The Condor 90:124–131

EXPERIMENTAL STUDY OF PREDATION ON EGGS OF GROUND-NESTING BIRDS: EFFECTS OF HABITAT AND NEST DISTRIBUTION[1]

JAROSLAV PICMAN
Department of Biology, University of Ottawa, 30 Somerset E., Ottawa, Ontario K1N 6N5, Canada

Abstract. Predation pressure on nests of ground-nesting birds was examined experimentally by offering predators artificial nests with small, white chicken eggs in three adjacent habitats: marsh, wet meadow, and upland thicket. In each habitat, 40 nests with eggs were distributed in three 80- × 80-m quadrats according to random, uniform, and clumped distribution patterns and nests were examined for predation on days 5 and 10. In three sets of experiments during which each quadrat in each habitat received all nest distribution treatments, predation rates were highest in the upland thicket, intermediate in the wet meadow, and generally low in the marsh. The pattern of nest distribution consistently affected predation rates in the upland thicket only, where the uniform distribution resulted in lower predation. In the upland thicket many predators were responsible for high predation and unpredictable predation patterns which presumably favor spacing out (uniform nest distribution) in this habitat. In contrast, low predation in the marsh, resulting from exclusion of many predators, appears to be unimportant in determining spatial distribution of marsh-nesting birds.

Key words: Egg predation; ground-nesting birds; effects of habitat; nest distribution.

INTRODUCTION

The evolution of avian reproductive strategies has presumably been driven by different temporal and spatial patterns of distribution of food (e.g., Horn 1968) and by the form and intensity of predation on adults and their nests (e.g., Kruuk 1964, Lack 1968, Ricklefs 1969). The effects of predation on avian reproductive strategies are complex and depend on a number of factors affecting predator-prey relationships such as prey defense, diversity and abundance of predators, the type of cues predators use to find prey, and temporal predictability of predation patterns.

Two main types of antipredation strategies may be favored. First, if prey cannot defend itself against predators, there should be selection for predator avoidance adaptations. These include concealment of the nest and its contents, spacing out that increases camouflage of nesting activities and breeding at inaccessible sites or in safer habitats (e.g., Nice 1957, Lack 1968, Burger 1974, Taylor 1976, McCrimmon 1980, Collias and Collias 1984, Nilsson 1984). Second, if prey can reduce the impact of predators through communal antipredator attacks or through dilution of predators' effects, this should favor higher local prey density and hence colonial pattern of distribution (e.g., Kruuk 1964, Robertson 1972, Andersson 1976, Andersson and Wiklund 1978).

Although nest predation may be important for the evolution of avian reproductive tactics, relatively little attention has been paid to antipredation adaptations with the exception of colonial nesting (e.g., McCrimmon 1980, Wiklund and Andersson 1980, Wiklund 1982). Different nest spacing patterns may in part represent adaptations to various predation pressures. A positive correlation between prey density and nest-predation rates reported, for example, in Great Tits, *Parus major* (Krebs 1971, Dunn 1977), and Field Sparrows, *Spizella pusilla* (Fretwell 1972), suggests that spacing out in prey is a predator avoidance strategy (Andersson and Wiklund 1978). On the other hand, colonial nesting by some birds could be a consequence of their preference for safe but limited breeding areas (e.g., Lack 1968, Wittenberger 1976, Orians 1980) and/or improved nest defense due to communal antipredator attacks (e.g., Andersson and Wiklund 1978).

Several field experiments have been conducted to test the antipredator role of avian nest dispersion. For example, Tinbergen et al. (1967), Goransson et al. (1975), and Page et al. (1983) found that high nest densities resulted in higher predation rates. However, there is lack of ex-

---

[1] Received 13 March 1987. Final acceptance 18 July 1987.

perimental data on the effect of different spatial patterns of distribution of nests on predation within as well as between habitats. Such information is important because it directly examines the effectiveness of spacing strategies of birds in a given area with respect to predation pressures, and it should help us to understand habitat selection. Thus, the purpose of this study was (1) to establish the relative importance of predation on clutches of ground-nesting birds occurring in three adjacent habitats: marsh, wet meadow, and upland thicket, and (2) to determine the effect of uniform, random, and clumped nest distributions on predation rates in the three habitats.

