

SOURCES OF NESTING MORTALITY AND CORRELATES OF NESTING SUCCESS IN YELLOW-HEADED BLACKBIRDS

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ABSTRACT.—The Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) is a polygynous, colonial, marsh-nesting passerine. We determined the causes of Yellow-headed Blackbird reproductive failure. For the population studied, predation was the most important source of nesting mortality, causing failure of 51% of all nests over a two-year period. The most important nest predator was the Marsh Wren (*Cistothorus palustris*), a conclusion supported by several lines of evidence. First, predators that were offered mixed-egg clutches consisting of Common Quail (*Coturnix coturnix*) and Yellow-headed Blackbird eggs destroyed only the blackbird eggs, which are smaller. Second, nesting success of Yellow-headed Blackbirds was positively correlated with their distance from Marsh Wrens. Third, all 26 photographs of predation events obtained at experimental nests showed Marsh Wrens pecking eggs. Yellow-headed Blackbirds recognized Marsh Wrens as a potential danger to their nests and aggressively excluded wrens from the vicinity of their territories. Marsh Wren attacks on blackbird nests and blackbird aggression towards wrens promoted spatial segregation of the breeding grounds of the two species. We conclude that nest predation is an important selective force that likely has played a role in shaping reproductive tactics in the Yellow-headed Blackbird. Received 24 September 1992, accepted 22 December 1992.

REPRODUCTIVE STRATEGIES of passerines could be characterized by the pattern of distribution of breeding individuals in space (colonial vs. overdispersed spacing tactics), by temporal organization of nesting attempts (synchronous vs. asynchronous), and by the number of mates (monogamous or polygamous mating patterns). The type of strategy that any given species will adopt is likely to be determined to a great extent by the distribution and predictability of food resources (e.g. Horn 1968) and by predation patterns (e.g. Kruuk 1964).

The North American marsh-nesting passerines present an interesting group of birds that are unique in at least two ways. First, in spite of the fact that most passerines are monogamous (e.g. Lack 1968), many marsh-nesting species are polygynous (Verner and Willson 1966, Orians 1969). Second, although coloniality is relatively rare among North American passerines, this nesting pattern is characteristic of several marsh-nesting blackbirds (e.g. Orians 1961, 1980). The marsh-nesting passerines thus offer an opportunity for a study of factors leading to the evolution of coloniality and polygyny.

The high frequency of polygyny and colon-

iality in marsh passerines possibly could be caused by two marsh characteristics. First, based on an extensive survey of nesting mortality, Ricklefs (1969) concluded that in temperate North America marsh-nesting passerines suffer the highest mortality, mostly due to predation. Second, marshes are extremely productive habitats that potentially could support high density populations of passerines breeding in them (Verner and Willson 1966). Because high predation and food abundance have likely played a role in shaping the reproductive strategies of marsh-nesting passerines, more data are needed on these factors and their relative importance.

The Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) is a polygynous, colonial, marsh-nesting passerine that occurs in the central and western parts of North America (Orians 1980). For many altricial birds, the period of greatest mortality is the egg and nestling stages (Ricklefs 1969). For temperate marsh-nesting passerines, including the Yellow-headed Blackbird, predation and nestling starvation seem to be the greatest sources of this mortality (Orians 1961, Young 1963, Willson 1966, Robertson 1972, 1973, Patterson et al. 1980, Richter 1984, Bancroft 1986, Picman et al. 1988, Westneat 1992). Therefore, it is important to look at these sources of mortality in order to gain a better under-

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standing of the observed reproductive pattern in Yellow-headed Blackbirds.

Our study was designed to examine sources of nesting mortality and provide information on foraging patterns of Yellow-headed Blackbirds in the Delta Marsh, Manitoba. Specifically, our goals were to: (1) assess the role of nest predation relative to other nest mortality factors in reproductive success; (2) determine which predators occur in our marsh and establish their relative importance; and (3) examine nest predation as a selective force in two consecutive years. Because earlier studies of this species (e.g. Willson 1966, Verner 1975, Bump 1986) and our preliminary observations suggested that predation by Marsh Wrens (*Cistothorus palustris*) could be important, additional goals were to: (4) assess the impact of Marsh Wrens on Yellow-headed Blackbird nesting success; (5) establish if Yellow-headed Blackbirds recognize Marsh Wrens as a specific nest predator and respond aggressively to them; and (6) examine the role of the interactions between Yellow-headed Blackbirds and Marsh Wrens in determining the pattern of their distribution in the marsh.

