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Nest predation rates in managed and reserved extensive northern hardwood forests

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Abstract

Depredation rates on artificial ground and shrub nests in large blocks of managed and remote reserved northern hardwood forests were studied in the White Mountain National Forest (WMNF) (303 930 ha) in New Hampshire, USA, from June to August 1991. Both types of nests were monitored by trip cameras that recorded depredations as eggs were removed. No differences in nest predation rates were found for either ground or shrub nests between managed and reserved forest blocks. Elevated nest predation rates are generally considered to be indicative of fragmented forest conditions; the results of this study suggest that extensive northern hardwood forests in northern New England are not fragmented by even-aged silviculture with clearcut regeneration, which is commonly used to manage northern hardwoods. All identified nest predators were mammals.

Keywords: Artificial nest; Nest predation; Remote-triggered camera; Hardwood

1. Introduction

Fragmentation of extensive forests into smaller patches has occurred in many temperate forest regions due to conversion to agricultural or urban land uses. Forest fragments have a higher proportion of exterior edge and so are more heavily influenced by their surroundings, i.e. the matrix in which they are embedded, than are larger, more intact forests. Such influences include higher rates of nest parasitism (Wilcove, 1985; Robinson, 1988; Paton, 1994) and higher rates of nest predation (Andren and Angelstam, 1988; Burger et al., 1994).

Nest predation limits the breeding success of open-nesting passerine birds (Ricklefs, 1969; Martin, 1991). The decline in populations of migratory birds that breed in forest habitats of the eastern USA has been attributed to elevated nest predation rates as a result of forest fragmentation (Wilcove, 1985; Terborgh, 1989; Askins et al., 1990). Artificial nests are tools for evaluating predation rates in various habitats (Loiselle and Hoppes, 1985; Martin, 1987; Gibbs, 1991).

Predation rates on both natural and artificial nests have been shown to be higher in small than in large fragments and are influenced by the distance to the forest edge (Gates and Gysel, 1978; Ambuel and Temple, 1983; Moller, 1988). Predation rates on artificial nests have been shown to be higher in isolated forest patches than in extensive forest (Wilcove, 1985; Andren et al., 1985). Studies of bird populations in fragmented forests — relatively small, isolated tracts of forest in essentially non-forest landscapes — suggest that nest predation is a type of

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edge effect (Angelstam, 1986; Andren and Angelstam, 1988). Elevated nest predation rates have therefore been proposed as indicators of forest fragmentation (Whitcomb et al., 1981; Small and Hunter, 1988).

Within extensive managed hardwood forest in the northeastern USA, no elevations in rates of nest predation were observed in young stands, nor was predation rate related to stand area, suggesting that the forest was not fragmented by even-aged management (DeGraaf and Angelstam, 1993). Although rates of nest predation did not differ among managed stands of various ages in the aforementioned study, the question remains whether predation rates differ between large blocks of mature northern hardwood forest that are subject to management and similar blocks that have been reserved from management (i.e. are wilderness).

The identification of nest predators can be problematic. Track-board nests are useful for obtaining predation rates and identifying predators on ground nests (Angelstam, 1986), but present several potential problems: inability to distinguish which predator actually preyed upon a nest if tracks of more than one species are present, obliteration of tracks by rain, and possible attraction of some predators by the track medium (DeGraaf and Angelstam, 1993). Also, track-boards are not practical for evaluating avian predation of arboreal cup nests. In several studies, predator identity was speculated (Rearden, 1951; Yahner and Wright, 1985; Angelstam, 1986).

Recently, more reliable techniques, such as remotely tripped cameras, have been developed for identifying nest predators, (Picman, 1988; Reitsma et al., 1990). Leimgruber et al. (1994) used cameras that were tripped by an infrared beam that was sensitive to sudden changes in the heat profile of the monitored area caused by predators in the vicinity of artificial nests.

Within extensive temperate forest, does even-aged management with clearcut regeneration result in elevated rates of predation on birds' nests within managed areas? This study used cameras tripped by actual egg removal to investigate potential differences in predation rates and predators on artificial nests in managed and reserved forest areas within extensive forest. No differences in predation rates are hypothesized for either ground or shrub nests.