METHODS

This study was conducted in June and July 1983 in the Mer Bleue Conservation Area near Ottawa, Ontario. Artificial nests with extra small chicken eggs (white) were placed in three habitats, a marsh, an adjacent wet meadow, and an upland thicket (located approximately 150 m from the marsh).

MARSH

This is a Cattail (*Typha* sp.) -dominated habitat with water depth of up to 130 cm and height of vegetation of up to 230 cm. The experimental quadrats were established along the shallow end of this marsh (water depth varied between 40 and 60 cm), where cattail vegetation formed a relatively uniform cover. Birds present in this marsh included, in approximately decreasing order of abundance, the Red-winged Blackbird (*Agelaius phoeniceus*), Swamp Sparrow (*Melospiza georgiana*), Common Grackle (*Quiscalus quiscula*), Black Tern (*Chlidonias niger*), Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), Marsh Wren (*Cistothorus palustris*), Mallard (*Anas platyrhynchos*), Common Moorhen (*Gallinula chloropus*), Least Bittern (*Ixobrychus exilis*), Common Snipe (*Gallinago gallinago*), and American Bittern (*Botaurus lentiginosus*). Of these species, the Mallard, Common Moorhen, Common Snipe, American Bittern, and Swamp Sparrow breed close to water level.

WET MEADOW

This habitat is dominated by grasses, sedges, *Carex* sp., bulrushes, *Scirpus* sp., and young willows, *Salix* sp., generally not higher than 70 cm. The wet meadow initially contained many pools of water (up to 25 cm deep) that dried up by early July. Avian species breeding in this habitat were the Swamp Sparrow, Bobolink (*Dolichonyx oryzivorus*), Red-winged Blackbird, and Eastern Meadowlark (*Sturnella magna*), all breeding on or near the ground.

UPLAND THICKET

The experimental quadrats were approximately 150 m from the edge of the marsh on an elevated ridge. The upland thicket was a semi-open habitat dominated by willows, hardhack, *Spiraea douglasii* sp., young poplars, *Populus* sp., birches, *Betula* sp., and alders, *Alnus* sp., all generally not exceeding 3 to 4 m. Raspberries, *Rubus* sp., grasses, and a large number of herbs formed the undergrowth in which nests were placed. The common birds in the study quadrats were the Yellow Warbler (*Dendroica petechia*), Common Yellowthroat (*Geothlypis trichas*), American Goldfinch (*Carduelis tristis*), and Brown-headed Cowbird (*Molothrus ater*). In addition, a number of other species such as the Song Sparrow (*Melospiza melodia*), House Wren (*Troglodytes aedon*), Gray Catbird (*Dumetella carolinensis*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), American Woodcock (*Scolopax minor*), and American Crow (*Corvus brachyrhynchos*) were present near the experimental quadrats. Of the species occurring in this habitat the Common Yellowthroat and American Woodcock build their nests on or near the ground.

In each habitat three 80- × 80-m quadrats were established. Yellow flagging tape tied to vegetation was used to mark corners of 20- × 20-m squares within these quadrats. Each quadrat was separated from the nearest quadrat by at least 20 m. In each of the three quadrats 40 nests were distributed according to the uniform, random, or clumped pattern (Fig. 1; the predetermined spacing patterns were confirmed statistically using the quadrat sampling technique; see Zar 1984). In cases of random and clumped nest distributions, the minimum distance between the nearest nests was 1 m. The actual location of nests was determined by estimating their position within 20- × 20-m quadrats and by the availability of suitable vegetation (an attempt was made to conceal the nests as much as possible). To control for possible differences between quadrats within habitats, the patterns of nest distribution were interchanged between quadrats so that each quadrat received all three nest distribution treatments (i.e., this experiment was con-

