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NEST DENSITY, PRODUCTIVITY, AND HABITAT SELECTION OF RED-SHOULDERED HAWKS IN A CONTIGUOUS FOREST

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ABSTRACT.—We measured habitat selection, productivity, and nest density of Red-shouldered Hawks (*Buteo lineatus*) breeding in a largely contiguous forest in northern Wisconsin. We located and followed the reproductive success of 71 breeding attempts within an estimated 26 territories between 2002 and 2006. Mean reproductive rates were 0.7 young per breeding attempt and 2.0 young per successful nest, and nest success averaged 35% per year. Annual nest density ranged from 0.10–0.16 nests per km^2. Micro- and macrohabitat variables were measured at 400-m^2 circular plots centered on nest trees and at random plots located in similar forest types. When compared to random plots, nesting areas were significantly shorter distances from the nearest lake or treeless wetland ($P <$ 0.001). The logistic regression model that provided the best fit for our data included the distance to nearest trail or road and the distance to nearest lake or treeless wetland. At the microhabitat scale, nesting areas had greater basal areas and fewer sapling-sized trees (i.e., trees 3–13 cm in diameter at breast height) than found at random plots. The low reproductive success in combination with the observed nest density suggests that immigration of Red-shouldered Hawks from outside the study area may be critical to maintaining this breeding population.

KEY WORDS: *Red-shouldered Hawk*; Buteo lineatus; *broadcast surveys*; *nest density*; *nesting habitat*; *reproductive rate.*

DENSIDAD DE NIDOS, PRODUCTIVIDAD Y SELECCIÓN DE HÁBITAT DE *BUTEO LINEATUS* EN UN BOSQUE CONTINUO

RESUMEN.—Medimos la selección de hábitat, la productividad y la densidad de nidos de individuos de *Buteo lineatus* que nidifican en un bosque mayoritariamente continuo en el norte de Wisconsin. Localizamos y seguimos el éxito reproductivo de 71 intentos de nidificación en un total estimado de 26 territorios, entre 2002 y 2006. Las tasas reproductivas promedio fueron 0.7 pichones por intento de nidificación y 2.0 pichones por nido exitoso, y el éxito de nidificación promedió 35% por año. La densidad anual de nidos fluctuó entre 0.10–0.16 nidos por km^2. Las variables de micro- y macro-hábitat fueron medidas en parcelas circulares de 400 m^2, centradas en los árboles con nidos y en parcelas al azar localizadas en bosques similares. En comparación con las parcelas al azar, las áreas de nidificación estuvieron a distancias significativamente más cortas del lago más cercano o el humedal no arbolado ($P <$ 0.001). El modelo de regresión logística que brindó el mejor ajuste para nuestros datos incluyó la distancia al sendero o camino más cercano y la distancia al lago o humedal no arbolado más cercano. A la escala de micro-hábitat, las áreas de nidificación tuvieron áreas basales más grandes y menos renovales de árboles (i.e., árboles 3–13 cm de diámetro a la altura del pecho) que lo encontrado en las parcelas al azar. El bajo éxito reproductivo, en combinación con la densidad de nidos observada, sugieren que la inmigración de individuos de *Buteo lineatus* desde fuera del área de estudio puede ser crítica para mantener esta población reproductiva.

[Traducción del equipo editorial]

Many studies in eastern North America have examined habitat selection of Red-shouldered Hawks (*Buteo lineatus*) using micro- and macrohabitat variables. In general, nesting habitats were described as large, remote, and contiguous tracts of mature forest (Titus and Mosher 1981, Bosakowski et al. 1992, McLeod et al. 2000, Naylor et al. 2004). However, Red-shouldered Hawks also nest and reproduce at high rates in largely fragmented habitats, including

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suburban areas (Dykstra et al. 2000). Some studies reported nest locations positively associated with distance to wetlands or surface water (Bednarz and Dinsmore 1981, Titus and Mosher 1981, Bryant 1986, Bosakowski et al. 1992, Dykstra et al. 2000) and structural characteristics (e.g., high basal area, high canopy height, and large-diameter trees) of mature forests (Titus and Mosher 1981, Morris and Lemon 1983, Woodrey 1986, Moorman and Chapman 1996, Dykstra et al. 2000, McLeod et al. 2000). In addition, some studies reported Red-shouldered Hawk nest sites negatively associated with distance to nearest road or building (Bednarz and Dinsmore 1982, Bosakowski et al. 1992), and treeless upland habitats (Moorman and Chapman 1996).