2. Study area

This study was conducted on the Saco Ranger District (44° 00′N, 71° 15′W) of the White Mountain National Forest (WMNF) in north-central New Hampshire, USA. The 303 930-ha WMNF is 97% forested (US Forest Service 1986: III-30). The Saco Ranger District comprises 81550 ha and is also 97% forested, primarily by deciduous and mixed coniferous woods. Mid-slopes are dominated by northern hardwood species, primarily sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*) and American beech (*Fagus grandifolia*) (Eyre, 1980: 31). Elevations above 900 m are dominated by red spruce (*Picea rubra*) and balsam fir (*Abies balsamea*). Paper birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*) are common associates of both northern hardwoods, red spruce and balsam fir. The study area and much of the surrounding forest supports primarily mature stands that regenerated after widespread unregulated logging in the late 1800s and extensive fires around 1900 that were fueled by slash from timber clearing (Belcher, 1980: x-xiii; US Forest Service, 1986: II-3). On managed areas of the District, even-aged methods have been continuously practised for the past 40 years. Over all cover-types, the forest is comprised of 87% mature stands, 5% poletimber stands and 8% regeneration/sapling stands; stand sizes are 5-80 ha and clearcut stands do not exceed 16 ha. Stands adjacent to clearcuts can not be cut until trees in the regenerating clearcut have attained a mean height of 10 m, which commonly occurs within 10-15 years (J.W. Lanier, WMNF, personal communication, 1992). In practice, however, adjacent stands are commonly cut many years after minimum height is attained, or are left unharvested.

Extensive wilderness areas, which have been reserved from timber management for 85-140 years, are located throughout the WMNF in general and the Saco District in particular. Such areas provide important scenic vistas or are located on sites protected by steep access. All species known or suspected to prey upon birds' nests normally occur in the study area, and include eastern chipmunk (*Tamias striatus*), red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomvs sabrinus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), gray fox (*Urocyon* *cinereoargenteus*), black bear (*Ursus americanus*), raccoon (*Procyon lotor*), fisher (*Martes pennanti*), mink (*Mustela vison*), ermine (*Mustela erminea*), long-tailed weasel (*Mustela frenata*), striped skunk (*Mephitis mephitis*) and bobcat (*Felis rufus*). Nest-robbing birds present include blue jay (*Cyanocitta cristata*), American crow (*Corvus brachyrhynchos*) and common raven (*Corvus corax*).

Natural forest disturbance in northern New Hampshire is predominantly by gap-phase regeneration caused by the death of one or a few trees (Runkle, 1990), although in the White Mountains blowdowns up to 1000 ha occur (Curtis, 1943), and occasional severe hurricanes cause widespread disturbance. Natural gaps occur frequently (weekly to monthly) and randomly throughout the forest, disturbing a small proportion (about 1%) of the area each year (Runkle, 1990). Localized blowdowns, caused by winds generated in the White Mountains, are more common in softwood stands — especially *Picea* and *Abies* due to their occurrence at higher elevations and their shallow-rootedness — than in hardwood stands. Also, wind damage is greater in softwood than in hardwood types (Curtis, 1943). Hurricanes extend into north-central New Hampshire infrequently; the last such storm, which caused extensive damage, occurred in 1938. Similar storms also occurred in 1635 and 1815 (Channing, 1939).

I chose six 64-ha study sites in northern hardwoods (300–670 m elevation): three in managed areas and three in areas historically reserved from management. Managed areas were comprised of 65% sawtimber stands (to stand diameter at breast height (dbh) > 25.4 cm), 17% poletimber stands (stand dbh 12.7–25.4 cm) and 18% seedling/sapling stands (stand dbh < 12.7 cm). Harvests were clearcuts < 16 ha in size that were approximately 10 years old and were naturally regenerated. Reserved areas were comprised of 96% sawtimber stands and 4% poletimber stands.

3. Materials and methods

3.1. Nest predation

To evaluate rates of predation on ground and low arboreal bird nests in managed and reserved forests, two types of artificial nests were each exposed to predators in two periods from 1 June to 9 August 1991. Ground nests consisted of a small, fresh chicken egg in a shallow depression on an 8 × 8 × 2 cm wood block which also contained a microswitch under the egg. The wood block was concealed in the litter. Shrub nests were aviculturists' wicker baskets, 10 cm in diameter and 5–6 cm deep, lined with a few dead leaves (Martin, 1987) and placed in sapling forks or crotches 1–1.5 m above the ground. Shrub nests were held in place by a wire wrapped discreetly around the supporting stems and contained a small chicken egg resting on a microswitch hidden in the bottom of the nest. The microswitches were connected by 4-m electric cables to 35-mm flash cameras aimed at the nests from a distance of 2–2.5 m to identify nest predators as they depredated nests. Cameras were mounted in inconspicuous weatherproof containers fastened to convenient tree trunks. All nests exposed to predation were thus monitored by cameras tripped by egg removal.

