Wilson Bull., 106(3), 1994, pp. 456–465

A CAMERA STUDY OF TEMPORAL PATTERNS OF NEST PREDATION IN DIFFERENT HABITATS

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ABSTRACT.—We examined composition of predator communities, relative importance of individual nest predators, and temporal patterns of nest predation in marsh, old field, scrubland, and forest habitats. To record predation, we photographed animals manipulating Japanese Quail (*Coturnix coturnix*) eggs in artificial dry grass nests. A total of 848 photos of nest visitors was obtained in all habitats by means of automatic cameras. The number of different species of egg predators/destructors was low in the marsh (4 species), intermediate in the old field (6 species), and higher in the scrubland and forest (9 species). However, in each of the four habitats there were only one or two major predators. The temporal patterns of predation differed between habitats and were mostly determined by the relative importance of mammalian (mostly nocturnal) and avian (exclusively diurnal) predators. *Received 12 April 1993, accepted 7 Oct. 1993.*

Although predation may be the major cause of nesting mortality of most species (e.g., Lack 1968, Ricklefs 1969), its role as a selective force shaping avian reproductive strategies has not been thoroughly examined. To understand predation as a selective force, we need data on temporal patterns of activities of different predators. More specifically, we need to establish the extent and relative importance of diurnal and nocturnal predation because predators operating at different times of day should present different selective pressures. The purposes of our study, therefore, were to (1) identify predators that attack passerine clutches in four different habitats (marsh, old field, scrubland, forest), (2) determine their relative importance, and (3) examine the temporal pattern of nest predation in these habitats.

METHODS

Between May and July 1986, we established automatic camera stations in four habitats (marsh, old field, scrubland, and forest) in the Mer Bleue Bog Conservation Area near Ottawa, Ontario, Canada (coordinates 45°23′N, 75°32′W). The marsh is extensive (about 30 ha; maximum water depth in the marsh center is about 120 cm) and has a relatively homogeneous cattail (*Typha* sp.) cover up to 220 cm high. The old field is a meadow habitat adjacent to the marsh, with grasses and various herbs dominating the plant community. The vegetation cover is low (a maximum of about 50 cm when the study was conducted). The scrubland was also adjacent to the marsh. Dominant shrubs in this habitat were meadow sweet (*Spirea* spp.) and willow (*Salix* spp.); of occasional trees, birch (*Betula* spp.) was most common. Shrubs and trees were interspersed in this habitat with small patches of grass. The forest was about 3 km from the other habitats and was dominated by mature, approximately 50-year-old deciduous and coniferous trees such as maple (*Acer* spp.), American

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beech (*Fagus grandifolia*), oak (*Quercus* spp.), birch (*Betula* spp.), spruce (*Picea* spp.), and Pine (*Pinus* spp.).

In each of the four habitats we established three 80 m × 80 m quadrats (neighboring quadrats were 20 m apart). In these quadrats, we offered predators experimental nests with Japanese Quail (*Coturnix coturnix*) eggs (depending on experiment, between 9 and 40 nests/quadrat and 1 egg/nest). We constructed experimental nests from dry grass (in size and shape similar to Red-winged Blackbird [*Agelaius phoeniceus*] nests). We distributed these nests with eggs according to random, clumped, and uniform spacing patterns (40 nests/quadrat) and in different densities (40, 25, and 9 nests/quadrat) throughout the experimental quadrats (results of these experiments will be reported elsewhere). In addition, in each habitat, 20 m from these quadrats, we placed a transect of 10 camera setups 10 m apart. Each camera setup consisted of a camera, a dry grass nest with one quail egg, and a mechanism that triggered the camera when a predator manipulated an egg (Picman 1987). Some camera setups were also equipped with a clock, placed approximately 30 cm from the nest, which allowed recording time when pictures of the predation events were taken (Picman 1987).

In each habitat, we had one transect with 10 camera setups (i.e., a total of 40 camera setups were operated simultaneously). Every two weeks we moved the camera transects to a new location (at least 100 m away from the original location) to reduce effects of habituation by predators to the nest location and to sample predation over a larger area. We operated the camera transects from the beginning of May until the end of July, 1986 (92 days, 3680 camera days, 920 in each habitat). We visited all setups once a day (usually between 09:00 and 12:00), replaced depredated eggs with new eggs, and re-set cameras. We kept notes on the appearance of depredated eggs and on the time of predation events.