Red-shouldered Hawks were listed as a threatened species in Wisconsin in 1979 because of suspected declines in suitable nesting habitat (Wisconsin Department of Natural Resources 1988). Analysis of data from the North American Breeding Bird Survey (1966–2004) showed that Red-shouldered Hawk abundance in Wisconsin had one of the largest negative trends for this species in North America (Sauer et al. 2005). Decreases in Red-shouldered Hawk abundance elsewhere have been attributed to reduced prey numbers (Campbell 1975) or displacement by Red-tailed Hawks (*Buteo jamaicensis*; Bednarz and Dinsmore 1982, Bryant 1986) that ultimately are caused by the direct loss, alteration, or fragmentation of nesting and foraging areas. Unfortunately, in many investigations, the direct effect of forest alteration on Red-shouldered Hawks is difficult to identify because of confounding factors such as multiple landowners, changes in land use and management philosophies, or a short study duration (i.e., 3 yr or less).

Broadcast surveys for Red-shouldered Hawks detected 43 and 23 responses in two 93-km^2 areas of the Menominee Indian Reservation located in northern Wisconsin (one area surveyed in 1999, one in 2000; D. Rieter unpubl. data). With the assumption that each response came from paired territorial birds (Henneman et al. 2007), the estimated densities for those areas were 0.27 and 0.15 pairs per km^2. If these estimates were correct, they represent moderate densities for breeding Red-shouldered Hawks in the northern portions of their breeding range. We initiated this study to determine whether these estimates, based on responses to broadcast surveys, were accurate.

Our goals in this study were to locate nests and monitor Red-shouldered Hawk occupancy and reproductive performance, and to identify nest and landscape habitat component(s) Red-shouldered Hawks select in an extensive, forested landscape. Measurements obtained from microhabitat variables may be used to develop forest structure thresholds that land managers can use to create or enhance nesting habitat for Red-shouldered Hawks.

METHODS

Study Area. Our study area (Fig. 1) was approximately 10 800 ha in size with >98% of it forested. The northern and western boundaries of the study area were defined by open agricultural lands with small woodlots, while the remaining boundaries followed ecological landscape divisions and forest types. The entire study area was located within the Menominee Indian Reservation (hereafter referred to as Menominee forest) and is property of the Menominee Indian Tribe. The Menominee forest is actively managed by Menominee Tribal Enterprises, with most forest types following single-tree or group selection silvaculture, in which trees are harvested in various size classes, either individually or in small groups, at regular intervals to maintain an uneven-aged forest. The structural characteristics of this forest are unique in this region because forest managers here have followed these harvest prescriptions for >50 yr (D. Cox pers. comm.). Following this method of timber management over many years has resulted in a relatively homogeneous (>99% of the forested area) mature, uneven-aged forest. Treeless habitat included lakes, streams, open wetlands, and small upland openings. Major forest types in order of decreasing abundance included northern hardwood (predominantly sugar maple [*Acer saccharum*], yellow birch [*Betula alleghaniensis*], American basswood (*Tilia americana*) and white ash [*Fraxinus americana*]), eastern hemlock (*Tsuga canadensis*)-northern hardwood, swamp conifer (*Thuja occidentalis* and *Pinus strobus*), eastern hemlock, and quaking aspen (*Populus tremuloides*). A diverse understory was found throughout the forest, with regenerating eastern hemlock common and some American yew (*Taxus canadensis*) present.

