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Effects of timber size-class on predation of artificial nests in extensive forest

Richard M. DeGraaf*[,a], Per Angelstam[b]
[a]*USDA Forest Service, Northeastern Forest Experiment Station, University of Massachusetts, Amherst, MA 01003, USA*
[b]*Grimsö Wildlife Research Station, Riddarhyttan, Sweden*

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Abstract

Depredation on artificial ground and cup nests in even-aged seedling/sapling, pole, and mature stands of continuous northern hardwood forest was studied in the White Mountain National Forest in New Hampshire, USA from May to June 1988. Track-board nests were used to identify predators of ground nests; plain ground nests and cup nests were used to investigate the effects of timber size-class on rates of predation. No elevation in nest predation rate was observed in the early stages of growth, nor was predation rate related to stand area. As elevated predation rates are usually taken to indicate the fragmentation of forest, the results of this study suggest that extensive hardwood-dominated forests in northern New England are not fragmented by even-aged management.

Introduction

Predation on birds' nests is generally considered to be a major cause of nesting mortality for many species (Skutch, 1949; Lack, 1954; Ricklefs, 1969). Avian reproductive strategies likely reflect adaptations to different spatial and temporal distributions of food (Horn, 1968) and to different types of predation on eggs, nestlings, and adults (Lack, 1968; Ricklefs, 1969). Predation rates on artificial and unattended real arctic loon nests were similar in Sweden (Gotmark et al., 1990). Predation rates on artificial nests have been shown to be higher in isolated woodlots 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 edge effect (Angelstam, 1986). Production of young has been reported to be negatively correlated to forest–farmland edges (Gates and Gysel, 1978). Nest predation has been implicated in the decline of local avifauna with increasing fragmentation of deciduous forests in agricultural landscapes (Whitcomb et al., 1981); nest predation rates

*Corresponding author.

increase as forest patch size decreases in agricultural or suburban landscapes (Ambuel and Temple, 1983; Wilcove, 1985).

In a primarily forested area in Maine, fragmented by roads, powerlines and fields and containing numerous streams and water bodies, predation on artificial nests was greatest in small tracts that were not bounded by water; large tracts and those bordered by large bodies of water had lower predation rates (Small and Hunter, 1988). In central Sweden, however, Angelstam (1986) found no increase in predation rates on artificial nests close to versus far from forest–farmland edges; within the forest, the predation rate on nests was similar in all habitats except recent clearcuts, where cover was sparse and predation rates higher.

The similarity of predation rates in forest habitats and agricultural lands was explained in terms of differences in productivity between habitats: highly productive habitats, such as landscape under intensive agriculture, produce more food for generalist predators, allowing higher densities of such predators and consequent higher nest predation rates in the edges of adjacent woodlands.

In essentially forested habitats, where agricultural land is a minor component of the landscape, productivity is lower, the densities of generalist predators are lower, so predation rates are low in both forest edges and interiors. Yahner and Wright (1985) similarly accounted for the absence of different predation rates at the edges and in the interiors of small (1 ha) aspen (*Populus* spp.) stands in Pennsylvania.

Does even-aged management with clearcut regeneration in extensive forest result in elevated rates of predation on birds' nests (a phenomenon indicative of forest fragmentation) in early seral stages? This study was conducted to investigate potential differences in predator use and predation rates on artificial nests in three timber size-classes within extensive managed forest, i.e. where no differences in productivity exist between habitats, and no differences in predation rates are hypothesized for either ground or cup nests.

