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SURVIVAL OF RED-HEADED WOODPECKERS' (*MELANERPES ERYTHROCEPHALUS*) NESTS IN NORTHERN NEW YORK

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ABSTRACT.—Populations of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) have declined throughout much of their range. Conservation management to arrest declines or increase populations is difficult, because many aspects of the species' demography remain poorly understood. To address this knowledge gap, we monitored Red-headed Woodpeckers' nests on Fort Drum Military Installation, in northern New York and modeled daily nest survival rate as a function of temporal and habitat-specific covariates. Red-headed Woodpeckers had low overall nest survival rates (nest survival = 32%), and predation was the leading cause (82%) of nest failure. Cavity concealment had the greatest influence on daily nest survival rate, whereby nests with greater vegetative structure surrounding (within 1 m² of) the nest cavity had higher survival rates, likely because of reduced nest predation. Our estimates of Red-headed Woodpeckers' nest survival were lower relative to other portions of their range and suggest that, at local scales, low reproductive rates near the periphery of the species' distribution may limit population growth. Received 21 January 2014. Accepted 4 June 2014.

Key words: cavity concealment, *Melanerpes erythrocephalus*, nest habitat, nest survival, New York, Red-headed Woodpecker.

The Red-headed Woodpecker (*Melanerpes erythrocephalus*) was historically common in the eastern and central United States, and it still has one of the largest breeding distributions of any woodpecker species in North America (Smith et al. 2000). Nevertheless, this species has experienced sharp, 40-year population declines across much of its range (Smith et al. 2000, Sauer et al. 2014). Breeding Bird Survey (BBS) data report an annual range-wide population decline of nearly 3%, resulting in its status as a "Watch List Species" by the National Audubon Society and Partners in Flight (Rich et al. 2004, Sauer et al. 2014). As would be expected (*sensu* Sexton et al. 2009), population decline has been greatest near the periphery of the species' distribution as its range has contracted over time. In New York State, estimated BBS declines of 9.2% annually are among the highest for any state within the Red-headed Woodpeckers' range (Sauer et al. 2014). This decline is corroborated by New York

State Breeding Bird Atlas data, which recorded Red-headed Woodpeckers in 70% fewer survey blocks during the 2000–2005 atlas compared to 1980–1985. As a consequence of these declines, the species is now listed as a New York State "Species of Greatest Conservation Need" (SGCN; McGowan and Corwin 2008).

A reduction in suitable breeding habitat appears to be an important factor contributing to population declines of Red-headed Woodpeckers (King et al. 2007, Kilgo and Vukovich 2014). However, the relative contribution of other potentially limiting factors remains poorly understood. This is in part because of the dearth of knowledge about the species' demography (e.g., Smith et al. 2000, Rodewald et al. 2005, King et al. 2007, Kilgo and Vukovich 2012). In particular, surprisingly few studies have quantified the nest survival, reproductive success, and productivity of Red-headed Woodpeckers, although these demographic parameters are well known to influence population dynamics (Martin 1995). Effective conservation monitoring and management depends on understanding and manipulating key demographic parameters (e.g., Crouse et al. 1987, Doak 1995, Katzner et al. 2007). In the case of Red-headed Woodpeckers' populations, reproductive success may be especially important in determining population trends, yet knowledge about this parameter is not well known.

A small but regionally important population of Red-headed Woodpeckers breeds regularly on Fort Drum Military Installation in northern New

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York. This population potentially represents one of the largest breeding populations of the species in the northeastern United States, and occurs at the northern limit of the species' distribution. Thus, work in this area could provide critical insight into the limiting factors associated with the demography of Red-headed Woodpeckers. In response to the paucity of information regarding breeding ecology in the northern portion of this species' range, the objectives of our study were to 1) quantify Red-headed Woodpeckers' nest survival, and 2) identify factors influencing nest survival for the Fort Drum breeding population.

METHODS

Study Area.—All fieldwork was conducted on Fort Drum, a large (43,442 ha) United States Army Installation located in Jefferson and Lewis counties, New York (44° 00' N, 75° 49' W). The study area is characterized by sandy soils and vegetation dominated by grasses (Poaceae) and sedges (Cyperaceae) with scattered forest patches. Dominant tree species within forest patches include northern red oak (*Quercus rubra*), white oak (*Q. alba*), eastern white pine (*Pinus strobus*), red pine (*P. resinosa*), and red maple (*Acer rubrum*). Understory vegetation includes lowbush blueberry (*Vaccinium angustifolium*) and seedlings from overstory trees.

