

Predation on Nesting Woodpeckers in British Columbia

ERIC L. WALTERS¹ and EDWARD H. MILLER²

Department of Biology, University of Victoria, P.O. Box 3020, Victoria, British Columbia V8W 3N5 Canada

¹Current address: Department of Biological Science, Florida State University, Tallahassee, Florida 32306-1100 USA

²Current address: Biology Department, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9 Canada

Walters, Eric L., and Edward H. Miller. 2001. Predation on nesting woodpeckers in British Columbia. *Canadian Field-Naturalist* 115(3): 413-419.

Predation on eggs, nestlings, and breeding adults of Red-naped Sapsuckers, *Sphyrapicus nuchalis*, Northern Flickers, *Colaptes auratus*, Hairy Woodpeckers, *Picoides villosus*, and Williamson's Sapsuckers, *S. thyroideus*, was documented in the Hat Creek valley, south-central British Columbia from 1989-1994. Predation by Black Bears (*Ursus americanus*), Deer Mice (*Peromyscus maniculatus*), and House Wrens (*Troglodytes aedon*) was observed; and predation by Long-tailed Weasels (*Mustela frenata*) was inferred.

Key Words: Red-naped Sapsucker, *Sphyrapicus nuchalis*, Williamson's Sapsucker, *S. thyroideus*, Hairy Woodpecker, *Picoides villosus*, Northern Flicker, *Colaptes auratus*, Black Bear, *Ursus americanus*, Deer Mouse, *Peromyscus maniculatus*, House Wren, *Troglodytes aedon*, nesting, predation, British Columbia.

Hole nesting in birds has evolved independently in many taxonomic groups. The generally accepted dogma is that hole nesting offers an advantage over open nesting (e.g., von Haartman 1957). Many authors (e.g., Lack 1954; Nice 1957) have provided evidence to suggest that nesting success is higher in hole-nesting species even though there is more constraint on choice of nesting location. Because predation can be a major cause of nest failure among species that nest in holes (Nilsson 1984), it has obvious implications for the evolution of life history traits (Martin 1995). Predation, therefore, must be a strong evolutionary force with respect to breeding biology (Alerstam and Högstedt 1981; Nilsson 1984). However, data concerning predation on hole-nesting species are difficult to obtain, requiring detailed life-history studies over successive breeding seasons (Greene 1986); and usually involve climbing trees, many of which are in various stages of decay. Recent advances in technology have allowed some researchers to utilize cameras to circumvent some of the problems associated with observing nests (e.g., Martin 1988; Picman and Schriml 1994; Thompson et al. 1999). The use of cameras for tree holes that are relatively high or for observing nocturnal predators, however, is still quite limited. Besides difficulties associated with nest monitoring, many studies of the reproductive success of hole-nesting species have relied upon nest box studies (e.g., van Balen and Potting 1990; Verhulst et al. 1995) rather than using natural cavities.

Our objectives are to document predation events, to identify the predators, and to describe the evidence that allows inferences about the species of predator that prey upon woodpecker nests. In this paper we define nest predation as any event that

results in the destruction of eggs or the death of a chick or adult during the nesting stage without regard to whether the "predator" actually ingested the egg, chick, or adult (cf. Sealy 1994). Under this definition, a predator may be motivated either by hunger or by a desire to obtain a nest or roost site.

Study Area and Methods

The study site was within the Hat Creek valley near Upper Hat Creek (25 km SW of Cache Creek), south-central British Columbia (50°46'N 121°38'W), at an elevation of approximately 1200 m. The slopes of the narrow valley are forested with second-growth Interior Douglas-fir (*Pseudotsuga menziesii*), Interior Spruce (*Picea engelmannii* × *glauca*), and pines (*Pinus contorta* and *P. ponderosa*), with some Trembling Aspen (*Populus tremuloides*). On the valley bottom the same tree species occur, but aspen and willow (*Salix* spp.) are more abundant. Further details about the study site are given by Walters (1996).