Study area

This study was conducted on the 21 200 ha Kilkenny Wildlife Management Area (44°30′N, 71°22′W) of the White Mountain National Forest (WMNF) in New Hampshire, USA (Fig. 1). This northernmost part of the WMNF lies between the Pilot, Pliny, and Crescent Ranges of the White Mountains, and is drained by the Upper Ammonoosuc River. Soils of the region are typically stony, sandy, and acidic. The Kilkenny Management Area is completely forested; agriculture has never been practiced on the study area. The area bounded by the White Mountain National Forest is 90% forested; 3% is in alpine tundra (White Mountain National Forest records). Northern New Hampshire is

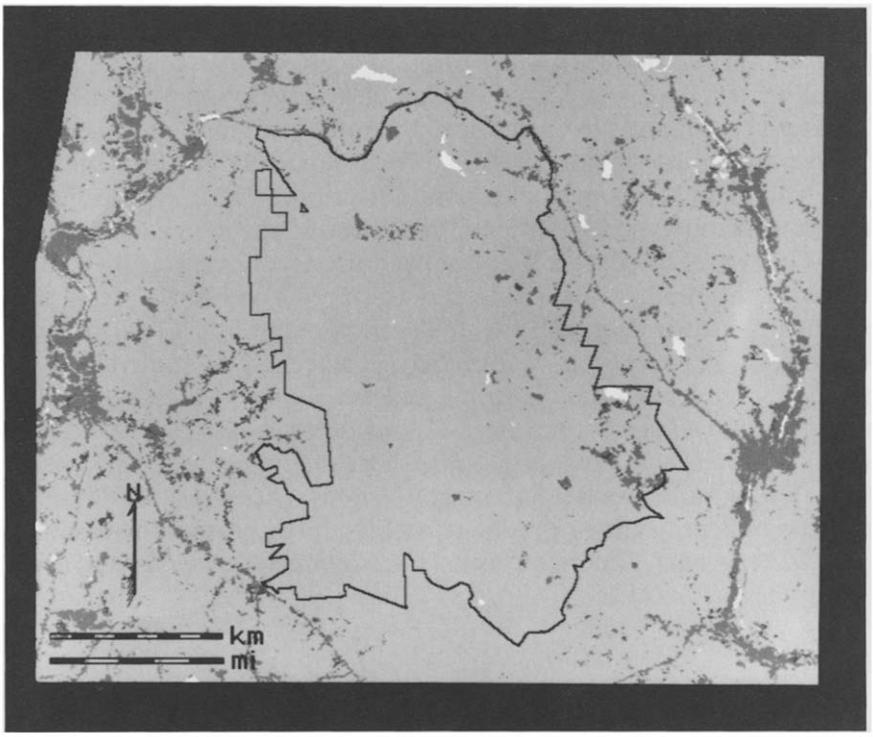

Fig. 1. A land-cover classification of the northern section of the White Mountain National Forest. The classification is based upon Multispectral Scanner (MSS) imagery obtained with the LANDSAT 5 satellite on 22 June 1985. The satellite data were used in 'corrected' form, i.e. both radiometrically corrected and geometrically corrected to the space-oblique mercator (SOM) projection with a 57 m per pixel resolution. Cloud cover over the entire scene was less than 10%, and no clouds appear within the forest boundary. The grey background represents forest cover, white areas represent water bodies, and the dark grey areas represent fields, clearcuts, roads and settled places.

92% forested, and in southern New Hampshire 80% is forest cover (Frieswyk and Malley, 1985). In the midwestern USA the landscape is comprised of forest islands in an agricultural matrix; high rates of nest parasitism by brown-headed cowbirds (*Molothrus ater*) occur in such forests (Wilcove, 1985; Robinson, 1988). Cowbirds have not been reported in clearcuts or at stand edges in intensively managed forest in New Hampshire (DeGraaf, 1992). The predominant forest cover types are northern hardwoods (*Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*) (60%), red spruce–balsam fir (*Picea rubens*, *Abies balsamea*) (20%), and balsam fir (5%). Paper birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*) are common associates of all types.

The study area supports primarily mature stands that grew after widespread unregulated logging in the late 1800s and extensive fires in 1903. Even-

aged management has been practiced for the last 35 years. Over all cover types, the forest is comprised of 87% mature forest, 5% poletimber, and 8% regeneration/sapling; stand sizes are 5–80 ha and clearcuts do not exceed 16 ha. Stands adjacent to clearcuts have not been cut until trees in the regenerating clearcut have attained a height of 10 m, which normally occurs within 10 years (J.W. Lanier, WMNF, personal communication, 1992). The study area contains a narrow unpaved 27 km forest road around the valley at an elevation of 400–700 m; road edges are not mowed nor is any vegetation change associated with the road. All species known to prey upon birds' nests normally occur in the study area, and include eastern chipmunk (*Tamias striatus*), red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys 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*).

