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Effects of Forest Harvesting on Nest Predation in Cavity-nesting Waterfowl

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Waterfowl populations in North America are threatened by habitat loss (Owen and Black 1990), but effects of habitat destruction and fragmentation on waterfowl nesting in forested landscapes are poorly known. Increased nest predation is often attributed to habitat fragmentation and may be particularly evident in smaller habitat patches and at habitat edges (Paton 1994, Andrén 1995). However, relatively few studies conducted in forest-dominated landscapes show edge effects at either natural or anthropogenic edges (Paton 1994, Andrén 1995, Pöysä et al. 1997). Lack of edge effects in forest-dominated landscapes may be due to relatively low predator species richness and abundance, and lack of predator attraction to edges (Andrén 1995). However, predator abundance and nest predation may increase with increased deforestation of the landscape (Andrén 1995, Hartley and Hunter 1998).

Effects of habitat destruction and fragmentation on nest predation of cavity-nesting waterfowl are unknown. We know of only one study of nest predation in cavity-nesting waterfowl in forest-dominated landscapes (Pöysä et al. 1997). This study found no edge effects at natural (lake) edges in a forested landscape, but did not investigate effects of forest harvesting. Thus, we experimentally investigated effects of forest harvesting on cavity-nesting waterfowl in the boreal mixedwood forest of western Canada, an important breeding and summering area for waterfowl. Although deforestation and fragmentation have proceeded relatively slowly in that region, large areas of forest have recently become available for harvesting. We used artificial waterfowl cavity nests to test the following hypotheses: (1) nest-predation levels in cutblocks (clearcuts with ≥8% of trees remaining) differ from predation levels in uncut forest, (2) nest-predation levels in riparian forest buffer strips differ from predation levels in uncut forest, (3) nest-predation levels in uncut forest vary with distance from the riparian forest edge, and (4) nest predation is higher around lakes in harvested versus unharvested landscapes.

Methods.—We conducted research from May through July in 1997 and 1998, in the boreal mixedwood forest surrounding 10 lakes in north-central Alberta, Canada. Six of the 10 study lakes were part of the TROLS (Terrestrial and Riparian Organisms, Lakes and Streams) project, a large-scale multidisciplinary study using experimental forest harvesting protocols at 12 lakes to determine effects of different buffer strip widths on aquatic and terrestrial boreal systems. Study lakes were in three clusters and ranged in size from 8.6 to 103.6 ha. Forests surrounding study lakes were dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), white spruce (*Picea glauca*), black spruce (*P. mariana*), and jack pine (*Pinus banksiana*).

Extensive commercial forest harvesting began in this region in 1993. Forest harvesting is carried out in two to three passes 10 years apart, creating a mosaic landscape of harvested patches of various ages and unharvested stands. Average cutblock size is approximately 30 ha and cutblocks contain ≥8% residual trees. When forest surrounding lakes is harvested, a forest buffer strip 100 m wide separates riparian vegetation and the adjacent lakeshore from harvesting activity. The purpose of buffer strips is to protect lake water quality. (Although riparian vegetation separated the forest from the lake edge around

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some study lakes, for clarity, we refer to the forest–riparian vegetation edge as the "lakeshore" hereafter.) Forest blocks around five study lakes were harvested once between September 1995 and April 1997 (harvested lakes). Harvesting removed about 10 to 40% of forest from the catchments of harvested lakes. Forest within 800 m of four of the five remaining study lakes was unharvested in both years of our study. The fifth lake was harvested to within 450 m in 1994. We refer to these five lakes as "unharvested lakes" hereafter. The amount of forest harvesting in catchments of unharvested lakes was 0 to 5%. Cavity-nesting waterfowl in the region include Bufflehead (*Bucephala albeola*), Common Goldeneye (*B. clangula*), Common Merganser (*Mergus merganser*), and Hooded Merganser (*Lophodytes cucullatus*). Potential mammalian predators of waterfowl cavity nests include short-tailed weasel (*Mustela erminea*), long-tailed weasel (*M. frenata*), mink (*M. vison*), marten (*Martes americana*), northern flying squirrel (*Glaucomys sabrinus*), and red squirrel (*Tamiasciurus hudsonicus*). Potential avian nest predators in the area include Common Raven (*Corvus corax*) and Gray Jay (*Perisoreus canadensis*), and although they are not true predators, Northern Flickers (*Colaptes auratus*) may also destroy eggs.