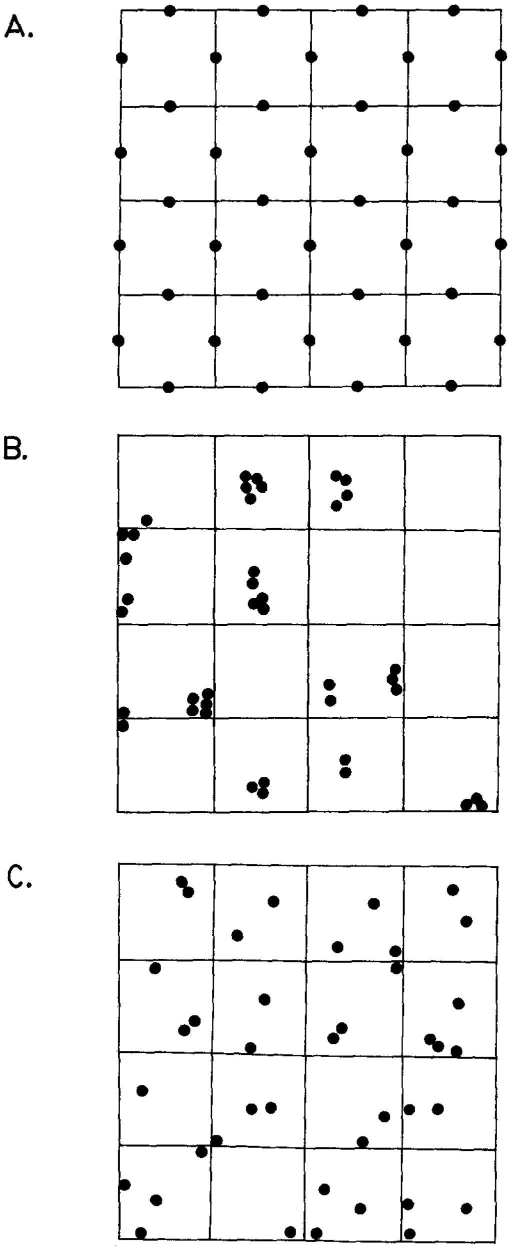

FIGURE 1. The uniform (A), clumped (B), and random (C) patterns of distribution of experimental nests (the same nest dispersion patterns were used in the three habitats throughout all experiments).

ducted three times in all habitats). The time period between the end and start of subsequent sets of this experiment was 5 days.

The nests (about 20 cm in diameter and 5 cm high) were built of dry grass in the wet meadow and upland thicket and of dry cattail leaves in the marsh. These nests were placed directly on the ground or in cattail at the water level. One extra small chicken egg was placed in each nest in a small depression.

To reduce the likelihood of nest discovery by predators due to frequent visits by researchers, all nests were examined for predation only twice, 5 and 10 days after their introduction. When a depredated nest was encountered, notes were taken on its appearance and its location was recorded on a map of the study area. Following the check on day 10, all nests and remaining eggs were removed. Fresh eggs were used for subsequent experiments.

RESULTS

THE APPEARANCE OF DEPREDATED NESTS

Two major signs of predation were the presence of pieces of eggshell of various sizes and disappearance of the whole egg. In the marsh, pieces of shell were found on or near the nests in the majority (92%) of cases of predation (in 8% of cases the whole egg disappeared). This sign of predation was also common in the wet meadow (77% of predation cases), but the complete disappearance of an egg was also common, accounting for 23% of all cases of predation. In a total of 42 cases of depredated nests in the wet meadow (all in the last experiment) a predator dug out a hole in or near (within 0.5 m) the nest. These holes were 5 to 10 cm in diameter and 5 to 15 cm deep. In the upland thicket most (54%) depredated eggs were removed by predators, and in the remaining cases (46%) broken eggs with holes of various sizes (sometimes with part of their contents) or pieces of eggshell were found on or near the nests. Differences in the appearance of depredated nests thus indicate that different predators operate in the marsh and upland habitats.

THE EFFECT OF HABITAT ON PREDATION

When data for the three series of experiments and all distribution patterns are pooled, predation rates on the experimental eggs differ significantly between the three habitats (Table 1). Checks 5 and 10 days after the start of the experiments showed that the highest egg losses occurred in the upland thicket, the intermediate losses in the wet meadow, and the marsh quadrats suffered the lowest predation. Differences in

TABLE 1. Predation rates in three habitats. Data from different distribution patterns and three time series of experiments for each habitat were combined.

Habitat	No. days after start	Percent (*n*) eggs		Total
		Depredated	Survived	
Marsh	5	8.3 (30)	91.7 (330)	100 (360)
	10	25.8 (93)	74.2 (267)	100 (360)
Wet meadow	5	24.7 (89)	75.3 (271)	100 (360)
	10	59.4 (214)	40.6 (146)	100 (360)
Upland thicket	5	51.1 (184)	48.9 (176)	100 (360)
	10	84.7 (305)	15.3 (55)	100 (360)

Note: Statistical comparison of predation rates in the three habitats: After 5 days: $\chi^2 = 166.2$; df = 2; $P < 0.001$. After 10 days: $\chi^2 = 255.9$; df = 2; $P < 0.001$.

predation rates between the three habitats were highly significant ($P < 0.001$) for both 5- and 10-day checks.

