general, to include more detailed measures of habitat and food availability. Further, our nest observation videos were recorded from the morning to early afternoon on non-rainy days, so we did not capture much variation in our time of day, temperature, or precipitation covariates. Future studies interested in how weather and time of day impact parental care should record observations with a wider variety of weather conditions and times.

Conclusion
Our study is the first to confirm equal biparental care in a truly monomorphic woodpecker species. The proportion of effort male and female Red-headed Woodpeckers dedicate to parental care is not unlike the contributions of many other dimorphic woodpecker species; males almost exclusively clean the nest of fecal material (Wozniak and Mazgajski 2003, Rossmanith et al. 2009, Chazarreta et al. 2011, Kozma and Kroll 2013, Gow et al. 2015, Tremblay et al. 2016). Dimorphic male woodpeckers also help females to provision nestlings (Jackson 1976b, Rossmanith et al. 2009, Chazarreta et al. 2011, Loverin et al. 2021), assist in diurnal incubation (Vehrencamp 2000, Pechacek et al. 2005), and

assist in diurnal brooding (Wiktander et al. 2000, Rossmanith et al. 2009, Chazarreta et al. 2011). Red-headed Woodpeckers divide parental care so that males excavate new nest cavities or defend their old ones, provision nestlings, clean the nest of nestling feces, and nocturnally incubate eggs and brood nestlings. Red-headed Woodpecker females produce eggs, provision nestlings, and carry out the majority of diurnal incubation and nestling brooding. This division of labor in Red-headed Woodpeckers likely results in a somewhat equal overall contribution of energy by both sexes, and theory suggests that such equal allocation of effort is most common in species with low levels of parental conflict (i.e., searching for extra-pair mating opportunities, Olson et al. 2007). This study, and others like it, can be used to further understand the link between parental care, parental conflict, and plumage similarities among mates (Verner and Willson 1969), particularly because sexual monomorphism and dimorphism are labile evolutionary traits (Price and Birch 1996).

Responses to this article can be read online at:
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Data Availability:

The data and code that support the findings of this study are available on GitHub at https://github.com/lawalter/rhwo-parental-care

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Appendix 1. A review of the size and plumage characteristics between sexes of every woodpecker species in the world.

Table A1.1. All woodpecker species were assessed to determine if sexes are dimorphic, similar, monochromatic, or monomorphic. Monomorphic species ($n = 2$) exhibit no plumage or size dimorphism that allow males and females to be distinguished in the hand. Monochromatic species ($n = 4$) have identical plumage between sexes, but exhibit size dimorphism. Species noted to be "similar" in appearance between sexes ($n = 20$) have nearly imperceptible differences in plumage characteristics. Species are arranged by morphism and scientific name.

Common name	Scientific name	Morphism
Red-headed Woodpecker	*Melanerpes erythrocephalus*	Monomorphic[1,2]
Lewis's Woodpecker	*Melanerpes lewis*	Monomorphic[1,3]
Red-breasted Sapsucker	*Sphyrapicus ruber*	Monochromatic[4]
Rufous-necked Wryneck	*Jynx ruficollis*	Monochromatic[5]
Guadeloupe Woodpecker	*Melanerpes herminieri*	Monochromatic[6]
Eurasian Wryneck	*Jynx torquilla*	Monochromatic[5]
Campo Flicker	*Colaptes campestris*	Similar[5]
Green-barred Woodpecker	*Colaptes melanochloros*	Similar[5]
Chilean Flicker	*Colaptes pitius*	Similar[5]
Andean Flicker	*Colaptes rupicola*	Similar[5]
Gray-capped Woodpecker	*Dendrocopos canicapillus*	Similar[5]
Pygmy Woodpecker	*Dendrocopos kizuki*	Similar[5]
Middle Spotted Woodpecker	*Dendrocopos medius*	Similar[7]
Sunda Woodpecker	*Dendrocopos moluccensis*	Similar[5]
Brown-capped Woodpecker	*Dendrocopos nanus*	Similar[5]
Golden-crowned Woodpecker	*Dendropicos xantholophus*	Similar[5]
Ground Woodpecker	*Geocolaptes olivaceus*	Similar[5]
Black-and-buff Woodpecker	*Meiglyptes jugularis*	Similar[5]
White-fronted Woodpecker	*Melanerpes cactorum*	Similar[5]
White Woodpecker	*Melanerpes candidus*	Similar[5]
Beautiful Woodpecker	*Melanerpes pulcher*	Similar[5]
Red-cockaded Woodpecker	*Picoides borealis*	Similar[3]
Grayish Piculet	*Picumnus granadensis*	Similar[5]
Ecuadorian Piculet	*Picumnus sclateri*	Similar[5]
Checkered Woodpecker	*Veniliornis mixtus*	Similar[5]
Red-naped Sapsucker	*Sphyrapicus nuchalis*	Similar[1,5]
Bay Woodpecker	*Blythipicus pyrrhotis*	Dimorphic[5]
Maroon Woodpecker	*Blythipicus rubiginosus*	Dimorphic[5]
Guayaquil Woodpecker	*Campephilus gayaquilensis*	Dimorphic[5]