We placed four transects of artificial cavity nests around each lake. Each transect consisted of four nests approximately 30 m apart. Transects were ≥200 m apart. Around harvested lakes, we placed one nest transect in a cutblock at 50 m from the forest–cutblock edge, therefore approximately 150 m from the lakeshore, and one nest transect 50 m from the lakeshore edge of a 100 m wide forest buffer strip. We also located one nest transect in uncut forest 50 m from the lakeshore, and one nest transect in uncut forest 150 m from the lakeshore. At unharvested lakes, we placed two nest transects 50 m from the lakeshore and two nest transects 150 m from the lakeshore. Nest transects were in the same areas in both years of the study, although nests were not always on the same trees both years. Locating nest transects at both 50 and 150 m from the lakeshore allowed investigation of different levels of predation at different distances from the lakeshore.

We constructed artificial cavity nests with dimensions approximating the mean dimensions of natural Bufflehead and Common Goldeneye nest cavities (Bellrose 1980, Gauthier 1993, Eadie et al. 1995). Nests consisted of two 4.6 L plastic buckets wired together to create a cylindrical cavity 18 cm in diameter and 39 cm long with a 10 cm diameter entrance hole. We covered cavities with coarse, light brown burlap fabric to reduce conspicuousness and ensure predators could grip the plastic surface. We also placed a 3 to 5 cm wide strip of burlap inside the nest cavity and attached this to the lower edge of the entrance hole to allow predators to escape from cavities.

To facilitate predator identification in 1998, we attached hair-catchers at cavity entrances. Hair-catchers consisted of a flexible plastic strip (0.16 × 3 × 29 cm) fitted around the lip of the entrance hole and secured with double-sided indoor–outdoor carpet tape (Manco brand product 10-1). We stuck a strip of carpet tape (3 × 32 cm) on the surface of the plastic strip to collect hairs and feathers of potential predators entering artificial nests. We also placed a small piece of carpet tape at the top of the burlap tongue inside the nest boxes. Carpet tape remained strongly adhesive throughout the experiment.

We nailed nest cavities to trees approximately 2 m above ground, and placed leaf litter on the bottom of cavities. We placed one small wax-filled chicken egg (Pasitschniak-Arts and Messier 1995) and one plasticine egg of approximately the same size into each cavity. Small chicken eggs approximated the size of real Bufflehead and Common Goldeneye eggs (Gauthier 1993, Eadie et al. 1995). Before placing nests in cavities, we scented each egg with two to three drops of commercially produced duck scent to reduce bias against olfactory predators caused by the absence of adult birds and down nest lining from artificial nests (Willebrand and Marcström 1988, Pasitschniak-Arts and Messier 1995). We wore latex gloves when handling nest contents to reduce human odor (Pasitschniak-Arts and Messier 1995).

Nest-predation trials were 30 days long, paralleling Bufflehead and Common Goldeneye incubation periods (Gauthier 1993, Eadie et al. 1995). To help maintain olfactory stimuli at nests throughout the experiment, we added two to three drops of duck scent to each remaining egg or to the empty nest 13 to 16 days after starting trials. At that time in 1998 we also removed carpet tape with hair adhering to it before adding a new piece of tape. If there were no hairs on the tape we placed another layer on top of the first, to maintain consistent adhesiveness among nests.

At the conclusion of artificial nest trials, we examined eggs for predation and hair-catchers for hair samples in 1998. We considered a nest depredated if one or both eggs were pecked, bitten, broken, or removed. When possible, we identified mammalian nest predators by comparing tooth marks left in eggs to impressions made in plasticine using museum specimens. We could not identify avian predators to species level from egg damage. We removed hair samples from carpet tape using carbon tetrachloride (CCl_4). After removal, we cleaned hairs by soaking them in CCl_4 (Pasitschniak-Arts and Messier 1995) for 15 to 30 min. We measured hair length and diameter and determined stricture location, color pattern and shield appearance. We used confocal laser scanning microscopy to examine medulla structure and scanning electron microscopy to examine scale patterns. We identified hairs to species level by using identification keys based on those characteristics

TABLE 1. Predators identified at artificial nests located in riparian forest buffer strips (BS) and cutblocks (CB) adjacent to harvested lakes, and in uncut forest 50 and 150 m from the forest edge adjacent to harvested and unharvested lakes (H 50, H 150, and U 50, U 150, respectively).