In the marsh, scrubland, and forest, we placed all nests 80–100 cm above ground (we attached nests to wooden stakes; see Picman 1987). We placed the camera setups in concealed locations (i.e., in dense vegetation) to simulate natural nest locations. In the old field, we placed nests on the ground to simulate passerines breeding in the grassland. For this reason, we had to shorten wooden stakes supporting the cameras so that, in the old field, the cameras would be approximately 20 cm above ground.

RESULTS

We obtained a total of 878 photos of different nest visits by eight mammalian (368 photos) and 17 bird (510 photos) species. To establish the status (i.e., predator vs accidental visitor) of individual species, we used information on the outcome of nest visits by individual species. In most cases, the mammalian visitors destroyed the quail eggs (Table 1), and we thus consider them as potential egg predators. Our results suggest that the striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), and red squirrel (*Tamiasciurus hudsonicus*) are the most important nest predators. These species were responsible for 96% of all mammalian predation events in our study area. The remaining mammals recorded by our cameras (short-tailed weasel [*Mustela erminea*], flying squirrel [*Glaucomys volans*], deermouse [*Peromyscus maniculatus*], chipmunk [*Eutamias* sp.], and woodchuck [*Marmota monax*]) were infrequent visitors at nests and had a small impact on experimental clutches.

TABLE 1
TOTAL NUMBER OF PHOTOGRAPHS OF PREDATORS AT EXPERIMENTAL NESTS IN DIFFERENT HABITATS

Predator	No. of photographed predation events in				Total	Percent of nest visits when eggs depredated
	Marsh	Meadow	Scrubland	Forest		
Raccoon	138 (46)[a]	2 (2)	13 (6)	62 (25)	215 (79)	97
Red squirrel	—	—	31 (8)	8 (8)	39 (16)	6
Short-tailed weasel	1 (1)	—	3 (3)	—	4 (4)	—
Flying squirrel	—	—	—	1 (1)	1 (1)	—
Deermouse	—	—	—	2 (2)	2 (2)	—
Striped skunk	—	101 (36)	—	—	101 (36)	100
Chipmunk	—	—	2 (2)	—	2 (2)	—
Woodchuck	—	4 (1)	—	—	4 (1)	—
Blue Jay	1 (1)	1 (0)	179 (82)	220 (202)	401 (285)	94
Broad-winged Hawk	—	—	—	14 (14)	14 (14)	91
Northern Harrier	2 (0)	1 (0)	—	—	3 (0)	—
Cooper's Hawk	—	—	—	1 (0)	1 (0)	—
Downy Woodpecker	—	—	—	1 (1)	1 (1)	—
Gray Catbird	—	—	6 (1)	—	6 (1)	—
American Crow	—	—	10 (5)	—	10 (5)	100
House Wren	—	—	2 (1)	—	2 (1)	—
Eastern Meadowlark	—	28 (6)	—	—	28 (6)	100
Red-winged Blackbird	29 (22)	—	—	—	29 (22)	21
Black-capped Chickadee	—	—	2 (2)	1 (1)	3 (3)	—
American Robin	—	—	—	1 (1)	1 (1)	—
Swamp Sparrow	1 (1)	—	—	—	1 (1)	—
American Goldfinch	—	—	7 (2)	—	7 (2)	—
Cedar Waxwing	—	—	1 (0)	—	1 (0)	—
Yellow Warbler	1 (1)	—	—	—	1 (1)	—
Thrush (sp. ?)	—	—	—	1 (1)	1 (1)	—
Total	173 (72)	137 (45)	256 (112)	312 (256)	878 (485)	
Total number of species	7	6	11	11	25	

[a] Number of events where time was recorded is given in parentheses. We assumed that broken or missing eggs were depredated. Percent of nest visits when eggs were depredated (i.e., were found broken or missing) was calculated for all photographed predation events for species of animals with at least 10 nest visits. Sample size: 920 nest days in each habitat.

TABLE 2

NUMBER OF PREDATORS IN THE FOUR HABITATS AS DETERMINED FROM PHOTOS OF PREDATION EVENTS

Habitat	Avian predators	Mammalian predators	All predators	Major predators[a]	Total
Marsh	2	2	4	1	142
Old field	3	3	6	2	137
Scrubland	5	4	9	2	248
Forest	5	4	9	2	310

[a] The major predators were defined as those that caused at least 10% of all cases of predation in a given habitat. Events that involved species not known to depredate on eggs or destroy eggs for other reasons were excluded from the total number of predation events in a given habitat. 920 nest days in each habitat.