The topology is generally flat to rolling, interspersed with areas of pitted outwash and other ice contact deposits located within the Green Bay Lobe Stagnation Moraine subsection of the National Hierarchical Framework of Ecological Units (McNab and Avers 1994). There were three seasonally occupied residences located near a lake in the study area; no other buildings were present. Road density

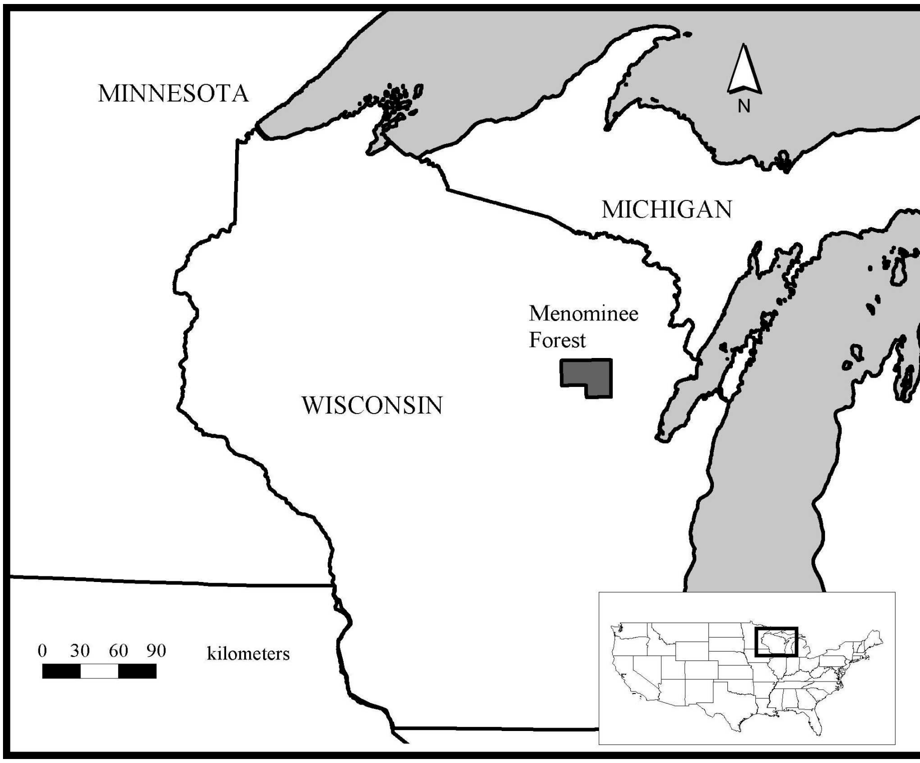

Figure 1. Location of Menominee Indian Reservation in Wisconsin.

was 785 m per km^2, however, 91% of the linear road length was unpaved and most roads were completely covered by forest canopy.

Surveys, Nest Searches, and Productivity Monitoring. We surveyed the entire study area annually for Red-shouldered Hawks using conspecific calls broadcast along forest roads and within roadless areas to locate occupied territories. Complete coverage was attained by establishing calling stations every 800 m along all roads and trails. Interior calling stations were added to areas located >800 m from a road station and surveyed on foot. After the first field season, if a known nest was found to be occupied, all stations within 400 m of the nest were skipped. We surveyed from 27 March to 22 May 2002, 4 April to 3 May 2003, 29 March to 4 May 2004, 28 March to 25 April 2005, and 24 March to 26 April 2006. All surveys occurred between 0.5 hr after sunrise to 1000 H Central Standard Time. Surveys were cancelled if wind speeds were consistently >16 km h^{-1} or steady precipitation occurred. We used a Western Rivers Electronic Game Caller with a 25-watt amplifier (Western Rivers, Lexington, TN U.S.A.) to broadcast the call. Survey protocol followed methods described by Iverson and Fuller (1991), McLeod and Andersen (1998) and Dykstra et al. (2001). At each survey station, one to four observers looked and listened along the road or trail. The survey consisted of a 20-sec call followed by a 40-sec listening period. This sequence was played six times in succession, followed by a 4-min listening period for a total survey time of 10 min per station. The loudspeaker was rotated 90° after each of the 20-sec calling sessions. When a response was detected, either aurally or visually, the broadcast caller was stopped and compass bearing of the first response detected was recorded. On many occasions, multiple observers spaced 50–100 m apart heard a response simultaneously. This allowed us to triangulate the location where a bird was first detected. Occasionally, multiple birds responded to a broadcast survey from different directions; these were recorded as potentially different territories.