Year	Predator	BS	CB	H 50	H 150	U 50	U 150
1997	Red squirrel	1	1		1	3	1
	Avian predator			1			
	Unidentified			3	4	4	2
1998	Red squirrel	3		3	1	5	8
	Red squirrel or northern flying squirrel					1	1
	Red squirrel or marten						1
	Short-tailed or long-tailed weasel	1					
	Avian predator					1	1
	Unidentified	2			3	5	3

(e.g. Adorjan and Kolenosky 1969, Wallis 1992) and samples taken from museum specimens.

We analyzed predation data in S-Plus 4.5 (MathSoft Inc. 1998) using generalized linear models (GLIM) with quasilikelihood functions. We used quasilikelihood functions in GLIM because those functions do not assume that errors conform to a particular distribution (McCullagh and Nelder 1989). We nested transects within lakes, and assumed that nests within transects were not always biologically and therefore statistically independent. We also included year (first or second summer of the study) in models, and examined interactions between transect type and year. We rejected null hypotheses at $P \leq 0.01$, rather than $P \leq 0.05$ because we conducted multiple comparisons with components of the data set (Miller 1981). We excluded nests destroyed by black bears (*Ursus americanus*) from analyses (54 in 1997, 56 in 1998). Black bears depredate nests of cavity-nesting waterfowl (Erskine 1972, Eadie et al. 1995), including those in nest boxes (J. E. Thompson pers. comm.). However, the artificial nest cavities we used were much more accessible and easier for black bears to destroy than natural cavities, and therefore did not provide a useful relative measure of black bear depredation of real cavity nests.

Results.—In 1997, we recorded 21 nest-predation events. Eleven of 48 nests (22.9%) were depredated at harvested lakes, compared to 10 of 58 nests (17.2%) at unharvested lakes (Table 1). Seven predation events were mammalian; tooth marks in eggs indicated that red squirrels were responsible for those. We identified one avian predation event based on egg damage. In the remaining 13 predation events, predators removed eggs and carried them away from nest sites; thus, we could not identify the predators.

In 1998 we recorded 39 nest-predation events. Thirteen of 38 nests (34.2%) were depredated at harvested lakes, compared to 26 of 66 nests (39.4%) at unharvested lakes (Table 1). Tooth marks in eggs demonstrated that red squirrels were responsible for 14 predation events. Analyses of hairs suggested that red squirrels were responsible for six additional predation events, in which eggs were removed from artificial nests. There were two avian predation events in 1998, identified by egg damage. Hair analyses suggested that two of the remaining 17 predation events were due to red squirrel or northern flying squirrel, one was due to short-tailed weasel or long-tailed weasel and one was due to red squirrel or marten. (Collection of multiple hair types at those nests, and difficulty distinguishing some hairs, precluded more precise identification.) Identities of predators in 13 events were unknown, due to egg removal and lack of hair samples.

Numbers of wax-filled chicken eggs versus plasticine eggs depredated did not differ significantly (1997: 15 wax-filled and 15 plasticine eggs taken; 1998: 39 wax-filled and 30 plasticine eggs taken; $G = 0.36$, $df = 1$, $P > 0.05$). Both eggs were removed from most nests (only plasticine egg removed: 7 nests; only wax-filled egg removed: 16 nests; both eggs removed: 38 nests).

At harvested lakes in both 1997 and 1998, nest predation was lower in cutblocks than on any other transect type. Only one nest in a cutblock was depredated (by a red squirrel) during our study. Nest predation was significantly lower in cutblocks than in uncut forest 150 m from the lakeshore; year did not significantly affect predation (Table 2, Fig. 1). (Extremely low predation in cutblocks precluded examination of an interaction between year and transect type using GLIMs.) Levels of nest predation in riparian buffer strips did not differ significantly from uncut forest 50 m from the lakeshore; again, effect of year was not significant, and there was no significant interaction between year and transect type, although standard errors were relatively large (Table 2, Fig. 1).