Methods

To evaluate the effects of timber size-class on predation of ground and low canopy bird nests, three types of artificial nests were exposed to predators twice in three periods from mid-May through mid-June 1988. Two types of ground nests (track-board and plain) were employed according to Angelstam (1986). Track-board nests were prepared by placing two small brown chicken eggs on boards 0.3 m×0.3 m and 0.6 cm thick, which were coated with a 3 mm layer of grease and covered by fine sand. The corners and edges of the track boards were camouflaged with vegetation, leaf litter and other forest floor debris. Tracks of avian and mammalian nest predators were identified according to Murie (1954). The manner in which eggs were destroyed or disturbed was ascribed to species according to Rearden (1951).

The second nest type, plain nests, consisted of two small brown chicken eggs placed together on the ground. A small piece of plastic flagging was hidden under the eggs in these plain nests so that the site could be found if the eggs were removed (Angelstam, 1986).

The third type of nest, cup 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 depending upon the height of a suitable location. Cup nests were held in place by a wire wrapped discreetly around supporting stems or twigs, and contained two very small brown chicken eggs.

Nest sites were marked at 240 m intervals along the forest road using a

random starting point for each exposure period. Stands containing nests were categorized by mean stem diameter at breast height (dbh) as either seedling/sapling (2.5–10 cm dbh), poletimber (12.5–27.5 cm dbh) or mature (over 30.0 cm dbh) by averaging the diameters of 20 randomly selected trees in each stand. Sizes (ha) of stands containing nests were obtained from WMNF records and categorized as 4–10, 11–20, 21–40, or more than 41 ha. Actual nest locations were not flagged or marked.

All nests were placed during 17:00–22:00 h by an investigator wearing rubber gloves and hip boots to minimize both visual detection by avian predators and human scent. Nests were not visited during exposure periods.

During the three nest exposure periods, one, two or all three nest types were used; 6 days elapsed between periods. One track-board nest was placed 40–45 m from the road edge in each of 61 stands in the first period and exposed to predators for 7 days. All three nest types were used in the second exposure period; each of 42 forest stands contained one nest of each type. Track-board nests were at least 35 m from the roadside, cup nests were at least 20 m from the track-board nests, and plain nests were at least 20 m from the cup nests. Nests were placed in random directions from each other and were exposed to predators for 8 days. In the third period, cup and plain nests were placed in 50 stands and exposed to predators for 8 days. Cup nests were at least 25 m from the roadside, and plain nests were randomly placed at least 25 m from cup nests. In Periods 1 and 2, when more than one nest type was employed, workers did not walk directly from one nest location to another. All distances were estimated. In all periods, a nest was considered depredated when either one or both eggs were removed or broken. At the end of each period, all nests, eggs and eggshells were removed from the forest.

Results

The rate of predation on track-board nests was greater ($\chi^2=44.2$, 1 d.f., $P<0.001$) than on either plain or cup nests (Table 1). Over all exposure periods, 23% of track-board nests ($n=103$) were preyed upon, compared with 9% of cup ($n=92$) and 8% of plain ($n=92$) nests. In the second period, the predation rate on track-board nests increased in all timber size-classes, even though nest locations were different ($\chi^2=16.4$, 1 d.f., $P<0.001$). In both Periods 1 and 2, track-board nests were depredated in proportion to their distribution by timber size-class ($\chi^2=2.33$, 1 d.f., $P=0.21$; $\chi^2=0.25$, 1 d.f., $P=0.59$, respectively). Loss rates of cup and plain nests did not increase in the subsequent period of exposure. Daily survival rates of track-board, plain, and cup nests were 0.937, 0.990 and 0.989, respectively (Table 2).

