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Red-headed Woodpecker Habitat Selection and Breeding Ecology on Fort Drum Military Installation, New York

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**Red-headed Woodpecker Habitat Selection and Breeding Ecology on Fort Drum Military
Installation, New York**

Jacob L. Berl

**Thesis submitted to the
Davis College of Agriculture, Natural Resources and Design
at West Virginia University
in partial fulfillment of the requirements
for the degree of**

**Master of Science
in
Wildlife and Fisheries Resources**

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Division of Forestry and Natural Resources

**Morgantown, West Virginia
2013**

KEYWORDS: forest management, *Melanerpes erythrocephalus*, nest-habitat thresholds,
nesting success, New York, red-headed woodpecker

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ABSTRACT

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Jacob L. Berl

Red-headed woodpecker (*Melanerpes erythrocephalus*) populations have declined range-wide over the past 40 years, although the causal mechanisms implicated in the observed declines remain poorly understood. Population decline has been most severe at the periphery of their range, particularly in the northeastern United States, coinciding with a region where there is little information regarding red-headed woodpecker habitat use or demography. A detailed knowledge of habitat requirements and population dynamics is prerequisite for the effective conservation and management of imperiled wildlife populations, and this knowledge gap likely precludes informed management decisions for red-headed woodpeckers in the northeastern portion of their range. In response to the extreme paucity of information regarding red-headed woodpecker habitat selection and breeding ecology in the northeastern United States, I conducted a field study on Fort Drum Military Installation, New York where a small but regionally important population of 10–15 adult red-headed woodpecker pairs regularly breeds. From May to August 2012–2013 I surveyed the installation for red-headed woodpecker breeding territories and located 15 and 11 territorial pairs in 2012 and 2013, respectively. I subsequently located nest cavities of breeding pairs to monitor reproductive success and conducted extensive habitat sampling to assess nest-habitat selection.

I used boosted regression trees (BRT) to identify red-headed woodpecker nest-habitat thresholds at multiple spatial scales. Red-headed woodpeckers exhibited nest-tree thresholds related to tree (1) decay class, (2) dead-limb length, and (3) diameter at breast height (dbh), while forest patch (i.e., surrounding vegetation) thresholds were related to (1) total dead-limb

length, (2) understory height, (3) average tree dbh, and (4) large tree (≥ 30 -cm dbh) density.

These results provide objective criteria for managing nesting habitat for red-headed woodpeckers, and indicate the relative importance of nest-tree and forest-patch characteristics on nest-site selection.

I modeled red-headed woodpecker daily nest survival rates (DSR) as a function of temporal and habitat-specific covariates using logistic-exposure models to identify factors influencing nest survival and better understand the underlying mechanisms affecting reproductive success and productivity. A total of 30 red-headed woodpecker nesting attempts by 22 breeding pairs were monitored over the course of the study and I documented low rates of reproductive success (overall nest success = 32%) and observed high rates ($>80\%$) of nest predation. DSR was most influenced by cavity concealment, such that nests with greater vegetative structure surrounding (within 1 m^2 of) the nest cavity had higher survival rates—an attribute that likely reduced nest predation.

I also sought to identify factors influencing large-scale selection of breeding habitats by red-headed woodpeckers, and used BRTs to compare characteristics (structure and composition) of forest stands occupied and unoccupied by breeding territories. Red-headed woodpeckers selected forest stands with greater overall stand decadence (decay) and shorter woody understory height. My results suggest that at coarse spatial scales (i.e., forest stands or habitat fragments) red-headed woodpecker selection of breeding habitats can be influenced by overall stand decadence and management strategies that recruit numerous decadent trees into forest stands will increase available habitat for this species. This study provides resource managers with meaningful estimates of red-headed woodpecker resource selection and reproductive success that can be used as guidelines to conserve habitat for this species.

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CHAPTER 1

RED-HEADED WOODPECKER LITERATURE REVIEW

LITERATURE REVIEW

Biology and Taxonomy

The red-headed woodpecker (*Melanerpes erythrocephalus*) is a member of the family Picidae, a large and diverse avian family that includes ~20 species of woodpeckers, sapsuckers, and their allies in North America (Smith et al. 2000). Red-headed woodpeckers are closely related to other members of the genus *Melanerpes*, comprised of 5 other species in the United States (acorn woodpecker [*Melanerpes formicivorus*], gila woodpecker [*Melanerpes uropygialis*], golden-fronted woodpecker [*Melanerpes aurifrons*], Lewis's woodpecker [*Melanerpes lewis*], and red-bellied woodpecker [*Melanerpes carolinus*]) (Smith et al. 2000).

Red-headed woodpeckers are medium-sized birds, weighing on average 70 g (Smith et al. 2000). Adults are conspicuously colored with a brilliant red head and nape, black across their primary and covert feathers, and contrasting white on secondary feathers. The species is considered gregarious in that they are social, extremely vocal, and easily identified (Rodewald et al. 2005).

Distribution and Population Status

Red-headed woodpeckers are widely distributed, occurring across much of the eastern United States (Smith et al. 2000, Rodewald et al. 2005, Vierling and Lentile 2006, King et al. 2007, Vierling and Gentry 2008). Historically, the red-headed woodpecker was locally abundant throughout its range, and has one of the largest breeding distributions of any woodpecker species in North America (King et al. 2007) ranging from Montana and Colorado to the west, Texas and Florida to the south, and north to New England and Canada (Smith et al. 2000, Rodewald 2005). Its core breeding distribution (i.e., highest breeding densities) occurs across much of the eastern

tallgrass prairie and central hardwoods interphase, encompassing the states of Illinois, Wisconsin, Iowa, Missouri, Indiana, and Ohio (Smith et al. 2000, Sauer et al. 2011).

Although widely distributed, this species has experienced sharp population declines across much of its range over the past 40 years (Smith et al. 2000, Rich et al. 2004, Rodewald et al. 2005, Vierling and Gentry 2008, Sauer et al. 2011). Breeding Bird Survey (BBS) data reports an annual range-wide population decline of nearly 3%, invoking its listing as a “Watch List Species” by the National Audubon Society and Partners in Flight (Rich et al. 2004, Sauer et al. 2011). Although the cause of population decline is poorly understood, potential explanations include removal of decadent trees and snags from timber harvesting and altered disturbance regimes (e.g. fire suppression) that reduce available habitat (Smith et al. 2000, King et al. 2007, Vierling and Gentry 2008). Red-headed woodpecker population declines have been greatest near the periphery of its range (Sauer et al. 2011) resulting in range contraction (Wilcove and Terborgh 1984, Rodriguez 2002). In New York State declines of 8.8% annually have been reported, constituting the greatest rate of decline for any state within the red-headed woodpeckers range (Sauer et al. 2011). This decline is corroborated by New York State Breeding Bird Atlas data, which recorded twice as many red-headed woodpeckers during the 1980–1985 survey compared to 2000–2005 (McGowan and Corwin 2008). This drastic decline resulted in the red-headed woodpeckers listing as a New York State “Species of Greatest Conservation Need” (Levine 1998, McGowan and Corwin 2008, Spiering 2009). Red-headed woodpecker populations are patchily distributed throughout the northeastern United States and remnant populations are typically small in size (i.e., a few breeding pairs; Spiering 2009).

Habitat Selection and Associations

Knowledge of habitat selection, particularly during the breeding season, is crucial in order to manage habitat for species of conservation concern (Anderson and Shugart 1974). Habitat associations and selection can be related to a variety of biotic and abiotic factors (Cody 1981, Stauffer and Best 1982, Doligez et al. 2002) and vary by spatial scale (Johnson 1980). This is true for many cavity nesting birds, which are known to have rather specific habitat criteria (Raphael and White 1984, Martin and Li 1992) relative to other avian guilds. Important nest-habitat features for cavity nesting birds include the presence of adequate snags or decadent trees for use as nesting substrate (Raphael and White 1984).

Red-headed woodpeckers have adapted to breed in a variety of open habitats including oak (*Quercus* spp.) savanna (King et al. 2007), oak and hickory (*Carya* spp.) woodlots (Conner 1976, Adkins-Giese and Cuthbert 2003), burned ponderosa pine (*Pinus ponderosa*) stands (Vierling and Lentile 2006), rural golf courses (Rodewald et al. 2005), urbanized landscapes (Shackelford and Conner 1997), bottomland hardwoods (Williams 1975, Conner et al. 1994), riparian corridors (Sedgwick and Knopf 1990), quaking aspen (*Populus tremuloides*) stands (Kronland 2007) and oak scrub forests (McNair 1996). Dependence on, and selection for, open habitats may be a factor leading to population decline in this species (Smith et al. 2000). Due to a range of anthropogenic factors (e.g., fire suppression and altered disturbance regimes) abundance of many disturbance-mediated habitat types in the eastern United States are declining—ultimately leading to the population reductions of bird species dependent on these landscapes (Davis et al. 2000). As a direct result of large-scale habitat loss, several bird species that inhabit open landscapes (e.g., temperate grasslands, oak savanna, early successional forests) of the eastern United States have experienced population decline in recent years (Askins 1993, Herkert 1994, Sauer et al. 2011).

Nest-site Selection

Nest-site selection is an integral component of avian breeding behavior (Dobkin et al. 1995, Martin 1995, Martin 1996, Misenhelter and Rotenberry 2000), and can be influenced by a variety of factors including competition (Svardson 1949), predation (Nilsson 1984), food abundance (Nilsson 1984), and habitat alteration (Stauffer and Best 1980). Therefore, a thorough understanding of habitat features that influence avian nest-site selection can better inform nest-habitat management decisions for target species—particularly for species experiencing sharp population declines (Jones 2001, Newlon and Saab 2011).

Although red-headed woodpeckers have historically been considered to be relatively plastic in their selection of cavity (hereafter termed nest) sites (Smith et al. 2000), habitat thresholds (i.e., limiting factors) do exist (King et al. 2007) and several studies have shown red-headed woodpeckers to be highly selective with regards to nest-site selection. For example, in Illinois, Reller (1972) observed red-headed woodpeckers breeding solely in the trunks of snags, with cavity heights ranging from 7–20 m. Sedgwick and Knopf (1990) found red-headed woodpeckers use of nest sites to be positively correlated with tree decadence and snag density in riparian woodlands in Colorado at both the nest tree and forest patch (i.e., vegetation immediately surrounding the nest tree) spatial scales. Vierling et al. (2009) found red-headed woodpeckers nesting in the Black Hills of South Dakota to select nest trees that were larger (37.8-cm dbh) and taller (10.7-m tree height) than randomly available trees. Furthermore, compared with random locations, red-headed woodpeckers selected open habitats with fewer large-diameter trees and lower shrub understory (i.e., more open habitats). In a similar study, Vierling and Lentile (2006) recorded red-headed woodpecker nests in stands with higher shrub density, distance to edge, higher burn severity, and greater nest tree diameter at breast height

(dbh) than random sites. In central Wisconsin, King et al. (2007) described red-headed woodpecker nest-site selection indicating selection for large cavity trees (e.g., 44.2-cm dbh and 16.3-m tall) and a habitat threshold associated with the density of dead-limb bearing trees. Red-headed woodpeckers also select nesting habitats with higher basal area, snag densities, cavity densities, decadent tree densities, and total dead-limb length (King et al. 2007).

Although red-headed woodpeckers use a variety of tree species in which to nest (e.g. > 20 different tree species reported), several studies have noted that certain tree species are selected at greater frequency than available. Red-headed woodpeckers have been shown to selectively nest in mature quaking aspen (Vierling and Lentile 2006), bigtooth aspen (*Populus grandidentata*) and northern pin oak (*Quercus ellipsoidalis*) (King et al. 2007, Adkins-Giese and Cuthbert 2005), American elm (*Ulmus americana*) (Jackson 1976), eastern cottonwood (*Populus deltoides*) (Gutzwiller and Anderson 1987, Sedgwick and Knopf 1990), and eastern white oak (*Quercus alba*) and hickory (Conner 1976). Woodpeckers often select, or excavate, nests at a specific directional orientation. Red-headed woodpeckers appear to select nest cavities oriented in a southwestern (Reller 1972) or southeastern (Conner 1975) direction. This selection behavior may be in part a response to fungal/vegetation growth on northerly facing surfaces of cavity trees, or for warmer thermal properties associated with southern cavity orientations (Conner 1975).

