

PATTERNS OF PREDATION ON PASSERINE NESTS IN MARSHES: EFFECTS OF WATER DEPTH AND DISTANCE FROM EDGE

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ABSTRACT.—We tested a hypothesis that the high densities of some passerines breeding in North American marshes result from greater safety of this habitat from predators as compared to upland habitats. We examined the relative importance of water depth and distance from the marsh edge in lowering predation rates on experimental nests with Blue-breasted Quail (*Coturnix chinensis*) eggs. In addition, using cameras we studied the role of water depth in determining the predator community. Our results showed that: (1) predation was lower in the marsh than in the adjacent upland; (2) predation rates decreased with increasing water depth in the marsh; (3) for the marsh nests, the distance to the marsh edge was relatively unimportant; (4) the diversity of nest predators decreased with increasing water depth; and (5) in the deep marsh areas, there was only one major predator, the Marsh Wren (*Cistothorus palustris*). We propose that the greater safety of deep-water marsh areas, the reduced complexity of the predator community, and the type of predators allowing effective nest defense by nest owners have played the key role in the evolution of reproductive strategies of marsh-nesting passerines. Received 10 October 1991, accepted 15 June 1992.

NORTH AMERICAN marshes are among the most productive habitats that also accommodate a diverse avian community (Verner and Willson 1966). Some passerines, such as the Red-winged Blackbird (*Agelaius phoeniceus*), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), and Tricolored Blackbird (*A. tricolor*), breed in marshes in high densities (e.g. Orians 1961, 1980), suggesting that marshes are highly suitable for these birds. This high suitability of marshes could be explained in terms of food abundance (e.g. Verner and Willson 1966, Orians 1980) and/or reduced nest predation (e.g. Robertson 1973, Wittenberger 1976). Food available on territories of the above blackbirds however, is relatively unimportant because individuals of all three species usually forage away from their territories (e.g. Orians 1980). On the other hand, water in marshes should prevent most of the typical terrestrial predators from reaching passerine nests located especially in the deeper marsh areas. This presumably lower vulnerability of deep-water marshes to predators should lead to intense competition among birds for these "safe" breeding grounds. Given these reasons, we have evaluated the effect of water depth on nest-predation patterns.

In addition to the safety due to the water below the nests, another feature of most marshes that could increase nesting success of marsh-nesting birds is the high and dense cattail (*Typha* sp.) vegetation. In many North American marshes, cattails form a dense and relatively uniform cover that is likely to provide well-concealed, and for most predators poorly accessible, nest locations. The amount of cattail vegetation between the nest and the marsh edge (i.e. distance to edge) might, therefore, also influence chances of nesting success and, hence, nest-site selection by marsh-nesting birds.

Predation on adults and their nests is an important selective factor that could play a role in the evolution of various reproductive strategies, such as the type and size of a territory, the type of spacing of nests, and the mating pattern. Therefore, to gain a better understanding of the adaptive value of reproductive strategies of any particular species, we need to know what role predation has been playing for that species.

The purpose of our research was to examine the nest predation patterns in an extensive marsh located near Ottawa, Ontario. More specifically, we examined the role of water depth in determining the predator community and nest-predation rates. Because distance from the marsh edge could influence nest-predation patterns, we also attempted to establish the importance of this nest-site characteristic. To

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achieve these objectives, we used experimental nests with Blue-breasted Quail (*Coturnix chinensis*) eggs that we distributed along transects throughout the marsh. This experimental procedure allowed us systematically to vary a selected nest-site characteristic (water depth or distance from edge), while keeping the other variable constant.

METHODS

Our study was conducted in 1985 and 1988 in the Ramsayville marsh in the Mer Bleue Bog Conservation Area near Ottawa, Ontario, Canada. The Ramsayville marsh (about 30 ha) is covered with dense and relatively uniform cattail vegetation. The water depth varies in this marsh from 0 cm (marsh edge) to about 120 cm in its center. Passerines breeding in this marsh include, in decreasing order of abundance, the Red-winged Blackbird, Swamp Sparrow (*Melospiza georgiana*), Common Grackle (*Quiscalus quiscula*), and Marsh Wren (*Cistothorus palustris*).