Pale-billed Woodpecker	*Campephilus guatemalensis*	Dimorphic[5]
Crimson-bellied Woodpecker	*Campephilus haematogaster*	Dimorphic[5]
Imperial Woodpecker†	*Campephilus imperialis*	Dimorphic[5]
Cream-backed Woodpecker	*Campephilus leucopogon*	Dimorphic[5]
Magellanic Woodpecker	*Campephilus magellanicus*	Dimorphic[5]
Crimson-crested Woodpecker	*Campephilus melanoleucos*	Dimorphic[5]
Powerful Woodpecker	*Campephilus pollens*	Dimorphic[5]
Ivory-billed Woodpecker†	*Campephilus principalis*	Dimorphic[3]
Robust Woodpecker	*Campephilus robustus*	Dimorphic[5]
Red-necked Woodpecker	*Campephilus rubricollis*	Dimorphic[5]
Golden-tailed Woodpecker	*Campethera abingoni*	Dimorphic[5]
Bennett's Woodpecker	*Campethera bennettii*	Dimorphic[5]
Green-backed Woodpecker	*Campethera cailliautii*	Dimorphic[5]
Brown-eared Woodpecker	*Campethera caroli*	Dimorphic[5]
Little Green Woodpecker	*Campethera maculosa*	Dimorphic[5]
Mombasa Woodpecker	*Campethera mombassica*	Dimorphic[5]
Buff-spotted Woodpecker	*Campethera nivosa*	Dimorphic[5]
Knysna Woodpecker	*Campethera notata*	Dimorphic[5]
Nubian Woodpecker	*Campethera nubica*	Dimorphic[5]
Fine-spotted Woodpecker	*Campethera punctuligera*	Dimorphic[5]
Reichenow's Woodpecker	*Campethera scriptoricauda*	Dimorphic[5]
Tullberg's Woodpecker	*Campethera tullbergi*	Dimorphic[5]
Chestnut-colored Woodpecker	*Celeus castaneus*	Dimorphic[1]
Chestnut Woodpecker	*Celeus elegans*	Dimorphic[1]
Blond-crested Woodpecker	*Celeus flavescens*	Dimorphic[1]
Cream-colored Woodpecker	*Celeus flavus*	Dimorphic[5]
Helmeted Woodpecker	*Celeus galeatus*	Dimorphic[5]
Scale-breasted Woodpecker	*Celeus grammicus*	Dimorphic[1]
Cinnamon Woodpecker	*Celeus loricatus*	Dimorphic[1]
Pale-crested Woodpecker	*Celeus lugubris*	Dimorphic[5]
Kaempfer's Woodpecker	*Celeus obrieni*	Dimorphic[5]
Rufous-headed Woodpecker	*Celeus spectabilis*	Dimorphic[5]
Ringed Woodpecker	*Celeus torquatus*	Dimorphic[5]
Waved Woodpecker	*Celeus undatus*	Dimorphic[1]
Red-headed Flameback	*Chrysocolaptes erythrocephalus*	Dimorphic[5]
White-naped Woodpecker	*Chrysocolaptes festivus*	Dimorphic[5]
Greater Flameback	*Chrysocolaptes guttacristatus*	Dimorphic[5]
Luzon Flameback	*Chrysocolaptes haematribon*	Dimorphic[5]