As with most North American woodpecker species (Kisiel 1972, Mannan et al. 1980, Brawn et al. 1982, Raphael and White 1984, Morrison and With 1987), the red-headed woodpecker is dependent on decadent trees or snags for both nesting and foraging habitats. Gutzwiller and Anderson (1987) among others (e.g. Vierling and Lentile 2006, Williams 1975) found red-headed woodpeckers nesting occurrence in Wyoming riparian woodlands to be

positively associated with large (>85-cm dbh) snags. However, red-headed woodpeckers are not completely dependent on snags, and have been known to nest in live trees (Conner 1976), decadent limbs of live trees (Rodewald et al. 2005), and even telephone poles (Spiering 2009).

Red-headed woodpeckers usually excavate their own nest cavities (King et al. 2007), but will in some circumstances utilize existing natural cavities (e.g., knotholes) (King et al. 2007) or usurp nest cavities from competitors (Kronland 2007). Nest cavity excavation by woodpeckers is an important ecological process, as many other non-excavating cavity nesting birds (e.g., black-capped chickadee [*Poecile atricapillus*], eastern bluebird [*Sialia sialis*], American kestrel [*Falco sparverius*]) and other animals (e.g. flying squirrel [*Glaucomys* spp.], bats [*Myotis* spp.]) are often reliant on woodpecker-excavated nest sites (Aitken and Martin 2007, Cockle et al. 2011).

Nest Success and Reproduction

There is a pressing need for further study to quantify red-headed woodpecker reproduction and productivity (Smith et al. 2000) because these demographic parameters are well known to influence population dynamics (Dinsmore et al. 2002). In South Dakota, Vierling and Gentry (2008) studied red-headed woodpecker breeding ecology in two different burned habitats, and found nest success rates (fledging ≥ 1 young) of 92% in old burn sites and 47% in recently burned sites. Furthermore, productivity (number of fledglings) was greater in old burn sites (2.8) than recently burned sites (1.6), and nest failure resulted primarily from predation in both cases. Rodewald et al. (2005) studied red-headed woodpecker habitat use and reproduction on golf courses in Ohio and recorded nest success rates of 70% and 80% at golf course and non-golf course nests, respectively. Vierling and Lentile (2006) found red-headed woodpecker average clutch size to be 5.4, with a nest daily survival rate (DSR) of 0.98 in South Dakota. To date, only one study has used the logistic-exposure method (Dinsmore et al. 2002, Bonnot et al. 2008) to

estimate red-headed woodpecker DSR in relation to temporal and habitat-specific covariates. Using this method, Hudson and Bollinger (2013) recently found that red-headed woodpecker nest survival increases with nest age and nest height in eastern Illinois. Additional estimates of nest survival are necessary to better understand the underlying mechanisms affecting red-headed woodpecker reproduction.

Red-headed woodpeckers appear to display high nest-site fidelity (Ingold 1991), yet this behavior has not been evaluated extensively or at northern latitudes where the populations are largely migratory. Red-headed woodpecker breeding phenology is dependent upon location and latitude, and nest initiation has been reported to be as early as April in southern climes (Ingold 1989) and as late as mid-July in northern regions (Reller 1972, Jackson 1976, Vierling and Lentile 2006). Double clutches have been recorded for red-headed woodpeckers on several occasions (Ingold 1987, McNair 1996) but the extent to which this behavior occurs at northern latitudes (where the breeding season is inherently shorter) is unknown.

Territoriality and Competition

Red-headed woodpeckers are extremely territorial, and display both intraspecific and interspecific agonistic behavior towards potential competitors. This behavior occurs during the non-breeding season when individuals will establish well defined territories around food caches (Kilham 1958, Muskovits 1978) and during the breeding season when territories are centered around nest trees (Atterberry-Jones and Peer 2010). Winter territory size range from 0.04 ha (Doherty et al. 1994), 0.1–0.2 ha (Kilham 1958), 0.97 ha (Muskovits 1978), and 0.8–1.2 ha (MacRoberts 1975). Territoriality during the breeding season is less studied, and documentation of breeding territory size is limited (Atterberry-Jones and Peer 2010, Kilgo and Vukovich 2012). However, territoriality is probable during the breeding season, as suitable nesting cavities are

likely to be a limiting resource and breeding pairs will defend resources surrounding nest locations (Rodewald et al. 2005, Vierling et al. 2009).

Red-headed woodpeckers are known to be aggressive towards potential interspecific and intraspecific competitors. Competition over nest sites (Jackson 1976, Ingold 1989) and foraging opportunities (Vierling et al. 2009) have been well documented. Potential interspecific competitors include the red-bellied woodpecker, Lewis's woodpecker, downy woodpecker (*Picoides pubescens*), pileated woodpecker (*Dryocopus pileatus*), American crow (*Corvus brachyrhynchos*), blue jay (*Cyanocitta cristata*), and tufted titmouse (*Baeolophus bicolor*) (Kilham 1958b, Bock et al. 1971, Reller 1972, Williams 1975, Pinkowski 1977, Moskovits 1978, Ingold 1989). In particular competition and behavioral interactions between red-headed woodpeckers and their ecological counterpart, red-bellied woodpeckers, have been well documented (Reller 1972, Ingold 1989, Ingold 1990, Ingold 1991). Furthermore, as a result of presumed competition, Vierling et al. (2009) documented niche partitioning between red-headed woodpeckers and the closely related Lewis' woodpecker co-occurring in recently burned forests in South Dakota. Ingold (1989, 1994) described nest cavity usurpation and competitive interaction over nest cavities between red-headed woodpeckers and the invasive European starling (*Sturnus vulgaris*). Nest usurpation by European starlings has been hypothesized as a factor leading to red-headed woodpecker population decline (Smith et al. 2000, Spiering 2009).

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CHAPTER 2

SCALE-DEPENDENT NEST-HABITAT THRESHOLDS FOR RED-HEADED

WOODPECKERS AT THE NORTHERN LIMIT OF THEIR RANGE

Scale-dependent Nest-habitat Thresholds for Red-headed Woodpeckers at the Northern Limit of Their Range

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ABSTRACT

Red-headed woodpecker (*Melanerpes erythrocephalus*) populations have declined range-wide in recent decades although the causal factors for these declines remain poorly understood. We evaluated red-headed woodpecker nest-site selection on Fort Drum Military Installation, in New York State near the northern limit of the species' range and identified nest-habitat thresholds (abrupt non-linear species-habitat relations) at the nest-tree and forest-patch spatial scales. Red-headed woodpeckers exhibited nest-tree thresholds related to tree (1) decay class, (2) dead-limb length, and (3) dbh, while forest patch (i.e., surrounding vegetation) thresholds were related to (1) total dead-limb length, (2) understory height, (3) average tree diameter at breast height (dbh), and (4) large tree (≥ 30 -cm dbh) density. Our results provide objective threshold criteria for managing nesting habitat for red-headed woodpeckers, and indicate the relative importance of nest-tree and forest-patch characteristics on nest-habitat selection.

KEYWORDS habitat thresholds, *Melanerpes erythrocephalus*, nest-habitat selection, New York State, oak-woodlands, red-headed woodpecker

A detailed knowledge of habitat requirements is prerequisite for the effective conservation of imperiled wildlife populations. The successful implementation of management plans for at-risk species is predicated on correctly identifying resource needs throughout the annual cycle (Morrison et al. 2006). For species with broad geographic distributions that occupy disparate habitat types throughout their range, identifying habitat needs can be challenging because resource requirements likely vary spatially and temporally.

Breeding populations of red-headed woodpeckers (*Melanerpes erythrocephalus*) occur across much of the eastern and central United States, yet populations are patchily distributed and uncommon throughout most of their range (Smith et al. 2000, McGowan and Corwin 2008). Furthermore, red-headed woodpecker nesting habitat is comprised of a variety of disparate habitat types, including oak (*Quercus* spp.) and pine (*Pinus* spp.) savanna, bottomland hardwood forest, burned ponderosa pine (*Pinus ponderosa*) forest, cottonwood and aspen (*Populus* spp.) riparian woodlands, agricultural woodlots, campgrounds, suburban parks and golf courses (Sedgwick and Knopf 1990, Vierling and Lentile 2006, Atterberry-Jones and Peer 2010, Kilgo and Vukovich 2012, Hudson and Bollinger 2013). Although these habitat types differ in species composition they retain similar structural properties. In particular, the importance of large decadent trees and snags for use as nest trees, with surrounding vegetation characterized by open understories, low basal area of trees, and high densities of dead-limb bearing trees has been well documented (Sedgwick and Knopf 1990, Rodewald et al. 2005, King et al. 2007, Frei et al. 2013). Despite being broadly distributed, and apparently capable of breeding in a variety of habitat types, red-headed woodpecker populations have experienced steady range-wide declines in recent decades (Sauer et al. 2012) and are considered a national species of conservation

concern (Rich et al. 2004). Furthermore, in spite of their status as an at-risk species, reasons for the observed population declines are uncertain making conservation planning difficult (but see Frei et al. 2013).

Identifying thresholds (abrupt non-linear changes) in species-habitat relations can be a useful tool to establish objective habitat management targets that meet the minimum requirements for species of conservation concern (Angelstam et al. 2003, Ficetola and Denoel 2009). King et al. (2007) identified a nest-habitat threshold for red-headed woodpeckers in central Wisconsin related to the density of dead-limb bearing trees, whereby the probability of red-headed woodpecker nesting occurrence increased with greater densities of dead-limb bearing trees surrounding the nest tree. Despite its apparent merit and applicability to conservation planning, the prevalence of red-headed woodpecker nest-habitat thresholds in other regions and habitat types has been largely unexplored.

Our objective was to examine red-headed woodpecker nest-site selection at the northern limit of its range, on Fort Drum Military Installation, in northern New York State. Specifically, we sought to (1) determine the relative influence of habitat characteristics on nest-habitat selection at multiple spatial scales, and (2) examine potential nest-habitat thresholds for breeding red-headed woodpeckers. Northern New York State represents the extreme northeastern periphery of the red-headed woodpecker distribution, and also coincides with a region where population decline has been particularly severe and limited information is available related to habitat use or nest-site selection (McGowan and Corwin 2008, Sauer et al. 2012). Substantial population decline often results in species range-contraction (Rodriguez 2002), and as such periphery populations can be important for maintaining long-term population persistence and genetic diversity—particularly when confronted with potential large-scale changes in land use

(Lesica and Allendorf 1995). Lastly, given the broad distribution and wide variety of habitat types used by this species, it is important to obtain regionally specific estimates of resource use on which to base management decisions.

STUDY AREA

This study was conducted on Fort Drum (44°00' N, 75°49' W), an active U.S. Army installation located in northern New York. The study area is characterized by sandy soils and open grasslands interspersed by forest patches that consisted mostly of oak-dominated woodlands. We partitioned the study area into 35 study sites ($\bar{x} = 9.0 \text{ ha} \pm 1.0 \text{ SE}$) based on forest stands delineated from Fort Drum's forest inventory data (Fig. 1; Fort Drum Forest Management Program, 2012). Individual study sites were selected *a priori* based on historic use by red-headed woodpeckers (J. Bolsinger, unpublished data). Study sites varied in tree composition and structure, but were generally dominated by northern red oak (*Quercus rubra*) and eastern white oak (*Q. alba*); other prevalent trees included red maple (*Acer rubrum*), red pine (*Pinus resinosa*), eastern white pine (*P. strobus*) gray birch (*Betula populifolia*), and bigtooth aspen (*Populus grandidentata*). Understory vegetation was characterized by woody shrubs including lowbush blueberry (*Vaccinium angustifolium*), labrador tea (*Rhododendron groenlandicum*) and seedlings from overstory trees, while herbaceous vegetation was dominated by grasses (Poaceae) sedges (Cypaceae), and ferns (Dryopteridaceae).

METHODS

Nest Searching and Monitoring

We conducted nest searching from early May to late June during two breeding seasons (2012–2013). We systematically surveyed study sites in a grid network and used audio playbacks of red-headed woodpecker calls and drumming at 200-m intervals to elicit responses from territorial

pairs (protocol following Dudley and Saab 2003). Nesting red-headed woodpeckers are highly territorial and generally respond well to playback calls (Rodewald et al. 2005, J. Berl personal observation), which aided in their detection. All study sites were surveyed three times per season, and we separated individual surveys by at least one week. When adult red-headed woodpeckers were detected along survey transects we used careful observation and behavioral cues (e.g., nest excavation, copulation, and chatter calls) to locate nest cavities. If we detected an individual on a survey but did not locate a nest cavity during the initial contact and observation, we returned to the site on ≥ 2 additional occasions to determine if the area contained a breeding territory.