Nest Searching.—We monitored Red-headed Woodpeckers' nesting activity on Fort Drum from 7 May to 10 August 2012 and 2013. We systematically searched ~500 ha of known woodpecker habitat using established nest searching protocol (Dudley and Saab 2003). We surveyed the study area using linear transect surveys, and used audio playbacks of Red-headed Woodpeckers' vocalizations at 200-m intervals to elicit responses from territorial individuals. Once Red-headed Woodpeckers were detected along a survey route, we used behavioral cues to locate nest cavities. If we could not locate a nest cavity upon initial contact, we would revisit the territory on at least 2 additional occasions to confirm breeding activity and locate nest cavities.

Nest Monitoring.—Once located, we monitored active Red-headed Woodpecker nests every 1–6 days (\bar{x} = 3.1 days) until completion (fledge or failure). Nest contents were visually confirmed during each nest check using an infrared wireless video camera (Luneau and Noel 2010) mounted onto a 15.2-m telescoping fiberglass pole. At each visit, we determined nest fate (successful, failed,

unknown), nesting stage (e.g., courtship, nest excavation, egg laying, incubation, nestling, and fledgling), and number of eggs or nestlings. We considered nest fate successful if ≥ 1 young fledged and failed otherwise (Dinsmore et al. 2002). Nest age was calculated by back-dating from known nesting-stage transition intervals (e.g., hatch date or fledge date), or by inspecting nestling feather development compared to digital video recordings obtained over the course of the study (JLB, unpubl. data). We assumed a 44-day nesting cycle beginning with the first egg laid (egg laying = 5 days; incubation = 12 days; nestling = 27 days; Smith et al. 2000).

Upon failure of a nesting attempt, we continued to monitor the breeding pair to determine if they attempted to re-nest and monitored all re-nesting attempts when possible. When possible, we categorized nest failures as being caused by (1) predation, (2) abandonment, (3) non-viable eggs, or (4) exposure, and we visually inspected nest cavities and surrounding vegetation for clues of the reason for failure. Potential indicators of nest predation events included changes in nest appearance, claw marks, egg shell remnants, and missing eggs or hatchlings (Dudley and Saab 2003). Nests were considered abandoned if all eggs and hatchlings remained within the nest cavities, but adults were not detected near the nest site for >2 nest checks. A nest was assumed to contain non-viable eggs if the incubation period was protracted beyond the expected hatch date (i.e., beyond 12 days), yet adults remained attentive to incubating the nest. Failure caused by exposure occurred when there was visual evidence of weather-related mortality (e.g., cavity flooding) and if eggs or nestlings remained in the cavity.

Habitat Variables.—Habitat features associated with nest-site selection can affect avian nest survival by influencing predation rates, nest defense, microclimates, and food abundance for provisioning young (e.g., Newlon and Saab 2011, Klassen et al. 2012, Kozma and Kroll 2012). We sampled habitat characteristics related to the nest cavity, nest tree, and surrounding vegetation that were thought to influence survival of Red-headed Woodpeckers' nests. We measured cavity height (m) using a telescoping pole and recorded cavity diameter (cm) by viewing with binoculars a ruler affixed to the end of the pole. We also recorded nest cavity concealment by standing 5 m from the base of the nest tree and visually estimating (in 10% increments) the amount of vegetative cover

within 1 m² of the nest cavity. We also measured a suite of characteristics of the nest tree. These included: diameter at breast height (dbh; cm), decay class (Newell et al. [2009]; 1 = vigorous tree, 2 = <33% dieback, 3 = 33–66% dieback, 4 = >66% dieback, 5 = recently dead tree, 6 = only large limbs remain, 7 = only bole >8 m, 8 = only bole <8 m), and total length (m) of dead limbs \geq 10-cm diameter. Furthermore, snag density \geq 10 cm dbh and average dbh of trees \geq 5 cm were measured within a 0.04-ha plot centered on the nest tree. Canopy cover (%) was estimated as the average of 4 densiometer recordings taken at the perimeter of the 0.04-ha plot in the four cardinal directions. We measured small tree and shrub-stem (<1.4 m height) density within a 0.01-ha subplot centered on the nest tree. We also calculated average height (cm) of understory vegetation within the subplot by measuring woody understory plants (<50 cm; principally *Vaccinium* spp.) along a 5-m transect in a random cardinal direction away from the nest tree. Habitat measurements were made after completion of each nesting attempt to reduce disturbance to active nests.