No avian predator tracks were observed on track-boards, but the tracks of four mammalian predators were identified over the two periods of exposure. Over both exposures and three timber size-classes, three nests were depre-

Table 1
Losses (%) among three types of artificial nests during three exposure periods by timber size-class, White Maintain National Forest, New Hampshire, 1988

Nest type	Period of exposure		
	1 (19–26 May)	2 (2–10 June)	3 (17–25 June)
Track-board			
Seedling/sapling	25 (n=4)	75 (n=16)	
Poletimber	44 (n=9)	83 (n=6)	
Mature	21 (n=48)	80 (n=20)	
Total	25 (n=61)	79 (n=42)	
Cup			
Seedling/sapling		25 (n=16)	20 (n=15)
Poletimber		0 (n=6)	9 (n=11)
Mature		0 (n=20)	0 (n=24)
Total		10 (n=42)	8 (n=50)
Plain			
Seedling/sapling		6 (n=16)	7 (n=15)
Poletimber		0 (n=6)	9 (n=11)
Mature		10 (n=20)	8 (n=24)
Total		7 (n=42)	8 (n=50)

Table 2
Losses and daily survival rates[1] among three types of artificial nests by timber size-class, White Mountain National Forest, New Hampshire, 1988

	Nest type		
	Track-board	Cup	Plain
Timber size-class			
Seedling/sapling	13 (65%)	7 (23%)	2 (6%)
	n=20	n=31	n=31
Poletimber	9 (60%)	1 (6%)	1 (6%)
	n=15	n=7	n=17
Mature	26 (38%)	0	4 (9%)
	n=68	n=48	n=44
Overall	48 (47%)	8 (9%)	7 (8%)
	n=103	n=92	n=92
Daily survival rate[1]	0.937	0.989	0.990

[1]Calculated after Mayfield (1975).

dated by red fox, six by striped skunk, four by fisher and four by raccoon (Table 3). Seven nests were depredated by predators unidentified by tracks in the first exposure period and 24 in the second period. Pooling results for two exposure periods, predation rates on track-board nests were not different

Table 3
Fate of track-board nests during two exposures to predators, White Mountain National Forest, New Hampshire, 1988

	Period of exposure		Total ($n=103$)
	1 (19–26 May) ($n=61$)	2 (2–10 June) ($n=42$)	
Nests depredated	15 (24.6%)	33 (78.6%)	48 (46.6%)
Depredated by:			
Striped skunk	4 (26.7%)	2 (6.1%)	6 (12.5%)
Raccoon	3 (20.0%)	1 (3.0%)	4 (8.3%)
Red fox	0	3 (9.1%)	3 (6.3%)
Fisher	1 (6.7%)	3 (9.1%)	4 (8.3%)
Unkonwn predator[1]	7 (46.6%)	24 (72.7%)	31 (64.6%)
Daily survival rate[2]	0.965	0.902	0.937
Nests depredated in:			
Seedling/sapling	1 (25.0%, $n=4$)	12 (75.0%, $n=16$)	13 (65.0%, $n=20$)
Poletimber	4 (44.4%, $n=9$)	5 (83.3%, $n=6$)	9 (60.0%, $n=15$)
Mature	10 (20.8%, $n=48$)	16 (80.0%, $n=20$)	26 (38.2%, $n=68$)

[1]Of 31 predated nests, it is likely that three were depretated by mink, two by fisher, 11 by black bear, and one by a coyote.
[2]After Mayfield (1975).

by timber size-class ($\chi^2=3.0$, 1 d.f., $P=0.09$). The predation rate on pooled track-board nests was not different from that expected in stands of 4–10, 11–20, 21–40, and more than 41 ha ($\chi^2=1.40$, 2 d.f., $P=0.49$).

Predation rates on cup and plain nests were much lower than on track-board nests, and neither differed among size-classes. Cup nests were never disturbed in mature stands (Table 1). Predation rates did not change between exposure periods for either cups or plain nests.