Buff-spotted Flameback	*Chrysocolaptes lucidus*	Dimorphic[5]
Crimson-backed Flameback	*Chrysocolaptes stricklandi*	Dimorphic[5]
Javan Flameback	*Chrysocolaptes strictus*	Dimorphic[5]
Yellow-faced Flameback	*Chrysocolaptes xanthocephalus*	Dimorphic[5]
Greater Yellownape	*Chrysophlegma flavinucha*	Dimorphic[5]
Chequer-throated Woodpecker	*Chrysophlegma mentale*	Dimorphic[5]
Banded Woodpecker	*Chrysophlegma miniaceum*	Dimorphic[5]
Bronze-winged Woodpecker	*Colaptes aeruginosus*	Dimorphic[5]
Black-necked Woodpecker	*Colaptes atricollis*	Dimorphic[5]
Northern Flicker	*Colaptes auratus*	Dimorphic[3]
Gray-crowned Woodpecker	*Colaptes auricularis*	Dimorphic[5]
Gilded Flicker	*Colaptes chrysoides*	Dimorphic[5]
Fernandina's Flicker	*Colaptes fernandinae*	Dimorphic[5]
Spot-breasted Woodpecker	*Colaptes punctigula*	Dimorphic[5]
Crimson-mantled Woodpecker	*Colaptes rivolii*	Dimorphic[5]
Golden-olive Woodpecker	*Colaptes rubiginosus*	Dimorphic[5]
Freckle-breasted Woodpecker	*Dendrocopos analis*	Dimorphic[5]
Sind Woodpecker	*Dendrocopos assimilis*	Dimorphic[5]
Stripe-breasted Woodpecker	*Dendrocopos atratus*	Dimorphic[5]
Brown-fronted Woodpecker	*Dendrocopos auriceps*	Dimorphic[5]
Crimson-breasted Woodpecker	*Dendrocopos cathpharius*	Dimorphic[5]
Darjeeling Woodpecker	*Dendrocopos darjellensis*	Dimorphic[5]
Arabian Woodpecker	*Dendrocopos dorae*	Dimorphic[5]
Himalayan Woodpecker	*Dendrocopos himalayensis*	Dimorphic[5]
Rufous-bellied Woodpecker	*Dendrocopos hyperythrus*	Dimorphic[5]
White-winged Woodpecker	*Dendrocopos leucopterus*	Dimorphic[5]
White-backed Woodpecker	*Dendrocopos leucotos*	Dimorphic[5]
Fulvous-breasted Woodpecker	*Dendrocopos macei*	Dimorphic[5]
Philippine Woodpecker	*Dendrocopos maculatus*	Dimorphic[5]
Yellow-crowned Woodpecker	*Dendrocopos mahrattensis*	Dimorphic[5]
Great Spotted Woodpecker	*Dendrocopos major*	Dimorphic[5]
Lesser Spotted Woodpecker	*Dendrocopos minor*	Dimorphic[5]
Sulu Woodpecker	*Dendrocopos ramsayi*	Dimorphic[5]
Syrian Woodpecker	*Dendrocopos syriacus*	Dimorphic[5]
Sulawesi Woodpecker	*Dendrocopos temminckii*	Dimorphic[5]
Abyssinian Woodpecker	*Dendropicos abyssinicus*	Dimorphic[5]
Little Gray Woodpecker	*Dendropicos elachus*	Dimorphic[5]
Elliot's Woodpecker	*Dendropicos elliotii*	Dimorphic[5]