Statistical Analysis.—We modeled Red-headed Woodpeckers' daily nest survival rate (DNS) using the logistic-exposure method implemented within Program MARK (Lebreton et al. 1992, Dinsmore et al. 2002). Models were fit using Program R 2.13.1 (R Core Development Team 2011) and the R package 'RMark' (Laake and Rexstad 2012). We modeled DNS in relation to *a priori* temporal and habitat-related explanatory variables that we expected would influence Red-headed Woodpeckers' nest survival (above and Table 1). We constructed competing models based on what we determined were biologically relevant and plausible explanations of Red-headed Woodpeckers' nest survival. Re-nesting attempts were included in our analysis of nest survival, because we wanted to evaluate overall productivity for the breeding population. We standardized nesting seasons between years by selecting 12 May as day 1 for the analysis and sequentially numbering days through 17 August.

We used an information-theoretic approach to evaluate competing models using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). Competing models were ranked by their Δ AIC_c values and evaluated by their model weights (w_i). Models with ≤ 2 Δ AIC_c were considered to be well

supported by the data (Burnham and Anderson 2002). We calculated parameter estimates (β), standard errors (SE), and 95% confidence intervals (CI) for variables of interest from top ranking models (Laake and Rexstad 2012). We also estimated effective sample size (n) as the sum of exposure days and daily intervals for which a nest failure occurred (Rotella et al. 2004). For comparisons with other studies, we provide naïve nest success estimates (number successful nests/number of nesting attempts) in addition to nest survival calculated from the product of daily survival rates for each day of the nesting period (i.e., DNS⁴⁴). We present means \pm standard errors (SE) throughout.

RESULTS

We monitored 36 nesting attempts by Red-headed Woodpeckers during 2012 (22) and 2013 (14). Of these, we were only able to observe 30 (17 in 2012 and 13 in 2013) with the wireless camera system. As a consequence, we had 22 first-nest attempts and 8 re-nest attempts ($n = 30$ total) usable for logistic-exposure analysis (effective sample size: $n = 648$). Clutch size of Red-headed Woodpeckers averaged 4.2 ± 0.22 eggs ($n = 27$), and earliest recorded nest initiation dates were 19 May 2012 and 12 May 2013. Overall, 42% ($n = 15$) of 36 Red-headed Woodpeckers' nests successfully fledged at least 1 young.

Nest survival based on Mayfield estimates (Mayfield 1961) was 32% (DNS = 0.974 ± 0.01) for nests monitored with the wireless video system ($n = 30$). Of these nests, predation was the primary cause of failure we observed (82%, $n = 14$), followed by exposure (12%, $n = 2$) and non-viable eggs (6%, $n = 1$). Nest failure most commonly occurred during the nestling (47%, $n = 8$) and incubation (41%, $n = 7$) stages, while 12% ($n = 2$) of nests failed during egg laying. Successful nests ($n = 13$) fledged on average 1.9 ± 0.26 young (range = 1–4) and overall productivity (# of young fledged/nesting attempts [$n = 30$]) was 0.83 young fledged per nesting attempt.

The best supported model of Red-headed Woodpeckers' daily nest survival (i.e., lowest AIC_c value and highest model w_i) included a main effect of cavity concealment (Table 3). Cavity concealment had a positive effect on nest survival (Table 4), with daily survival rates increasing when vegetative cover surrounding the nest cavity increased (Fig. 1). Models including terms for

TABLE 1. Explanatory variables and hypotheses used in candidate logistic-exposure models to evaluate variation in survival of Red-headed Woodpeckers' nests on Fort Drum Military Installation, New York, during May–August, 2012–2013.