At both harvested and unharvested lakes, predation did not differ significantly in uncut forest at 50 versus 150 m from the lakeshore, and at harvested lakes, predation levels were not significantly differ-

TABLE 2. Results of generalized linear model analyses of predation at artificial cavity nests. Results significant at $P \leq 0.01$.

Null deviance	Residual deviance	Variables	SE	df	F	P
		Cutblocks vs. uncut forest 150 m from the lakeshore, at harvested lakes:				
49.59	38.69	Transect type	1.76	1, 46	10.55	0.002
		Year	0.42	1, 47	0.13	0.72
		Buffer strips vs. uncut forest 50 m from the lakeshore, at harvested lakes:				
49.08	33.47	Transect type	2.63	1, 34	1.30	0.26
		Year	2.29	1, 35	4.47	0.04
		Year × Transect type interaction	1.23	1, 32	2.74	0.11
		Uncut forest 50 m vs. 150 m from the lakeshore, at harvested lakes:				
51.73	50.25	Transect type	1.27	1, 35	0.18	0.67
		Year	1.29	1, 36	0.03	0.87
		Year × Transect type interaction	0.77	1, 33	0.05	0.82
		Uncut forest 50 m vs. 150 m from the lakeshore, at unharvested lakes:				
145.67	128.02	Transect type	2.21	1, 121	0.05	0.82
		Year	0.75	1, 122	9.87	0.002
		Year × Transect type interaction	0.49	1, 119	1.70	0.19
		Uncut forest 50 m from the lakeshore at harvested vs. unharvested lakes:				
92.46	86.25	Transect type	1.85	1, 70	1.83	0.18
		Year	1.21	1, 71	1.06	0.31
		Year × Transect type interaction	0.67	1, 68	0.22	0.64
		Uncut forest 150 m from the lakeshore at harvested vs. unharvested lakes:				
107.52	92.03	Transect type	1.75	1, 86	1.83	0.18
		Year	1.00	1, 87	6.08	0.02
		Year × Transect type interaction	0.60	1, 84	2.33	0.13
		Harvested lakes vs. unharvested lakes:				
247.51	230.59	Transect type	1.15	1, 207	0.13	0.72
		Year	0.55	1, 208	9.60	0.002
		Year × transect type interaction	0.35	1, 205	1.36	0.25

ent between years; the deviance values show that the model fitted the data very poorly (Table 2, Fig. 1). However, at unharvested lakes, there was a highly significant year effect (Table 2, Fig. 1); in 1998, predation increased 13% at transects 50 m from the lakeshore and 32% at transects 150 m from the lakeshore, compared to 1997. At both harvested and unharvested lakes, there was no significant interaction between year and transect type (Table 2).

Nest predation in uncut forest around harvested lakes, versus unharvested lakes, did not differ significantly at either 50 or 150 m from the lakeshore (Table 2, Fig. 1). Also, there were no significant year effects on nest predation at either distance from the lakeshore (Table 2, Fig. 1), and there were no significant year by transect type interactions (Table 2). Although not a statistically significant difference, in 1997 nest predation in uncut forest 150 m from the lakeshore was almost 40% higher at harvested lakes than unharvested lakes. In 1998, however, the difference was only 2%, due to increased predation at unharvested lakes.

When results for all nest transects were combined, lake treatment (harvested vs. unharvested) did not affect nest predation levels (Fig. 2); however, year did. Overall, predation was higher in 1998. The effect of year did not differ significantly between lake treatments (Table 2).

Discussion.—Almost all nest predators identified in our study were mammalian, and almost all mammalian predation events were unambiguously attributed to red squirrels. Pöysä et al. (1997) corroborate our findings by suggesting that waterfowl cavity nests are more frequently depredated by mammals than by birds. However, we may have underestimated the importance of avian predation if avian predators removed eggs from artificial cavity nests (Haskell 1995).