THE EFFECT OF SPATIAL DISTRIBUTION OF NESTS ON PREDATION

In the marsh, on the fifth day, the egg-predation rates were higher when nests were clumped (Table 2). However, on day 10, predation rates were similar for all nest-distribution patterns (Table 2). In the wet meadow, predation rates were significantly different for the three nest-distribution patterns on day 5 (lower for random than for uniform and clumped distributions), but were not significantly different on day 10 (Table 2). Finally, in the upland thicket quadrats, the uniformly distributed nests suffered significantly lower predation than those with random and clumped nest distributions on days 5 and 10 (Table 2).

THE EFFECT OF TIME ON PREDATION

The necessity of conducting the experiments at three different times might have introduced a bias due to changing predation pressures. In addition, habituation by predators to the experimental nests with eggs available in a given habitat over a longer period of time might result in increased predation rates during experiments conducted later. I tested this by combining data from quadrats with different distributions of nests and comparing predation rates within individual habitats in the three consecutive series of experiments. In all three habitats predation rates during the three series of experiments differed significantly for checks after 5 and 10 days (Table 3). In the wet meadow there was the same, systematic seasonal trend for checks on days 5 and 10 indicating that predation rates gradually increased with time (Table 3). In the upland thicket predation rates peaked during the second experiment for both checks. In contrast, in the marsh, nest-predation rates followed different seasonal patterns during the two checks (Table 3).

THE EFFECT OF LOCATION WITHIN A HABITAT ON PREDATION

In any given habitat predation might also be site specific due to differences between experimental quadrats in vegetation structure, local predators and their densities, and other features that might affect nest predation. To test this, I combined

TABLE 2. Predation rates (% and in parentheses no. depredated eggs) in three habitats with respect to the spatial distribution of nests. Data from the three time series of experiments were combined. The sample size for each distribution pattern in each habitat is 120 nests.

Habitat	No. days after start	Distribution of nests			χ^2	df	*P*
		Uniform	Random	Clumped			
Marsh	5	5.8 (7)	4.2 (5)	15.0 (18)	10.69	2	<0.005
	10	23.4 (28)	26.6 (32)	27.5 (33)	0.61	2	>0.5
Wet meadow	5	30.8 (37)	14.2 (17)	29.2 (35)	10.87	2	<0.005
	10	64.6 (77)	62.5 (75)	60.0 (72)	0.45	2	>0.5
Upland thicket	5	36.7 (44)	64.2 (77)	65.0 (78)	25.24	2	<0.001
	10	70.0 (84)	94.6 (113)	90.0 (108)	30.95	2	<0.001

TABLE 3. The effect of time on predation rates (% and in parentheses no. depredated eggs) in three habitats. Data from quadrats with different nest distributions were combined for individual habitats. During individual time series of experiments a total of 120 nests were offered to predators in each habitat.

Habitat	No. days after start	Experiment number 1	2	3	χ^2	df	*P*
Marsh	5	20.8 (25)	2.5 (3)	1.7 (2)	36.87	2	<0.001
	10	31.6 (38)	8.4 (10)	37.6 (45)	29.84	2	<0.001
Wet meadow	5	0.8 (1)	22.5 (27)	50.8 (61)	81.08	2	<0.001
	10	5.0 (6)	76.7 (92)	96.6 (116)	231.27	2	<0.001
Upland thicket	5	47.5 (57)	77.5 (93)	28.3 (34)	58.98	2	<0.001
	10	71.6 (86)	96.6 (116)	85.5 (103)	29.14	2	<0.001

data from three consecutive series of experiments for individual quadrats (each quadrat received all three patterns of nest distribution) and compared predation losses for the three quadrats in each habitat. In the wet meadow and upland thicket habitats all quadrats suffered similar egg losses during checks on days 5 and 10 (Table 4). Therefore, in these habitats, quadrat location did not play an important role. In the marsh, however, according to both checks one quadrat lost significantly more eggs to predators than the other two (Table 4).