Type	Variable name	Description	Hypothesis
Temporal	Nest age	Age of the nest (in days)	Nest age influences survival because of changes in offspring and parental behavior throughout the nesting cycle
	Time	Julian date in nesting season	Time of nest initiation influences survival because of temporal variation in predation rates and food abundance
	Year	Year of study (2012 or 2013)	Annual changes in predation pressure and resource availability influence nest survival
Habitat	Nest attempt	Nest attempt (first or re-nest)	Nest attempt (first clutch or re-nest) influences nest survival
	Cavity diam.	Cavity diameter (cm)	Variation in cavity diameter influences nest detectability and accessibility to predators
	Cavity ht.	Cavity height (m)	Cavity height influences nest detectability and accessibility to predators and offers different microenvironments that may affect survival
	Concealment	Cavity concealment (%)	Vegetative structure surrounding the cavity entrance influences nest detectability and accessibility to predators
	Tree dbh	Nest tree diameter at breast height (cm)	Variation in nest tree size affects cavity placement and microclimates
	Tree decay	Nest tree decay class	Nest tree decay state influences the amount of vegetative cover near the nest site and can affect both nest and adult survival
	Tree dll	Nest tree dead-limb length (m)	Dead-limb length affects nest survival by decreasing vegetative cover and is maladaptively selected (Frei et al. 2013)
	Canopy cover	Canopy cover (%)	Canopy cover influences predation rates by facilitating movements of arboreal predators and affects parents ability to defend the nest cavity
	Snag den.	Snag density (0.04-ha)	Snag density influences the number of available cavity sites for inter- and intra-specific competitors and density of cavity-seeking predators (e.g., flying squirrels) and affect their predation efficiency (i.e., dilution effect)
	Understory	Understory height (cm)	Understory vegetation affects predator densities (e.g., small mammals) and Red-headed Woodpecker foraging efficiency and provisioning
Stems	Woody stem density (0.01-ha)	Midstory vegetation affects predator densities (e.g., small mammals) and Red-headed Woodpecker foraging efficiency and provisioning	

TABLE 2. Descriptive statistics for habitat variables used in candidate logistic-exposure models of survival of Red-headed Woodpeckers' nests on Fort Drum Military Installation, New York, during May–August, 2012–2013. See Table 1 for variable descriptions.

Variable	Mean	SE	Range
Cavity diam.	6.82	0.21	5.71–9.52
Cavity ht.	8.75	0.49	4.51–13.03
Concealment	34.00	4.35	0.00–90.00
Tree dbh	44.28	2.61	24.40–72.20
Tree decay	4.26	0.36	1.00–8.00
Tree dll	11.73	2.06	0.00–36.00
Canopy cover	73.10	3.32	31.62–96.62
Snag den.	1.43	0.26	0.00–4.00
Understory	6.58	1.26	0.00–23.60
Stems	14.73	2.72	0.00–53.00

canopy cover and year also received moderate support (Table 3), although both models were $>2 \Delta AIC_c$ units below the top-ranked model. The probability of daily nest survival decreased as canopy cover surrounding the nest tree increased, suggesting nest survival was greater in relatively open canopies (Table 4). Nest survival also varied by year, and daily survival rates were substantially lower in 2012 (0.959 ± 0.01 ; nest survival = 16%) compared to 2013 (0.986 ± 0.01 ; nest survival = 54%).

DISCUSSION

Red-headed Woodpeckers on Fort Drum appear limited by their relatively low reproductive success. This is notable because other primary

TABLE 3. Relative support for 18 candidate logistic-exposure models of Red-headed Woodpeckers' daily nest survival rate (DNS) on Fort Drum Military Installation, New York, during May–August, 2012–2013. K indicates the number of model parameters, AIC_c is Akaike's information criterion corrected for small sample size, ΔAIC_c is the difference in AIC_c units from the best approximating model, while w_i is the model weight. See Table 1 for description of model variables.