Because Yellow-headed Blackbirds are dominant in direct behavioral interactions with Marsh Wrens (e.g. Verner 1975), wrens presumably can destroy contents of unguarded nests only. Therefore, blackbird nests should be most vulnerable to wren attacks when female owners are foraging and cannot effectively guard them. To establish if foraging activities by nesting females result in increased vulnerability of their nests, we collected data on the location of foraging grounds for breeding female Yellow-headed Blackbirds and estimated the overall foraging effort in different feeding areas. Finally, to determine which variable(s) contributes to the variance in yellowhead nesting success, we conducted a multivariate analysis of nesting success as a function of a number of environmental variables. Obtaining this background information on the role of predation in reproductive success and location of foraging grounds was the first step in our study of the adaptive value of reproductive strategies of the Yellow-headed Blackbird.

METHODS

General breeding information and nesting success.—Our study was conducted in an extensive freshwater marsh bordering the southern end of Lake Manitoba at the

University of Manitoba Field Station, Delta Marsh. We conducted fieldwork between 1 May and mid-July 1983, 20 April and 1 July 1984, and 20 and 28 May 1987. The emergent vegetation of the study area (ca. 5 ha in 1983 and 7 ha in 1984) was dominated by cattails (*Typha* sp.), bulrushes (*Scirpus* sp.), and reeds (*Phragmites* sp.), in that order. The only abundant passerine species breeding in the marsh were the Yellow-headed Blackbird and Marsh Wren. We concentrated on two Yellow-headed Blackbird colonies in 1983 and three in 1984, which were separated by narrow strips of reeds. To facilitate the recording of spatial information, the study site was divided into 20 × 20 m quadrats and subsequently mapped. Territorial males were captured early in May using a decoy trap baited with an "intruding" male Yellow-headed Blackbird, and were given a unique color-band combination. Male territories were determined through observation of male movements, their territorial displays, singing locations, and interactions with neighbors and strange intruders.

To establish how foraging activities of females affect vulnerability of their nests to Marsh Wrens, we conducted the following study. In 1984, between 26 May and 13 June 1988, we recorded 22 1-h time budgets for selected breeding females. Eleven were in the incubation stage, with the remaining 11 in the nestling stage. Two of the incubating females were later excluded from the analysis because one had laid an egg during the observation period, and the other had an egg hatch. All time budgets were conducted between 0530 and 0930 CST. Activities of the females were divided into the following five categories: (1) time on nest; (2) time foraging on resident male's territory; (3) time foraging in marsh outside resident male's territory; (4) time foraging off marsh; (5) other (perched, preening, sexual chases, mobbing, chasing wrens, interacting with other females).

Biweekly searches of the marsh for nests provided the information on the breeding pattern and nesting success of Yellow-headed Blackbirds. When a new nest was found, a numbered label was attached to surrounding vegetation, 1 m from the nest, and its location in a given quadrat was recorded on the map of the study area. At this time, the following nest-site characteristics were recorded: (1) water depth below nest; (2) height of nest above floor of marsh, measured from top of nest; (3) vegetation height from floor of marsh to top of supporting vegetation; (4) type of vegetation used for nest support; and (5) vegetation density at nest. The vegetation density was estimated using a 50-cm-long stick with 20 evenly spaced bright red spots (1-cm diameter). This stick was placed on top of the nest and the number of unobstructed dots was counted from a distance of 2 m.