Once potential nests were identified, we confirmed nesting activity by inspecting cavity contents using a wireless video camera (Luneau and Noel 2010) affixed to a telescoping fiberglass pole. In instances when we were unable to view cavity contents due to nest height (i.e., >14 m) or vegetative obstruction, we confirmed nesting activity if we (1) observed adults enter the nest cavity and remain for ≥ 5 minutes, (2) observed adults provisioning young, or (3) heard nestling vocalizations.

Habitat and Vegetation Measurements

We recorded habitat variables at 3 spatial scales by measuring characteristics of the nest cavity, nest tree, and forest patch (3rd and 4th order selection *sensu* Johnson 1980). We collected habitat variables following King et al. (2007) with minor modifications (see Table 1 for description of habitat variables). We directly measured characteristics of nest cavities and nest trees, while characteristics of the forest patch (i.e., surrounding vegetation) were recorded within 0.04-ha (11.3-m radius) circular plots centered on the nest tree (Martin et al. 1997).

To evaluate nest-site selection in relation to available habitat, we collected analogous habitat data at randomly located availability plots dispersed among study sites ($n = 50$). We constrained the distribution of availability plots to study sites that were occupied by a territorial red-headed woodpecker pair in at least one year of the study ($n = 11$). We ensured that the number of availability plots per study site ($\bar{x} = 2 \pm 0.26$ SE) was proportional to study site area, and confirmed that all availability plots were ≥ 25 m from known nest trees. Availability plots were located using a random point generator in ArcGIS 10.0 (ESRI, Redlands, CA) and we navigated to within 10 m of the random UTM coordinates using a handheld GPS. We centered availability plots on a random focal tree (≥ 10 -cm dbh) located nearest the randomly selected coordinates and conducted vegetation measurements analogous to those conducted at nest sites (Table 1) with the exception of nest-cavity characteristics.

Analytical Methods

Nest-cavity characteristics.—We were unable to compare characteristics of nest cavities to available cavities because too few ($n = 5$) random focal trees contained cavities; only cavity orientation allowed for comparison between observed and random. We generated a paired ($n = 24$) random set of nest-cavity orientations (N, NE, E, SE, S, SW, W, NW) and used Chi-squared analysis to determine if nest cavity orientation differed from random.

Nest-tree and forest-patch thresholds.—We used boosted regression trees (BRT) to model differences in habitat characteristics between nest sites and random sites at both the nest-tree and forest-patch spatial scales. BRTs construct a large number of simple regression trees that recursively partition the response variable given a candidate set of predictor variables, and then uses a stochastic machine learning technique (boosting) to ensemble individual regression trees—a procedure that greatly improves model predictive performance (De'ath and Fabricius

2000, Elith et al. 2008). We selected this form of analysis over traditional generalized linear model approaches (i.e., logistic regression) because BRTs are able to model complex non-linear relations (Elith et al. 2008) that are required to identify habitat thresholds in species-habitat relations (Ficetola and Denoel 2009). Furthermore, BRTs are robust to multicollinearity among predictor variables and can accommodate data from virtually any distribution (Elith et al. 2008). This enabled us to incorporate all collected variables into BRT models without the need for data transformation or culling of variables due to multicollinearity.

We constructed BRT models using the ‘dismo’ package (Hijmans et al. 2013) in program R version 2.13.1 (R Core Development Team 2011) and specified a Bernoulli response distribution to accommodate our binary (used *versus* available) data structure (Elith et al. 2008). Fitting BRT models requires the specification of several model parameters, including the model learning rate (specifies the contribution of each simple regression tree to the boosted model), the bag fraction (determines the proportion of model training data used) and tree complexity (determines the number of modeled interactions). Model parameters were set as recommended by Elith et al. (2008): learning rate = 0.005, bag fraction = 0.50, tree complexity = 1. We also used 10-fold cross-validation to calculate the optimal number of regression trees for each BRT model using the ‘gbm.step’ function (Hijmans et al. 2013). Model predictive performance was assessed using cross-validated estimates of area under the curve (AUC) of the receiving operator characteristic (ROC), which is a measure of discrimination (Bradley 1997). We considered models with AUC scores ≥ 0.70 to have acceptable discrimination efficiency and models with AUC scores ≥ 0.90 to have excellent discrimination efficiency.

The relative influence of each predictor variable on response variables was assessed by the average number of times a given predictor variable was selected for partitioning and

weighted by the squared model improvement resulting from the successive partitions. We then used a cross-validated simplification algorithm to sequentially remove predictor variables that contributed little to model performance, as measured by changes in predictive deviance (Elith et al. 2008, Hijmans 2013); this procedure resulted in a reduced predictor set that included only significant variables. Habitat thresholds were identified using BRT partial dependence plots, which assess the marginal effect of each predictor on the response, while holding all other predictors constant (Friedman 2001). We defined habitat threshold values by the first abrupt change in slope (i.e., distinct increase or decrease in marginal effect) along a gradient of predictor values (Cutler et al. 2007, Ficetola and Denoel 2009, Feld 2013).

RESULTS

We located 19 nests in 2012 and 11 nests in 2013 for a total of 30 red-headed woodpecker nest trees over the course of the study; however, we only retained 24 nests for use in analyses because 6 nests were re-nest attempts (after nest failure) within the same year.

Nest-cavity Characteristics

Red-headed woodpeckers nested in several different tree species, including red oak (71%), white oak (8%), red maple (8%), eastern cottonwood (*P. deltoides*; 8%), and red pine (5%). Nests were located in both limbs (54%) and boles (46%) of trees, and in live (13%) and dead (87%) substrates. Cavities were typically placed high in trees, averaging $10.1 \text{ m} \pm 0.68 \text{ SE}$ from the ground. The majority of red-headed woodpecker nest cavities faced north (25%) and east (21%), but observed orientations did not significantly differ from random ($\chi^2 = 44.51$, $df = 49$, $P = 0.656$).

Nest-tree Thresholds

The simplified (final) model evaluating nest-tree thresholds indicated excellent discrimination efficiency (cross-validated AUC: $\bar{x} = 0.90 \pm 0.35$ SE), and retained 3 predictor variables that best characterized red-headed woodpecker nest trees. Red-headed woodpecker nest-tree selection was most influenced by tree (1) decay class, (2) dead-limb length, and (3) dbh (Table 2). Inspection of partial dependence plots indicated strong (i.e., an abrupt change in slope) nest-tree thresholds related to each of these variables as specified by the first major break point in marginal effect (Fig. 2). Nest-tree use by red-headed woodpeckers increased when trees exceeded a decay class threshold value of ≥ 3 , which corresponds to trees with $\geq 33\%$ decadent canopies (Fig. 2). Nest-tree thresholds also existed for tree dead-limb length of ≥ 4 m and for tree dbh of ≥ 34 cm (Fig. 2) with probability of use increasing when these minimal thresholds were exceeded.

Forest-patch Thresholds

Our simplified model evaluating forest-patch thresholds exhibited acceptable cross-validated discrimination efficiency (cross-validated AUC: $\bar{x} = 0.80 \pm 0.56$ SE). At the forest-patch scale, red-headed woodpecker nest-site selection was most influenced by (1) total dead-limb length, (2) understory height, (3) average tree dbh, and (4) density of large trees (trees ≥ 30 -cm dbh) surrounding the nest tree (Table 3). Probability of forest patch use by red-headed woodpeckers substantially increased when dead-limb length surrounding the nest tree (0.04-ha) exceeded a minimum threshold of 17 m (Fig. 3). The height of woody understory vegetation had a negative influence on red-headed woodpecker nest-site selection, with the probability of site use decreasing when understory heights were >12 cm (Fig. 3); however this was a ‘smooth threshold’, as defined by Ficetola and Denoel (2009), and should therefore be considered with some flexibility. The probability of forest patch use also greatly increased when average tree dbh

exceeded a 30-cm threshold, and when large tree density exceeded a minimum threshold of four (per 0.04 ha) within the forest patch (Fig. 3).

DISCUSSION

We evaluated red-headed woodpecker nest-site selection at the northern limit of its range and found strong evidence of nest-habitat thresholds at multiple spatial scales. The existence of nest-habitat thresholds and non-linear species-habitat relations has been well documented for other woodpecker species (e.g., Butler et al. 2004), which as a group are known to have relatively specific habitat requirements—often related to the presence of dead wood (Muller and Butler 2010). Our findings support and expand upon the work of King et al. (2007), which previously described the presence of a nest-habitat threshold for red-headed woodpeckers.

Nest-tree Thresholds

Although previous authors have described red-headed woodpecker nest-tree characteristics, none have identified objective nest-tree threshold criteria. In our study, we demonstrated nest-tree thresholds related to tree decay state, dead-limb length and dbh, which suggests that red-headed woodpeckers select for microhabitat characteristics (i.e., features of the nest tree) in addition to habitat features at larger spatial scales.

Our demonstrated nest-tree decay threshold (tree decay class ≥ 3) is associated with trees that have $\geq 33\%$ decadent canopy (Figure 2), which indicates that red-headed woodpeckers do not necessarily require nest trees that are in advanced decay stages (i.e., snags) but also select nest trees with only partial crown decadence. Red-headed woodpeckers are known to nest in dead portions of otherwise live trees (Rodewald et al. 2005, King et al. 2007, Hudson and Bollinger 2013) and over 54% of nests on Fort Drum were located in dead limbs (21% in dead limbs of otherwise live trees). Furthermore, we detected a nest-tree threshold related to tree dead-limb

length, which is known to be an important nest-tree characteristic for red-headed woodpeckers in cottonwood floodplains (Sedgwick and Knopf 1990), oak savanna (King et al. 2007), and agricultural woodlots (Frei et al. 2013). This indicates broad-scale selection for nest trees with ample-dead limb length, probably because dead-limbs are frequently used as cavity sites (see citations above) and drumming substrates (Reller 1972). Conversely, Frei et al. (2013) found dead-limb length to be an important determinant of red-headed woodpecker nest-tree selection in southern Ontario, but also suggested that the selection of this characteristic resulted in maladaptive habitat use because unsuccessful nests had higher dead-limb lengths compared to successful nests. However, given the demonstrated wide-spread selection for and use of dead-limbs by red-headed woodpeckers, it would be surprising if this habitat feature consistently resulted in maladaptive habitat use across the species range.

We also detected a minimum nest-tree dbh (>33 cm) threshold that was likely a result of the association between tree dbh and the development of dead-wood characteristics (i.e., decay state and dead limbs) in larger and older trees (Sedgwick and Knopf 1990). Although red-headed woodpeckers probably do not select nest trees based on dbh *per se* (but rather other characteristics related to large trees), a minimum nest-tree dbh threshold provides useful forest management guidelines for recruiting trees that are likely to develop suitable nest-tree characteristics for red-headed woodpeckers.

Forest-Patch Thresholds

Red-headed woodpeckers exhibited nest-habitat thresholds at the forest-patch scale (0.04-ha), which has been previously demonstrated in other habitat types (King et al. 2007). Interestingly, our forest-patch habitat thresholds were related to: (1) total dead-limb length, (2) understory height, (3) average tree dbh, and (4) large-tree density, and did not correspond to the dead-limb

tree density threshold previously identified by King et al. (2007). There are several potential reasons why our forest-patch thresholds differed from that of King et al. (2007). Primarily, differences in forest-patch thresholds could indicate variation in red-headed woodpecker nest-site selection in disparate habitat types across its range. As previously described, red-headed woodpeckers have a broad distribution and resource requirements may accordingly vary by habitat and landscape composition, which affirms the need for habitat-specific estimates of resource use throughout their range. Furthermore, dissimilarities in statistical methodology may contribute to the observed differences between studies. King et al. (2007) used logistic regression to develop their nest-habitat threshold, however, the validity of using logistic regression to identify abrupt thresholds in complex non-linear species-habitat relations has been recently criticized (Ficetola and Denoel 2009). Somewhat ironically, our most influential forest-patch threshold variable (total dead-limb length) was not included in the threshold model used by King et al. (2007) because of its correlation to dead-limb tree density (i.e., it was culled due to collinearity)—a consequence that further supports the use of modeling approaches (e.g., BRT and Generalized Additive Models [GAMs]) that can detect non-linear relations and also accommodate multicollinearity among predictor variables.