Woodpecker nests were studied from late April to late July 1989-1994. Nest monitoring varied among years. In 1989 and 1991, nests were monitored up to three times; in 1990 and 1992, they were visited approximately 20 times; and in 1993 and 1994, nests were visited daily. Emphasis was on finding nests of the Red-naped Sapsucker (*Sphyrapicus nuchalis*), the most abundant breeding species in the area. Other common breeding woodpeckers were the Northern Flicker (*Colaptes auratus*), Hairy Woodpecker (*Picoides villosus*), and Pileated Woodpecker (*Dryocopus pileatus*). Downy Woodpeckers (*Picoides pubescens*) and Williamson's Sapsuckers (*Sphyrapicus thyroideus*) bred regularly in the area but were uncommon.

Nests were found by various means: nesting signs

(e.g., recent excavations, wood chips on ground), audible cues (e.g., drumming, vocalizations, nestling calls), observing adults feeding young, or by direct observations of birds (Jackson 1977). In 1992-1994 we checked nest contents with a mirror and flashlight (nest contents were not checked prior to 1992). Predation was assumed when all eggs or nestlings were missing from the nest (except when fledging was expected), or if eggshells, feathers, or other signs (e.g., sticks in the hole entrance) were in the nest cavity or on the ground below the nest (Johnsson 1994). The identity of the predator was determined by either observation of the predation

event or indirectly by examining the result of the predation event (e.g., use of sticks by wrens, bear claw marks). All of our observations of predation events were opportunistic in nature and occurred while we were checking the status of each nest.

Results

The number of woodpecker nests monitored varied among years (Table 1). We found evidence of 23 cases of nest predation out of a total of 239 nests during our study: probable mustelid, 12; Black Bear (*Ursus americanus*), 4; House Wren (*Troglodytes aedon*), 3; Deer Mouse (*Peromyscus maniculatus*),

TABLE 1. Numbers of woodpecker nests with eggs or young and the outcome associated with each.

Species	Year	Total	Cause of Failure				Unknown	Outcome	
			Predation					Successful	Unknown
			Weasel	Bear	Mouse	Wren			
RNSA	1989	39	-	-	-	-	-	39	
	1990	36	-	-	-	3	22	11	
	1991	19	-	-	-	-	-	19	
	1992	24	1	-	-	-	21	1	
	1993	25	2	-	1	-	20	-	
	1994	30	3	-	-	3	19	-	
NOFL	1989	1	-	-	-	-	-	1	
	1990	9	-	1	-	-	3	4	
	1991	2	-	-	-	-	-	2	
	1992	11	1	2	1	-	2	5	
	1993	9	1	-	-	-	7	1	
	1994	11	2	-	1	-	1	-	
HAWO	1989	3	-	-	-	-	-	3	
	1990	3	-	-	-	-	1	2	
	1991	0	-	-	-	-	-	-	
	1992	3	1	-	-	-	2	-	
	1993	2	1	-	-	-	1	-	
	1994	3	-	-	-	-	3	-	
WISA	1989	1	-	-	-	-	1	-	
	1990	0	-	-	-	-	-	-	
	1991	1	-	-	-	-	-	1	
	1992	1	-	1	-	-	-	-	
	1993	0	-	-	-	-	-	-	
	1994	0	-	-	-	-	-	-	
DOWO	1989	0	-	-	-	-	-	-	
	1990	1	-	-	-	-	1	-	
	1991	0	-	-	-	-	-	-	
	1992	1	-	-	-	-	-	1	
	1993	0	-	-	-	-	-	-	
	1994	1	-	-	-	-	1	-	
PIWO	1989	0	-	-	-	-	-	-	
	1990	0	-	-	-	-	-	-	
	1991	0	-	-	-	-	-	-	
	1992	0	-	-	-	-	-	-	
	1993	1	-	-	-	-	1	-	
	1994	2	-	-	-	-	1	-	
Total		239	12	4	3	3	17	110	90

RNSA = Red-naped Sapsucker; NOFL = Northern Flicker; HAWO = Hairy Woodpecker, WISA = Williamson's Sapsucker, DOWO = Downy Woodpecker, and PIWO = Pileated Woodpecker.

3; and Cooper's Hawk (*Accipiter cooperii*), 1. We also found 17 nests where the young died of unknown causes.