Avian visitors included predatory birds such as (in the decreasing order of number of visits) Blue Jay (*Cyanocitta cristata*), Broad-winged Hawk (*Buteo platypterus*), American Crow (*Corvus brachyrhynchos*), Northern Harrier (*Circus cyaneus*), and Cooper's Hawk (*Accipiter cooperii*), all of which regularly destroyed the experimental eggs (Table 1). In addition to these predators, our cameras recorded visits of several species that are known to attack and destroy eggs of other passerines for reasons other than predation. These included the Gray Catbird (*Dumetella carolinensis*), House Wren (*Troglodytes aedon*), and Eastern Meadowlark (*Sturnella magna*); see Belles-Isles and Picman (1986a, b) and Picman (1992). Although the Black-capped Chickadee (*Parus atricapillus*) has been reported to attack eggs (Belles-Isles and Picman 1988), more recent data indicate that egg attacks are a relatively rare phenomenon in this species (J. Picman and S. Pribil, unpubl. data). We believe that eight bird visitors recorded by our cameras (Downy Woodpecker [*Picoides pubescens*], Swamp Sparrow [*Melospiza georgiana*], American Robin [*Turdus migratorius*], Red-winged Blackbird [*Agelaius phoeniceus*], American Goldfinch [*Carduelis tristis*], Cedar Waxwing [*Bombycilla cedrorum*], Yellow Warbler [*Dendroica petechia*], and an unidentified thrush [*Catharus* sp.]) were not nest predators. The Red-winged Blackbird, American Goldfinch, and Swamp Sparrow never attacked experimental clutches during experiments conducted near their active nests (J. Picman, unpubl. data). Photos of these species probably represent accidental visits. In the following analyses of temporal patterns of nest predation in different habitats we considered only the predatory species.

The rates of photographed nest visits by predators were highest in the forest, intermediate in the scrubland, and lowest in the marsh and old field (Table 2; $\chi^2 = 102.25$; df = 3; $P < 0.001$). The number of species of predators (avian, mammalian, or all combined) was highest in the

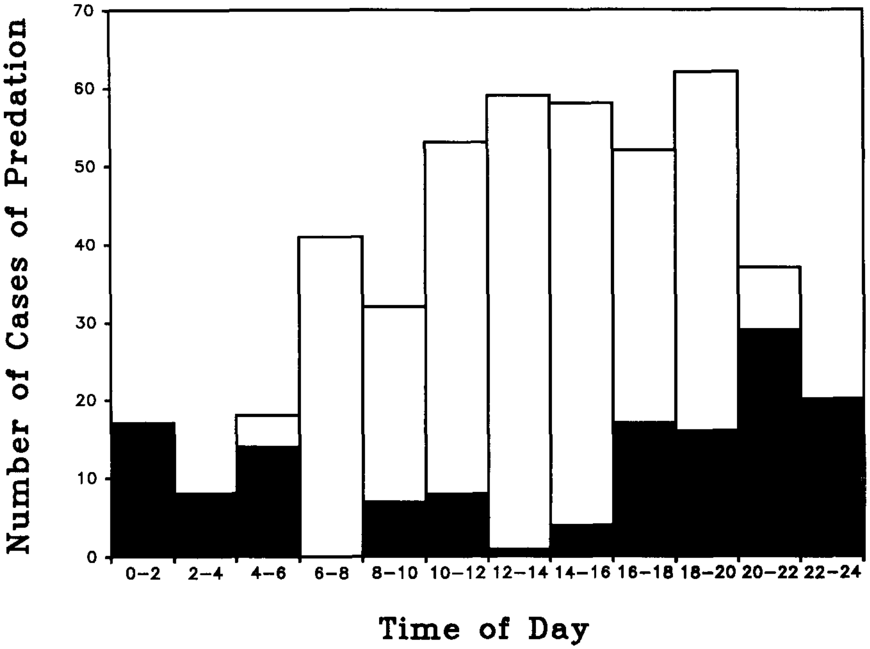

FIG. 1. The frequency of occurrence of predation as a function of time of day for all habitats combined. The black bars indicate the frequency of occurrence of mammalian predation. The avian predation is represented by open bars that were added on top of the black bars.

scrubland and forest habitats, intermediate in the old field, and lowest in the marsh (Table 2). However, in each of these habitats there were only one or two major (i.e., responsible for at least 10% of all cases of predation in a given habitat) nest predators (Table 2). Thus, with respect to the frequency of occurrence of predation events, each community of predators in our study areas was dominated by one or two species.