Red-headed woodpeckers have long been known to select habitats characterized by large, sparsely distributed trees and open understories (Smith et al. 2000), and we identified forest-patch thresholds that correspond to these structural attributes. We found that total dead-limb length surrounding the nest tree was the most influential threshold at the forest-patch scale, which further demonstrates the importance of dead limbs to this species (Sedgwick and Knopf 1990, King et al. 2007, Frei et al. 2013). Dead limbs on trees surrounding the nest site may be important resources for use as roosting and nesting cavities (Sedgwick and Knopf 1990,

Rodewald et al. 2005), as well as perching sites during foraging bouts (Reller 1972, Frei et al. 2013). Red-headed woodpeckers commonly flycatch and ground forage during the nesting period (Reller 1972), and will utilize exposed dead limbs as perch sites to secure food resources (J. Berl personal observation). Recruitment of dead limbs into forest stands is often associated with trees that are large, mature, and in a state of decline (Sedgwick and Knopf 1990), or from self-pruning tree species (e.g., oaks and American elm [*Ulmus americana*]) that will recruit dead limbs prior to reaching advanced decay stages. Furthermore, management strategies such as girdling tree limbs can increase dead-limb length within a target forest patch, and may also enhance red-headed woodpecker nest success (Hudson and Bollinger 2013) in certain situations. In landscapes where dead limbs are often removed for safety or aesthetic reasons (e.g., suburban areas, parks or campgrounds) we recommend careful inspection of dead-limb bearing trees to ensure that dead limbs are removed only in the most necessary situations (Sedgwick and Knopf 1990).

Red-headed woodpecker nest-site selection on Fort Drum was also negatively influenced by understory vegetation, whereby a threshold existed for forest patches with woody understory vegetation height < 12 cm. Although previous studies have indicated a selection for dense understories in other habitat types (e.g., burned pine forest; Vierling and Lentile 2006), our understory vegetation threshold may be associated with the tendency of red-headed woodpeckers to ground forage near nest trees. We frequently observed red-headed woodpeckers ground foraging for hard mast and insects during late spring and early summer, often selecting areas devoid of understory vegetation (with the exception of leaf litter) that likely allowed birds clear access to food resources (e.g., acorns) and visibility to detect approaching predators. Subsequently, forest management practices that maintain open understories while also recruiting

and retaining mature, large-diameter trees within forest patches will increase available habitat for red-headed woodpeckers. On Fort Drum, certain military training activities (e.g., troop bivouacking and tracked-vehicle maneuvering) have likely perpetuated habitat for red-headed woodpeckers on the installation because these activities successfully manage understory vegetation. Additional management practices such as prescribed burning (King et al. 2007), cattle and sheep grazing (Conner 1976, Newlon and Saab 2011), or mechanical removal of under- and mid-story woody stems can be used to reduce undesirable understory vegetation, while maintaining large-diameter overstory trees that are required by red-headed woodpeckers.

MANAGEMENT IMPLICATIONS

When applied properly, identification of habitat thresholds can be an effective management tool for the conservation of imperiled wildlife populations because habitat management and restoration remain the most widely used conservation strategies implemented by land and resource managers (Huggett 2005, Ficetola and Denoel 2009). We found strong evidence for multivariate red-headed woodpecker nest-habitat thresholds at multiple spatial scales. As such, habitat loss is likely a key factor limiting red-headed woodpecker populations (Smith et al. 2000, King et al. 2007) as the distribution of suitable habitat (i.e., habitats that meet or exceed the multivariate threshold criteria) is diminished as a result of land use change. Furthermore, there is increasing evidence that red-headed woodpeckers have relatively specific nest-habitat requirements (King et al. 2007) and identifying habitat-specific thresholds in other regions and landscapes will improve range-wide conservation efforts.

In conclusion, we provide objective minimal nest-habitat requirements for red-headed woodpeckers that can inform management decisions for this species. Habitat management for red-headed woodpeckers in the northeastern United States should strive to meet or exceed the

minimum nest-habitat thresholds described above, and we propose the use of multivariate thresholds to identify areas of suitable habitat that are of high conservation value for this species, or to identify specific habitat features that require management or restoration to increase available habitat.

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Table 1. Nest-habitat variables collected at red-headed woodpecker nest sites and random sites on Fort Drum Military Installation, New York, during May–August, 2012–2013.

Habitat variable	Description
Cavity	
Cavity height (m)	Estimated using a clinometer
Cavity diameter (cm)	Measured with ruler affixed to a telescoping pole
Cavity location	Bole or limb
Substrate diameter (cm)	Measured with ruler affixed to a telescoping pole
Cavity age	New or old
Cavity orientation	recorded using compass and back-azimuth
Substrate type	Dead or live
Tree^a	
Tree species	Recorded when determinable
Tree dbh (cm)	Measured using calipers
Tree height (m)	Estimated using a clinometer
Limb tree	Presence/absence of dead limb ≥ 10 cm diameter
No. of dead limbs	Number of dead limbs ≥ 10 cm diameter
Dead-limb length	Visually estimated length of dead limbs ≥ 10 cm diameter
Tree decay class	Ranked 1–8, following Newell et al. (2009): 1 = vigorous tree, 2 = < 33% dieback, 3 = 33–66% dieback, 4 = > 66% dieback, 5 = recently dead tree, 6 = dead tree, only large limbs remain, 7 = dead tree, only bole > 6 m remains, 8 = dead tree, only bole < 6 m remains
Tree state	Live or dead
Tree top cond.	Unbroken or broken
Tree bark	Visually estimated % bark coverage
Forest patch^b	
Mean tree dbh (cm)	Mean dbh of trees ≥ 5 cm dbh
Canopy height (m)	Mean height of 5 largest trees nearest the nest tree estimated with clinometer
Canopy cover (%)	Mean of 4 densiometer readings recorded at the plot edges in the 4 cardinal directions
Understory height (cm)	Mean height of understory vegetation recorded along 5 m transect from focal tree
Dead-limb density	Number of dead limbs ≥ 10 cm diameter
Total dead-limb length (m)	Visually estimated length of dead limbs ≥ 10 cm diameter
Mean tree decay class	Mean decay class for trees ≥ 5 -cm dbh. Ranked 1–8, defined following Newell et al. (2009)
Snag density	Density of snags ≥ 10 cm dbh
Limb-tree density	Density of dead-limb trees with ≥ 1 decadent limb ≥ 10 cm

	diameter
Small tree density	Density of small trees; 5–15 cm dbh
Medium tree density	Density of medium trees; 15–30 cm dbh
Large tree density	Density of big trees; > 30 cm dbh
Total tree density	Density of all trees; $\geq$ 5-cm dbh

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^aMeasured at the nest tree and random focal tree

^bMeasured within 0.04-ha plots centered on nest tree and random focal tree

Table 2. Relative influences of habitat variables on nest-tree use by red-headed woodpeckers on Fort Drum Military Installation, New York, during May–August, 2012–2013. Relative influences are given for both the fully parameterized (global) and simplified (final) models. See Table 1 for description of habitat variables.

Variable	Relative % influence	
	Full	Simplified
tr.dec	45.50	48.63
tr.dll	27.39	33.08
tr.dbh	16.17	18.30
tr.dl	4.08	—
tr.ht	3.11	—
tr.top	1.60	—
tr.sp	1.19	—
tr.state	0.55	—
tr.bark	0.39	—
tr.limb	0.00	—

Table 3. Relative influences of habitat variables on forest patch use by red-headed woodpeckers on Fort Drum Military Installation, New York, during May–August, 2012–2013 as derived from boosted regression tree (BRT) models. Relative influence values are given for both fully parameterized (global) and simplified (final) models. See Table 1 for description of habitat variables.

Variable	Relative % Influence	
	Full	Simplified
tot.dl	23.22	36.95
ave.under	11.94	23.30
ave.dbh	9.92	22.19
bt.den	11.49	17.57
ave.dec	12.59	—
mt.den	10.67	—
lt.den	6.83	—
can.ht	4.52	—
st.den	3.67	—
snag.den	2.40	—
can.cov	1.71	—
tot.dl	0.66	—
tot.tr	0.39	—

FIGURE CAPTIONS

Figure 1. Location and distribution of forested study sites monitored for breeding red-headed woodpeckers within Fort Drum Military Installation, New York during May–August, 2012–2013.

Figure 2. Partial dependence plots indicating the marginal effect of nest-tree characteristics on red-headed woodpecker nest-site selection on Fort Drum Military Installation, New York, during May–August, 2012–2013. Nest-tree thresholds were identified by the first abrupt change in marginal effect. Relative percent influence of habitat variables are given in parentheses.

Figure 3. Partial dependence plots indicating the marginal effect of influential forest patch characteristics on red-headed woodpecker forest patch use on Fort Drum Military Installation, New York, during May–August, 2012–2013. Nest-tree thresholds were identified by the first abrupt change in marginal effect. Relative percent influence of habitat variables are given in parentheses.

Figure 1.

Figure 2.

Figure 3.

CHAPTER 3
RED-HEADED WOODPECKER NEST SURVIVAL AND REPRODUCTION
IN NEW YORK STATE

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RED-HEADED WOODPECKER NEST SURVIVAL AND REPRODUCTION
IN NEW YORK STATE

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ABSTRACT.—Red-headed Woodpecker (*Melanerpes erythrocephalus*) populations have declined range-wide, and estimates of reproductive success and factors influencing nest survival remain poorly understood. In response to this knowledge gap, we monitored Red-headed Woodpecker nesting success at the northeastern extent of the species range during two breeding seasons (2012 and 2013) and modeled daily nest survival rate (DSR) as a function of temporal and habitat-specific covariates. We monitored 30 Red-headed Woodpecker nesting attempts over the course of the study and found low overall rates of reproductive success (nest success = 32%) and documented high rates (>80%) of nest predation. DSR was most influenced by cavity concealment, whereby nests with greater vegetative structure surrounding (within 1 m²) the nest-cavity had higher survival rates—an attribute that likely reduced nest predation. Our estimates of Red-headed Woodpecker nesting success were lower relative to other portions of their range and suggest that, at local scales, low reproductive rates may be implicated in population decline on the periphery of the species' distribution.

The Red-headed Woodpecker (*Melanerpes erythrocephalus*) was historically common in the eastern and central United States, and has one of the largest breeding distributions of any woodpecker species in North America (Smith et al. 2000). Although widely distributed, this species has experienced sharp population declines across much of its range over the past 40 years (Smith et al. 2000, Sauer et al. 2012). Breeding Bird Survey (BBS) data reports 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. 2012). As would be expected (*sensu* Sexton et al. 2009), population decline has been greatest near the periphery of its distribution as the species range has contracted over time. In New York State, BBS declines of 8.8% annually have been reported, constituting the greatest rate of decline for any state within the Red-headed Woodpecker range (Sauer et al. 2011). 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 and resulted in their listing as a New York State “Species of Greatest Conservation Need” (McGowan and Corwin 2008).

The cause of population decline in this species is poorly understood, and there is a generally accepted need for further assessment of Red-headed Woodpecker habitat use and demography (e.g. Smith et al. 2000, Rodelwald et al. 2005, King et al. 2007, Kilgo and Vukovich 2012). Surprisingly few studies have quantified Red-headed Woodpecker nest survival, reproductive success, and productivity, although these demographic parameters are well known to influence population dynamics (Dinsmore et al. 2002). Hudson and Bollinger (2013) recently found Red-headed Woodpecker nest survival in eastern Illinois to be influenced by nest age and cavity height, suggesting that Red-headed Woodpecker reproductive success can be affected by both temporal (nest age) and habitat-related (cavity height) parameters. Additional estimates of

nest survival and reproductive success are necessary for effective management of this rapidly declining species (Smith et al. 2000), particularly in the northeastern United States where no study of Red-headed Woodpecker breeding ecology has previously occurred. Moreover, there is a need to further identify factors influencing nest survival to better understand the underlying mechanisms affecting reproductive success and productivity.

A small but regionally important population of 9–15 adult Red-headed Woodpecker pairs regularly breeds on Fort Drum Military Installation, in northern New 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 its distribution. In response to the paucity of information regarding Red-headed Woodpecker breeding ecology in the northern portion of its range, the objectives of our study were to (1) quantify nest survival and reproductive success 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 angustifolia*) and seedlings from overstory trees.