Twelve occurrences of nest predation (six Red-naped Sapsucker, four Northern Flicker, two Hairy Woodpecker) were presumed to be by a mustelid, probably the Long-tailed Weasel (*Mustela frenata*) given that it was the only mustelid observed in the study area. Killed were both adult woodpeckers and large nestlings, all within nesting cavities. In the first case of predation on sapsuckers, some hairs (light brown in colour and >3 cm) were found at the cavity entrance and the eggs were gone. In the second, shell fragments were observed within a sapsucker cavity followed by a dead adult male in the cavity the next day. The third event occurred when a large sapsucker nestling was found partly eaten at the base of a nest tree. In the fourth, flesh plus crushed shells were present in the sapsucker nest. The fifth nest was observed late in the day as both parents were feeding the young. Early the following day the male was gone and the chicks were found dead in the cavity. Finally, of three sapsucker nestlings within a few days of fledging, one was found dead in the nest and the others alive at the base of the nest tree. The dead

chick was removed, and the live chicks were returned to their nest. The next day one chick was dead inside the cavity and the other chick was alive at the base of the nest tree. We placed this chick on the trunk of the tree; it fledged successfully. Three adult Northern Flickers were depredated while incubating or brooding. Hairy Woodpecker adult males were preyed upon at night when brooding large young. Both nests were in the same tree in successive years. In each case at least one of the young was removed from the cavity. Nine of the twelve nests where suspected mustelid predation occurred were from two areas (<5 ha) within our 80 ha study site. In all nests where mustelid predation is suspected, no tooth marks were evident around the cavity entrance.

Evidence of predation or attempted predation by Black Bears was of three types: fresh scarring of trees by claws; scarring around nest holes by teeth; and mortality of chicks or adults. Many old nest trees (10/25 in 1993 and 11/30 in 1994 for Red-naped Sapsuckers) had numerous scars caused by the claws of bears during climbing (Figure 1). We noted four instances where apparently successful predation by bears had occurred and eight more attempts. In one case, a low (approximately 1.5 m above ground) Northern Flicker nest in a rotten stub of a large Interior Spruce had been exposed when the stub was ripped open. Bloody pinfeathers (remiges) of the nestlings were around the base of the stub. The tall grass around the stub was beaten down, suggesting the presence of a large mammal, and fresh bear feces lay a few meters away. In another case, a Williamson's Sapsucker nested in a Trembling Aspen 1.8 m above the ground. When the nest was checked, bite marks (consistent with a bear) were evident around the entrance (Figure 2) and the remains of the incubating male were in the intact nest cavity. We also found six Red-naped Sapsucker nests, one Northern Flicker nest, and one Hairy Woodpecker



FIGURE 1. Portion of a Trembling Aspen trunk used for nesting by Red-naped Sapsuckers over many seasons. Note the extensive scarring on the trunk, caused by Black Bears climbing up the tree.



FIGURE 2. Nest hole of Williamson's Sapsucker, showing marks from lower canines of Black Bear; the adult male died in the nest cavity from injuries received from the bear.

nest in which a bear had climbed to the cavity and clawed at the entrance but was not successful in gaining access to the nest. The nests had been checked less than 24 hours earlier.

We observed one occurrence of egg predation by a Deer Mouse and suspected it in two other nests. A female Northern Flicker flew and called agitatedly as we checked her nest. A Deer Mouse was visible in the nest, amidst the eggs, and two of the six eggs were smashed. Six hours later the entire clutch had been destroyed and only broken, flattened eggshells remained. Single nests of a Northern Flicker and a Red-naped Sapsucker were found with broken and flattened full or partial clutches in the cavity.

House Wrens depredated three Red-naped Sapsucker nests. At one, eggshell fragments were inside and outside the nest cavity. The next day, House Wrens were observed entering and exiting the cavity and there were twigs in the cavity (no twigs were present the day before). Two other predation events occurred such that freshly dead Red-naped Sapsucker chicks were found in their nests, sticks over them, and House Wrens were nearby. In all cases, House Wrens later nested within the sapsucker cavities.

One instance of predation of an adult Red-naped Sapsucker by a Cooper's Hawk was observed. The radiotagged sapsucker, five days after successfully fledging four young, was found dead in a Cooper's Hawk nest.

Discussion

In spite of any extra protection afforded cavity nesters, woodpeckers in our study suffered substantial losses in the breeding season. We cannot, however, estimate the proportion of nests that were depredated because nest-monitoring effort differed among years.