Nests were placed in a 16-point grid in each area (three managed, three reserved); points were located systematically 200 m apart. Each study area was embedded in the surrounding forest matrix and was > 1000 m from a maintained road or other forest edge. Nests were exposed to predators in two trials per nest type: ground nests were exposed for 1-week and 2-week periods; shrub nests were exposed for two 1-week periods. Successive trials were conducted at the same general grid point, but nests were relocated randomly about 20 m from the site of the first nest in each subsequent trial. All trials were separated by 1-week periods when no nests were present. All eggs were placed in nests during 17:00–22:00 h by an investigator wearing rubber boots and gloves to minimize both visual detection by potential avian predators and human scent. Nests were not visited during exposure periods. The order in which eggs were placed and nests checked was varied each trial to avoid leaving a regular scent trail through each study area. In all trials, a nest was considered depredated if an egg was removed or broken.

3.2. Vegetation sampling

Vegetation was measured after Welsh and Healy (1993) in order to characterize each study area. Tree species, dbh and height (m) of all trees > 2.5 cm dbh was recorded on 0.02 ha (8-m radius) circular plots centered at 16 grid points in each area. Heights of most trees were estimated, but consistency of estimates was maintained by measuring the height of at least one dominant or co-dominant tree and at least one understory tree in each plot with a clinometer. Basal area (BA) and density (trees ha^{-1}) were calculated by size class (sapling, poletimber, sawtimber). For shrubs and seedlings < 2.5 cm dbh, stems were counted by height class (< 0.5, 0.5–0.9, 1.0–1.9, > 2 m) on five 0.001-ha (1.78-m radius) circular plots at each grid point and 7.1 m in each cardinal compass direction from the grid point. Ground cover was estimated by counting the number of 'hits' on ground vegetation seen through a sighting tube, 15 cm long by 2.5 cm in diameter fitted with cross hairs, at 1-m intervals on random diameters of the 8-m radius tree measurement plots and averaging values.

Table 1

Loss rates and daily survival rates (exposures/treatment combined) of ground and shrub nests ($n = 16$ per block) during four exposure periods in managed and reserved forest blocks, WMNF, New Hampshire, 1991

Block	Nest type			
	Ground		Shrub	
	Exposure		Exposure	
	1 week	2 weeks	1 week	1 week
Reserved				
1	0.062	0.125	0.062	0.187
2	—	0.375	—	0.750
3	—	0.812	0.500	—
Daily survival rate [a]	0.979		0.978	
Managed				
1	0.375	1.0	0.875	0.937
2	—	0.125	—	—
3	0.125	0.250	0.312	—
Daily survival rate [a]	0.957		0.939	

[a] Calculated after Mayfield (1975); total exposure per treatment is 1008 days for ground and 560 days for cup nests.

3.3. Analyses

Differences in rates of nest predation were examined by goodness-of-fit test (Zar, 1974: 41). Mean values of measures of understory, vegetation structure and ground cover at depredated and undepredated nests were compared by independent samples *t*-test (Zar, 1974: 107). Effect of management on nest predation was evaluated using contingency tables. Daily nest survival rates were calculated after Mayfield (1975).

4. Results

Over all exposure periods, 27.1% of 192 ground nests and 36.3% of 160 shrub nests were depredated. Rates of predation on ground nests were not different ($\chi^2 = 10.19$, 5 d.f., $P = 0.081$) between the first 1-week exposure period and the second 2-week exposure period. Thus, exposure periods were pooled; predation rates on ground nests were not different ($\chi^2 = 1.65$, 5 d.f., $P = 0.875$) between managed and reserved blocks. Given an effect size of 0.96 and sample size of 192 ground nests, the power (Cohen 1988: 216) to fail to reject the null hypothesis is 90% at $\alpha = 0.01$. Camera malfunctions due to weather and other damage necessitated using two instead of three blocks per treatment in the second shrub nest exposure period while still maintaining 16 nests per block. Predation rates on pooled shrub nest trials were not different ($\chi^2 = 1.33$, 4 d.f., $P = 0.825$). Given an effect size of 0.91 and sample size of 160 shrub nests, the power to fail to reject the null hypothesis is 90% at $\alpha = 0.01$. Daily nest survival rates (1 − mortality rate) for ground nests in managed and reserved blocks (16 nests per block, three blocks per treatment, one 1-week and one 2-week exposure period) were 0.957, 0.979, respectively. Daily survival rates for shrub nests (16 nests per block, three blocks per treatment in first exposure, two blocks per treatment in second exposure, two 1-week exposure periods) were 0.939 in managed blocks and 0.978 in reserved blocks (Table 1).