Nest Searching.—We monitored Red-headed Woodpecker nesting activity on Fort Drum from early-May to mid-August of 2012 and 2013. We systematically searched ~500 ha of available habitat using established nest searching protocol (Dudley and Saab 2003). Briefly, we

surveyed the study area using linear transect surveys, and used audio playbacks of Red-headed Woodpecker vocalizations at 200-m intervals to illicit 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 ≥ 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 until completion (fledge or failure) with most checks at 3–4 day intervals. 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, nesting stage (e.g., courtship, nest excavation, egg laying, incubation, nestling, and fledgling) and number of eggs/nestlings. 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).

We considered nest fate “successful” if ≥ 1 young fledged, or “failed” if the nest did not fledge young (Dinsmore et al. 2002). Upon failure of a nesting attempt, we continued to monitor the breeding pair to determine if they attempted to re-nest; we monitored all re-nesting attempts when possible. Red-headed Woodpeckers frequently re-nest after nest failure (Ingold 1987), particularly when failure occurs early in the breeding season. We included re-nest attempts in our analysis of nest survival because we wanted to evaluate overall reproductive success and productivity for the breeding population. We categorized nest failures as (1) predation, (2) abandonment, (3) non-viable eggs, or (4) exposure and we visually inspected nest cavities and

surrounding vegetation for clues to ascertain the cause of failure. Potential indicators of nest predation events included changes in nest appearance, claw marks, egg shell remnants, and missing eggs/hatchlings (Dudley and Saab 2003). Nests were considered abandoned if all eggs/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 infertile eggs if the incubation period was protracted beyond the expected date (i.e., beyond 12 days) yet adults remained attentive to incubating the nest. We considered failure due to exposure when there was visual evidence of weather related mortality (e.g., cavity flooding) and if eggs/nestlings remained in the cavity.

Vegetation Sampling.—Upon completion of each nesting attempt, we sampled vegetative characteristics related to the (1) nest cavity, (2) nest tree, and (3) surrounding vegetation. We measured cavity height (m) using a telescoping pole and recorded cavity diameter (cm) by viewing a ruler affixed to the end of the pole with binoculars. We also recorded nest cavity concealment by visually estimating (in 10% increments) the amount of vegetative cover surrounding (within 1 m²) the nest cavity while standing 5 m from the base of the nest tree and directly facing the cavity. We also measured characteristics of the nest tree, including diameter at breast height (dbh; to nearest 0.1 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 ≥10-cm diameter. Furthermore, snag density ≥10-cm dbh and average dbh of trees ≥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. We also measured small tree and shrub-stem density (<1.4 m) and average understory height (to nearest 1 cm) surrounding the nest tree (0.01-ha plot).

Statistical Analysis.—Red-headed Woodpecker daily nest survival was modeled using the logistic-exposure method implemented within Program MARK as outlined by Dinsmore et al. (2002). Models were fit using the R package RMark (Laake and Rexstad 2012). We modeled daily nest survival in relation to *a priori* temporal and habitat related explanatory variables thought to influence Red-headed Woodpecker reproductive success (Table 1). In favor of using all possible variable combinations, we constructed competing models based on biologically relevant and plausible explanations of Red-headed Woodpecker nest survival given the study system. We used an information-theoretic approach to evaluate 19 competing models using Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). Competing models were ranked by their ΔAICc values (i.e., the difference between each model and the most parsimonious model, given the data) and evaluated by their model weights (w_i); models with $\leq 2 \Delta\text{AICc}$ 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 number of exposure days in addition to the number of intervals for which a failure occurred (Rotella et al. 2004). For comparisons with other studies, we provide naïve nest success estimates (# successful nests / # of nesting attempts) in addition to nest success calculated from the product of daily survival rates for each day of the nesting period (i.e., DSR^{44}). Means are presented $\pm$ standard errors (SE) throughout.

RESULTS

We monitored 36 Red-headed Woodpecker nesting attempts during 2012 (22) and 2013 (14); however, we were only able to monitor 30 nesting attempts (17 and 13 in 2012 and 2013, respectively) with the wireless camera system (i.e., useable for logistic-exposure analyses)

representing 22 first-nest attempts and 8 re-nest attempts (effective sample size: $n = 648$). Red-headed woodpecker clutch size 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 Red-headed Woodpecker nests ($n = 36$) successfully fledged at least 1 young; however, our estimate of nesting success calculated from daily survival rates (Mayfield 1961) was much lower (daily survival rate = 0.974 ± 0.01 ; nest success = 32%). Including only nests that we monitored with the video system ($n = 30$), predation was the primary cause of nest failure (82%, $n = 17$), followed by exposure (12%, $n = 2$) and infertile 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 Woodpecker daily nest survival rates (i.e., lowest AICc value and highest model w_i) included a main effect of cavity concealment (Table 2). Cavity concealment had a positive effect on nest survival (Table 3), with daily survival rates increasing when vegetative cover surrounding the nest cavity increased (Figure 1). Models including terms for canopy cover and year also received moderate support (Table 2) although both models were $> 2 \Delta\text{AICc}$ 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 3). Nest survival also varied by year, and daily survival rates were substantially lower in 2012 (0.959 ± 0.01 ; nest success = 16%) compared to 2013 (0.986 ± 0.01 ; nest success = 54%).

DISCUSSION

Our study was the first to evaluate Red-headed Woodpecker reproductive success in the northeastern United States, and we found that habitat characteristics (not temporal attributes) most influenced Red-headed Woodpecker nest survival within mixed-oak woodlands in northern New York. Nest cavity concealment had the greatest influence on nest survival, and cavities with more vegetative concealment had higher nesting success. We documented high rates of nest predation (> 80%) throughout our study, and substantial vegetative cover surrounding the nest cavity likely reduced the incidence of nest predation because vegetative cover can affect predator foraging efficiency by concealing nest locations and restricting access to cavity contents.

Nest concealment is known to improve nesting success for a variety of open-cup and cavity nesting avian species (Li and Martin 1991, Segura et al. 2012), and in our study greater vegetative cover surrounding the nest cavity may have subsequently impeded the ability of predators to detect Red-headed Woodpecker cavities. In particular, nest cavities located in dead limbs of 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 Red-headed Woodpecker selection of dead limbs (from both live trees and snags) for use as nesting substrates 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 in part explain the widespread selection for and use of this habitat feature. Nest predation is well known to influence avian reproductive strategies and nest-site selection (Martin 1995, Fontaine and Martin 2006) and 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 may therefore be limited by the availability of high-quality nest trees that offer both decadent substrates (dead wood) and cavity concealment (surrounding vegetation structure). Red-headed Woodpeckers are considered weak excavators (Jackson 1975) and likely use trees in advanced decay stages (e.g., only large limbs or bole remain and bark removed) because these trees have sufficient decadent substrates that are necessary for cavity creation (Hudson and Bollinger et al. 2013), albeit a lack of vegetative cover for cavity concealment. Frie et al. (2013) recently suggested that Red-headed Woodpecker selection of nest trees with abundant dead-limb length (i.e., snags and advanced decay-stage trees) resulted in maladaptive habitat use because unsuccessful nests had higher dead-limb length compared to successful nests. Although we found no difference in mean dead-limb length between successful ($11.3 \text{ m} \pm 2.94$) and unsuccessful ($12.1 \text{ m} \pm 2.95$) nests in our study (Wilcoxon ranked test: $W_{28} = 111.5$, $P = 0.98$), our results may in part supplement their hypothesis because nest trees with substantial dead-limb length likely provide minimal cavity concealment, and may consequently result in lower reproductive success. Therefore, although Red-headed Woodpeckers often select forest patches based on overall stand decadence (Sedgewick and Knopf 1990, King et al. 2007), high-quality nest trees (structurally complex trees with both decadent substrate and vegetative cover) may also be important because they provide nesting conditions necessary for successful reproduction.

We also found that nest survival decreased as canopy cover increased. Our results contradict those of Frei et al. (2013), which found that successful nests typically occurred in closed canopy forest patches. We are unsure why our findings differed, but suggest that closed canopy forest patches may have enabled arboreal nest predators (e.g., flying squirrels [*Glaucomys* spp.] and red squirrels [*Tamiasciurus hudsonicus*]) to better detect and access nest

cavities. Furthermore, adult Red-headed Woodpeckers will actively defend nest cavities from approaching inter- and intra-specific predators (JLB, pers. obs.), and open canopies may have allowed for better aerial maneuverability nearby the nest tree, thereby enabling parents to defend their nest from approaching predators (Kozma and Kroll 2012).

Interestingly, we did not find nest age to influence nest survival, which is a temporal attribute that often influences avian nest survival rates and was recently found to affect Red-headed Woodpecker nesting success in Illinois (Hudson and Bollinger 2013). Roughly equal numbers of nests failed during the incubation and nestling stages, and this symmetry in nest failure may explain the constant-age nest survival rates observed in our study. Conversely, we found disparate nesting success between years of our study, which suggests Red-headed Woodpecker reproduction is contingent upon annual nesting conditions. We hypothesize that the observed yearly differences in nesting success were related to annual variation in predation pressure. 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 regulating changes in predation rates, and suggest further research to investigate and identify Red-headed Woodpecker nest predators.

Red-headed Woodpecker populations are rapidly declining range-wide, and estimating reproductive success and identifying factors influencing nest survival is an important process in developing conservation strategies for this species (Smith et al. 2000). Red-headed Woodpeckers in our study area experienced relatively low reproductive success, particularly when compared with other cavity-nesting species that typically have high rates of nesting success (e.g., > 50%;

Martin and Li 1992). Our estimate of nesting success (32%; range = 16–56%) is somewhat lower than previous estimates of reproductive success for Red-headed Woodpeckers, which have been reported 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, Canada (76%; Frei et al. 2013). Our study occurred at the northern and eastern limit of the Red-headed Woodpecker distribution, and reproductive success may subsequently be lower relative to other portions of their range. Whether low rates of reproductive success and productivity are implicated in Red-headed Woodpecker population declines at the regional scale (i.e., northeastern portion of its range) remains to be determined, and should be considered in future conservation and management plans for this species.

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Table 1. Explanatory variables used in candidate logistic-exposure models to evaluate variation in Red-headed Woodpecker nest survival on Fort Drum Military Installation, New York, during May–August, 2012–2013.

Hypothesis	Variable	Description
Temporal	NestAge	Age of the nest (in days)
	Time	Julian date in nesting season
	Year	Year of study (2012 or 2013)
	NestAttempt	Nest attempt (first or re-nest)
Habitat	Diam	Cavity diameter (cm)
	CavHt	Cavity height (m)
	Conceal	Cavity concealment (%)
	TrDbh	Nest tree diameter at breast height (dbh)
	TrDec	Nest tree decay class
	TrDl	Nest tree dead limb length (m)
	CanCov	Canopy cover (%)
	SnagDen	Snag density
	AveUnder	Understory height (cm)
	Stems	Woody stem density
	AveDbh	Average tree dbh

Table 2. Relative support for 19 candidate logistic-exposure models of Red-headed Woodpecker daily nest survival rate (DSR) on Fort Drum Military Installation, New York, during May–August, 2012–2013. K indicates the number of model parameters, AICc is Akaike’s information criterion corrected for small sample size, ΔAICc is the difference in AICc units from the best approximating model, while w_i is the model weight. See Table 1 for description of model variables.

Model	K	AICc	ΔAICc	w_i
S(~Conceal)	2	116.94	0.00	0.33
S(~CanCov)	2	118.99	2.04	0.12
S(~Year)	3	119.33	2.39	0.10
S(~1)	1	120.17	3.23	0.06
S(~AveDbh)	2	120.91	3.96	0.04
S(~TrDbh)	2	121.27	4.33	0.04
S(~Stems)	2	121.41	4.46	0.03
S(~NestAge)	2	121.64	4.70	0.03
S(~TrDll)	2	121.74	4.80	0.03
S(~SnagDen)	2	121.76	4.82	0.03
S(~AveUnder)	2	121.91	4.96	0.03
S(~Diam)	2	122.05	5.11	0.03
S(~CavHt)	2	122.06	5.12	0.03
S(~Time)	2	122.08	5.14	0.02
S(~TrDec)	2	122.15	5.21	0.02
S(~TrDbh + TrDec)	3	122.72	5.77	0.02
S(~NestAttempt)	3	122.74	5.79	0.02
S(~Stems + AveUnder)	3	123.42	6.48	0.01
S(~NestAge + Time)	3	123.64	6.69	0.01

Table 3. Model parameter estimates for top 3 ranking logistic-exposure models of Red-headed Woodpecker daily nest survival rate (DSR) 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(~Conceal)	Intercept	2.74	0.45	1.86	3.62
	Conceal	0.28	0.14	0.01	0.56
S(~CanCov)	Intercept	5.61	1.26	3.14	8.08
	CanCov	-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

Figure Captions

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

Figure 1.