To examine nest predation patterns, we offered predators artificial nests with one quail egg in May and June 1988. These nests were made from dry grass by pressing two layers of grass in a cup of size and shape similar to a Red-winged Blackbird nest. The two layers of grass were held together by several strips of transparent and odorless glue. The experimental nests were then attached, using string, to clumps of cattail in concealed situations resembling nest sites chosen by Red-winged Blackbirds in this area.

Prior to the field experiments, quail eggs were treated with 20% acetic acid for 20 min and then thoroughly washed in running water for 10 min. The treatment made the shells thinner and, thus, allowed small predators, such as Marsh Wrens, to puncture them (see Picman et al. 1988).

We distributed the experimental nests with quail eggs along several transects (between-nest distances were 10 m). The placement of the nest transects and their length were determined according to the purpose of a given experiment. In the first experiment, we examined the role of water depth by placing nests with eggs along four transects of a similar length (with 30, 30, 31, and 31 nests) running from the deep-water marsh area into an adjacent upland (i.e. transects placed perpendicular to marsh edge). The distance between the neighboring transects was 50 m. To establish the relative roles of water depth and distance from the marsh edge, we introduced two sets of nest transects. In one set, three nest transects (with 26 nests in each transect) were placed at similar distances (90 m) from the marsh edge, but had different water depths. In the second set, two nest transects (with 27 and 26 nests) were placed at different distances from the marsh edge (30 and 110 m, respec-

tively) but in areas with similar water depth. Nests along the transects were checked on days 1 and 4 after their introduction.

To establish the effect of water depth on the types of predators operating in our marsh, we used automatic camera setups in 1985 and 1988 that were triggered by nest visitors manipulating quail eggs (see Picman 1987). These cameras were set up near experimental nests along two camera transects of the same length (a total of 30 setups) that ran perpendicular to the marsh edge from the deep areas of the marsh into the adjacent upland. In 1985, the two camera transects were 100 m apart. In 1988, the two camera transects were placed 50 m outside the four water-depth-gradient transects. These camera transects were operated in May and June of 1985 and 1988. All nests along these transects were visited every day, or every second day if predation was low. In case of a predation event, the depredated egg was replaced with a new egg and the camera was reset.

RESULTS

Predation generally was lower in the marsh than in the adjacent upland during both nest checks (Table 1). Within a marsh, water depth had a significant effect on predation during both nest checks. In the marsh, predation was relatively high on nests with eggs that were placed in the shallow area (water depth 0–20 cm), lower in the area with medium (21–40 cm) water depth, but increased again in the deep marsh area (water depth >40 cm; Table 1). Overall, the mean water depth and distance from marsh edge were greater for successful than for depredated nests (Table 2). Because in this experiment all four transects were run perpendicular to the marsh edge, these results do not allow us to establish the relative roles of water depth and distance from marsh edge in determining this predation pattern.

When we controlled distance from edge but varied water depth by placing three transects in shallow, intermediate, and deep marsh areas, water depth had a significant effect of predation rates during both nest checks (Table 3). Finally, when we controlled water depth and varied distance from edge, predation rates did not differ significantly among nests placed at different distances from the marsh edge (Table 4). This suggests that distance from the marsh edge was relatively unimportant.

The camera study of predators operating in different water-depth areas of the marsh and in the adjacent upland indicated that the number of species photographed at the experimental

TABLE 1. Effect of water depth on survival of experimental nests with quail eggs on days 1 and 4 after initiation of experiment.^a

Water depth (cm)	Number (%) nests depredated on		Total nests
	Day 1	Day 4	
Upland			
0	32 (80)	39 (98)	40
Marsh			
0-10	24 (56)	43 (100)	43
11-20	9 (50)	15 (83)	18
21-30	7 (32)	15 (68)	22
31-40	1 (8)	6 (46)	13
>40	14 (54)	17 (65)	26
Combined	55 (45)	96 (79)	122