Mammalian predation (Fig. 1) was greatest between 20:00 and 22:00 h and was high between 16:00 and 06:00 h. Mammalian predation was infrequent between 06:00 and 16:00 h. In contrast, avian predation was high during the day and absent during the night (i.e., between 22:00 and 04:00 h). When the records of avian and mammalian predators were combined, there was a peak of predation between 10:00 and 20:00 h, evidently because of generally high avian predation at this time of day (Fig. 1).

Predation patterns in the four habitats varied significantly throughout the day for individual habitats (Table 3). In the marsh and old field, where predation patterns were similar in time, the highest proportion (50% and

TABLE 3

PREDATION[a] AS A FUNCTION OF TIME OF DAY IN THE MARSH, OLD FIELD, SCRUBLAND, AND FOREST

Habitat	22:00–04:00	04:00–10:00	10:00–16:00	16:00–22:00	Chi-square
Marsh	13/0 (13)[a]	5/1 (6)	5/0 (5)	24/0 (24)	19.17*
Old field	16/0 (16)	5/0 (5)	1/3 (4)	17/3 (20)	16.96*
Scrubland	2/0 (2)	4/23 (27)	3/26 (29)	8/42 (50)	42.89*
Forest	14/0 (14)	7/46 (53)	3/128 (131)	12/44 (56)	112.97*

[a] Mammalian/avian predation (total cases).

* P (two-tailed) < 0.001.

44%, respectively) of predation occurred late in the afternoon and in the evening. In the scrubland, however, predation was high throughout the day, with the peak between 16:00 and 22:00 h. In the forest, predation was generally high throughout the day and peaked between 10:00 and 16:00 h (Table 3).

Our data allowed closer examination of temporal patterns of nest predation by several species for which we had at least 20 records of the time of a predation event. Raccoons and striped skunks made most visits of experimental nests between 16:00 and 04:00 (Table 4), whereas Blue Jays were generally important throughout the day (i.e., between 04:00 and 22:00 h, Table 4). Unfortunately, for the remaining predators we did not obtain enough photos of predation events to be able to present a similar analysis of their predatory activity pattern throughout the 24-h cycle.

TABLE 4

THE TEMPORAL PATTERN OF PREDATION BY PREDATOR SPECIES FOR WHICH AT LEAST 30 RECORDS OF TIME OF THE PREDATION EVENT WERE OBTAINED

		Number of predation events that took place between:			
Predator	Habitat	22:00–04:00	04:00–10:00	10:00–16:00	16:00–22:00
Raccoon	Marsh	13	4	5	24
	Scrubland	1	3	1	1
	Forest	11	3	3	8
	Combined	25	10	9	33
Striped skunk	Old field	15	4	1	16
Blue Jay	Scrubland	0	21	21	40
	Forest	0	38	120	44
	All combined	0	59	141	84

DISCUSSION

Results of our camera study suggest that the cattail marsh had the lowest number of different types of predators, most likely because the deep water of the marsh prevented predators from effectively searching this habitat. Raccoon depredation, the single major cause of egg mortality in the marsh, was mostly in shallow marsh areas (Picman et al. 1993). Marsh Wrens (*Cistothorus palustris*) were absent during this study but are important nest predators when present (Picman et al. 1993). Because Marsh Wrens are diurnal, their presence could change the temporal pattern of predation activities in the marsh (Table 1). Composition of a predator community, and consequently the temporal pattern of predation in some habitats, may thus vary between years, depending on changes in the predator community.

In spite of the discovery that in some habitats up to nine predator species were recorded, each habitat had at most two major predator species. The presence of such a small number of major nest predators in each of the four habitats could be explained in several ways. First, it is possible that the ''major'' predators were highly mobile animals that could exploit the food source (experimental clutches) more effectively. Second, the ''major'' predators could have been nest specialists that are behaviorally more effective in searching for bird nests. Third, following the experimental increase in food (egg) availability, some predators may have specialized on this food source (i.e., exhibited the functional response). And fourth, the increased nest density in our study areas may have attracted more individuals of the ''major'' predator species (i.e., a predator may have exhibited a numerical response). Establishing the plausibility of the above explanations would require recognition of individual predators and data on their foraging behavior following the introduction of experimental clutches. In addition, we would also have to examine the effect of selective removals of the ''major'' predators on foraging activity of the ''minor'' predators. Such removal experiments should allow us to establish if the ''minor'' predators are generally less effective in finding nests or if their potential effects have been masked by increased (or more effective) foraging activity of the ''major'' predators.