Model	K	AIC_c	ΔAIC_c	w_i	Deviance
S(~Concealment)	2	116.94	0.00	0.34	112.93
S(~Canopy cover)	2	118.99	2.04	0.12	114.97
S(~Year)	3	119.33	2.39	0.10	113.30
S(~.)	1	120.17	3.23	0.07	118.17
S(~Tree dbh)	2	121.27	4.33	0.04	117.26
S(~Stems)	2	121.41	4.46	0.04	117.39
S(~Nest age)	2	121.64	4.70	0.03	117.62
S(~Tree dll)	2	121.74	4.80	0.03	117.72
S(~Snag den.)	2	121.76	4.82	0.03	117.74
S(~Understory)	2	121.91	4.96	0.03	117.89
S(~Cavity diam.)	2	122.05	5.11	0.03	118.04
S(~Cavity ht.)	2	122.06	5.12	0.03	118.04
S(~Time)	2	122.08	5.14	0.03	118.07
S(~Tree decay)	2	122.15	5.21	0.03	118.13
S(~Tree dbh + Tree decay)	3	122.72	5.77	0.02	116.68
S(~Nest attempt)	3	122.74	5.79	0.02	116.70
S(~Stems + Understory)	3	123.42	6.48	0.01	117.39
S(~Nest age + Time)	3	123.64	6.69	0.01	117.60

cavity nesting species typically have high nest survival (e.g., >70%; Martin and Li 1992). Our estimate of nest survival (32%; yearly range = 16–56%) is generally lower than previous estimates of reproductive success for Red-headed Woodpeckers in Ohio (70–80%; Rodewald et al. 2005), South Dakota (47–92%; Vierling and Gentry 2008), Illinois (56%; Hudson and Bollinger 2013), and southern Ontario (76%; Frei et al. 2013). To some extent this would be expected because reproductive success is often lower near the periphery of a range, where limited resources can result in reduced fitness (Sexton et al. 2009).

Habitat characteristics largely determined Red-headed Woodpeckers' nest survival within our study area. In particular, nest cavity concealment

had the greatest influence on DNS, and cavities with more vegetative concealment had higher nest survival. Since predation was the greatest cause of nest failure, it seems logical to conclude that increased vegetative cover reduces nest predation. Nest concealment is known to improve nest survival for a variety of open-cup and cavity-nesting avian species. The mechanism for this is thought to be linked to the effect of vegetative cover on predator foraging efficiency, through concealment of nest locations and restriction of access to cavity contents (Li and Martin 1991, Segura et al. 2012).

Nest-cavity placement can affect the amount of vegetative structure surrounding cavity openings. In particular, nest cavities located in dead limbs of

TABLE 4. Model parameter estimates for top three ranking logistic-exposure models of Red-headed Woodpeckers' daily nest survival rate (DNS) on Fort Drum Military Installation, New York, during May–August, 2012–2013. Parameter estimates (β) are presented with standard errors (SE) and upper and lower 95% confidence intervals (CI).

Model	Parameter	β	SE	Lower CI	Upper CI
S(~Concealment)	Intercept	2.74	0.45	1.86	3.62
	Estimate	0.28	0.14	0.01	0.56
S(~Canopy cover)	Intercept	5.61	1.26	3.14	8.08
	Estimate	-0.03	0.02	-0.06	0.00
S(~Year)	Intercept	2.52	0.00	2.52	2.52
	2012	0.65	0.00	0.65	0.65
	2013	1.77	0.00	1.77	1.77

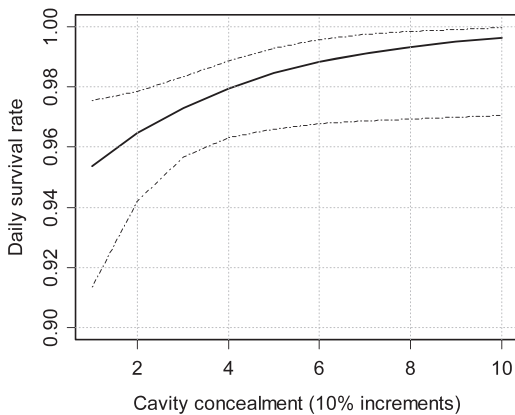


FIG. 1. Influence of cavity concealment on Red-headed Woodpeckers' daily nest survival rate (DNS) on Fort Drum Military Installation, New York, during May–August, 2012–2013. Dashed lines indicate 95% confidence intervals.