Multiple observers searched for nests near most responses by walking a line along the compass bearing of the original response. One observer walked the line from the calling station and the others walked parallel lines approximately 25–35 m apart, examining each tree within view. For most searches, observers walked >800 m along the compass line or until an occupied nest was found. When an occupied nest was located, the tree was marked and coordinates were determined with a Global Positioning System.

We used productivity definitions described by Jacobs and Jacobs (2002) to allow comparisons between our study and others in the region. An occupied nest was defined as one that was rebuilt or had fresh green vegetation on the nest edge, or one that had two territorial adults present near it. A breeding attempt was defined as a nest where young, eggs, or eggshells were observed, or an adult was observed in the nest with downy breast feathers present on the nest edge. A successful nest had at least one young reach banding age (i.e., approximately 21 d) or older. All nests found occupied during searches or where a breeding attempt occurred were visited at least twice prior to young fledging. If a nest appeared failed during any visit, we climbed the nest tree and searched the nest site area for evidence to determine a cause. We used a territory reoccupancy definition similar to that reported by Dykstra et al. (2000). Territory and nesting densities were calculated using the entire study area.

Habitat Assessment. We collected microhabitat data within a 400-m² circle plot centered at nest trees and random locations. Nest tree plots were sampled after the young had fledged or nest failed, and random plots were located using a random point generating script developed for ArcView® (ESRI, Redlands, CA U.S.A.) GIS software. Because all Red-shouldered Hawk nests were found within northern hardwood and hemlock-hardwood forest types, we stratified the study area by forest type and restricted random plot locations to these forest types. In general, we collected data using methods outlined by James and Shugart (1970), with several modifications and additions. We measured heights of four canopy trees throughout the plot, nest tree height, and nest height with a clinometer. Canopy closure was measured with a concave densitometer at 4, 8, 12, and 16 m along a random compass bearing through the center of each plot. We measured diameter at breast height (DBH) of all trees and shrubs >2 cm, and heights of all understory woody species between 1.2 and 6.1 m. All trees and shrubs >1.2 m tall were identified to species. Downed woody debris (DWD) was defined as all fallen trees and large branches >5 cm in diameter and >1 m in length, and stumps within the plots. Volume of each DWD piece was calculated by measuring the total length (or height for stumps) and diameter of each end. If a piece of DWD extended beyond a plot boundary, we measured only what was within the plot. Distance variables <120 m from plot center were measured with a meter tape, all others were measured remotely using aerial photographs, USGS 7.5-minute topographical maps, a Geographical Information System (GIS), and ArcView® software. For each territory with different nest trees used in different years, we measured habitat data at plots from all years, and used mean values for statistical analyses. Descriptions of all habitat variables measured at each nest and random plot are provided in Table 1.

Statistical Analyses. Univariate comparisons between nest and random plots were made using a Student's *t*-test and Mann-Whitney *U*-test for normally distributed and nonparametric data, respectively. For univariate statistical tests, the level of significance was adjusted using a modified Bonferroni procedure (Holm 1979). Variables with nonparametric data (TRDIS and CONBA) were transformed using a square-root transformation (Zar 1999). Next, all habitat variables were screened using the Pearson correlation coefficient (Zar 1999) to identify highly correlated pairs, with the least important variable eliminated. A threshold value of $R \geq 0.70$ was used for elimination. We used logistic regression on all possible habitat models to explain variation of the dependent variable (i.e., nest vs. random plots; following McDonald et al. 2005). Interactions and quadratic variables were ignored. The regression models were ranked by Akaike's Information Criterion (AIC_c) adjusted for small sample sizes (Akaike 1973). Next, AIC differences for each model were calculated and the "best" models (i.e., AIC_c differences ≤ 2) were retained for further analysis. From this sample, we calculated Akaike's weights and the relative importance value (Burnham and Anderson 2002) for each model and variable, respectively.