During these checks, the contents of all nests were examined and recorded. A nest was considered active only once a clutch was initiated. If a nest failed, the nest area was examined for possible causes of nesting

failure. If a nest lost its eggs or nestlings, it was considered to have been destroyed by a predator. Most often the depredated nests contained egg-shell fragments, dried egg contents or dried blood (in some instances these also were found on nearby vegetation), punctured eggs or dead young with various signs of injuries, or some combination of the above. Nests in which incubation or brooding was discontinued, but with nest contents undisturbed, were considered to have been abandoned. Other reasons for nesting failure included infertile eggs, nestling starvation, or poorly constructed nests, which resulted in the nest contents eventually falling into the water. Finally, nests that fledged at least one young were considered to have been successful.

Impact of Marsh Wrens relative to other predators.—In 1984, in another marsh located approximately 1 km from the main study area, we caused nests and territories to be abandoned by removing 13 of 21 territorial males and all active nests during a two-day period (31 May and 1 June). On 4 June, as part of another study in which we examined the antipredation value of Yellow-headed Blackbird colonial nesting, we placed 160 blackbird nests in the removal area. These nests were distributed uniformly in two high-density (internest distance of 5 m) and two low-density (internest distance of 15 m) plots. One Yellow-headed Blackbird egg and one Common Quail (*Coturnix coturnix*) egg were placed in every other nest, while the remaining nests contained two Yellow-headed Blackbird eggs. We examined all nests for predation on days 1, 3, 6, and 9 after the eggs were put out. In addition, three transects of a total of 31 experimental Yellow-headed Blackbird nests were simultaneously established 40 m apart in an active Yellow-headed Blackbird colony (nests were placed along these transects at 10-m intervals). All experimental nests contained one Yellow-headed Blackbird egg and one Common Quail egg, and were examined for predation on days 1, 3, 6, and 9 after establishment.

Since Marsh Wrens are rarely able to puncture and destroy quail eggs (Picman 1977), experimental nests in which the quail egg was intact (or had small peck holes the size of a Marsh Wren bill), but from which the blackbird egg disappeared or was found with various amounts of damage were considered as having been depredated by a Marsh Wren. Since both types of eggs were collected fresh and were refrigerated for no longer than a week before being used in this experiment, it is unlikely that predators would prefer one egg type over the other.

In 1987, we conducted a camera study to identify animals visiting experimental nests from photographs of predation events. We used 11 camera setups, which photograph the manipulator of a Common Quail egg placed in an artificial nest on a trigger (Picman 1987a). We used quail eggs as a stimulus for the following reasons: (1) Marsh Wrens cannot break quail eggs and this made it possible for us to reuse

the same nests in subsequent trials: (2) a large number of quail eggs were available for experimental studies of nest predation; and (3) Marsh Wrens respond in a similar way to eggs of different sizes and colors (Picman 1977). These setups were placed at 10-m intervals along a transect through the Yellow-headed Blackbird colony for a period of five days. Because no predation occurred during this time, the camera setups with nests were placed outside the blackbird colony (along edge of marsh), where Marsh Wrens were defending their territories, for additional two days. These setups were checked twice a day and, if a predation event had occurred, the camera was reset and a broken egg replaced.

Response of blackbirds to wren songs.—The response of male and female Yellow-headed Blackbirds to Marsh Wren songs was examined through playback experiments. Ten active blackbird nests were chosen at random in the study area in 1983. At each we played 10 min of Marsh Wren songs after a 10-min preplayback period of silence. The preplaybacks began once the local birds resumed normal activities after the intrusion of the observer. As a control experiment, five of these nests (randomly chosen) were also played 10 min of the Common Yellowthroat's (*Geothlypis trichas*) repertoire, again after a 10-min preplayback period. These controls were conducted randomly either one day before ($n = 2$), or one day after ($n = 3$) the experimental trials. All of the playbacks were conducted between 0500 and 1000, and none were conducted during inclement weather.

The playback experiments were conducted by placing a speaker on a 2-m-high stake, 3 m from an active blackbird nest. The observer could control the playback recordings using a portable cassette recorder wired to the speaker at a distance of 20 m. Responses of the Yellow-headed Blackbirds were scored as follows: (0) no response; (1) fly near to speaker, but no closer than 3 m, alert; (2) approach speaker from 1 to 3 m away, agitated; (3) approach speaker less than 1 m away, sometimes hovering over speaker, agitated.