Cardinal Woodpecker	*Dendropicos fuscescens*	Dimorphic[5]
Gabon Woodpecker	*Dendropicos gabonensis*	Dimorphic[5]
African Gray Woodpecker	*Dendropicos goertae*	Dimorphic[5]
Olive Woodpecker	*Dendropicos griseocephalus*	Dimorphic[5]
Melancholy Woodpecker	*Dendropicos lugubris*	Dimorphic[8]
Bearded Woodpecker	*Dendropicos namaquus*	Dimorphic[5]
Brown-backed Woodpecker	*Dendropicos obsoletus*	Dimorphic[5]
Speckle-breasted Woodpecker	*Dendropicos poecilolaemus*	Dimorphic[5]
Fire-bellied Woodpecker	*Dendropicos pyrrhogaster*	Dimorphic[5]
Mountain Gray Woodpecker	*Dendropicos spodocephalus*	Dimorphic[5]
Stierling's Woodpecker	*Dendropicos stierlingi*	Dimorphic[5]
Black-rumped Flameback	*Dinopium benghalense*	Dimorphic[5]
Spot-throated Flameback	*Dinopium everetti*	Dimorphic[5]
Common Flameback	*Dinopium javanense*	Dimorphic[5]
Olive-backed Woodpecker	*Dinopium rafflesii*	Dimorphic[5]
Himalayan Flameback	*Dinopium shorii*	Dimorphic[5]
Andaman Woodpecker	*Dryocopus hodgei*	Dimorphic[5]
White-bellied Woodpecker	*Dryocopus javensis*	Dimorphic[5]
Lineated Woodpecker	*Dryocopus lineatus*	Dimorphic[5]
Black Woodpecker	*Dryocopus martius*	Dimorphic[5]
Pileated Woodpecker	*Dryocopus pileatus*	Dimorphic[5]
Black-bodied Woodpecker	*Dryocopus schulzi*	Dimorphic[5]
Pale-headed Woodpecker	*Gecinulus grantia*	Dimorphic[5]
Bamboo Woodpecker	*Gecinulus viridis*	Dimorphic[9]
Heart-spotted Woodpecker	*Hemicircus canente*	Dimorphic[5]
Grey-and-buff Woodpecker	*Hemicircus concretus*	Dimorphic[5]
Buff-rumped Woodpecker	*Meiglyptes tristis*	Dimorphic[5]
Buff-necked Woodpecker	*Meiglyptes tukki*	Dimorphic[5]
Golden-fronted Woodpecker	*Melanerpes aurifrons*	Dimorphic[3]
Red-bellied Woodpecker	*Melanerpes carolinus*	Dimorphic[3]
Golden-naped Woodpecker	*Melanerpes chrysauchen*	Dimorphic[5]
Golden-cheeked Woodpecker	*Melanerpes chrysogenys*	Dimorphic[5]
Yellow-tufted Woodpecker	*Melanerpes cruentatus*	Dimorphic[5]
Yellow-fronted Woodpecker	*Melanerpes flavifrons*	Dimorphic[5]
Acorn Woodpecker	*Melanerpes formicivorus*	Dimorphic[3]
Hoffmann's Woodpecker	*Melanerpes hoffmannii*	Dimorphic[5]
Gray-breasted Woodpecker	*Melanerpes hypopolius*	Dimorphic[5]
Puerto Rican Woodpecker	*Melanerpes portoricensis*	Dimorphic[5]