The methods used in experimental predation studies are likely to affect predation patterns. For example, predation rates on eggs in artificial nests constructed from dry grass may differ from those on eggs in real nests (Storaas 1988, O'Reilly and Hannon 1989; but see Major 1990). The experimental approach could also affect the nest predation patterns because of the inability of observers to simulate the location of natural nests. Furthermore, frequent visits of experimental nests could attract predators, thereby increasing predation rates on artificial clutches (but see MacIvor et al. 1990). Our results on the composition of predator communities in different habitats and the relative role of individual species of predators could have been influenced by our field methods and hence must be interpreted with caution. Specifically, our frequent visits of camera setups (once every day), creating disturbance, leaving scent paths leading to nests, and the use of camera setups which made the nests more conspicuous could have made it easier for at least some predators to find our experimental nests. On the other hand, the presence of human observers and camera setups might deter some predators, whose importance could thus be underestimated in our results. Unfortunately, we were unable to control for such effects and cannot establish their importance. However, because we used the same methods in all habitats, we believe that differences in predation that we observed between habitats, and at different times of day within individual habitats, are real.

Our data indicate that egg predation may occur at any time of day. Avian predators in our study area were exclusively diurnal, whereas mammalian predators exhibited the highest level of activity during late afternoon, evening and at night. The presence of avian and mammalian predators and their relative abundances seem to determine the temporal pattern of nest predation in different habitats. Thus, mostly mammalian predation in the marsh and old field habitats resulted in a predation peak characteristic of mammalian predators (i.e., late evening/night). In contrast, more frequent avian predation in the scrubland and forest resulted in more intense predation during the day (i.e., between 04:00 and 22:00 h) in these two habitats.

Our results on the temporal pattern of nest predation could have been influenced by the timing of our daily checks of the camera setups. Assuming high levels of predation, we should expect more predation soon after our checks of the camera transects when new eggs were placed in the experimental nests. Because all checks of camera transects were done between 9:00 and 12:00 h, the highest predation should occur early in the afternoon. In the forest, where predation was highest, 52% of all predation events occurred in the time period following the check (Table 3). This evidence supports the view that in the forest the timing of camera checks may have biased the data on the temporal pattern of predation events. In the scrubland, where predation was the second highest, only 27% of all predation events occurred immediately after the check. Therefore, in this habitat the timing of our camera transect checks did not seem to affect temporal patterns of predation. This is further supported by the observation that in the scrubland predation was highest between 16:00 and 22:00 h (Table 3). In contrast, where predation is generally low, and/

or where most predation occurs at night, we should expect little or no effect of our nest checks on temporal patterns of nest predation. This prediction is supported by data from the old field and marsh habitats, where only 9–10% of all predation events occurred during the time period following our check.

The belief that timing of our checks may have had different effects on the temporal pattern of predation in different habitats, depending on intensity of predation and types of predators present, is further supported by data on three most common predators, the raccoon, Blue Jay, and striped skunk, which occurred in habitats with different intensities of predation. In the forest (the highest predation; Table 1; J. Picman, unpubl. data), Blue Jays were the most important predator and caused most egg losses between 10:00 and 16:00 h; i.e., soon after our checks of camera transects (usually 09:00–12:00 h). This diurnal predator was responsible for almost 50% of all egg losses during our camera study. On the other hand, the temporal patterns of activities of raccoons and striped skunks (to a great extent nocturnal predators), which were important but a far less frequent cause of egg losses in their respective habitats (Table 4), do not seem to have been influenced by the timing of our checks of camera transects (Tables 1, 4).

ACKNOWLEDGMENTS

We thank the National Capital Commission for a permit to conduct this research in the Mer Bleue Bog Conservation Area. B. Jobin, J. McAllister, and D. Beedell provided assistance with the fieldwork. S. Pribil helped us with preparation of Figure 1. C. R. Blem, W. H. Buskirk, D. Klem, Jr., and S. Pribil helped to improve this manuscript through many constructive comments. This research was supported by a NSERC grant to the senior author.

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