RESULTS

Territory Density and Reoccupancy. A Red-shouldered Hawk response was detected at 210 of 564 (37%) survey stations during this study. This response rate was probably conservative because we skipped some survey stations located near known nests that were found occupied prior to completing adjacent surveys. Ninety-four percent (197/210) of

Table 1. Univariate comparisons of habitat variables measured at Red-shouldered Hawk nest area ($N = 24$) and random ($N = 20$) plots.

VARIABLE	DESCRIPTION	NEST PLOTS		RANDOM PLOTS		P-VALUE[a]
		MEAN	(±SD)	MEAN	(±SD)	
TRDIS[b]	Distance to nearest road (m)	5	2.8	7	2.9	0.008
STDIS	Distance to nearest stream (m)	481	323.0	687	337.5	0.04
WETDIS	Distance to nearest wetland (m)	270	203.1	829	443.0	<0.001
CANHT	Canopy height (m)	28	3.6	26	3.7	0.16
CANDEN	Canopy density (% open)	10	4.3	12	7.4	0.22
DWD	Downed woody debris volume (m^3 per ha)	65.4	68.7	89.7	51.0	0.20
SAP	Trees 3–13 cm DBH (per plot)	22	8.6	32	11.7	0.004
POLES	Trees 14–28 cm DBH (per plot)	6	2.7	6	3.1	0.78
SMSAW	Trees 29–38 cm DBH (per plot)	2	1.3	2	1.8	0.54
LASAW	Trees 39–55 cm DBH (per plot)	2	1.2	1	1.0	0.16
VLSAW	Trees >55 cm DBH (per plot)	2	0.8	1	1.3	0.09
SP10	Number of tree species >10 cm DBH	4	0.9	4	1.1	0.41
BA	Basal area for trees >10 cm DBH (m^2 per ha)	30.2	7.4	24.5	9.2	0.03
CONBA[b]	% basal area from conifer species	20	18	24	26	0.18
SLS	Shrubs 1.2–3.0 m tall and <3 cm DBH	100	61	90	95	0.67
TLS	Shrubs 3.1–6.1 m tall and <3 cm DBH	20	12	19	20	0.86
TPERHA	Tree density per ha	287	67.9	259	77.9	0.21
SPERHA	Shrub density per ha	3547	1609.0	3519	2929.6	0.97

[a] Level of statistical significance ($P < 0.003$) adjusted using the Bonferroni procedure (Holm 1979).
[b] Values in table are square root transformations.

responses were detected aurally only or visually and aurally. Throughout the entire study period only two Red-tailed Hawks and one Great Horned Owl (*Bubo virginianus*) were observed or heard.

We estimated there were 26 different territories located in the study area during 2002–2006. All territories had at least one breeding attempt during the study period; six had breeding attempts each year. Occupied territory density ranged from a low of 0.13 per km^2 in 2003 to a high of 0.18 per km^2 in 2005 and 2006. Nesting density, based on documented breeding attempts, ranged from 0.10 nests per km^2 in 2003 to 0.16 nests per km^2 in 2005. Mean territory reoccupancy rate was 71%, with a low of 60% in 2003 and a high of 84% in 2006 (Table 2).

Productivity. On average, Red-shouldered Hawks produced 0.7 ± 0.4 young per breeding attempt (Table 2), and 2.0 ± 0.6 young per successful nest annually during our study. In most years, nest success was <30% (Table 2). Little or no evidence for the cause(s) of failure was found at most failed nests. Of the 46 failed breeding attempts, five failed during incubation, 15 during the nestling period, and for 26 the time of failure was unknown.