Black-cheeked Woodpecker	*Melanerpes pucherani*	Dimorphic[5]
Yucatan Woodpecker	*Melanerpes pygmaeus*	Dimorphic[5]
Jamaican Woodpecker	*Melanerpes radiolatus*	Dimorphic[5]
Red-crowned Woodpecker	*Melanerpes rubricapillus*	Dimorphic[5]
Velasquez's Woodpecker	*Melanerpes santacruzi*	Dimorphic[5]
Hispaniolan Woodpecker	*Melanerpes striatus*	Dimorphic[6]
West Indian Woodpecker	*Melanerpes superciliaris*	Dimorphic[5]
Gila Woodpecker	*Melanerpes uropygialis*	Dimorphic[5]
Rufous Woodpecker	*Micropternus brachyurus*	Dimorphic[5]
Southern Sooty-Woodpecker	*Mulleripicus fuliginosus*	Dimorphic[5]
Ashy Woodpecker	*Mulleripicus fulvus*	Dimorphic[5]
Northern Sooty-Woodpecker	*Mulleripicus funebris*	Dimorphic[5]
Great Slaty Woodpecker	*Mulleripicus pulverulentus*	Dimorphic[5]
Antillean Piculet	*Nesoctites micromegas*	Dimorphic[5]
White-headed Woodpecker	*Picoides albolarvatus*	Dimorphic[5]
Black-backed Woodpecker	*Picoides arcticus*	Dimorphic[5]
Arizona Woodpecker	*Picoides arizonae*	Dimorphic[5]
American Three-toed Woodpecker	*Picoides dorsalis*	Dimorphic[3]
Smoky-brown Woodpecker	*Picoides fumigatus*	Dimorphic[5]
Nuttall's Woodpecker	*Picoides nuttallii*	Dimorphic[5]
Downy Woodpecker	*Picoides pubescens*	Dimorphic[3]
Ladder-backed Woodpecker	*Picoides scalaris*	Dimorphic[5]
Strickland's Woodpecker	*Picoides stricklandi*	Dimorphic[5]
Eurasian Three-toed Woodpecker	*Picoides tridactylus*	Dimorphic[5]
Hairy Woodpecker	*Picoides villosus*	Dimorphic[3]
White-browed Woodpecker	*Piculus aurulentus*	Dimorphic[5]
Stripe-cheeked Woodpecker	*Piculus callopterus*	Dimorphic[5]
Bar-throated Woodpecker	*Piculus capistratus*	Dimorphic[5]
Golden-green Woodpecker	*Piculus chrysochloros*	Dimorphic[5]
Yellow-throated Woodpecker	*Piculus flavigula*	Dimorphic[5]
Dot-throated Woodpecker	*Piculus laemosticus*	Dimorphic[5]
White-throated Woodpecker	*Piculus leucolaemus*	Dimorphic[5]
Lita Woodpecker	*Piculus litae*	Dimorphic[5]
Belem Woodpecker	*Piculus paraensis*	Dimorphic[5]
Atlantic Woodpecker	*Piculus polyzonus*	Dimorphic[5]
Rufous-winged Woodpecker	*Piculus simplex*	Dimorphic[5]
Golden-yellow Woodpecker	*Piculus xanthochlorus*	Dimorphic[5]
White-wedged Piculet	*Picumnus albosquamatus*	Dimorphic[5]