CHAPTER 4

DETERMINATES OF FOREST STAND USE BY RED-HEADED WOODPECKERS

WITHIN HETEROGENEOUS OAK WOODLANDS

**Determinates of Forest Stand Use by Red-headed Woodpeckers within Heterogeneous Oak
Woodlands**

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Abstract

The effective conservation and management of at-risk wildlife populations is predicated on correctly identifying habitat requirements at multiple spatial scales. *Melanerpes erythrocephalus* Linnaeus (Red-headed Woodpecker) populations have declined range-wide, and few studies have evaluated large-scale selection of breeding habitat or identified characteristics of forest stands that influence occupancy of breeding territories by this species. We evaluated the influence of forest stand characteristics (structure and composition) on occupancy patterns by Red-headed Woodpeckers in heterogeneous *Quercus* spp. (oak) woodlands in northern New York. Occupied stands had greater overall tree decadence (decay) and shorter woody understory height than unoccupied stands. Furthermore, forest stands occupied by Red-headed Woodpeckers were dominated by *Quercus rubra* Linnaeus (Red Oak) and *Q. alba* Linnaeus (White Oak), whereas unoccupied stands had greater densities of secondary species such as *Acer rubrum* Linnaeus (Red Maple) and *Pinus rigida* Miller (Pitch Pine). Our results suggest that at larger spatial scales (i.e., forest stands or habitat fragments) Red-headed Woodpecker selection of breeding habitats was influenced by overall stand decadence and management strategies that recruit large numbers of decadent trees into forest stands will increase suitable habitat for this species.

Key Words: forest stand, habitat use, *Melanerpes erythrocephalus*, New York, oak-woodlands, Red-headed Woodpecker

Melanerpes erythrocephalus Linnaeus (Red-headed Woodpecker) is a primary cavity nesting species that has experienced range-wide population decline over the past 40 years and is considered a national species of conservation concern (Smith et al. 2000, Rich et al. 2004). Red-headed Woodpecker population declines have been particularly severe near the periphery of their

distribution in the northeastern United States, coinciding with a region where there is little knowledge of nesting habitat requirements (McGowan and Corwin 2008, Sauer et al. 2011). Red-headed Woodpecker population decline in the northeastern United States has resulted in disparate and patchily distributed remnant populations dispersed among remaining tracts of available habitat (e.g., oak-pine woodlands and beaver ponds) (McGowan and Corwin 2008).

Information regarding Red-headed Woodpecker habitat use in the northeastern United States remains primarily anecdotal, and this paucity of information likely precludes effective conservation and management strategies for this species in the region. Throughout other portions of their range, key features often associated with Red-headed Woodpecker nesting habitat include habitat types characterized by open understories, low shrub cover, and ample decadent (decayed) woody substrates (Sedgewick and Knopf 1990, Rodewald et al. 2005, Vierling and Lentile 2006, King et al. 2007). Furthermore, the majority of research investigating Red-headed Woodpecker nesting habitat use has focused on fine-scale assessments of nest-site selection (i.e., features of the nest tree and immediately surrounding vegetation) (Sedgewick and Knopf 1990, Adkins-Giese and Cuthbert 2005, Rodewald et al. 2005, King et al. 2007, Hudson and Bollinger 2013) and few studies have described larger-scale selection of breeding habitats (i.e., 2nd order selection *sensu* Johnson 1980) (Gutzwiller and Anderson 1987, Rodewald et al. 2005, Frie et al. 2013).

Here, we sought to evaluate patterns of forest stand use by Red-headed Woodpeckers within *Quercus* spp. (oak) woodlands in northern New York at the northeastern extent of their range. Specifically, our objectives were to determine how forest-stand characteristics (structure and composition) influenced patterns of Red-headed Woodpecker use within heterogeneous oak woodlands. We selected forest stands as our sampling unit because forest management activities

(e.g., silvicultural treatments or prescribed burning) are often implemented at this spatial scale. Moreover, given the steady and continued Red-headed Woodpecker population declines in the region, there are likely to be future management efforts targeted at providing suitable breeding habitat for this species in the northeastern United States, and throughout its range.

Methods

Study Area

All field activities were 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). Although the majority of Fort Drum is composed of northern hardwood forest (Dobony and Rainbolt 2008), a small portion of the installation consists of mixed-oak woodlands, including oak savannah and sandplain grassland—both of which are rare habitat types in New York and elsewhere in the northeastern United States. These habitats are characterized by sandy soils and grasslands dominated by Poaceae (grasses) and Cyperaceae (sedges) interspersed by forested areas.

We used Fort Drum forest inventory data (Forest Management Program, Fort Drum Military Installation, 2012) to delineate 35 individual forest stands on the installation (Figure 1). Forest stands selected for study were chosen *a priori* based on stand characteristics and historical knowledge of Red-headed Woodpecker distribution on the installation (J. Bolsinger, Fort Drum Military Installation, New York, unpubl. data). Forest stands ranged in size from 1.6 to 30.4 ha ($\bar{x} = 9.0 \text{ ha} \pm 1.0 \text{ SE}$) and varied in composition, structure and spatial arrangement. Dominant overstory trees within forest stands typically included *Q. rubra* Linnaeus (Northern Red Oak) and *Q. alba* Linnaeus (Eastern White Oak), with lesser amounts of *Acer rubrum* Linnaeus (Red Maple), *Pinus strobus* Linnaeus (Eastern White Pine), *P. resinosa* Solander (Red Pine), *P. rigida*

Miller (Pitch Pine), *Populus grandidentata* Michaux (Bigtooth Aspen), and *Betula populifolia* Marsh (Gray Birch) also present. Woody understory vegetation included *Vaccinium angustifolia* Aiton (Lowbush Blueberry), *Rhododendron groenlandicum* Kron (Labrador Tea), *Rubus* spp. (Raspberry and Blackberry), and seedlings from overstory trees.

Surveys and Territory Monitoring

We conducted surveys for breeding Red-headed Woodpeckers from early May to late June 2012 and 2013. Forest stands were surveyed using a grid network and we used audio playbacks of Red-headed Woodpecker calls and drumming at 200-m intervals to elicit responses from territorial individuals (Dudley and Saab 2003). All forest stands were surveyed on 3 occasions per season, and we separated individual surveys by at least one week. When adult Red-headed Woodpeckers were detected along survey transects we used careful observation and behavioral cues (e.g., nest excavation, copulation, and chatter calls) to locate nest trees. Once we identified the nest-site for territorial pairs, we would return to the territory every 2–4 days to demarcate the territory boundary using a handheld GPS (Atterberry-Jones and Peer 2010).

We classified forest stands as occupied if they were used (i.e., we identified a nest tree and breeding territory within forest stand boundaries) by a territorial Red-headed Woodpecker pair in at least one year of the study. Unoccupied forest stands did not contain a Red-headed Woodpecker territory in either year of the study. In one instance in 2012 we were unable to locate the nest tree of a territorial pair, but considered the forest stand occupied because we delineated the territory within the forest stand boundary and consistently observed territorial individuals within the forest stand. Although it is possible that we may have missed Red-headed Woodpecker territories in unoccupied forest stands, we contend that it is unlikely any forest

stands were misclassified as unoccupied because of the thorough survey effort and high detectability of Red-headed Woodpeckers within the study area.

Vegetation Sampling and Forest Stand Characteristics

We collected extensive forest stand inventory data during each year of the study to compare the composition and structure between stands occupied and unoccupied by Red-headed Woodpeckers. Stand inventory data were collected within circular vegetation plots (0.04 ha, 11.3-m radius) randomly distributed throughout forest stands using a random point generator in ArcGIS 10.0 (ESRI, Redlands, CA). The total number of inventory plots per forest stand ($\bar{x} = 4.42 \pm 0.50$ SE, range = 2–16) was proportional to forest stand size, and we ensured that at least 0.01% of each stand was sampled each year. We constrained our vegetation sampling to 1 July – 31 July of each year to control for seasonal changes in vegetation structure and composition.

Within inventory plots, we measured characteristics of forest stands thought to influence selection of nesting and foraging resources by Red-headed Woodpeckers (Table 1; Sedgwick and Knopf 1990, Vierling and Lentile 2006, King et al. 2007).

Statistical Analyses

We summarized individual forest stand structure and composition data by averaging values from inventory plots within each stand and between years. We used boosted regression trees (BRT) to model differences in habitat characteristics and identify variables most influential in discriminating between occupied and unoccupied forest stands. Although seldomly used in ecological studies, BRTs are a novel analytical technique that achieve high predictive performance by combining a stochastic machine learning technique (boosting) to ensemble several relatively simple regression trees (De'ath and Fabricius 2000, Elith et al. 2008). BRTs are robust to multi-collinearity among predictor variables and can accommodate data from non-

normal distributions (De'ath and Fabricius 2000), and therefore we did not transform our predictor variables or cull variables due to multi-collinearity. We developed BRT models using the 'dismo' package (Hijmans et al. 2013) in program R version 2.13.1 (R Core Development Team 2011) and specified a Bernoulli response distribution that accommodated our binary (occupied *versus* unoccupied) data structure. Fitting BRT models requires the specification of several model parameters, including the model learning rate, bag fraction, and tree complexity (see Elith et al. 2008 for detailed description of model parameters). We set our model parameters as follows: learning rate = 0.001, bag fraction = 0.75, tree complexity = 1. We used the 'gbm.step' function (Hijmans et al. 2013) and 10-fold cross-validation to calculate the optimal number of regression trees used in the boosted model. Model predictive performance was assessed using cross-validated estimates of area under the curve (AUC) of the receiving operator characteristic (ROC), which is a measure of model discrimination efficiency (Bradley 1997). We considered models with mean AUC scores ≥ 0.70 to have acceptable discrimination efficiency and models with mean AUC scores ≥ 0.90 to have excellent discrimination efficiency.

We used the relative percent influence of predictor variables to identify stand characteristics that most strongly discriminated between occupied and unoccupied forest stands. Relative influence of each predictor variable on the response (occupied *versus* unoccupied) was assessed by the average number times a given predictor variable was selected for partitioning and weighted by the squared model improvement resulting from the successive partitions (Elith et al. 2008). We then used BRT partial dependence plots to inspect the relation between influential predictors and the response.

Results

Patterns of Forest Stand Occupancy

Eleven (34%) of the 35 forest stands surveyed were occupied by territorial Red-headed Woodpeckers in at least one breeding season. Five forest stands (14%) were occupied in both years and six stands (17%) were occupied in only one year. We located 15 breeding territories on Fort Drum during the 2012 field season and 11 in 2013. We found 1.4 (± 0.30 SE; range = 1–4) Red-headed Woodpecker territories per stand in 2012 and 1.3 (± 0.21 SE; range = 1–2) in 2013.

Forest Stand Characteristics

We completed 155 forest inventory plots during 2012–2013. Our BRT model comparing structural characteristics between occupied and unoccupied forest stands achieved acceptable discrimination efficiency (mean cross-validated AUC = 0.85 ± 0.06 SE). Overall, the average decay class of trees within forest stands had the greatest effect on occupancy by breeding Red-headed Woodpeckers on Fort Drum, with a relative influence of nearly 68% (Table 2). Red-headed Woodpeckers occupied forest stands with higher overall stand decadence compared to unoccupied stands (Table 2) and the probability of forest stand use greatly increased as mean tree decay increased (Figure 2). Understory woody vegetation height was the second most influential (16% relative influence) stand characteristic (Table 2), and had a negative effect on stand occupancy whereby Red-headed Woodpeckers selected forest stands with lower understory heights (Figure 2). All other habitat variables had less than 10% relative influence, and were not considered to be important predictors in discriminating between occupied and unoccupied forest stands.