Spatial segregation of wrens and blackbirds.—To determine whether or not Marsh Wrens and Yellow-headed Blackbirds were spatially segregated, the presence or absence of their nests was recorded for 10 × 10 m quadrats covering suitable habitat in the study area. Four possible situations arose for any given quadrat: (1) no nests; (2) one or more wren nests only; (3) one or more blackbird nests only; (4) nests of both species present. A chi-square test was used to determine if nest locations for wrens and blackbirds were significantly segregated (Smith 1980).

Correlates of nesting success.—Because nesting success is a binary variable (failed or successful), a BMDP program for a stepwise logistic regression (Dixon 1985) was used to determine the correlates of nesting success. This analysis yields logistic regression coefficients (b) and their significance, as determined by a chi-square test. Twenty-two independent variables

were originally entered. However, because of inter-correlations and missing values, the final analysis included the following independent variables: (1) distance to nearest Marsh Wren nest, (2) harem size, (3) distance to edge of colony, (4) distance to open water, (5) water depth at nest, (6) nest height, (7) relative vegetation density at nest, (8) vegetation height at nest, (9) date nest received its first egg, (10) distance to nearest conspecific neighbor, and (11) location within colony (center vs. periphery). Centrally located nests were in territories surrounded by other blackbird territories. Peripheral nests were in male territories located at the colony edge. The statistical significance was set at the 0.05 probability level. All nests were included in this analysis.

RESULTS

General breeding information.—The first male Yellow-headed Blackbird arrived at the marsh in late April (20 April in 1984), while the first females began arriving in early May (4 May in 1984). Males established territories in the deeper regions of the marsh, near open water, where they eventually acquired up to seven females. Most territories were established in cattail-dominated areas of the marsh. Few males defended areas dominated by reeds, vegetation that normally is associated with the shallower regions of the marsh.

We captured and color banded 42 of 67 territorial males in 1983. In 1984, in the same area, there were 65 territorial males of which 51 were banded (18 were returning males banded in 1983 and 33 were new unbanded males). The third colony, studied only in 1984, included 24 territorial males, none of which were banded. Once males established a territory, they tended to return to the same marsh and usually to the same territory, or settled very close to their previous territory (unpubl. data). By late June, dispersion from the breeding grounds had begun, and flocks of feeding birds became prominent outside of the marsh.

Females alone constructed their nests (usually taking two to three days) and the first females initiated their nests in the second week of May. Most nests (82%) were built in cattails, with 12% in different combinations of cattails, bulrushes, and reeds, and only a few (6%) in bulrushes exclusively. All nests were constructed in the deep-water marsh areas (mean water depth for all active blackbird nests was 38.1 ± 8.0 cm in 1983 and 29.0 ± 6.9 cm in 1984). Clutch initiation began in mid-May and the peak

of laying for first eggs was on 25 May 1983 and 26 May 1984. The number of eggs in a clutch varied from one to five, with most having three or four eggs. Incubation required about 12 days after the second egg was laid.

In general, females were highly synchronous in their nesting activities (ca. 60% of clutch initiations occurred within a five-day period; Fig. 1). Females generally were single brooded; however, some re-nested if their first attempt failed early in the cycle. Internest distances for simultaneously active nearest neighbors varied from 2 to 33 m, and averaged 6.0 m in 1983 and 6.2 m in 1984.

In general, females alone were feeding the young during the nestling stage (ca. 12 days). Females feeding young spent on average more than twice as much time foraging than did incubating females (see Table 1). Most foraging activity for both groups of females was done outside of the marsh (Table 1). Most trips were in the direction of a forested dune ridge that separates Lake Manitoba from the marsh, where many adult Yellow-headed Blackbirds were commonly seen foraging (unpubl. data). This ridge was characterized by its frequent outbreaks of midge (*Chironomidae*) mating swarms, which provided a superabundant food source to the local insectivorous community. Only 7 of 67 territorial males were observed feeding nestlings in 1983.

Nesting success.—We studied 447 active nests of which 229 (51%) eventually failed due to predation, 182 (41%) fledged at least one young, and the remaining 36 (8%) were abandoned or failed for other reasons (Table 2). Of the 229 depredated nests, 143 (62%) failed during egg stages, and the remaining 86 (38%) failed while containing nestlings.