Bar-breasted Piculet	*Picumnus aurifrons*	Dimorphic[5]
Plain-breasted Piculet	*Picumnus castelnau*	Dimorphic[5]
Chestnut Piculet	*Picumnus cinnamomeus*	Dimorphic[5]
White-barred Piculet	*Picumnus cirratus*	Dimorphic[5]
Ocellated Piculet	*Picumnus dorbignyanus*	Dimorphic[5]
Golden-spangled Piculet	*Picumnus exilis*	Dimorphic[5]
Tawny Piculet	*Picumnus fulvescens*	Dimorphic[5]
Rusty-necked Piculet	*Picumnus fuscus*	Dimorphic[5]
Speckled Piculet	*Picumnus innominatus*	Dimorphic[5]
Lafresnaye's Piculet	*Picumnus lafresnayi*	Dimorphic[5]
Ochraceous Piculet	*Picumnus limae*	Dimorphic[5]
Arrowhead Piculet	*Picumnus minutissimus*	Dimorphic[5]
Mottled Piculet	*Picumnus nebulosus*	Dimorphic[5]
Black-dotted Piculet	*Picumnus nigropunctatus*	Dimorphic[5]
Olivaceous Piculet	*Picumnus olivaceus*	Dimorphic[5]
Orinoco Piculet	*Picumnus pumilus*	Dimorphic[5]
Spotted Piculet	*Picumnus pygmaeus*	Dimorphic[5]
Rufous-breasted Piculet	*Picumnus rufiventris*	Dimorphic[5]
White-bellied Piculet	*Picumnus spilogaster*	Dimorphic[5]
Scaled Piculet	*Picumnus squamulatus*	Dimorphic[5]
Speckle-chested Piculet	*Picumnus steindachneri*	Dimorphic[5]
Fine-barred Piculet	*Picumnus subtilis*	Dimorphic[5]
Ochre-collared Piculet	*Picumnus temminckii*	Dimorphic[5]
Varzea Piculet	*Picumnus varzeae*	Dimorphic[5]
Japanese Woodpecker	*Picus awokera*	Dimorphic[5]
Gray-headed Woodpecker	*Picus canus*	Dimorphic[5]
Lesser Yellownape	*Picus chlorolophus*	Dimorphic[5]
Black-headed Woodpecker	*Picus erythropygius*	Dimorphic[5]
Crimson-winged Woodpecker	*Picus puniceus*	Dimorphic[5]
Red-collared Woodpecker	*Picus rabieri*	Dimorphic[5]
Iberian Woodpecker	*Picus sharpei*	Dimorphic[5]
Scaly-bellied Woodpecker	*Picus squamatus*	Dimorphic[5]
Levaillant's Woodpecker	*Picus vaillantii*	Dimorphic[5]
Streak-breasted Woodpecker	*Picus viridanus*	Dimorphic[5]
Eurasian Green Woodpecker	*Picus viridis*	Dimorphic[5]
Laced Woodpecker	*Picus vittatus*	Dimorphic[5]
Streak-throated Woodpecker	*Picus xanthopygaeus*	Dimorphic[5]
Orange-backed Woodpecker	*Reinwardtipicus validus*	Dimorphic[5]

Okinawa Woodpecker	*Sapheopipo noguchii*	Dimorphic[1]
Rufous Piculet	*Sasia abnormis*	Dimorphic[5]
African Piculet	*Sasia africana*	Dimorphic[5]
White-browed Piculet	*Sasia ochracea*	Dimorphic[5]
Williamson's Sapsucker	*Sphyrapicus thyroideus*	Dimorphic[5]
Yellow-bellied Sapsucker	*Sphyrapicus varius*	Dimorphic[5]
Red-stained Woodpecker	*Veniliornis affinis*	Dimorphic[5]
Scarlet-backed Woodpecker	*Veniliornis callonotus*	Dimorphic[5]
Golden-collared Woodpecker	*Veniliornis cassini*	Dimorphic[5]
Choco Woodpecker	*Veniliornis chocoensis*	Dimorphic[5]
Yellow-vented Woodpecker	*Veniliornis dignus*	Dimorphic[5]
Dot-fronted Woodpecker	*Veniliornis frontalis*	Dimorphic[5]
Red-rumped Woodpecker	*Veniliornis kirkii*	Dimorphic[5]
Striped Woodpecker	*Veniliornis lignarius*	Dimorphic[5]
Yellow-eared Woodpecker	*Veniliornis maculifrons*	Dimorphic[5]
Bar-bellied Woodpecker	*Veniliornis nigriceps*	Dimorphic[5]
Little Woodpecker	*Veniliornis passerinus*	Dimorphic[5]
Blood-colored Woodpecker	*Veniliornis sanguineus*	Dimorphic[5]
White-spotted Woodpecker	*Veniliornis spilogaster*	Dimorphic[5]
Cuban Green Woodpecker	*Xiphidiopicus percussus*	Dimorphic[5]
Gray-and-buff Woodpecker	*Hemicircus concretus*	Dimorphic[5]

†Extinct.
[1]Short (1982), [2]Frei et al. (2020), [3]Sibley (2014), [4]Johnson and Johnson (1985), [5]Gorman (2014), [6]Selander (1966), [7]Pasinelli (2000), [8]Winkler et al. (2010), [9]Round et al. (2012)

Appendix 2. Photographs of Red-headed Woodpecker chicks taken between June and July in 2017 and 2018 at Fort A.P. Hill, Virginia, USA. Photos were taken using a wireless cavity inspection camera with a wireless monitor (IBWO, Little Rock, Arkansas, USA) on an extendable 15 m Crain CMR Series Measuring Rod (SECO Manufacturing, Redding, California, USA). All photos are from nests with known hatch dates. Differences in speed of development may be due to brood size or hatching asynchrony.