^a Upland vs. marsh (all depths combined): day 1, $X^2 = 14.77$, $df = 1$, $P < 0.001$; day 4, $X^2 = 7.68$, $df = 1$, $P < 0.01$. Effect of water depth (marsh only): day 1, $X^2 = 11.89$, $df = 4$, $P < 0.025$; day 4, $X^2 = 24.28$, $df = 4$, $P < 0.001$.

nests decreased with increasing water depth (Table 5). In the upland, cameras recorded 11 species of animals. Of these, seven are generally recognized as egg predators, while the four remaining species could not be considered as predators (American Goldfinch, Common Yellowthroat, Swamp Sparrow, and Black-capped Chickadee). In each of the shallow- and intermediate-water-depth marsh areas, six species were photographed at the nests, but in both cases two definitely were not predators (Red-winged Blackbirds and Swamp Sparrows failed to peck eggs in trials done earlier in this marsh; Picman unpubl. data). In the deep marsh areas, three species were recorded at the nests, but only one of these could be considered a predator (the Marsh Wren). Also, in the marsh only one or a small number of major predators were responsible for most egg attacks. Thus, in the deep marsh, only Marsh Wrens were important

TABLE 2. Mean water depth and distance from edge of marsh (\pm SD) for successful and depredated nests on days 1 and 4. Comparison of successful and depredated nests with *t*-test.^a

Day	Successful	Depredated	<i>t</i> -value
Water depth (cm)			
1	23.8 \pm 19.5	12.4 \pm 19.4	-3.74
4	35.0 \pm 16.0	15.1 \pm 19.5	-4.65
Distance to edge (m)			
1	93.3 \pm 58.8	41.9 \pm 48.2	-6.12
4	121.3 \pm 49.6	57.8 \pm 56.0	-5.11

^a For each test, $df = 161$ and $P < 0.001$.

TABLE 3. Effect of water depth on survival of experimental nests. Three transects of artificial nests ($n = 24$ each) were introduced parallel to edge of marsh (90 m from edge) in areas with different water depths.^a

Transect	Water depth	Mean water depth \pm SD (cm)	Percent nests depredated on	
			Day 1	Day 4
A	Shallow	0.0 \pm 0.0	62.5	100.0
B	Intermediate	21.2 \pm 6.8	3.8	84.6
C	Deep	29.2 \pm 19.3	7.7	46.2

^a Test for effect of water depth on survival of experimental clutches: day 1, $X^2 = 29.36$, $df = 2$, $P < 0.001$; day 4, $X^2 = 22.53$, $df = 2$, $P < 0.001$.

predators. In the medium-water-depth marsh area, raccoons, long-tailed weasels, and Marsh Wrens (depending on year of study) were important. Finally, in the shallow areas, raccoons, long-tailed weasels, and American Crows were important (Table 5). In the upland, up to seven different predators attacked eggs, but of these raccoons, Gray Catbirds, and red squirrels seemed to be the most important (Table 5).

DISCUSSION

Our study demonstrated that water depth played an important role in influencing nest-predation patterns in our study area. However, one problem arises from the examination of data collected during the two sets of predation trials (Tables 1 and 3). Table 1 indicates that predation on experimental nests in the marsh was relatively high in the deepest marsh area. In contrast, Table 3 shows that, in the experiment in which we controlled for the effect of distance from the marsh edge, predation decreased with increasing water depth. The difference in pre-

TABLE 4. Effect of distance from edge on survival of experimental clutches. Two transects of nests introduced parallel to edge of marsh (30 m and 110 m from edge) in areas with water of similar depth.^a

Transect	Dis- tance from edge (m)	Mean water depth \pm SD (cm)	Percent nests depredated on		
			Day 1	Day 4	<i>n</i>
A	30	50.2 \pm 17.6	19	48	27
B	110	42.3 \pm 15.2	4	31	26

^a Statistical comparison of water depth between two transects: $t = 1.74$, $P > 0.08$. Comparison of predation rates between two transects: day 1, $X^2 = 2.84$, $P > 0.05$; day 4, $X^2 = 1.67$, $P > 0.1$.