The number of plasticine and wax-filled chicken eggs attacked by predators did not differ signifi-

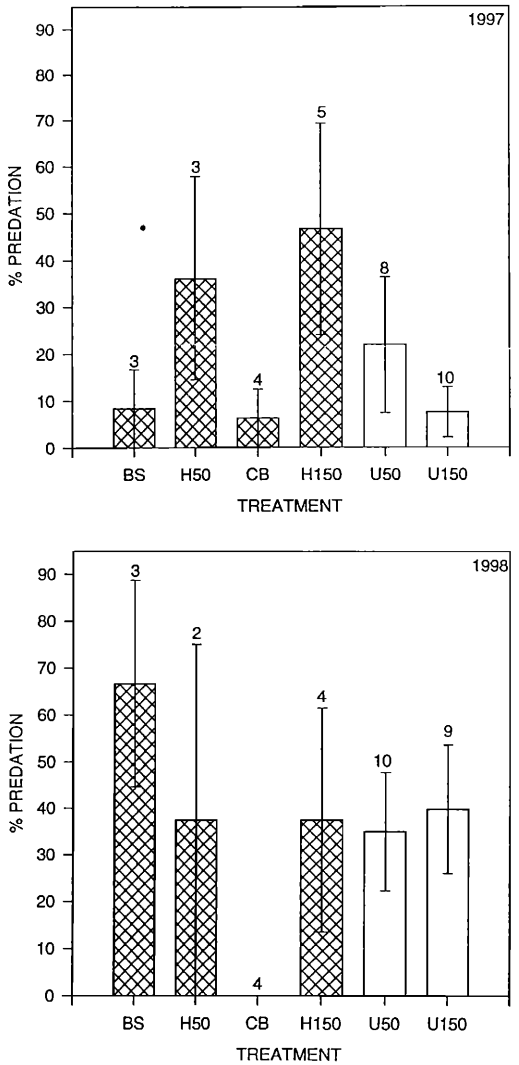

FIG. 1. Nest-predation levels (mean percent per transect ±1 SE) in 1997 and 1998 in riparian buffer strips abutting cutblocks (BS), 50 m from the lakeside forest edge at harvested lakes (H50), cutblocks (CB), 150 m from the lakeside forest edge at harvested lakes (H150), and 50 and 150 m from the lakeside forest edge at unharvested lakes (U50 and U150, respectively). Numbers above bars are number of transects included. Hatched bars = transects at harvested lakes, open bars = transects at unharvested lakes.

cantly. In most nests, both eggs were depredated, removing potential analytical problems associated with differential depredation of plasticine and real eggs in nest predation experiments (Bayne et al. 1997).

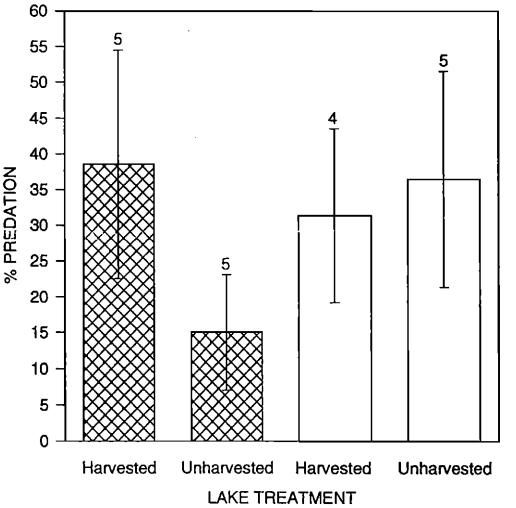

FIG. 2. Nest-predation levels (mean of percent predation per lake, for each lake type ±1 SE) in 1997 (hatched bars) and 1998 (open bars) at harvested and unharvested lakes. (Predation at all transects combined for each lake.) Numbers above bars are number of lakes included. (In 1998, all nests at one harvested lake were destroyed by bears, therefore four lakes were included in analyses.)