Forest stands occupied by Red-headed Woodpeckers were dominated by oaks (Table 3), with Red Oak and White Oak comprising over 65% of trees within these stands. Conversely, unoccupied stands had greater relative abundances of secondary tree species, including Red Maple, Pitch Pine, and White Pine (Table 3).

Discussion

Red-headed Woodpeckers on Fort Drum occupied mix-oak woodlands that were more decadent and had shorter understory height than unoccupied woodlands. At smaller spatial scales, Red-headed Woodpeckers are known to select nest trees and nest patches (i.e., vegetation immediately surrounding the nest tree within territories) with abundant decadent woody substrates because snags and dead limbs are commonly used for nest-cavity locations (Gutzwiller and Anderson 1987, Sedgwick and Knopf 1990, Rodewald et al. 2005, Hudson and Bollinger 2013). Our results suggest that this pattern of habitat selection also persists at larger spatial scales as well (i.e., 2nd order, forest-stand selection) whereby Red-headed Woodpeckers identify suitable nesting habitat based on overall stand decadence. King et al. (2007) identified a nest-habitat threshold for Red-headed Woodpeckers in central Wisconsin related to the density of dead-limb bearing trees—indicating the need for numerous decadent trees near nest sites. Moreover, King et al. (2007) suggested that when selecting a nest site, overall stand decadence (macrohabitat selection) likely supersedes the importance of individual nest trees (microhabitat selection) for nesting pairs. Our results support the hypothesis that overall stand decadence is a key factor influencing Red-headed Woodpecker selection of particular forest stands and nesting areas. The majority of available Red-headed Woodpecker habitats (e.g., grassland and woodlot edges, savanna and parklands) in the northeastern United States have been severely altered because of their suitability for development or conversion to agriculture (Lorimer and White 2003). In recent decades, land use practices such as firewood cutting, fire suppression, salvage logging, and removal of snags and dead limbs for aesthetic reasons or safety considerations have substantially reduced the distribution and quality of highly decayed forest stands throughout the eastern United States. Subsequently, remaining tracts of available forested areas may lack

sufficient densities of decadent trees that are required by breeding Red-headed Woodpeckers (King et al. 2007).

Red-headed Woodpeckers also selected forest stands on Fort Drum with short (<15 cm) woody understory heights, which is a structural attribute that enhances their ability to flycatch and ground forage. Unlike most woodpecker species, Red-headed Woodpeckers frequently flycatch and ground foraging during the breeding season (Reller 1972) and a reduction of near-ground vegetation likely allows better access to food resources. When choosing among particular forest stands for breeding, individual Red-headed Woodpecker pairs must select habitats that provide both nesting substrates (i.e., decadent trees) and suitable foraging areas. Frie et al. (2013) found Red-headed Woodpeckers to select forested woodlots in southern Ontario that maximized foraging conditions (forest openness and length of dead limbs) but not nesting resources. In our study area, breeding pairs likely selected forest stands that maximized both nesting and foraging resource requirements because occupied stands were both highly decayed (nesting substrates) and had open understories (foraging habitat). Interestingly, we did not find forest stand size to influence occupancy by Red-headed Woodpecker territories (<1 % relative influence).

Gutzwiller and Anderson (1987) found that Red-headed Woodpecker selection of habitat fragments (2rd order selection) in Wyoming riparian woodlands was most influenced by habitat area, with the probability of use increasing for fragments >2 ha in size. The majority of forest stands (94 %) in our study area were larger than the minimal criteria described by Gutzwiller and Anderson (1987), and it is therefore possible that stand area was not a limiting factor influencing Red-headed Woodpecker selection of individual forest stands on Fort Drum.

Tree species composition has rarely been indicated as a significant factor in Red-headed Woodpecker nest-tree and nest-patch selection (Conner 1976, Adkins-Giese and Cuthbert 2003,

Hudson and Bollinger 2013); however, forest stand composition may influence their selection of breeding habitat at larger spatial scales. For example, Rodewald et al. (2005) found that Red-headed Woodpeckers selected golf courses in central and northern Ohio with nearly twice as many hard-mast trees compared to golf courses where breeding territories were absent. Consistent with that observation, forest stands on Fort Drum occupied by Red-headed Woodpeckers were dominated by Red Oak and White Oak, which are the principal hard mast producing tree species within the study area. Red-headed Woodpecker selection of oak-dominated forest stands may be related to the availability of hard mast, which is an important food resource for these birds throughout the annual cycle (Reller 1972, Doherty et al. 1996).

Although unoccupied forest stands were also dominated (i.e., highest relative abundance) by oaks, they had greater densities of secondary species, most notably Red Maple and Pitch Pine, than occupied stands. Red Maple is a moderately shade-tolerant tree species that has increased in abundance throughout the eastern United States in recent decades as maturing forests develop mesophytic properties (Nowaki and Abrams 2008). In our study area, we noted that several unoccupied forest stands contained mature oak over-stories, yet mid-stories were dominated by emerging stems (1–15-cm dbh) of Red Maple and other shade-tolerant species—a structural characteristic that reduces the ability of Red-headed Woodpeckers to flycatch and ground forage. Without adequate disturbance regimes such as fire or grazing to reduce the density of emergent shade-tolerant saplings and other mid-story trees, potentially suitable forest stands (e.g., mature oak-dominated forest with open understories) can quickly become unsuitable as succession increases the height and density of lower- and mid-story vegetation. For example, we noted that several occupied forest stands on the installation were also commonly used for military training activities such as troop bivouacking and tracked-vehicle maneuvering—activities that have

successfully managed understory vegetation to levels desired by red-headed woodpeckers. Furthermore, we also observed that several unoccupied forest stands contained high densities (>40 %) of Pitch Pine, which is a shade-intolerant species that produces open-understory stands and is well adapted to sandy and other poor-quality soils. However, unlike oaks that self-prune to produce decadent substrates even in the absence of mature or late decay-stage trees, the majority of Pitch Pines in our study area rarely developed dead wood characteristics (mean tree decay class = 1.20 ± 0.05 SE; <33% decadent crown) and likely lacked sufficient stand-level tree decay properties required to support Red-headed Woodpecker breeding territories.

Red-headed Woodpecker populations are rapidly declining in the northeastern United States and they are listed as either endangered, threatened or of special concern in several states (Smith et al. 2000, McGowin and Corwin 2008). At large spatial scales, Red-headed Woodpeckers apparently select forest stands based on overall stand decadence, and management activities that enhance overall stand decadence will likely increase available habitat for this species. Therefore, in areas of the northeastern United States where current Red-headed Woodpecker populations exist, or where they have been recently extirpated, we encourage management activities that promote the development of large patches (> 2 ha) of late-decay stage forest stands and the removal of secondary non-oak under- and mid-story trees (e.g., Red Maple). For example, management practices such as prescribed burning (Vierling and Lentile 2006, King et al. 2007, Vierling and Gentry 2008) or tree girdling (Hudson and Bollinger 2013) can quickly recruit large numbers of decadent trees into target forested areas. Given their at-risk species status, future conservation strategies should manage habitat for this species at multiple spatial scales (e.g., nest tree, nest patch, and forest stand) and additional research investigating Red-headed Woodpecker resource selection and population dynamics (e.g., meta-population

dynamics among disparate breeding populations throughout the northeastern United States) will further inform management decisions.

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Table 1. Habitat variables collected within 0.04-ha stand inventory plots and used to discriminate between forest stands occupied and unoccupied by Red-headed Woodpeckers on Fort Drum Military Installation, New York, during May–August, 2012–2013.

Variable	Description
Tree decay class	Average decay class for trees ≥ 5 -cm dbh. Ranked 1–8, defined following Newell et al. (2009): 1 = vigorous tree, 2 = < 33% dieback, 3 = 33–66% dieback, 4 = > 66% dieback, 5 = recently dead tree, 6 = dead tree, only large limbs remain, 7 = dead tree, only bole > 6 m remains, 8 = dead tree, only bole < 6 m remains
Understory height (cm)	Average height of woody understory vegetation recorded along 5 m transect in random cardinal direction
Tree dbh (cm)	Mean dbh of trees ≥ 5 -cm dbh
Small tree density	Density of small trees; 5–15-cm dbh
Sapling density	Density of saplings; 0–5-cm dbh
Medium tree density	Density of medium trees; 15–30-cm dbh
Total tree density	Density of all trees; ≥ 5 -cm dbh
Limb-tree density	Density of dead-limb trees with ≥ 1 decadent limb ≥ 10 -cm diameter
Stand area (ha)	Area of forest stand
Dead-limb length (m)	Estimated length of decadent limbs ≥ 10 cm diameter
Dead-limb density	Number of dead limbs ≥ 10 cm diameter
Canopy height (m)	Mean height of 5 largest trees nearest the nest tree
Large tree density	Density of large trees; > 30 cm dbh
Snag density	Density of snags ≥ 10 cm dbh
Stem density	Density of woody stems 0.5–1.5 m in height
Canopy cover (%)	Average of 4 densiometer readings recorded at the plot edges in the 4 cardinal directions

Table 2. Summary statistics and relative percent influence of variables used to discriminate between Red-headed Woodpecker occupied and unoccupied forest stands on Fort Drum Military Installation, New York, during May–August 2012–2013. Relative percent influence values are derived from Boosted Regression Tree (BRT) models and indicate the relative effect of habitat variables on forest stand occupancy. Summary statistics (mean and standard error [SE]) of habitat variables are provided for comparison between occupied and unoccupied forest stands.

Stand variable	Relative influence (%)	Occupied stands (<i>n</i> = 11)		Unoccupied stands (<i>n</i> = 24)	
		Mean	SE	Mean	SE
Decay class of trees	67.9	1.95	0.11	1.45	0.08
Understory height (cm)	16.0	12.34	1.70	15.78	1.73
Tree dbh (cm)	6.9	24.53	2.00	20.93	2.09
Small tree density	2.6	8.91	3.45	12.89	2.67
Sapling density	1.6	14.75	3.48	20.79	4.74
Medium tree density	1.2	5.00	0.88	5.42	0.97
Total tree density	0.8	17.59	3.94	21.48	3.38
Limb-tree density	0.8	3.29	0.54	2.20	0.39
Stand area (ha)	0.8	12.54	2.34	7.38	1.44
Dead-limb length (m)	0.4	20.25	5.14	11.10	2.29
Dead-limb density	0.4	8.03	1.61	4.88	0.83
Canopy height (m)	0.2	10.93	0.44	10.55	0.46
Large tree density	0.2	3.68	0.39	3.17	0.49
Snag density	0.1	1.22	0.35	0.73	0.23
Stem density	0.0	22.36	5.01	26.54	6.63
Canopy cover (%)	0.0	71.47	4.26	71.62	4.84

Table 3. Tree composition and relative abundance (%) within forest stands occupied and unoccupied by Red-headed Woodpeckers on Fort Drum Military Installation, New York, during May–August, 2012–2013.

Species	Occupied Stands (<i>n</i> = 11)		Unoccupied Stands (<i>n</i> = 24)	
	<i>n</i>	%	<i>n</i>	%
Northern red oak (<i>Quercus rubra</i>)	515	50.44	642	32.25
Eastern white oak (<i>Quercus alba</i>)	153	14.99	163	8.19
Red maple (<i>Quercus rubrum</i>)	128	12.54	342	17.18
Bigtooth aspen (<i>Populus grandidentata</i>)	68	6.66	30	1.51
Red pine (<i>Pinus resinosa</i>)	62	6.07	88	4.42
Black cherry (<i>Prunus serotina</i>)	29	2.84	71	3.57
Eastern white pine (<i>Pinus strobilus</i>)	20	1.96	229	11.50
Gray birch (<i>Betula populifolia</i>)	12	1.18	96	4.82
Paper birch (<i>Betula papyrifera</i>)	9	0.88	17	0.85
Pitch pine (<i>Pinus rigida</i>)	9	0.88	269	13.51
Scots pine (<i>Pinus sylvestris</i>)	9	0.88	2	0.10
Pin cherry (<i>Prunus pennsylvanica</i>)	5	0.49	3	0.15
American beech (<i>Fagus grandifolia</i>)	1	0.10	2	0.10
Quaking aspen (<i>Populus tremuloides</i>)	1	0.10	5	0.25
Eastern cottonwood (<i>Populus deltoides</i>)	0	0.00	7	0.35
Eastern hemlock (<i>Tsuga canadensis</i>)	0	0.00	22	1.10
Yellow birch (<i>Betula alleghaniensis</i>)	0	0.00	3	0.15
Total	1021		1991	

Figure Captions

Figure 1. Location and distribution of forest stands occupied and unoccupied by Red-headed Woodpeckers on Fort Drum Military Installation, New York, during May–August, 2012–2013.