Nest Site Habitat. All Red-shouldered Hawk breeding attempts were made in sugar maple (*N*

Table 2. Red-shouldered Hawk nesting success, productivity, and territory reoccupancy within the Menominee forest, 2002–2006.

PARAMETER	2002	2003	2004	2005	2006	MEAN	SD
Number of occupied territories	15	14	18	19	19	17.0	2.3
Number of breeding attempts	13	11	15	17	15	14.2	2.3
Number of successful attempts	6	3	3	5	8	5.0	2.1
Number of young fledged	10	8	4	8	20	10.0	6.0
Young per breeding attempt	0.8	0.7	0.3	0.5	1.3	0.7	0.4
Nest success (%)	46	27	20	29	53	35.0	13.9
Territory reoccupancy (%)	—	60	61	79	84	71.0	12.3

Table 3. Best five ($\Delta AIC_c \leq 2$) of 255 possible logistic regression models to predict nesting areas of Red-shouldered Hawks in the Menominee forest. Rankings based on AIC_c, where AIC values were corrected for small sample size.

VARIABLES[a]	K[b]	AIC_c	Δ_i[c]	MODEL LIKELIHOOD	w_i[d]
TRDIS, WETDIS	4	39.62	0.00	1.00	0.359
WETDIS	3	40.76	1.14	0.57	0.203
TRDIS, WETDIS, SAP	5	41.33	1.71	0.43	0.153
TRDIS, WETDIS, DWD	5	41.35	1.73	0.42	0.151
TRDIS, WETDIS, SLS	5	41.58	1.96	0.38	0.135

[a] TRDIS = distance to nearest road; WETDIS = distance to nearest wetland; SAP = number of trees per plot 3–13 cm dbh; DWD = volume of downed woody debris; SLS = number of shrubs 1.2–3.0 m tall and <3 cm dbh.

[b] Number of estimable parameters in the logistic regression model.

[c] $\Delta_i = AIC_{ci} - AIC_c$ min.

[d] Akaike weights (Burnham and Anderson 2002).

= 22) or yellow birch ($N = 26$) trees. Nest trees had a mean height of 30.6 ± 4.3 m and mean DBH of 64.3 ± 11.2 cm. On average, nests were placed 15.9 ± 2.3 m above ground, or at 52% of nest tree height. Red-shouldered Hawk nesting areas were significantly closer to lakes or treeless wetlands (WETDIS) than random plots (Table 1). No other univariate comparison was significantly different. Four other variables were nearly significantly different (based on modified level of statistical significance $P < 0.003$); thus, it appears that Red-shouldered Hawks selected nesting areas based on additional characteristics. For example, nesting area plots were found a shorter distance from the nearest road or trail (TRDIS, $P = 0.008$) and stream (STDIS, $P = 0.04$) than random plots (Table 1). In addition, mean basal area (BA, $P = 0.03$) was greater and the number of sapling-sized stems (SAP, $P = 0.004$) less at nesting areas than random plots, respectively (Table 1).

We reduced the number of habitat predictor variables to eight (TRDIS, WETDIS, CANDEN, DWD, SLS, SAP, LASAW, and BA) based on field observations and multicollinear analysis. This provided 255 possible models for testing. Akaike's Information Criterion identified the logistic regression model with variables TRDIS and WETDIS as the best (i.e., minimum AIC_c) to predict Red-shouldered Hawk nesting areas in the study area (Table 3). This model was nearly twice as likely as the next highest ranked model to be the best-fit for our data. Distances to the nearest wetland (WETDIS, 100%) and trail or road (TRDIS, 79%) were the only variables with relative importance values >15%.

DISCUSSION

Distance to the nearest treeless wetland or lake (WETDIS) was the best distinguishing variable in nesting area selection by Red-shouldered Hawks in our study area. The positive association between Red-shouldered Hawk nesting areas and wet habitats has been described before (Titus and Mosher 1981, Bednarz and Dinsmore 1981, Bosakowski et al. 1992, Bloom et al. 1993, Dykstra et al. 2000, McLeod et al. 2000). Amphibians found in these wetlands provide an important food source during the nesting period (Craighead and Craighead 1956, Portnoy and Dodge 1979, Bednarz and Dinsmore 1981, Welch 1987).