otherwise live trees ($n = 8$) typically had higher cavity concealment (mean vegetative cover = $46.2\% \pm 8.01$) relative to cavities located in snags ($n = 15$; mean vegetative cover = $20.7\% \pm 3.45$). Several previous studies have demonstrated that Red-headed Woodpeckers select dead limbs (from both live trees and snags) for nesting throughout their range and in a variety of habitat types (Sedgwick and Knopf 1990, Rodewald et al. 2005, Vierling and Lentile 2006, King et al. 2007, Frei et al. 2013). Increased cavity concealment associated with nests located in dead limbs of live and recently dead trees may therefore be important to providing both suitable nesting substrate and protection from predators. Nest predation is known to influence reproductive strategies and nest-site selection in other birds (Martin 1995, Fontaine and Martin 2006). Therefore, Red-headed Woodpeckers may attempt to mitigate the effects of predation by excavating (or selecting) nest cavities in substrates with ample vegetative cover.

Red-headed Woodpeckers are considered weak excavators (Jackson 1975) which likely explains their selection of severely decayed nest trees (e.g., only large limbs or bole remain and bark removed) (Hudson and Bollinger 2013). In northern New York however, such nest trees often offer minimal cavity concealment. Frie et al. (2013) suggested that Red-headed Woodpeckers' selection of nest trees with long dead-limb lengths (i.e., snags and advanced decay-stage trees) was maladaptive because unsuccessful nests occurred in trees with greater dead-limb length compared to

successful nests. We found no difference in dead-limb length on trees used for successful ($11.3 \text{ m} \pm 2.94$) and unsuccessful ($12.1 \text{ m} \pm 2.95$) nests. However, if longer dead-limb lengths result in lesser cavity concealment and thus greater nest failure rates, then our results may indirectly support this hypothesis. Therefore, high-quality nest trees (structurally complex trees with both decadent substrate and vegetative cover) may be important resources for Red-headed Woodpeckers, because these trees provide nesting conditions necessary for successful reproduction and adult survival (Kilgo and Vukovich 2012)

Forest canopy structure can affect avian reproductive success by influencing predator assemblages and movement (Klassen et al. 2012). On Fort Drum, nest survival may have decreased in closed canopy forest patches that facilitated movement of arboreal nest predators (e.g., flying squirrels [*Glaucomys* spp.] and red squirrels [*Tamiasciurus hudsonicus*]) and enabled them to better detect and access nest cavities. Furthermore, adult Red-headed Woodpeckers actively defend nest cavities from approaching inter- and intra-specific predators (Berl et al. 2013), and open canopies may allow for better aerial maneuverability and thus more effective nest defense (Kozma and Kroll 2012).

Nest age, a temporal parameter that influences Red-headed Woodpeckers' nest survival in Illinois (Hudson and Bollinger 2013), was not important to nest survival in northern New York. In our study, constant-age nest survival rates suggest that predation rates are not disproportionately influenced by increased vocalizations and noise from chicks during the nestling stage (Hudson and Bollinger 2013). Conversely, we found disparate nest survival between years, which suggests Red-headed Woodpeckers' reproduction is contingent upon annual nesting conditions. The yearly differences in nest survival we observed may have been related to annual variation in predation pressure (i.e., predator switching). Nest predation rates are known to vary seasonally and annually (Morrison and Bulger 2002) as generalist nest predators (e.g., squirrels [Sciuridae] and black bear [*Ursus americanus*]) adjust foraging patterns in relation to fluctuating food resources such as hard and soft mast. However, because we were unable to identify nest predators, we cannot speculate the specific mechanisms that may have regulated changes in predation rates at this particular site.

Many populations of Red-headed Woodpeckers are declining across the species' range, and our ability to estimate reproductive success and identify factors that influence nest survival are important processes in developing conservation strategies for this species (Smith et al. 2000). At the edge of their distribution, Red-headed Woodpeckers may be limited by the availability of high-quality nest trees that offer both decadent substrates (dead wood) and cavity concealment (surrounding vegetation structure). The low rates of nest survival and productivity we document may be important limitations to the demography of Red-headed Woodpeckers at a regional scale (i.e., northeastern portion of range). These factors should therefore be considered in future conservation and management plans for this species.

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