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YELLOW-HEADED BLACKBIRD NEST DEFENSE: AGGRESSIVE RESPONSES TO MARSH WRENS[1]

STEPHEN R. BUMP[2]
Department of Biology and the Ecology Center, Utah State University, Logan, UT 84322

Abstract. Marsh Wrens (*Cistothorus palustris*) destroyed Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) eggs presented on wren territories and probably disrupted at least 10 of 189 yellowhead nesting attempts. Male yellowheads discriminated among Marsh Wren, Song Sparrow (*Melospiza melodia*), and Common Yellowthroat (*Geothlypis trichas*) songs, with the greatest proportion of aggressive approaches in response to broadcast Marsh Wren songs. The proportion of aggressive approaches by male yellowheads to Marsh Wren playbacks beside yellowhead nests was 27% and did not change with the stage of the nest; but the proportion of aggressive responses by females did vary, and was highest (53%) in response to playbacks beside nests containing eggs. Male responses are interpreted as reflecting territorial defense against Marsh Wrens, and female responses as a localized nest defense against egg predators.

Key words: Marsh Wrens; Cistothorus palustris; *Yellow-headed Blackbirds;* Xanthocephalus xanthocephalus; *song stimuli; acoustical signals; egg predation.*

INTRODUCTION

Marsh Wrens (*Cistothorus palustris*) destroy eggs and occasionally attack young nestlings of Red-winged Blackbirds (*Agelaius phoeniceus*) (Picman 1977, 1980). Since Marsh Wrens can be a major source of redwing nesting failure (Picman 1980), those blackbirds that successfully exclude Marsh Wrens from the vicinity of their own nests might experience reduced egg losses. Aggression by Red-winged and Yellow-headed (*Xanthocephalus xanthocephalus*) blackbirds toward Marsh Wrens has been described only briefly by Nero (1956), Orians and Willson (1964), Burt (1970), Verner (1975), and Picman (1982). Burt characterized attacks by yellowheads as much more intense than attacks by redwings, and he reported five chases during which male yellowheads actually captured Marsh Wrens and pecked them vigorously. There appears to be considerable antagonism between Marsh Wrens and yellowheads; however, no extensive studies have been done to determine the frequency of these encounters or to elucidate and quantify the nature of the response by yellowheads to the presence of Marsh Wrens.

Although Marsh Wrens often are difficult to locate visually, males are vociferous. Recognition of Marsh Wren songs may be advantageous to blackbirds since it probably is more efficient energetically to monitor evanescent wrens acoustically than to rely on visual cues. Marsh Wren songs, characterized by broad ranges in frequency and sharply broken and repetitive components, fit Marler's (1959:175) criteria for ease in locating the sound source. According to Picman (1977) male Marsh Wrens often sing while puncturing eggs. Yellowheads that respond aggressively to Marsh Wren vocalizations may reduce losses of eggs or of young nestlings caused by Marsh Wren pecking behavior.

The major objectives of this study were (1) to determine whether Marsh Wrens peck Yellow-headed Blackbird eggs, (2) to examine yellowhead responses to broadcast Marsh Wren songs, (3) to compare yellowhead responses to Marsh Wren songs at different nesting stages, and (4) to investigate roles of male and female yellowheads in nest defense against Marsh Wrens.

STUDY AREAS

I performed playback experiments on two study sites, Benson (41°48′N, 111°56′W; elev. 1,347 m, 290 field hr) and Dry Lake (41°34′N, 111°58′W; elev. 1,710 m, 70 field hr), between 30 April and 24 July 1981 in Cache County, Utah. Ten additional playback experiments were performed at Benson between 1 and 15 May 1982. The marshes at Benson supported extensive stands of hardstem bulrushes (*Scirpus acutus*) mixed with small, scattered clumps of cattails (*Typha latifolia*). Exposed vegetation from previous years was present year-round. Dry Lake forms seasonally from spring rains and snow melt from adjacent mountains. As the lake evaporates in late summer, horses from adjacent pastures move in and eat the vegetation, so each spring Dry Lake is left without emergent vegetation from past years. The principal emergents at Dry Lake were hardstem bulrushes, and later, Olney three-square (*Scirpus americanus*). Overnight temperatures were lower at Dry Lake than at Ben-

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[2] Present address: 3516 Russell Blvd. Apt. 30, St. Louis, MO 63104.

son, presumably due to elevational difference. Marshes at both sites were adjacent to alfalfa and corn fields.

Marsh Wrens were actively building nests by 23 March 1981, when male Yellow-headed Blackbirds began to arrive at Benson. Song Sparrows and, later, Common Yellowthroats were heard regularly in Benson marshes. At Dry Lake, however, yellowheads were the only passerines I saw on the marshes until 24 July, when Marsh Wrens were seen and heard singing there. At Benson, the presence of old vegetation enabled territorial establishment by yellowheads soon after males arrived, but at Dry Lake nesting was delayed until early June when emergent hardstem bulrushes became available to the birds. Female yellowheads began laying eggs at Benson during the first week in May, whereas few nests at Dry Lake contained eggs by mid-June. The sparse vegetation at Dry Lake was exposed to strong afternoon winds, which occasionally leveled stands of bulrushes. A storm deluged the Benson area, causing water levels to rise over 60 cm between 19 and 29 May 1981.

METHODS

Yellow-headed Blackbird eggs were collected from flooded nests and were refrigerated until several hours before being presented to Marsh Wrens. A yellowhead nest was tied to bulrushes at five locations, each near the song perch of a different Marsh Wren, and two eggs were placed in the nest for each trial. Observations were made 7 m from the nest, and wren activity at the nest was filmed during two of the five trials with an Argus 815 Super 8 movie camera. Trials were terminated either at the end of 1 hr or when eggs were destroyed by the wren.