During our two-year study we observed three cases of nest depredation by long-tailed weasels (*Mustela frenata*), with six instances where a weasel or some other small mammal was likely responsible. There were also five cases in which nests were pulled down, probably by a large mammalian predator such as mink (*M. vison*). Finally, there were 48 cases where Marsh Wrens were seen either leaving a recently depredated nest ($n = 14$) with punctured eggs, or were observed singing nearby ($n = 34$).

The importance of Marsh Wrens as nest predators was further demonstrated by the following evidence. First, in all 26 cases when a camera was triggered by a predator, Marsh Wrens were

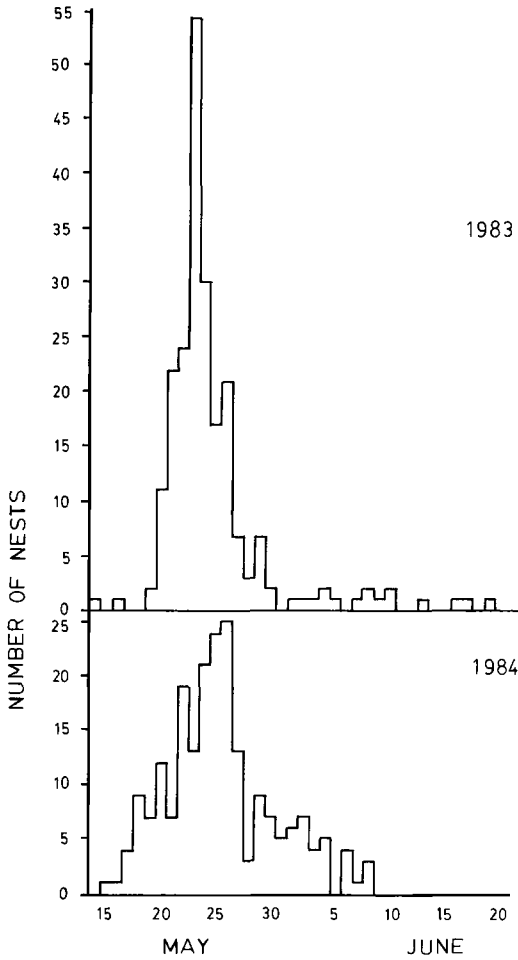


Fig. 1. Initiation of egg laying by female Yellow-headed Blackbirds as function of time for 1983 and 1984.

photographed on the nests. Because direct observations of wrens at the camera setups showed that Marsh Wrens trigger these cameras by pecking the quail egg placed on the trigger loop (Picman 1987a, unpubl. data), the cameras were not triggered accidentally. Second, in the experimental blackbird colonies, almost all (98%)

TABLE 2. Nesting success and causes of nesting failure (percent) for all Yellow-headed Blackbird nesting attempts in 1983 and 1984.

Nest outcome	1983	1984	Com- bined
Successful	31	51	41
Depredated	59	44	51
Abandoned	9	4	7
Failed for other reason	1	1	1
Total no. nests	226	221	447

depredated nests ($n = 64$) were judged to have been depredated by Marsh Wrens (i.e. in these mixed clutches, only blackbird eggs were depredated, but the thick-shelled quail eggs survived). Similarly, of 31 nests set out in transects through an active Yellow-headed Blackbird colony, 26 (84%) were destroyed by day 9, and 25 (96%) of these we considered to have been depredated by Marsh Wrens. This also demonstrates that Marsh Wrens can enter the Yellow-headed Blackbird breeding colony and destroy eggs in unguarded nests. Third, nesting success of Yellow-headed Blackbirds increased with distance of their nests from the nearest Marsh Wren nest in both 1983 and 1984 (Table 3).

Responses to playbacks.—The playback of empty tape did not elicit any response from blackbirds from the control and experimental categories. The playbacks of Common Yellowthroat songs (to the control group) also failed to elicit any response from the Yellow-headed Blackbirds. However, Marsh Wren song playbacks elicited aggressive responses from all 10 females and in 9 of 10 males (Fig. 2). Yellow-headed Blackbirds of both sexes, thus, seem to recognize Marsh Wrens as potential danger to their nests.