Where more than two nest types were located in one stand, predation on one nest type was independent of predation on the other type(s). In the second exposure period, in which all three nest types were used, 71% (30/42) of the stands had predation on track-board nests only; only 7% (3/42) of the stands had predation on more than one nest. In the third exposure period, in which no track-board nests were used, plain nests were disturbed in 6% (3/50) of the stands; only 2% (1/50) of the stands had predation on both the cup and plain nests. Rates of predation on cup and plain nests were similar in Periods 2 and 3, even though Period 2 also employed track-board nests. The similar rate of predation between Periods 2 and 3 is evidence that predators were not detecting a nest from another nest location. If such were the case, a higher predation rate on multiple nests in a stand would have been observed, especially in view of the high predation on track-board nests in Period 2.

Regarding the number of eggs taken, both were removed from 11 of 15

depredated track-board nests in Period 1, and both from all 33 depredated nests in Period 2. Of seven depredated plain nests, six lost both eggs. All eight cup nests depredated over both exposures remained upright. Of these, five lost one egg; in two cases, one egg remained in the nests while eggshells were below, and in three other cases, one unbroken egg was found beneath empty nests.

Discussion

The only predators present in the study area that are large enough to take the eggs without leaving tracks on the boards were fisher, raccoon, coyote, and black bear; based upon the evidence at 11 depredated nests by unknown predators (chewed boards—upper canines more than 5 cm apart, clawed boards—2 cm between each claw, and consumption of the track medium), black bears were probably the species involved. Consumption of lubricating grease and oil by black bears is common and they are probably attracted by the odor (L. Rogers, personal communication, 1991). Black bears are quick to learn new food types from one experience (Bacon and Burghardt, 1975). Thus, bears were probably more attracted to track-board nests by the smell of the grease than were other mammalian predators, and may have consumed eggs incidentally. Future studies of nest predation using track media should control for scent if black bears are present. Indistinct tracks of mink were left on three track-boards, and of fisher on two others. The depredated cup nests may have been robbed by crows or ravens, the only birds large enough to remove eggs from the nest. Predation by arboreal mammals cannot be excluded, however. Nests more than 1 m above the ground have been reported to be more susceptible to avian predation than ground nests in deciduous forest in Pennsylvania (Yahner and Scott, 1988; Yahner et al., 1989). However, in conifer forest in Arizona, predation rates on artificial cup nests placed 0.5–2 m above the ground were lower than on similar nests placed on the ground (Martin, 1987).

No clear evidence was found that predation rates on artificial nests differ by timber size-class or stand size in extensive forest. Track-board nests in both exposures were depredated in almost exact proportion to their distribution by seral stage. Managed extensive forest, comprised of a mosaic of even-aged stands, does not produce habitat conditions that differentially attract generalist predators that prey on bird nests. Elevated nest predation rates as an edge effect in habitat islands have been reported in forest–farmland ecotones in northern Europe (Angelstam, 1986; Andren and Angelstam, 1988), and in eastern USA in forest–suburb landscapes (Wilcove, 1985); in both continents, the edge-related increase in predation was mainly from predators living in the surrounding non-forest matrix. This elevation in artificial ground nest predation rate has been shown to level off 200–500 m from the edge in

large forest fragments in forest–farmland landscapes (Angelstam, 1986). The predation rate on plain nests in the present study (8%) was about the same as the overall predation rate (6%) on similar nests in continuous coniferous forest in Sweden (Andren et al., 1985). In forest-dominated landscapes in Maine, Small and Hunter (1988) found no evidence that predation on artificial nests increased at the edges of forests fragmented by roads, powerlines and fields; predation was greatest in small tracts, however. Northern hardwood forests normally regenerate readily after clearcutting—hardwood tree species normally have stem densities of more than 175 000 ha^{-1} and heights of 1–2 m 3 years after clearcutting (Marquis, 1965). There are essentially no differences in foliage profiles among stands more than 30 years old; foliage profiles in stands of widely disparate ages are similar because northern hardwood species reach their maximum height of about 26 m fairly early in the life of the stand (Aber, 1979).