DISCUSSION

Results of this study suggest that nest predation rates are consistently lower in the marsh and higher in the adjacent upland habitats. This is presumably due to the fact that the three habitats differ greatly in the accessibility of nests to different predators. In the marsh, dense vegetation and deep water restrict predation to only a few well-adapted predators such as the mink, *Mustela vison.* Mink had been observed in this marsh on several occasions prior to these experiments and the importance of mink depredation on waterfowl nests in marshes has been well documented (e.g., Sargeant et al. 1973). In addition, placement of nests in dense vegetation at the water level presumably prevented aerial detection by avian predators. The low diversity of predators in this marsh was demonstrated in 1985 and 1986 when I used cameras to photograph predators removing eggs from experimental nests (see Picman 1987). In this study I offered predators artificial nests with quail eggs and found that raccoons, *Procyon lotor,* and, in shallow water, weasels, *Mustela* sp., were responsible for almost all egg losses (Picman, unpubl. data). Low predation in this marsh relative to adjacent upland habitats is consistent with the finding that ducks that nest over water have higher reproductive success than those which nest on land (Nice 1957).

In the upland thicket, nests were exposed to many terrestrial and avian predators such as raccoons, weasels, red foxes, *Vulpes vulpes,* skunks, *Mephitis mephitis,* cats, *Felix domesticus,* Herring Gulls, *Larus argentatus,* American Crows, *Corvus brachyrhynchos,* and Blue Jays, *Cyanocitta cristata,* which were all present in or near the study area. These and other predators were previously implicated by many other authors (e.g.,

TABLE 4. The effect of location of quadrats within a habitat on predation rates (% and in parentheses no. depredated eggs) on experimental eggs. For individual quadrats, data from the three series of experiments with different nest distributions were combined. A total of 120 eggs was offered to predators in each quadrat.

Habitat	No. days after start	Quadrat A	B	C	χ^2	df	*P*
Marsh	5	1.7 (2)	16.7 (20)	6.7 (8)	18.33	2	<0.001
	10	18.4 (22)	35.8 (43)	23.4 (28)	10.18	2	<0.01
Wet meadow	5	25.8 (31)	20.8 (25)	27.5 (33)	1.55	2	>0.9
	10	56.6 (68)	65.8 (79)	64.2 (77)	2.43	2	>0.2
Upland thicket	5	49.2 (59)	54.2 (65)	50.0 (60)	0.69	2	>0.9
	10	80.0 (96)	85.8 (103)	88.4 (106)	3.39	2	>0.1

Balser et al. 1968, Chesness et al. 1968, Goransson et al. 1975, Picozzi 1975, Potts 1980, Page et al. 1983), although evidence for their impact on birds' nesting success is generally indirect. The camera study of predation that I conducted in 1985 and 1986 with quail eggs showed that, in the decreasing order of significance, Blue Jays, raccoons, Gray Catbirds, *Dumetella carolinensis,* red squirrels, *Sciurus carolinensis,* weasels, and American Crows were important predators in this habitat (Picman, unpubl. data). The greater diversity of predators could thus explain the highest predation rates in this habitat.

The wet meadow was originally partially protected against terrestrial predators by up to 25-cm deep pools of water scattered through it. Presumably for this reason predation in this habitat was more similar to the marsh than to the upland thicket. However, later when these pools dried up, nests in this habitat became more vulnerable to all terrestrial predators operating in the upland and this presumably resulted in higher predation. The camera study of predation on quail eggs conducted in 1986 in a nearby old field showed that skunks, *Mephitis mephitis,* and Eastern Meadowlarks, *Sturnella magna,* were the most important predators (Picman, unpubl. data). However, in addition to these predators, Herring Gulls, Northern Harriers, *Circus cyaneus,* American Crows, and mink were also observed on or near the experimental quadrats in 1983.

The proposition that different predators were operating in the three habitats is also supported by different appearance of depredated nests in these habitats. Differences in the number of predators operating in the three habitats could, thus, explain the lowest level of nest predation in the marsh and consistently the highest predation levels in the upland thicket.