Spatial segregation of wren and blackbird nests.—In both years, Marsh Wrens were breeding in the shallow-water areas along the outside edges of the marsh, whereas Yellow-headed Blackbirds occupied the centrally located, deep-water

TABLE 1. Mean (\pm SD) time spent in various activities by female Yellow-headed Blackbirds in egg and nesting stages. Observation period per female was 60 min.

Nesting stage of female (n)	Time (min)		Time foraging (min)		
	On nest	Other ^a	In marsh	On territory	Off marsh
Incubation (9)	44.1 \pm 9.4	2.5 \pm 3.4	0.8 \pm 1.8	4.3 \pm 7.1	10.6 \pm 8.8
Nesting (11)	19.8 \pm 14.3	4.2 \pm 10.4	6.0 \pm 12.6	5.5 \pm 5.5	24.4 \pm 9.8

^a Time spent perched, preening, in sexual chases, mobbing, chasing Marsh Wrens, and interacting with other females.

TABLE 3. Percent (number) Yellow-headed Blackbird nests depredated for four categories of increasing nearest Marsh Wren nest distance in 1983 and 1984 (only successful and depredated nests included). Correlation analysis* performed with original, individual data points.

Distance (m) from nearest wren nest	Percent depredated (n in parentheses)
1983 (r = 0.150*)	
0-15	79 (29)
>15-25	73 (55)
>25-35	58 (59)
>35	60 (60)
1984 (r = 0.204**)	
0-10	58 (50)
>10-20	54 (65)
>20-30	37 (71)
>30	30 (23)

* One-tailed test. *, P < 0.05; **, P < 0.01.

marsh areas (see also Leonard and Picman 1986). In the majority of cases during 1983, only Marsh Wren nests (n = 66 quadrats) or Yellow-headed Blackbird nests (n = 142 quadrats) were present in "inhabited" quadrats. In only 11 quadrats (5% of 219 quadrats that had at least one nest), nests of both species were present on the same quadrat. Nesting sites of wrens and blackbirds were highly significantly spatially segregated (Table

TABLE 4. Analysis of the spatial pattern of distribution of Yellow-headed Blackbird and Marsh Wren nests built before 23 June 1983, and 24 June 1984. Based on presence or absence of nests of these species in 10 × 10 m quadrats.

Yellow-headed Blackbirds	No. quadrats with nests of Marsh Wrens		Total
	Present	Absent	
1983 (X² = 23.72***)			
Present	11	142	153
Absent	66	178	244
Total	77	320	387
1984 (X² = 19.54***)			
Present	13	130	143
Absent	125	342	467
Total	138	472	610

***, P < 0.001.

4). Similar results on spatial segregation between these species were obtained in 1984 (Table 4).

Correlates of nesting success.—The stepwise logistic regression analysis of nesting success against 11 independent variables for 1983 indicated that distance to the edge of the colony was the only significant variable that was entered into the equation (b = 0.059, X² = 16.7, df = 1, P < 0.001). The farther a nest was from the edge, the greater the chance that it would survive until fledging. In 1984, the date of clutch initiation (b = -0.128, X² = 27.1, df = 1, P < 0.001) and the distance to the nearest Marsh Wren nest (b = 0.033, X² = 4.3, df = 1, P = 0.039) were the only variables entered into the equation. The greater the distance a nest was located from Marsh Wrens, the greater the chances of nesting success for Yellow-headed Blackbirds; the earlier clutch initiation began, the greater the chances of success.