Figure 2. Partial dependence plots indicating the marginal effect of predictor variables on forest stand occupancy by Red-headed Woodpeckers on Fort Drum Military Installation, New York, during May–August, 2012–2013.

Figure 1.

Figure 2.

CHAPTER 5

**MANAGEMENT IMPLICATIONS FOR RED-HEADED WOODPECKERS ON FORT
DRUM MILITARY INSTALLATION, NEW YORK**

Management Implications for Red-headed Woodpeckers on Fort Drum Military Installation, New York

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INTRODUCTION

Red-headed woodpecker populations are declining at alarming rates and are considered a national species of conservation concern (Rich et al. 2004, Sauer et al. 2011). In the northeastern United States, population declines have been particularly severe (e.g., >5% per year) and the species is listed as endangered, threatened, or of special concern in several U.S. states and Canadian provinces (Smith et al. 2000). In New York, the red-headed woodpecker is considered a “Species of Greatest Conservation Need” and is listed as Special Concern (McGowan and Corwin 2008). Limited information exists regarding red-headed woodpecker habitat use and reproductive success in New York and elsewhere in the Northeast, which further complicates management and conservation strategies for this species in the region. A better understanding of habitat use and local population dynamics will greatly improve management decisions for this species in the region.

As a result of long-term population declines, red-headed woodpeckers are uncommon and sparsely distributed in the northeastern United States (Smith et al. 2000). When present, they are

typically found in small numbers (a few pairs) in distinct and isolated habitat patches, such as beaver ponds, remnant oak savanna, golf courses, or other habitats characterized by abundant snags and open understory (McGowan and Corwin 2008). Red-headed woodpeckers were historically common throughout much of the eastern United States where large expanses of savanna and other park-like habitats were maintained by natural and human-induced disturbances (e.g., fire) created open understories and recruited snags and partially decayed trees into forest stands (Smith et al. 2000, Brawn et al. 2005). The majority of historic red-headed woodpecker habitat (e.g., oak savanna) in the Northeast has been lost as a result of conversion to agriculture and development (Nuzzo 1986, Askins 1993), and subsequently remaining meta-populations are patchily distributed in disparate areas of available habitat (such as Fort Drum). Future conservation of red-headed woodpeckers at the regional scale presents significant challenges because of the difficulty in managing small and disparate meta-populations, each with variable local population dynamics.

We studied a small (10–15 adult pairs) breeding population of red-headed woodpeckers on Fort Drum Military Installation, New York (Figure 1) which represents one of the largest breeding populations in the state. The primary goal of this research was to provide natural resource biologists on Fort Drum with objective guidelines for managing habitat for this species on the installation, and to provide baseline demographic information (i.e., reproductive success) of the breeding population. Specifically, our objectives were to (1) evaluate red-headed woodpecker nest-habitat selection at multiple spatial scales, and (2) examine reproductive success and factors influencing nest survival. Here, we overview the pertinent findings from our research and provide habitat management recommendations for red-headed woodpeckers on Fort Drum.

MANAGEMENT IMPLICATIONS

Nesting Habitat

Given our findings (Chapters 2–4), red-headed woodpeckers consistently selected for three key habitat features at multiple spatial scales: large trees, dead wood, and open understories (Figure 2). Red-headed woodpeckers are known to select for these structural attributes in many different habitat types throughout their range (Sedgewick and Knopf 1990, Rodewald et al. 2005, Vierling and Lentile 2006, King et al. 2007, Frie et al. 2013, Hudson and Bollinger 2013). Therefore, nesting habitats for red-headed woodpeckers on Fort Drum should be dominated by large (>30-cm dbh) decadent trees with minimal understory vegetation. Forest management activities that negatively affect stand decadence or reduce the amount of dead wood within forest stands that are being managed for red-headed woodpeckers should be strongly discouraged. For example, common practices such as firewood cutting should either be restricted in areas that are currently managed for red-headed woodpeckers, or limited to live trees <30-cm dbh and targeted at those with minimal decay properties. In particular, dead limbs were consistently selected by red-headed woodpeckers at multiple spatial scales, and their removal should be conducted only in the most necessary situations. Forest management practices that promote the recruitment of decadent trees and dead limbs into forest stands will likely increase available habitat for this species on Fort Drum. For example, tree girdling can quickly recruit snags and partially decayed trees into target forest stands—particularly if the stand does not meet minimal dead wood threshold criteria (Chapter 2). Furthermore, because red-headed woodpecker nest survival was positively affected by cavity concealment, the presence of structurally complex trees (i.e., those that have both live and dead portions) will also provide nesting substrates necessary for successful reproduction (Figure 3).

As a result of the widespread loss of savanna and other park-like habitats throughout the eastern United States, there has recently been intensified interest in restoration of these disturbance-mediated habitat types (Brawn et al. 2001, Brawn 2005, Grundel and Pavlovic 2007). On Fort Drum, several forest stands have potential for restoration/management opportunities—particularly stands with mature oak overstories. Without adequate natural or mechanical disturbance in previous decades, several oak-dominated forest stands within the study area have developed mesophytic properties as succession has increased the density of shade-tolerant species (e.g., maples [*Acer* spp.]) within forest stands (Figure 4–6). In these cases, nest-habitat results from my study (Chapters 2 and 4) can be used as guidelines for restoring and/or managing forest stands (or areas within a given stand) to suitable nesting habitats for red-headed woodpeckers on the installation. Management strategies based on prescribed fire have been very successful in maintaining suitable red-headed woodpecker nesting habitat (Brawn 2005, Vierling et al. 2006, King et al. 2007) because low-intensity fires effectively remove understory vegetation while simultaneously recruiting snags and partially decayed trees into burn areas (Figure 7). However, in situations where management prescriptions such as prescribed fire are not preferred, surrogate disturbance activities such as mechanical tree harvest, vegetation removal, and herbicide treatments can be used to manage habitat for this species. For example, in stands that have developed mesophytic properties, mechanical removal of undesirable understory and mid-story vegetation can restore oak-dominated stands to habitats with savanna-like structural attributes.

Throughout their range red-headed woodpeckers have adapted to human-modified habitats that structurally mimic natural savanna-like habitats, such as city parks or golf courses (Smith et al. 2000, Rodewald et al. 2005, Hudson and Bollinger 2013). Interestingly, military

training and installation maintenance activities have likely sustained suitable nesting habitat for red-headed woodpeckers on Fort Drum (e.g., western forest stands of Training Area 5D; Figure 1). For example, activities such as bivouacking and tracked-vehicle maneuvering within oak-woodlands on the installation have probably maintained suitable nesting habitat by reducing or suppressing understory vegetation (Figure 8). In addition, grassland areas on Fort Drum that are maintained by mowing and that have sufficient large decadent tree densities will likely support red-headed woodpecker nesting (e.g., the Ammunition Supply Point [ASP] bunker area). Red-headed woodpeckers on Fort Drum commonly used mowed and un-mowed grasslands as foraging areas for ground foraging and aerial flycatching, often “commuting” considerable distances (e.g., >150 m) from nest trees to foraging areas. This behavior indicates a disjuncture between optimal foraging areas (i.e., stands with open understories or open grasslands) and suitable nesting areas (i.e., areas with ample decadent trees). Although we could not directly quantify foraging habitat surrounding nest sites, areas of open grassland may be important foraging areas for red-headed woodpeckers on Fort Drum—however, additional research would be necessary to fully understand the importance of open grasslands for these birds on the installation. When identifying target forest areas for habitat management, decadent stands juxtaposed to open grasslands likely provide ideal nesting and foraging conditions.

Reproductive Success

We documented high annual variation in red-headed woodpecker nesting success, and rates of reproduction (overall productivity = 0.83 young fledged per nesting pair) that are below replacement levels (Chapter 3). This is of substantial and immediate concern given the inherently small size (10–15 pairs) and migratory status of the Fort Drum breeding population. Continued monitoring of red-headed woodpecker reproduction is certainly warranted, and will further

improve reproductive success estimates to elucidate long-term trends in reproductive success and population size. Furthermore, marking (banding) birds will provide insight to the fidelity and recruitment of individuals to Fort Drum, which can be used to estimate population persistence (e.g., population viability modeling). Fort Drum is an important breeding area for red-headed woodpeckers in the northeastern United States, and actively managing oak-dominated woodlands on the installation will be important step in maintaining and/or increasing the Fort Drum red-headed woodpecker population.

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FIGURES

Figure 1. Distribution of forest stands occupied and unoccupied by red-headed woodpeckers on Fort Drum Military Installation, New York, during May–August, 2012–2013. Fort Drum Training Areas are labeled in black, while individual forest stands are labeled in white.

Figure 2. Photograph showing habitat features selected for by red-headed woodpeckers on Fort Drum, including numerous large-diameter trees with decadent substrates and an open understory. Photograph was taken in Forest Stand 16, in Training Area 5D.

Figure 3. Photograph of a successful red-headed woodpecker nest, with the cavity located in a structurally complex nest tree with both dead substrates and live vegetation that provide concealment. Photograph was taken in Forest Stand 0, in Training Area 5D.

Figure 4. Photograph from an area unoccupied by red-headed woodpeckers showing an oak-dominated forest stand that has developed dense understory and mid-story vegetation.

Photograph was taken in Forest Stand 6, in Training Area 5D.

Figure 5. Photograph from an area unoccupied by red-headed woodpeckers showing an oak-dominated forest stand that has developed dense understory and mid-story vegetation.

Photograph was taken in Forest Stand 13, in Training Area 5D.

Figure 6. Photograph from an area unoccupied by red-headed woodpeckers showing a pine- and oak-dominated forest stand that has developed dense understory and mid-story vegetation.

Photograph was taken in Forest Stand 11, in Training Area 5D.

Figure 7. Photograph indicating how low-intensity fire can remove undesirable understory vegetation while recruiting decadent trees into target forest stands. Photograph was taken in Forest Stand 18, in Training Area 8A.

Figure 8. Photograph showing how military maneuvering within oak-dominated forest stands can maintain open understories that are selected for by red-headed woodpeckers. Photograph was taken in Forest Stand 0, in Training Area 5D.

APPENDICIES

APPENDIX A. Figures indicating representative trees of various decay stages used to assign individual trees to pre-defined decay classes. Tree decay class system used in this study followed Newell et al. (2009) and corresponds to % crown decadence.

Figure 1. Tree decay class 1; vigorous tree with live crown and no partial decadence.

Figure 2. Tree decay class 2; vigorous tree with <33% crown dieback.

Figure 3. Tree decay class 3; declining tree with 33–66% crown dieback.

Figure 4. Tree decay class 4; declining tree with >66% crown dieback.

Figure 5. Tree decay class 5; recently dead tree that retains primary and secondary limbs and braches.

Figure 6. Tree decay class 6; dead tree that retains only large primary limbs.

Figure 7. Tree decay class 7; dead tree only bole remains >8 m.

Figure 8. Tree decay class 8; dead tree only bole remains <8 m.

APPENDIX B. Figures indicating various cavity concealment classes used in logistic-exposure models of red-headed woodpecker nest daily survival rates (DSR). Cavity concealment was assessed based on % vegetative structure (live or dead) surrounding (within 1 m² of) nest cavities and categorized into 10% increments (e.g., cavity concealment category 2 corresponds to 20–30% concealment).

Figure 1. Nest cavity with no cavity concealment and vegetative structure surrounding the cavity (category 1; 0–10% concealment).

Figure 2. Nest cavity with very minimal cavity concealment and vegetative structure surrounding the cavity (category 1; 0–10% concealment).

Figure 3. Nest cavity with marginal cavity concealment and vegetative structure surrounding the cavity (category 3; 30–40% concealment).

Figure 4. Nest cavity with marginal cavity concealment and vegetative structure surrounding the cavity (category 4; 40–50% concealment).

Figure 5. Nest cavity with considerable cavity concealment and vegetative structure surrounding the cavity (category 6; 60–70% cavity concealment).

Figure 6. Nest cavity with substantial cavity concealment and vegetative structure surrounding the cavity (category 8; 80–90% cavity concealment).