Janzen (1978), who examined predation on eggs of ground-nesting birds in Costa Rica, concluded that the rate of disappearance of eggs from experimental nests was lowest in the swamp, highest in the deciduous forest, and intermediate in the rain forest. Results of his and my experiments from tropical and temperate zones, respectively, suggest that marshes and swamps may generally provide better protection against many predators. However, Ricklefs (1969) concluded that, of all temperate zone passerines, the marsh-nesting species suffer the highest nest mortality rates. These contradictory conclusions could be explained by different predation rates on nests of passerines and other, larger species of birds that breed in marshes. For example, in North American marshes, Marsh Wrens (*Cistothorus palustris*) and Sedge Wrens (*Cistothorus platensis*) may be responsible for much of nesting mortality of other small, co-occurring birds (Picman 1977, Picman and Picman 1980). On the other hand, wrens cannot break larger eggs and, thus, other predators such as mink and raccoon must be involved in predation on nests of larger species. Therefore, predation by small passerines can be excluded from this study. In addition, Ricklefs (1969) did not take into consideration differences in behavior and ecology between species breeding in different habitats which are likely to affect their reproductive success. This view is supported by data on Red-winged Blackbirds that show that populations nesting in marshes are more successful than those from adjacent uplands (e.g., Robertson 1972).

As indicated by both checks, the spatial distribution of nests had a systematic effect on predation in the upland thicket only, where uniform distribution and, thus, spacing out consistently resulted in lower predation rates (Table 2). In contrast, the type of nest distribution did not affect predation rates in the wet meadow and marsh quadrats on day 10. Significant differences in predation rates between various nest spacing patterns on day 5 could be explained by random patterns of predation in habitats with small predator diversity and generally low predation rates over a short period of time. For this reason data from day 10 should better reflect the long-term value of different nest spacing patterns in these two habitats.

Different types of predators present in the three habitats could also explain different effects of nest-distribution patterns on predation rates. The presence of many avian and terrestrial predators in the upland thicket resulting in relatively unpredictable predation patterns is likely to prevent the evolution of any specific antipredator strategies. Intense and relatively unpredictable predation should favor more generalized strategies such as camouflage of nesting activities through spacing out and concealment of nests. On the other hand, generally predictable predation patterns resulting from the low diversity of predators, should favor specific antipredator strategies. Finally, when predation is unimportant, selection for antipredation adaptations should be weak. This situation appears to be characteristic of the marsh quadrats that generally suffered low losses to predation and where the spatial distribution of nests had no effect on nest-predation rates on day 10. Results from the marsh quadrats are consistent with observations that some marsh-nesting species such as the American Bittern, rails, and most waterfowl space themselves out, whereas others such as some gulls and Black Terns are colonial (e.g., Harrison 1978).

There are several problems associated with the experimental design adopted in this study. First, although the density of experimental nests was not high for some species breeding in marshes (e.g., gulls and terns), it was high for any medium-sized ground-nesting species occurring in upland habitats. Because high density of prey is likely to attract more predators, this study may overestimate nest-predation rates in the upland habitats as compared to natural nests. However, one of the main objectives of these experiments was to compare predation on nests in different habitats and this required that the density and pattern of distribution of nests were kept constant between habitats. In addition, the fact that the uniform distribution of nests in the upland thicket consistently suffered lower predation rates suggests that the nest density was not too high to mask the effects of the type of nest distribution on nest predation. Second, it has been suggested that the presence of parents on or near the nest may attract predators (Skutch 1949, Willis 1973; but see Gottfried and Thompson 1978). The experimental setup would thus underestimate predation. Third, the use of white hens' eggs could have made the nests more vulnerable to predators. Unfortunately, no data on reproductive success of any medium-sized ground-nesting birds from this area are available to determine to what extent the data on nest predation are biased. However, regardless of any such bias, results from different habitats should still reflect relative differences in predation pressures on nests of birds breeding in these habitats.

In conclusion, this study suggests that nest-predation patterns greatly differ between the three adjacent habitats and that they should exert different selective pressures on reproductive strategies of birds breeding there. However, to fully understand the role of nest predation in the evolution of different spacing strategies of birds, we need to determine what is the relative importance of different nest predators, which cues they use to find nests, and how predictable nest-predation patterns are in time and space.

ACKNOWLEDGMENTS

I would like to thank J.-C. Belles-Isles, D. Beedel, and J. McAllister for field assistance. S. Hamill kindly allowed me to conduct this research in the Mer Bleue Conservation Area owned by the National Capital Commission. B. M. Gottfried, G. LaPointe, M. Leonard, and an anonymous reviewer provided constructive comments on this manuscript. This research was supported by the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

ANDERSSON, M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. Ibis 118:208–217.

ANDERSSON, M., AND WIKLUND, C. G. 1978. Clumping versus spacing out: experiments on nest predation in fieldfares (*Turdus pilaris*). Anim. Behav. 26:1207–1212.