DISCUSSION

For this population of Yellow-headed Blackbirds, predation was the most important source of nesting mortality, accounting for 86% of all nesting failures. It was the cause of failure for 51% of all active nests during the two years of our study. Starvation did account for some losses (0.5%), mostly through brood reduction, but in general, food did not appear to be a major limiting factor. Females fed most frequently on a forested dune ridge, where an abundant food source of midges could be found. Furthermore,

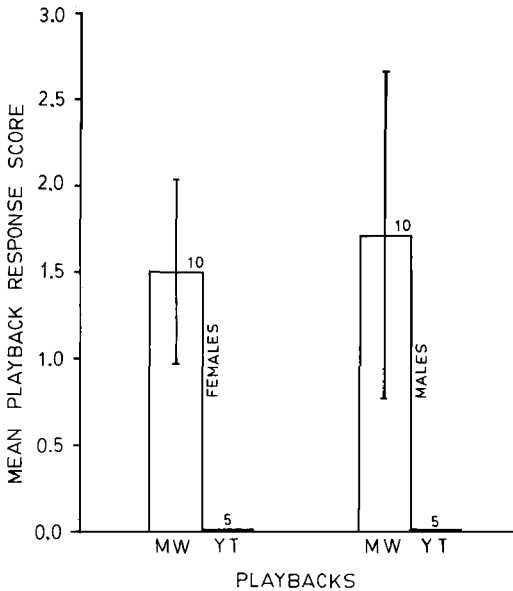


Fig. 2. Mean levels of response (±SD) of male and female Yellow-headed Blackbirds to playbacks of Marsh Wren (MW) and Common Yellowthroat (YT) songs. Sample sizes given above bars.

only 10.5% of males in 1983 were observed feeding nestlings, which is consistent with the observations of Roberts (1909) and Fautin (1941). However, both Willson (1966) and Gori (1984) have reported frequent feeding of young by males. In the marsh studied by Willson, starvation was a major cause of nestling mortality and Gori (1984) reported that, in general, paternal investment in feeding nestlings is greater in unproductive marshes. Therefore, variation in male feeding of nestlings may in part be related to differences between these studies in food abundance.

Marsh Wrens have been identified by other authors as nest predators for both Yellow-headed Blackbirds and Red-winged Blackbirds (*Agelaius phoeniceus*; Orians and Willson 1964, Burt 1970, Verner 1975, Picman 1977, 1980, 1987b, Ritschel 1985, Bump 1986, Picman et al. 1988). Picman (1977, 1980, 1987b), Bump (1986), and Ritschel (1985) considered Marsh Wrens as the most important predator operating in marshes they studied. For the population of Yellow-headed Blackbirds we studied, Marsh Wrens also are the most important predator accounting for most cases of nest depredation. This conclusion is based on three types of evidence. First, during our experiments with nests containing mixed-egg clutches, almost always only the Yellow-headed Blackbird egg was depredated. This clearly implicates Marsh Wren attacks because other predators likely would have destroyed the quail egg as well. Second, the number of successful (nonmanipulated) Yellow-headed Blackbird nests increased with increasing distance of blackbirds from the nearest Marsh Wren nest. Third, the camera study of nest predators revealed only Marsh Wrens.

Although our results suggest that Marsh Wrens are important predators on Yellow-headed Blackbird eggs, wrens also are likely to be a cause of many nestling blackbird losses. Marsh Wrens are known to kill or injure nestling Red-winged Blackbirds and Marsh Wrens (Picman 1977, unpubl. data). The fact that the foraging female Yellow-headed Blackbirds spent more time away from the marsh during the nestling than incubation period suggests that wrens should have more opportunities to visit unguarded blackbird nests during the nestling stage.

Results of the playback experiments are consistent with the finding that the Marsh Wren is an important predator on blackbird nests at Del-

ta Marsh. Both male (with one exception) and female Yellow-headed Blackbirds consistently responded in an aggressive manner to the playbacks of Marsh Wren songs, but failed to respond to playbacks of Common Yellowthroat songs (control). The yellowthroat is another marsh-nesting passerine, present at Delta Marsh, and not known to be a threat to Yellow-headed Blackbird reproductive success. This result is similar to the findings of Bump (1986) and suggests that Yellow-headed Blackbirds recognize Marsh Wrens as a potential danger possibly throughout their breeding range. Presumably, more aggressive responses could have been elicited from the blackbirds if a visual cue of a Marsh Wren had been used in addition to the playback of the wren song (Bump 1986). Nonetheless, naturally occurring agonistic interactions between Yellow-headed Blackbirds and Marsh Wrens have been well documented (Verner 1975, Bump 1986, Leonard and Picman 1986). Typically, adult Yellow-headed Blackbirds chased nearby wrens (usually singing males) from their perches down into the vegetation, and would either continue the chase in the vegetation, or simply perch above the wren.