Fig. A2.1. A newly hatched Red-headed Woodpecker chick.

Fig. A2.2. Red-headed Woodpecker chicks aged approximately 1 day.

Fig. A2.3. Six-day-old chicks still have their eyes closed and no emergent pinfeathers.

Fig. A2.4. A single chick, aged 7 days, with emerging pinfeathers.

Fig. A2.5. Chicks aged 11 days with emerging pinfeathers. Eyes are beginning to open and chicks are beginning to cling to cavity walls.

Fig. A2.6. A pair of 16-day-old chicks with feathers covering most of their body, but bare feather tracts still visible on head and scapulars.

Fig. A2.7. Day 18 chicks, clinging higher on the cavity walls with feathers fully covering their bodies.

Fig. A2.8. Day 21 chicks have well-developed feathers with a pattern on their primaries and secondaries visible.

Fig. A2.9. Day 28 chicks are fully developed with typical juvenile plumage.

Appendix 3. Variation in Red-headed Woodpecker provisioning proportions by brood for all pairs at Fort A.P. Hill, Virginia, USA.
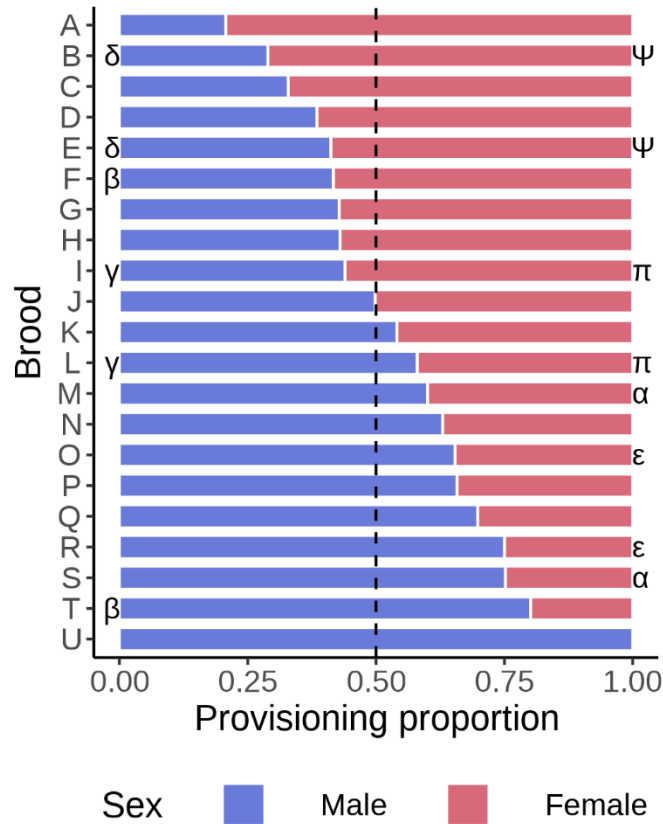

Fig. A3.1. Individual woodpeckers that participated in raising more than one brood are noted with Greek letters. In 2018, a pair raised two broods (B and E) at the same snag. The pair that raised brood I in 2017 and brood L in 2018 used the same snag for both years. Male β used the same snag in 2017 (brood T) to nest in 2018 (brood F), but with a new female mate. Female α and ε relocated to a new snag after 2017, both with a new male partner in 2018. Note that for brood U, the female was indeed alive and visited the nest during the video recording but did not participate in any parental care activities.