Evidence suggested that mustelids may be the most common predators of woodpecker nests in our study area. In England, almost all (96%) of the predation on tit (*Parus* spp.) nests in nest boxes was by mustelids (Dunn 1977). Sleeman (1993) even speculates that many hole-nesting fauna found in Britain are not found in Ireland because of predation pressure by *M. erminea*. Of known predation events in our study, we attribute 55% to mustelids; but one would expect relative abundances of predators to vary among geographic areas. For example, in Sweden, woodpeckers were the chief predator (48%) of tits nesting in nest boxes (Nilsson 1984).

Interestingly, presumed predation by mustelids occurred in certain parts of our study area from year to year. Individual mustelids learn where nests are (Johnson 1947) and revisit them from one year to another (Sonerud 1985a,b; 1989). This may explain what we attribute to mustelid predation in our study, and why (in some species) nestling predation in new

cavities may be less than in old ones (Nilsson et al. 1991). Because mustelids in our study area tend to be nocturnal (Burt and Grossenheider 1980; but see Johnson 1947; Pettingill 1976; Kilham 1977b; and Daily 1993) and our nest monitoring was diurnal, we are not able to state conclusively that mustelids were responsible for the predation events we attributed to them. However, we found hairs at the entrance to the cavity in one case similar to what Kilham (1977b) reported after he had observed a weasel depredating a Yellow-bellied Sapsucker (*Sphyrapicus varius*) nest. In contrast, Crockett (1975, page 93) observed "the total destruction" of a Williamson's Sapsucker nest by *M. frenata*. Similarly, Erskine and McLaren (1972) report several Northern Flicker nests that were destroyed by assumed *M. erminea*.

Successful predation by Black Bears on nesting adult Red-naped Sapsuckers and Northern Flickers has been reported by Franzreb and Higgins (1975) and DeWeese and Pillmore (1972), respectively. Similar to some of the nests in our study, the latter authors noted that bears gained entrance to nest cavities in living aspen. How Black Bears capture adult woodpeckers and probably advanced nestlings is largely unknown. Dixon (1927) reported a Black Bear trying to gain access to a Black-backed Woodpecker (*Picoides arcticus*) nest by gnawing at the entrance hole. Our Williamson's Sapsucker observation suggested that the bear gnawed at the nest entrance and caught the inhabitant as it exited. Adults and advanced nestlings are prone to scramble out of the nest when disturbed (e.g., by a human climbing the nest tree). Northern Flickers are particularly susceptible to predation by bears at our field site, as Northern Flickers nest close to the ground in rotten snags. Because it has been assumed that hole nesting offers a refuge against predation (Lack 1968), Redondo and de Reyna (1988) claimed that the young of hole-nesting species produce calls with wider frequency ranges and less attenuable signals than those of open-nesting species (cf. Popp and Ficken 1991). The incessant calling of young in some species may be a cue to which Black Bears (and other predators) are attuned and thus a paradox seems apparent. Counter to the views of Redondo and de Reyna (i.e., ecological release of nestling vocalization), perhaps the vocal cues emitted by the young of hole-nesting species are constrained such that the signal will carry outside of the nest (i.e., so the parents can hear the young). It does not appear that Black Bears randomly climb trees. We compared the frequency with which available trees (i.e., > 12 cm diameter at breast height) in a 1 ha area surrounding the nest tree (N = 17) exhibited bear claw marks compared with nest trees. Frequency of bear claw marks differed significantly (Fisher's Exact Test, $p < 0.001$) between nest trees (11 / 30 Red-naped Sapsucker nests in 1994) and available trees

(190 / 4155), suggesting that bears are selectively climbing nest trees.

Deer Mice have been reported to be significant predators on ground-nesting birds (Maxson and Oring 1978; Reitsma et al. 1990). However, we are only aware of one study that reported predation by *Peromyscus* spp. on a hole-nesting species: Guillory (1987) observed predation by *P. leucopus* and *P. gossypinus* on Prothonotary Warbler (*Protonotaria citrea*) nests. Our findings of Deer Mice predation appear to be the first for a woodpecker nest. We estimate that at least 14% of our predation events were due to Deer Mice.