TABLE 5. Frequency of visits to experimental nests placed in marsh and adjacent upland by different animals as determined in camera study. The two numbers represent percentage of all cases in a given category in two years of study (1985/1988).

Nest visitor	Percent of all visits in			
	Upland	Marsh with water depth (cm)		
		0-20	21-40	41-more
Raccoon (<i>Procyon lotor</i>)	14.3/52.4	71.2/66.7	50.0/66.7	3.7/5.0
Long-tailed weasel (<i>Mustela frenata</i>)	14.3/14.3	24.7/5.6	25.0/22.2	0/0
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	21.4/0	0/0	0/0	0/0
Moose (<i>Alces alces</i>)	0/0	0/5.6	0/0	0/0
Blue Jay (<i>Cyanocitta cristata</i>)	4.8/14.3	0/0	0/0	0/0
American Crow (<i>Corvus brachyrhynchos</i>)	4.8/0	0/16.6	0/0	0/0
Gray Catbird (<i>Dumetella carolinensis</i>)	21.4/0	0/0	0/0	0/0
Black-capped Chickadee (<i>Parus atricapillus</i>)	2.4/0	0/0	0/0	0/0
Swamp Sparrow (<i>Melospiza georgiana</i>)	0/4.8	4.1/0	8.3/0	0/0
American Goldfinch (<i>Carduelis tristis</i>)	0/4.8	0/0	0/0	0/0
Common Yellowthroat (<i>Geothlypis trichas</i>)	0/9.5	0/0	0/0	0/0
Virginia Rail (<i>Rallus limicola</i>)	0/0	0/0	4.2/0	0/0
House Wren (<i>Troglodytes aedon</i>)	14.3/0	0/0	0/0	0/0
Marsh Wren (<i>Cistothorus palustris</i>)	0/0	0/0	12.5/0	85.2/45.0
Red-winged Blackbird (<i>Aegialius phoeniceus</i>)	0/0	0/5.6	0/11.1	11.1/50.0
Total visits	42/21	73/18	24/18	27/20

dition rates in deep marsh areas between the two experiments designed to examine the effect of water depth on predation was caused by Marsh Wrens. In the first study, wrens (as indicated by the presence of their nests) were close (i.e. 10-15 m) to some experimental nests in the deep end of the four nest transects running perpendicular to the marsh edge (see Table 1). In the second study, wrens were far away (i.e. >30 m) from the three nest transects testing the role of water depth (distance to edge controlled; see Table 3). Because Marsh Wrens apparently prefer deep-water marsh areas (Leonard and Picman 1986), their presence will have the greatest effect on nests in these areas. The intensity of predation in the deep marsh areas, thus, reflects the number and proximity of Marsh Wrens.

In contrast to water depth, the distance from the marsh edge was relatively unimportant. Data on the role of water depth (Table 4) indicate, however, that nests located farther from the marsh edge experienced slightly lower predation than those located closer to the edge (differences of 15 and 17% on days 1 and 4, respectively). It is possible that a larger sample could result in a significant difference. However, our data suggest that water depth is much more important in nesting success than distance to the marsh edge.

The lower predation in deep-water areas clearly is a result of the exclusion of many pred-

ators that occur in upland habitats. The camera study of predators in sites with different water depths and in the adjacent upland demonstrated that the predator community is more diverse in the upland, where different avian and mammalian predators present danger to both adult passerines and their nests. In contrast, in the deep marsh areas, only Marsh Wrens were important. However, in other marshes, mink (*Mustela vison*) also may play a role. We have observed minks on several occasions in the marsh we studied, but cannot be certain that this predator was constantly present throughout our investigation.