The finding that those Yellow-headed Blackbird nests located at the edge of the colony suffered a higher rate of nesting failure is consistent with our data that Marsh Wrens, which apparently were responsible for most blackbird nesting mortality, must enter the breeding blackbird colony from outside. Similarly, the Yellow-headed Blackbird nesting success was positively correlated with the distance to the nearest Marsh Wren nest in the other year. Because both distance to the edge of the colony and distance to Marsh Wrens were significantly interrelated in both years, Yellow-headed Blackbirds should preferentially nest as far as possible from Marsh Wrens to reduce the impact of the latter's nest-destroying behavior.

Our study established that: (1) predation was responsible for most of the Yellow-headed Blackbird nesting losses, and (2) Marsh Wrens were the most important nest predator in our marsh. Yellow-headed Blackbirds, however, should be able to protect effectively their nests against Marsh Wrens. The relatively high impact wrens had on our study blackbird population could be explained by location of foraging grounds of the breeding females. Because female Yellow-headed Blackbirds did most of their foraging outside the marsh, this evidently

allowed Marsh Wrens to visit and destroy contents of many unguarded nests.

In one year, females nesting earlier suffered on average a lower rate of depredation. This could be explained in at least two ways. First, earlier nesters are often older, more experienced females (Coulson and White 1958, Crawford 1977). These individuals are likely to choose safer nesting sites, and more effectively defend their nests against potential predators (i.e. may be more effective in excluding Marsh Wrens from the immediate vicinity of their nests). Second, since Yellow-headed Blackbirds are highly synchronous in their nesting activities (Fig. 1), early nesters potentially could maximize the benefit from predator satiation and dilution effects, as well as increased group vigilance and predator mobbing during the period of highest vulnerability to Marsh Wren predation (egg and early nestling stages). Difference between 1983 and 1984 most likely could be explained by different temporal patterns of female settlement (as indicated by initiation of egg laying) in these years. If we examine the peak of egg-laying activities in 1983 and 1984, then in five days of the peak of laying, 65 and 39% of all nests, respectively, had the first egg laid during this period. Because initiation of nesting was less synchronous in 1984, early females could have benefitted more from antipredation behavior of their neighbors than females nesting later. In contrast, greater nesting synchrony in 1983 presumably resulted in similar effects of antipredation behavior of neighbors on nesting success of most females and, consequently, in the lack of a significant effect of the initiation of egg laying on nesting success.

Destruction of Yellow-headed Blackbird eggs by Marsh Wrens and blackbird aggression towards wrens presumably resulted in the spatial segregation of their breeding areas. Yellow-headed Blackbirds physically dominate Marsh Wrens in direct behavioral interactions and, thus, should be able to exclude wrens from the preferred, deep-water marsh areas. This view is supported by the finding that, following removal of Yellow-headed Blackbirds from one breeding colony, Marsh Wrens immediately expanded their territories to include the vacated deep-water marsh areas (Leonard and Picman 1986). The spatial segregation of the two species in our marsh, thus, is a result of interference competition between these passerines rather than of their different microhabitat preferences.

Strong predation pressures are well documented for Temperate Zone marsh-nesting passerines (Ricklefs 1969). For many marsh-nesting blackbirds, predation is considered to be an important source of egg and nestling mortality (e.g. Orians 1961, 1973, 1980, Willson 1966, Robertson 1972, 1973, Holm 1973, Caccamise 1976, Picman 1980, Bancroft 1986, Picman et al. 1988, Westneat 1992); the population of Yellow-headed Blackbirds we studied is no exception. Selection should, therefore, act on Yellow-headed Blackbirds to minimize nest predation. Gregarious nesting, common to many marsh-nesting blackbirds, may reduce predation through: group vigilance and mobbing; predator dilution and satiation effects; and geometric effects. These potential antipredation benefits of colonial nesting by Yellow-headed Blackbirds and their possible implications for polygyny in this species are yet to be examined.

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