BALSER, D. S., H. H. DILL, AND H. K. NELSON. 1968. Effect of predator reduction on waterfowl nesting success. J. Wildl. Manage. 32:669–682.

BURGER, J. 1974. Breeding adaptations of Franklin's gull (*Larus pipixcan*). Anim. Behav. 22:521–567.

CHESNESS, R. A., M. M. NELSON, AND W. H. LONGLEY. 1968. The effect of predator removal on pheasant reproductive success. J. Wildl. Manage. 32:683–697.

COLLIAS, N. E., AND E. C. COLLIAS. 1984. Nest building and bird behavior. Princeton Univ. Press, NJ.

DUNN, E. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. J. Anim. Ecol. 46: 634–652.

FRETWELL, S. D. 1972. Populations in a seasonal environment. Princeton Univ. Press, NJ.

GORANSSON, G., J. KARLSSON, S. G. NILSSON, AND S. ULFSTRAND. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study. Oikos 26:117-120.

GOTTFRIED, B. M., AND C. F. THOMPSON. 1978. Experimental analysis of nest predation in an old-field habitat. Auk 95:304–312.

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

JANZEN, D. H. 1978. Predation intensity on eggs on the ground in two Costa Rican forests. Am. Midl. Nat. 100:467–470.

KREBS, J. R. 1971. Territory and breeding density in the great tit, *Parus major* L. Ecology 52:2–22.

KRUUK, H. 1964. Predators and anti-predator behaviour of the black headed gull (*Larus ridibundus* L.). Behaviour Suppl. 11:1–129.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

MCCRIMMON, D. A. 1980. The effects of timing of breeding, dispersion of nests, and habitat selection on nesting success of colonial waterbirds. Trans. Linn. Soc. N.Y. 9:87–102.

NICE, M. M. 1957. Nesting success of altricial birds. Auk 74:305–321.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand. 15:167–175.

ORIANS, G. H. 1980. Adaptations of marsh-nesting blackbirds. Monogr. Pop. Biol. No. 14. Princeton Univ. Press, NJ.

PAGE, G. W., L. E. STENZEL, D. W. WINKLER, AND C. W. SWARTH. 1983. Spacing out at Mono Lake: Breeding success, nest density, and predation in the snowy plover. Auk 100:13–24.

PICMAN, J. 1977. Destruction of eggs by the long-billed marsh wren (*Telmatodytes palustris palustris*). Can. J. Zool. 55:1914–1920.

PICMAN, J. 1987. An inexpensive camera setup for the study of predation at artificial nests. J. Field Ornithol. 58:372–382.

PICMAN, J., AND A. K. PICMAN. 1980. Destruction of nests by the Short-billed Marsh Wren. Condor 82: 176–179.

PICOZZI, N. 1975. Crow predation on marked nests. J. Wildl. Manage. 39:151–155.

POTTS, G. R. 1980. The effects of modern agriculture, nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). Adv. Ecol. Res. 11:2–81.

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

ROBERTSON, R. J. 1972. Optimal niche space of the red-winged blackbird (*Agelaius phoeniceus*). I. Nesting success in marsh and upland habitat. Can. J. Zool. 50:247–263.

SARGEANT, A. B., S. H. ALLEN, AND R. T. EBERHARDT. 1973. Selective predation by mink, *Mustela vison*, on waterfowl. Am. Midl. Nat. 89:208–214.

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

TAYLOR, J. R. 1976. The advantage of spacing out. J. Theor. Biol. 59:485–490.

TINBERGEN, N., N. IMPEKOVEN, AND D. FRANCK. 1967. An experiment on spacing-out as a defense against predation. Behaviour 28:307–321.

WIKLUND, C. G. 1982. Fieldfare (*Turdus pilaris*) breeding success in relation to colony size, nest position and association with Merlins (*Falco columbarius*). Behav. Ecol. Sociobiol. 11:165–172.

WIKLUND, C. G., AND M. ANDERSSON. 1980. Nest predation selects for colonial breeding among Fieldfares, *Turdus pilaris*. Ibis 122:363–366.

WILLIS, E. O. 1973. Survival rates for visited and unvisited nests of Bicolored Antbirds. Auk 80: 145–155.

WITTENBERGER, J. F. 1976. The ecological factors selecting for polygyny in altricial birds. Am. Nat. 110:779–799.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.