House Wrens often peck at and perforate eggs, in conspecific and heterospecific nests, and then remove them (White and Kennedy 1997). One adaptive interpretation (among several) placed on this behavior is that it is an interference mechanism (Belles-Isles and Picman 1986). In our study, House Wrens benefited through such behavior by disrupting the nesting cycle of Red-naped Sapsuckers, who abandoned their nesting attempt, or spent more time away in preparation for another breeding attempt. In the latter case, sapsucker re-use of the nest cavity was discouraged because the wrens put nesting material in the cavity. Kennedy and White (1992) have noted the discouraging effect of sticks on other species. We suspect that the placement of nesting material (e.g., sticks) on sapsucker nestlings within our study may have caused their death.

Other species may have been responsible for the unknown cases of predation. For example, both Red Squirrels (*Tamiasciurus hudsonicus*) and Northern Flying Squirrels (*Glaucomys sabrinus*) are present in the study area. The former is known to depredate Yellow-bellied Sapsucker nests (Lawrence 1967; Erskine and McLaren 1972) but we have no evidence (e.g., none of the depredated nests was chewed around the entrance hole) to suggest that squirrels depredated any nests. In fact, we had several nest trees where both squirrels (*T. hudsonicus* and *G. sabrinus*) and sapsuckers coexisted without any apparent negative effect on the sapsucker nests. Although Raccoons, *Procyon lotor*, are known to prey upon Yellow-bellied Sapsucker nests (Kilham 1971, 1977a), they do not occur in our study area.

We have outlined the nature of predation events on four woodpecker species, all of which excavate cavities in which to nest. Given the extent to which these cavity nesters are susceptible to predation may lead one to question the adaptiveness of hole nesting as an anti-predation strategy. As some have suggested (e.g., Alerstam and Högstedt 1981), perhaps hole nesting is the ancestral trait and open nesting is derived. Thus, open-nesting species that are secretive in their foraging might overcome the risk of predation relative to the cost of finding or constructing a suitable hole in which to nest. Under this scenario,

hole-nesting species are not seeking refuge from predatory events but, in fact, have less chance of being depredated than if they were to become open nesters. Lack (1954) and Nice (1957) both estimated that the proportion of eggs in completed clutches that give rise to flying young was approximately 45-46% in open-nesting species compared with 66-67% in hole-nesting species. One would expect predation to be lower in hole-nesters that excavate within relatively hard trees as opposed to species that use softer wood. Supporting this contention is the work of Christman and Dhondt (1997) who found that nest predation in Black-capped Chickadees (*Poecile atricapilla*), a species that excavates within soft and often rotten wood, is as high as 62%. In our study, Northern Flickers tended to nest in softer trees, and we recorded a predation event in 21% of our nests. On the other hand, Red-naped Sapsuckers tended to nest in live aspen (i.e., relatively hard wood; Schepps et al. 1999), and we recorded a predation event in only 6% of those nests. Neither figure should be interpreted as overall predation frequency because the number of nest observations differed from year to year. Besides the integrity of the substrate, Northern Flickers may have been exposed to higher predation rates than sapsuckers because the cavity entrance of Northern Flicker nests is larger. Several researchers (e.g., Sandström 1991; Sonerud 1985b) found that cavities with larger entrance holes were more prone to predation. Ironically, Martin and Li (1992) did not observe any predation on Northern Flicker or Red-naped Sapsucker nests during three breeding seasons in Arizona. We hypothesize that this finding may be due to the fact that their site differed from ours with respect to potential predators (e.g., the Arizona field site had less bears, personal observation (ELW)) and cavity-nesting species tended to nest higher in trees in Arizona (i.e., reducing potential for depredation, personal observation (ELW)). In fact, Li and Martin (1991) reported that nest success was lower for species with lower nest height in their study area.