Over all 352 nests, 114 (31%) were depredated. Of these, cameras recorded 53 (48%) nest depredations in which predators were identified. In 57 (52%) of depredations, either the camera failed to work or the aim of the camera had been changed by unknown factors, perhaps wind or animal activity. One ground nest was trampled by moose (*Alces alces*) and six cameras were destroyed (chewed) by black bears.

Table 2
Fate of ground and shrub nests (exposure periods combined) in three managed and three reserved forest blocks, WMNF, New Hampshire, 1991

	Block				Total
	Managed ($n = 3$)		Reserved ($n = 3$)		
	Ground ($n = 96$)	Shrub ($n = 80$)	Ground ($n = 96$)	Shrub ($n = 80$)	
Nests depredated	30 (31%)	34 (42%)	22 (23%)	27 (30%)	114 (31%)
Nest predator:					
Fisher	6 (20%)	13 (38%)	3 (14%)	5 (21%)	27 (25%)
Black bear	—	14 (41%)	—	6 (25%)	20 (18%)
Raccoon	1 (3%)	—	—	3 (13%)	4 (4%)
Mouse	1 (3%)	—	2 (10%)	—	3 (3%)
Snowshoe hare	1 (3%)	—	1 (5%)	—	2 (2%)
Red squirrel	—	—	1 (5%)	—	1 (1%)
Unknown	21 (73%)	7 (21%)	15 (68%)	13 (54%)	57 (52%)

One additional nest was trampled by moose (*Alces alces*).

Table 3
Characteristics of vegetation on three managed and three reserved areas in the WMNF, New Hampshire, 1991

	Managed		Reserved	
	Mean	SD	Mean	SD
Overstory				
Live trees > 10.0 cm dbh				
Density (stems ha^{-1})	550	204	447	334
Basal area (m^2 ha^{-1})	29.6	10.2	24.2	16.4
Stand dbh	26.8	5.4	26.6	5.3
All trees > 2.5 cm dbh (live and dead)				
Density (stems ha^{-1})				
Saplings	1813	2185	973	404
Poletimber	284	242	344	156
Sawtimber	139	107	154	82
Height < 10 m	1586	1918	870	335
Height 10–20 m	522	429	477	264
Height > 20 m	129	109	124	94
Softwoods	147	288	75	124
Hardwoods	2091	2071	1396	465
Understory				
Number of woody stems < 2.5 cm dbh per 0.001 ha by height class (m)				
< 0.5	303	287	269	189
0.5–1.0	38	31	37	38
1.0–2.0	25	38	11	8
> 2.0	29	55	3	3
Ground cover				
Ground cover (%)	30.8	17.4	27.9	14.7

Fishers and black bears accounted for 47 (43%) of nest depredations.

All nest predators identified were mammals (Fig. 1). Nest predators identified (in decreasing frequency of depredation) were: fisher, black bear, raccoon, mouse (*Peromyscus* spp.), snowshoe hare and red squirrel (Table 2).

Percent ground cover (arc-sin transformation) did not differ at depredated or undepredated ground ($t = 0.599$, d.f. = 13, $P = 0.560$) or shrub ($t = 0.869$, d.f. = 50, $P = 0.389$) nests. The densities of understory stems in height classes 1 and 2 (< 0.5 m and 0.5–1.0 m tall, respectively) did not differ between depredated or undepredated ground nests, but densities of stems in height classes 3 and 4 (1.0–2.0 m and > 2.0 m, respectively) were significantly different (were greater – $t = 3.100$, d.f. = 90, $P = 0.003$; $t = 3.382$, d.f. = 85, $P = 0.001$, respectively) at undepredated than at depredated ground nests. No habitat variables were significantly different between depredated and undepredated shrub nest locations. Vegetation characteristics were similar on managed and reserved areas (Table 3).