Both the ''best'' habitat model (i.e., TRDIS and WETDIS) and univariate comparisons could be used to identify probable Red-shouldered Hawk nesting areas across the entire Menominee forest and other similar forests in the region (e.g., national, state, and county forests). They could also serve as useful tools in stratifying, by habitat, large blocks of public and private land for future surveys, because the data needed to populate these types of models are readily available for all areas with remotely-sensed landcover data (e.g., Landsat Thematic Mapper data) and a trail and road layer. It is likely that other habitat variables like forest fragmentation, mean tree diameter, and distance to nearest building would be equally or more important in areas without extensive forest coverage. Hence, we discourage the application of this model to those landscapes.

The positive association of nest locations with seasonal jeep trails we found differed from most studies that examined this or a similar variable. One study found nests at a greater distance from roads than random plots (Bosakowski et al. 1992), while several others found no significant difference in distance to road between nests and random plots (Morris and Lemon 1983, Dykstra et al. 2000, and McLeod et al.

2000). A possible explanation for this difference in our study was that all nests were near trails that received very little or no traffic during the breeding season. Most of the vehicular activity on these trails occurred during fall and winter for hunting and logging activities. In addition, these trails may provide excellent flight and foraging corridors. We observed many trails with small ephemeral or permanent wet areas that contained large numbers of amphibians. The affinity that Red-shouldered Hawks had for stream habitats in our study was no different than that reported in other predominantly forested (Titus and Mosher 1981, Moorman and Chapman 1996) and more fragmented habitats (Bednarz and Dinsmore 1982, Dykstra et al. 2000) elsewhere in eastern North America.

Red-shouldered Hawk productivity has substantial annual variability in eastern North America (reviewed in Dykstra et al. 2008). The low reproductive rates we observed were similar to results (0.69 young per breeding attempt) reported for Red-shouldered Hawks in northeast Wisconsin (J. Jacobs unpubl. data), but much lower than levels (1.36 young per breeding attempt) reported in central Wisconsin <100 km away (E. Jacobs unpubl. data) during the same period. We believe that limited prey availability or poor adult foraging success were responsible for low productivity and nest success. In our Menominee forest study and two other Red-shouldered Hawk studies in central and northeast Wisconsin, prey delivery rates (as determined by video recordings) were positively correlated to each area's productivity (E. Jacobs pers. comm.). Also, we observed sibling aggression (i.e., fighting and injuries) at five nests and adult cannibalism of nestlings at one nest, both typical responses to food shortage at raptor nests (Newton 1979). There was no evidence of Red-shouldered Hawk pairs being replaced by sympatric competitors (e.g., Red-tailed Hawk and Great Horned Owl) or depredation of adults or nests during this study.

This is one of a small number of Red-shouldered Hawk studies in which a remote, contiguous forest was systematically surveyed and an attempt was made to locate all breeding attempts. Logistical constraints (e.g., poor access and weather) limited the study to one broadcast survey per station per year. It wasn't until the 2004 nesting season that we were confident a response from a new area actually was from adults occupying a new territory. Thus, we believe nest densities recorded in 2004–2006 (mean density = 0.15 nests per km^2) reflected a total census for the study area, while those from 2002 and 2003 may have been conservative.

The combination of a contiguous and mature-structured forest, availability and spatial pattern of treeless wetlands, and low interspecific competition and predation present in the Menominee forest may explain both the moderate nest density and high territory reoccupancy rates observed during this study. Although acceptable nesting habitat appears abundant, productivity of Red-shouldered Hawks in the Menominee forest was lower than that reported in all other studies for this species (Dykstra et al. 2008), except one from northern Minnesota (McLeod 1996). We suspect that Red-shouldered Hawks are immigrating from other areas to replace adults lost in the Menominee forest, and these birds are retained because of low predation and little competition for space from other raptors.

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