Artificial nest cavities were depredated significantly less in cutblocks than in comparable unharvested forest. Similarly, Ratti and Reese (1988) and Rudnicky and Hunter (1993) found predation of artificial ground and shrub nests was lower in clearcuts in a forest-dominated landscape. Red squirrels and martens tend to avoid clearcuts for at least six years after harvesting (Kirkland 1977, Snyder and Bissonette 1987, Thompson et al. 1989, Whitfield and Hall 1997). Because most of the mammalian nest predators in our study were red squirrels, lack of predation in cutblocks concurs with squirrel avoidance of harvested areas. Weasels do not exhibit clear responses to clearcutting, although data are sparse (Simms 1979, Thompson et al. 1989, Hansson 1994). Although there are few records of cavity-nesting waterfowl in clearcuts (R. G. Anderson and S. Woodley pers. comm.), if birds are able to nest in residual trees in cutblocks, they may experience lower nest predation and potentially higher nesting success for up to six years after forest harvesting.

Predation of artificial cavity nests in riparian forest buffer strips did not differ significantly from unharvested riparian forest. Red squirrel abundance in riparian forest buffer strips is not known to differ from unharvested forest (Whitfield and Hall 1997). However, Vander Haegen and DeGraaf (1996) found higher predation of open-cup nests in 20 to 80 m wide riparian buffer strips than in intact riparian sub-boreal Acadian forest. They identified red squirrels and

Blue Jays (*Cyanocitta cristata*) as important nest predators. In contrast, avian predators did not depredate nests in buffer strips in our study, unless they were removing eggs from nests, and thus could not be identified.

Paton (1994) concluded that nest predation was most likely to increase within 50 m of habitat edges, but studies in forest-dominated landscapes have failed to find edge effects (Andrén 1995). Similarly, predation on real and artificial waterfowl cavity nests is not known to increase in forests closer to lakeshores (Pöysä et al. 1997). Our study concurs with those conclusions. Nest transects in buffer strips were 50 m from both the lakeshore and cutblock edge, and predation levels in buffer strips did not differ from intact riparian forest. Predation on artificial cavity nests also did not differ in intact forest at 50 versus 150 m from the lakeshore, around either harvested or unharvested lakes. Mean nest-predation levels in uncut forest patches in our study were close to ranges found in artificial nests and real Common Goldeneye nests in nest boxes near lake shorelines in Sweden and Finland. Predation of cavity nests in these locales can range from 10 to 88% (Eriksson 1979, Fredga and Dow 1984, Pöysä et al. 1997).

Although negative edge effects due to clearcutting have not been demonstrated at smaller spatial scales (Andrén 1995), depredation of artificial ground nests can increase with increasing amounts of clearcutting at the landscape level (Hartley and Hunter 1998). However, our results for artificial cavity nests did not support that conclusion; predation levels did not differ around harvested and unharvested lakes. That may be due to the currently low level of forest harvesting in the landscape around our study sites.

Effect of year was significant in our study in analyses comparing nest predation at 50 versus 150 m from the lakeshore at unharvested lakes, reflecting the very low nest predation levels at 150 m from the lakeshore around unharvested lakes in 1997. Predation levels in buffer strips also differed greatly between years; however, the low number of nest transects and high variability in predation prevented that difference being statistically significant. Those patterns contributed to a significant year effect when we compared total predation at harvested versus unharvested lakes. Changes in nest predation between years of our study may be due to changes in the abundance and distribution of nest predators, for example the red squirrel, as a result of changes in squirrel food supply and weather conditions (Kemp and Keith 1970, Rusch and Reeder 1978, Gurnell 1983).

Our results show that 1 to 30 months after low-level forest harvesting, depredation of waterfowl artificial cavity nests did not increase, and predation was not higher at 50 m compared to 150 m from the forest edge adjacent to lakeshores. However, predation levels may change with increasing deforestation in the landscape, and increasing time since forest harvesting, especially if habitat changes induced by forest harvesting affect red squirrel abundance and distribution. The loss of nest cavities may negatively affect waterfowl more strongly than changes in nest predation due to harvesting, particularly at higher levels of forest harvesting. Also, when harvesting is extensive in the landscape, older trees, which are more likely to harbor nest cavities, may become concentrated into buffer strips adjacent to lakes. That may increase the risk of nest predation for cavity-nesting waterfowl by creating highly rewarding foraging patches for nest predators. Studies of real waterfowl cavity nests are required to determine the importance of those processes in the boreal forest of western North America.

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