5. Discussion

High predation rates in small (< 100 ha) forest blocks versus large forest blocks have been attributed to higher abundances of generalist predators, e.g. raccoons, crows and jays (Wilcove, 1985; Reese and Ratti, 1988). Numbers of these predators are considered low in large forest blocks and thus predation rates have been assumed to be low in large forests (Gates and Gysel, 1978; Yahner and Scott, 1988). I observed predation rates that exceed those reported for large (> 300 ha) forest blocks in previous artificial nest studies (Wilcove, 1985: 9%; Small and Hunter, 1988: 3–9%; Yahner and Scott, 1988: 9%; Leimgruber et al., 1994: 19.7%). In the present study no avian nest predators were identified, possibly due to the eggs used, but likely, also, to the low abundance of such predators in the study areas. Extensive bird surveys in the study area immediately preceding (1989–1990) the present study showed crows to be absent and blue jays to be present in low abundances (Welsh and Healy, 1993).

Large mammals were the primary predators. Black bears have been reported as predators on artificial nests previously (DeGraaf and Angelstam, 1993); black bears are quick to learn new food types from one experience (Bacon and Burghardt, 1975). Fishers have been shown to have quite varied diets; no studies of food habits to date record taking eggs from nests (Coulter, 1966; Powell, 1982: 108–109;

Fig. 1. Predators depredating artificial nests in the White Mountains, New Hampshire, USA, clockwise from top left: raccoon (*Procyon lotor*), red squirrel (*Tamiasciurus hudsonicus*), black bear (*Ursus americanus*), fisher (*Martes pennanti*) at cup nest, snowshoe hare (*Lepus americanus*) and fisher at ground nest.

Arthur et al., 1989). In another study conducted in the White Mountains, red squirrels and chipmunks were found to be important predators on artificial nests (Reitsma et al., 1990), yet few red squirrels and no chipmunks depredated nests in the present study, although mice were photographed attempting to depredate nests. Mouse predation is probably underestimated in studies using chicken or Japanese quail (*Coturnix coturnix*) eggs, because the eggs are too large to break or remove. An assessment of mouse predation would require very small eggs, e.g. those of Zebra finch (*Taenopygia* spp.), which are not commonly available commercially.

Clearly, nest predation rates are not solely a function of forest size; predator species and abundance and vegetation characteristics are also important. High foliage and spatial vegetation densities are associated with reduced nest predation in woodlands (Martin, 1991; Leimgruber et al., 1994). There is some evidence in the present study that understory stem density is related to predation rates on ground nests.

This study used cameras to record actual egg removal from artificial nests, not merely predator presence in the vicinity of the nest. This study was also conducted in extensive forest (> 300000 ha). It may be that nest predators and predation rates are different at such a scale, and that study location, landscape character, forest size and vegetation interact to support predator assemblages that produce characteristic nest predation patterns in extensive North American forest, as was reported for fragmented forests in western Europe (Nour et al., 1993). Comparison of nest predation rates between the New World and the Old World are possible for forest fragment/farmland landscapes. Studies in the USA (Wilcove, 1985) and Sweden (Andrén and Angelstam, 1988), conducted in similar landscapes, showed the same results: increasing nest predation rate within forest patches as distance from farmland–forest edge decreased; in both studies the edge-related increase in predation was primarily due to generalist predators residing in surrounding farmland. Whether similar patterns in nest predation exist between eastern North American and European extensive forests is not known; Europe has a longer history of fragmentation and a larger, more abundant and more diverse corvid fauna than does eastern North America. It is possible, however, that predation rates are similar in extensive managed and reserved European forests.

From a forest management perspective, the key question is, does even-aged silviculture with clearcut regeneration increase fragmentation in extensive forests as revealed by elevated nest predation rates? In the present study, such rates were not greater in managed extensive northern hardwood forests than those in similar reserved forests. New England northern hardwoods regenerate quickly after clearcutting; foliage profiles in stands of widely disparate ages are similar because northern hardwoods reach their height of about 26 m fairly early in the life of the stand (Aber, 1979). Rapid regeneration of cut stands and low numbers of generalist predators (as in a forest/agricultural landscape) likely contribute to the similarity of nest predation rates in managed and reserved extensive northern hardwood forests.

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