Acknowledgments

We are indebted to Ken and Gina Reynolds, Brand 88 Ranch, for allowing us to work and stay on their property, and for their strong support of our work there. The ranch managers, Tim and Lois Malpass, helped us on many occasions, and extended numerous courtesies. John Cooper was instrumental in the initial development of the study and he kindly provided data on several bear predation events. Financial and logistic support was provided by: Natural Sciences and Engineering Research Council of Canada (operating grants to EHM); King-Platt Memorial Scholarship and Fellowship (awarded to ELW); British Columbia Ministry of Environment, Parks and Lands (Wildlife Branch); British

Columbia Ministry of Forests (Silviculture and Research branches); Canadian Wildlife Service; Copley Bros. Construction; and British Columbia Ministry of Tourism, Recreation and Culture (Royal British Columbia Museum). For their assistance, encouragement, and advice, we thank Joe Antos, Alan Burger, Trudy Chatwin, Don Clark, Andrew Derocher, Jakob Dulisse, Michael Dunn, Mike Fenger, Elizabeth Hunter, Frances Jones, Sarah Jones, Kathy Martin, Peter Miller, Rissa Miller, Ross Miller, Cathy Mutter, Bev Mutter, Roy Mutter, Brian Nyberg, Karen Walters, Larry Walters, and Ted White. Frances James, Julie Jo Walters, Spencer Sealy, and Tony Erskine graciously offered constructive criticisms of earlier versions of this manuscript for which we are grateful.

Literature Cited

- Alerstam, T., and G. Högstedt. 1981. Evolution of hole-nesting in birds. *Ornis Scandinavica* 12: 188-193.
- Balen, J. H. van, and R. P. J. Potting. 1990. Comparative reproduction biology of four Blue Tit populations in the Netherlands. Pages 19-38, in *Population biology of passerine birds: an integrated approach*. Edited by J. Blondel, A. Gosler, J.-D. Lebreton, and R. McCleery. NATO ASI Series G: Ecological Sciences, volume 24, Springer-Verlag, Berlin.
- Belles-Isles, J. C., and J. Picman. 1986. House Wren nest-destroying behavior. *Condor* 88: 190-193.
- Burt, W. H., and R. P. Grossenheider. 1980. A field guide to the mammals. Peterson Field Guide Series, Number 5. Houghton Mifflin Co., Boston, Massachusetts.
- Christman, B. J., and A. A. Dhondt. 1997. Nest predation in Black-capped Chickadees: how safe are cavity nests? *Auk* 114: 769-773.
- Crockett, A. B., Jr. 1975. Ecology and behavior of the Williamson's Sapsucker in Colorado. Ph.D. dissertation, University of Colorado, Boulder, Colorado.
- Daily, G. C. 1993. Heartwood decay and vertical distribution of Red-naped Sapsucker nest cavities. *Wilson Bulletin* 105: 674-679.
- DeWeese, L. R., and R. E. Pillmore. 1972. Bird nests in an aspen tree robbed by black bear. *Condor* 74: 488.
- Dixon, J. 1927. Black Bear tries to gnaw into a woodpecker's nest. *Condor* 29: 271-272.
- Dunn, E. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *Journal of Animal Ecology* 46: 633-652.
- Erskine, A. J., and W. D. McLaren. 1972. Sapsucker nest holes and their use by other species. *Canadian Field-Naturalist* 86: 357-361.
- Franzreb, K. E., and A. E. Higgins. 1975. Possible bear predation on a Yellow-bellied Sapsucker nest. *Auk* 92: 817.
- Greene, H. W. 1986. Natural history and evolutionary biology. Pages 99-108 in *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates*. Edited by M. E. Feder and G. V. Lauder. University of Chicago Press, Chicago, Illinois.
- Guillory, H. D. 1987. Cavity competition and suspected predation on Prothonotary Warblers by *Peromyscus* spp. *Journal of Field Ornithology* 58: 425-427.
- von Haartman, L. 1957. Adaptation in hole-nesting birds. *Evolution* 11: 339-347.
- Jackson, J. A. 1977. How to determine the status of a woodpecker nest. *Living Bird* 15: 205-221.
- Johnson, R. A. 1947. Role of male Yellow-bellied Sapsucker in the care of the young. *Auk* 64: 621-623.
- Johnsson, K. 1994. Colonial breeding and nest predation in the Jackdaw *Corvus monedula* using old Black Woodpecker *Dryocopus martius* holes. *Ibis* 136: 313-317.
- Kennedy, E. D., and D. W. White. 1992. Nest building in House Wrens. *Journal of Field Ornithology* 63: 35-42.
- Kilham, L. 1971. Reproductive behavior of Yellow-bellied Sapsuckers. I. Preference for nesting in *Fomes*-infected aspens and nest hole interrelations with flying squirrels, raccoons, and other animals. *Wilson Bulletin* 83: 159-171.
- Kilham, L. 1977a. Altruism in nesting Yellow-bellied Sapsucker. *Auk* 94: 613-614.
- Kilham, L. 1977b. Nesting behavior of Yellow-bellied Sapsuckers. *Wilson Bulletin* 89: 310-324.
- Lack, D. 1954. *The natural regulation of animal numbers*. Clarendon Press, Oxford.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Methuen & Co Ltd., London.
- Lawrence, L. de K. 1967. A comparative life-history study of four species of woodpeckers. *Ornithological Monograph Number 5*, American Ornithologists' Union.
- Li, P., and T. E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. *Auk* 108: 405-418.
- Martin, T. E. 1988. On the advantage of being different: nest predation and the coexistence of bird species. *Proceedings of the National Academy of Sciences* 85: 2196-2199.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65: 101-127.
- Martin, T. E., and P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* 73: 579-592.
- Maxson, S. J., and L. W. Oring. 1978. Mice as a source of egg loss among ground-nesting birds. *Auk* 95: 582-584.
- Nice, M. M. 1957. Nesting success in altricial birds. *Auk* 74: 305-321.
- Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance on nest predation and competition. *Ornis Scandinavica* 15: 167-175.
- Nilsson, S. G., K. Johnsson, and M. Tjernberg. 1991. Is avoidance by black woodpeckers of old nest holes due to predators? *Animal Behaviour* 41: 439-441.
- Pettingill, O. S., Jr. 1976. Observed acts of predation on birds in northern lower Michigan. *Living Bird* 14: 33-41.
- Picman, J., and L. M. Schriml. 1994. A camera study of temporal patterns of nest predation in different habitats. *Wilson Bulletin* 106: 456-465.
- Popp, J., and M. S. Ficken. 1991. Comparative analysis of acoustic structure of passerine and woodpecker nestling calls. *Bioacoustics* 3: 255-274.
- Redondo, T., and L. A. de Reyna. 1988. Locatability of begging calls in nestling altricial birds. *Animal Behaviour* 36: 653-661.
- Reitsma, L. R., R. T. Holmes, and T. W. Sherry. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest

- predation in a northern hardwood forest: an artificial nest experiment. *Oikos* 57: 375-380.
- Sandström, U. 1991. Enhanced predation rates on cavity bird nests at deciduous forest edges — an experimental study. *Ornis Fennica* 68: 93-98.
- Schepps, J., S. Lohr, and T. E. Martin. 1999. Does tree hardness influence nest-tree selection by primary cavity nesters? *Auk* 116: 658-665.
- Sealy, S. G. 1994. Observed acts of egg destruction, egg removal, and predation on nests of passerine birds at Delta Marsh, Manitoba. *Canadian Field-Naturalist* 108: 41-51.
- Sleeman, D. P. 1993. Habitats of the Irish stoat. *Irish Naturalist's Journal* 24: 318-321.
- Sonerud, G. A. 1985a. Nest hole shift in Tengmalm's owl *Aegolius funereus* as defence against nest predation involving long-term memory in the predator. *Journal of Animal Ecology* 54: 179-192.
- Sonerud, G. A. 1985b. Risk of nest predation in three species of hole nesting owls: influence on choice of nesting habitat and incubation behaviour. *Ornis Scandinavica* 16: 261-269.
- Sonerud, G. A. 1989. Reduced predation by pine martens on nests of Tengmalm's Owl in relocated boxes. *Animal Behaviour* 37: 332-334.
- Thompson, F. R., W. Djak, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. *Auk* 116: 259-264.
- Verhulst, S., J. H. van Balen, and J. M. Tinbergen. 1995. Seasonal decline in reproductive success of the Great Tit: variation in time or quality? *Ecology* 76: 2392-2403.
- Walters, E. L. 1996. Habitat and space use of the Red-naped Sapsucker, *Sphyrapicus nuchalis*, in the Hat Creek Valley, south-central British Columbia. M.Sc. thesis, University of Victoria, Victoria, British Columbia.
- White, D. W., and E. D. Kennedy. 1997. Effect of egg covering and habitat on nest destruction by House Wrens. *Condor* 99: 873-879.

Received 20 July 1999

Accepted 8 August 2001