Another explanation for lower predation in deep-water marsh areas is based on presumably more efficient nest defense by Red-winged Blackbirds in these areas. In our marsh, the density of Red-winged Blackbirds was higher in deep-water than in shallow-water areas (J. Picman and T. Ewanovich unpubl. data). Red-winged Blackbirds generally exhibit a high level of aggression towards potential nest predators (e.g. Nero 1956), and their nest defense may improve with increasing density of breeding individuals in a given area (Picman et al. 1988). This could explain why we failed to obtain any photographs of avian predators such as American Crows and Blue Jays in marsh areas with deeper water (Table 5). Although we cannot establish the relative importance of deep water and antipredator defense by Red-winged Black-

birds in predator exclusion, we suggest that both may have played a role in our study area.

Different predation rates on passerine nests and different predators operating in marshes and uplands indicate that birds breeding in these habitats are exposed to different selective pressures. In the upland habitats, the diversity of predators and of foraging tactics should select for predator-avoidance strategies such as nest concealment and crypticity of nesting activities. In marshes, on the other hand, water depth should determine the reproductive strategies of passerines breeding there. Thus, those species that breed in shallow areas should presumably adopt the predator-avoidance strategies (e.g. nest concealment, camouflage) because in this portion of the marsh habitat both typical marsh predators (e.g. Marsh Wrens) and upland predators (e.g. raccoons, long-tailed weasels, American Crows, Blue Jays) could occur. However, in the deep-water marsh areas, where Marsh Wrens seem to play the dominant role as predators, the antipredation strategies could include increased density of breeding individuals, which should lead to better predator detection and improved antipredator defense (e.g. Picman 1980, Picman et al. 1988). This proposition is supported by the fact that the two blackbird species that breed in deep marsh areas only (e.g. Yellow-headed and Tricolored blackbirds) are highly colonial. In contrast, the Red-winged blackbird and other passerines that breed in shallow marsh areas and adjacent uplands (e.g. Swamp Sparrows and sometimes Marsh Wrens) are present in much lower densities (e.g. Orians 1961; L. Schriml and J. Picman unpubl. data). Additional support for this hypothesis comes from a study of Red-winged Blackbird densities in different water-depth areas of a single marsh, which indicates that the density of breeding Red-winged Blackbirds increases with increasing water depth (J. Picman and T. Ewanovich unpubl. data).

Marsh-nesting passerines are more frequently polygynous than species breeding in uplands. This phenomenon has been traditionally explained by high availability and heterogeneous distribution of passerine food resources (e.g. Verner and Willson 1966, Orians 1969). This explanation, however, is untenable for at least some of these species because the most-highly polygynous passerines (Red-winged, Yellow-headed, and Tricolored blackbirds) generally forage away from their territories and

away from their breeding marshes (e.g. Orians 1961, 1980, Picman 1980, Isabelle 1988). For this reason, passerine food contained within territories of these birds could not have played a role in the evolution of their polygynous mating pattern. Contrary to this hypothesis, we propose that polygyny in marsh-nesting birds such as blackbirds has been favored by reduced nest-predation rates. It is possible that the polygynous mating pattern could be a result of ability of some males to monopolize the high-quality (i.e. safer, deep-water) breeding areas that are preferred by females. The test of this hypothesis will require that we examine the intensity of competition among males and females for breeding grounds in the deep-water and shallow-water marsh areas, and establish its effect on distribution of individuals of both sexes.

Polygyny in some marsh-nesting species could also be promoted by a small nest predator that is common in many North American marshes (Marsh Wren), whose impact the co-occurring birds could reduce through nest defense. In Red-winged and Yellow-headed blackbirds, this nest defense is further improved through reduced distances between female neighbors. Predation, thus, may favor clumping by females (Picman et al. 1988, Isabelle 1988). The female clumping tendency could, in turn, allow some males to monopolize high-quality breeding grounds or female clumps, thereby leading to resource-defense or harem-defense polygyny (see Emlen and Oring 1977).

In conclusion, we suggest that different nest-predation patterns in marshes may have led to the evolution of reproductive strategies such as colonial nest dispersion and high degrees of polygyny observed in some marsh-nesting passerines. More data on predation patterns for nests of individual marsh-nesting species would allow us to examine the role of their nest distribution and polygynous mating pattern in reducing nest predation.

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