If extensive forest were fragmented by even-aged management, elevated nest predation rates would be expected to differ by timber size-class or stand area (Andren and Angelstam, 1988; Small and Hunter, 1988). Lacking the population augmentation provided by suburbs and agricultural lands, mid-sized omnivores and carnivores (generalist predators) do not overrun stands in intensively managed forest as they do in more settled landscapes. The results of the present study, in which track-board nests were depredated in proportion to their distribution by seral stage and area, and in which predation rates on cup and plain nests were low, suggest that even-aged management in extensive hardwood-dominated forests does not contribute to fragmentation in northern New England.

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References

Aber, J.D., 1979. Foliage height profiles and succession in northern hardwood forests. Ecology, 60: 18–23.

Ambuel, B. and Temple, S.A., 1983. Area-dependent changes in the communities and vegetation of southern Wisconsin forests. Ecology, 64: 1057–1068.

Andren, H. and Angelstam, P., 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology, 69: 544–547.

Andren, H., Angelstam, P., Lindstrom, E. and Widen, P., 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. Oikos, 45: 273–277.

Angelstam, P., 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos, 47: 365–373.

Bacon, E.S. and Burghardt, G.M., 1975. Learning and color discrimination in the American black bear. Int. Conf. Bear Res. Manage., 3: 27–36.

DeGraaf, R.M., 1992. Effects of even-aged management on forest birds at northern hardwood stand interfaces. For. Ecol. Manage., 46: 95–110.

Frieswyk, T.S. and Malley, A.M., 1985. Forest statistics for New Hampshire—1973 and 1983. Res. Bull. NE-88, Broomall, PA; US Dept. Agric. For. Serv. Northeastern For. Exp. Stn., 100 pp.

Gates, J.E. and Gysel, L.W., 1978. Avian nest dispersion and fledgling success in field–forest ecotones. Ecology, 59: 871–883.

Gotmark, F., Neergaard, F.R. and Aklund, M., 1990. Predation of artificial and real arctic loon nests in Sweden. J. Wildl. Manage., 54: 429–432.

Horn, H., 1968. The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*). Ecology, 49: 682–694.

Lack, D., 1954. The Natural Regulation of Animal Numbers. Clarendon Press. Oxford, 343 pp.

Lack, D., 1968. Ecological Adaptations for Breeding in Birds. Methuen, London, 409 pp.

Marquis, D.A., 1965. Regeneration of birch and associated hardwoods after patch cutting. Res. Pap. NE-32, USDA Forest Service, Upper Darby, PA, 13 pp.

Martin, T.E., 1987. Artificial nest experiments: effects of nest appearance and type of predator. Condor, 89: 925–928.

Mayfield, H.F., 1975. Suggestions for calculating nest success. Wilson Bull., 87: 456–466.

Murie, O.J., 1954. A Field Guide to Animal Tracks. Houghton Mifflin, Boston, MA, 375 pp.

Rearden, J.D., 1951. Identification of waterfowl nest predators. J. Wildl. Manage., 15: 386–395.

Ricklefs, R.E., 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool., 9: 1–48.

Robinson, S.K., 1988. Reappraisal of the costs and benefits of habitat heterogeneity for nongame wildlife. Trans. North Am. Wildl. Nat. Res. Conf., 53: 145–155.

Skutch, A.F., 1949. Do tropical birds rear as many young as they can nourish? Ibis, 91: 430–455.

Small, M.F. and Hunter, M.L., 1988. Forest fragmentation and avian nest predation in forested landscapes. Oecologia, 76: 62–64.

Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K. and Bystrak, D., 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: R.L. Burgess and D.M. Sharpe (Editors), Forest Island Dynamics in Man-dominated Landscapes. Springer, New York.

Wilcove, D.S., 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology, 66: 1211–1214.

Yahner, R.H. and Scott, D.P., 1988. Effects of forest fragmentation on depredation of artificial nests. J. Wildl. Manage., 52: 158–161.

Yahner, R.H. and Wright, A.L., 1985. Depredation on artificial ground nests: effects of edge and plot age. J. Wildl. Manage., 49: 508–513.

Yahner, R.H., Morrell, T.E. and Rachael, J.S., 1989. Effects of edge contrast on depredation of artificial avian nests. J. Wildl. Manage., 53: 1135–1138.