I outlined territories of male Yellow-headed Blackbirds on maps of the study areas. Yellowheads were not banded, yet several males were recognizable by plumage characteristics that developed later in the season. Perches from which a male yellowhead regularly sang and displayed uncontested by conspecifics were considered to be within his territory, and I assumed that nests circumscribed by his flights between perches also belonged to that male. When there was a question about nest "ownership" I assumed that a nest belonged to the female that flew up from the vicinity of that nest when I approached the marsh, and that females were mated to the male on whose territory they spent most time. Nevertheless, during experiments I often could not be sure that a female responding to playbacks beside a nest was the same female which had laid, or eventually would lay, eggs in that nest.

I found yellowhead nests by carefully searching each study area once a week for the first two to three weeks, and then by perusing the territories and adjacent areas immediately following playbacks on those territories. I numbered each nest, tied a short yellow flag above it, and recorded its contents.

I divided the phenological sequence of nesting into five stages. Yellowhead territories without any structurally complete nests were designated *prenesting*. Structurally complete nests that contained no eggs were *prelaying*. The *egg* stage referred to nests containing one or more eggs. *Nestlings* denoted nests that contained nestlings and no eggs. Active nests were nests that contained eggs or nestlings. Except in four cases, playbacks were not done beside nests containing a combination of eggs and nestlings, so that I could determine whether yellowheads defended one stage more aggressively than another.

I assessed the response of yellowheads to Marsh Wren songs by a series of playback experiments. Vocalizations of Song Sparrows (*Melospiza melodia*) and Common Yellowthroats (*Geothlypis trichas*), commonly heard at Benson, were used as controls. Songs used for playbacks were recorded near Benson on a Uher 4000 Report-L tape recorded at 19 cm/sec with a Sony 265 microphone mounted on a 58-cm parabolic reflector. Volume was roughly standardized. Common Yellowthroat tapes were modified to repeat a song every 10 sec; Song Sparrow and Marsh Wren tapes did not require such modification. Yellow-headed Blackbird tapes repeated a song every 15 sec. The four resulting playback tapes (Marsh Wren, Song Sparrow, Common Yellowthroat, and Yellow-headed Blackbird) each lasted 2 min.

Playback equipment consisted of the Uher tape recorder played at 19 cm/sec; 25 m of speaker wire; and a 20-cm, 8-ohm, 10-watt Quam speaker mounted on a wooden tripod. The speaker face was covered with a black nylon cloth.

Of the 169 playback trials, 129 were conducted on Benson marshes and 40 on Dry Lake (Table 1). Territories and nests sampled were selected the day prior to trials. Trials on adjacent territories were avoided for 24 hr to reduce habituation, and I waited at least 24 hr after inspecting nests on a territory before doing a trial on that territory. Nests had to be accessible and males had to be present on the territory before setting up a trial; if males were absent, I moved to the next designated territory. Territories closer to shore were sampled more readily than others and may be overrepresented since I did not sample all territories equally, although I did sample every ter-

TABLE 1. Number of playbacks presented to Yellow-headed Blackbirds according to song type, type of response elicited, and nesting stage. The number of trials in which a similar response category, male or female, resulted from both playbacks within a trial (Marsh Wren and alternate) is enclosed in parentheses.

Nesting stage	Alternate playbacks: Song Sparrow	Alternate playbacks: Common Yellowthroat	Alternate playbacks: Yellow-headed Blackbird	Alternate playbacks: Total	Marsh Wren playbacks
Prenesting					
Playbacks	7	8	9	24	24
Male responses	7 (7)	8 (8)	9 (9)	24 (24)	24 (24)
Female responses	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Prelaying					
Playbacks	18	18	14	50	50
Male responses	18 (16)	16 (15)	13 (11)	47 (42)	44 (42)
Female responses	4 (0)	4 (2)	4 (3)	12 (5)	14 (5)
Eggs					
Playbacks	14	17	17	48	48
Male responses	12 (10)	12 (10)	15 (6)	39 (26)	29 (26)
Female responses	8 (7)	15 (11)	6 (5)	29 (23)	30 (23)
Nestlings					
Playbacks	8	8	31	47	47
Male responses	8 (6)	8 (7)	27 (25)	43 (38)	39 (38)
Female responses	2 (2)	1 (0)	8 (5)	11 (7)	15 (7)
Total					
Playbacks	47	51	71	169	169
Male responses	45 (39)	44 (40)	64 (51)	153 (130)	136 (130)
Female responses	14 (9)	20 (13)	18 (13)	52 (35)	59 (35)

ritory I had access to and could define. Trials were conducted between 0600 and 2100.

In each trial two playbacks, Marsh Wren and alternate-species playback (Song Sparrow, Common Yellowthroat, or Yellow-headed Blackbird), were presented on yellowhead territories. The speaker was placed 1 m from a nest or, for prenesting territories, near the territory center. The order of presentation was chosen for convenience and usually alternated between trials (e.g., Marsh Wren playback first, Song Sparrow second; Song Sparrow first, Marsh Wren second; Marsh Wren first, Common Yellowthroat second; etc.). Alternate species' songs were selected for playback arbitrarily with a conscious attempt to have all categories represented, yet without a system that would have ensured equal representation of all categories. Thus, sampling was not random and potentially may have biased experimental results; however, the order in which playbacks were presented was not related to male yellowhead responses during either wren or alternate playbacks (Table 2), although admittedly sample sizes were small.

The first series of sample periods began 8 min after the speaker was in place and I was positioned for observation. Each sample period lasted 1 min. Before starting playbacks I recorded male yellowhead activities during the first sample period and Marsh Wren activities during the second. Playback was initiated then, and I noted male and female yellowhead responses during the third sample period and Marsh Wren activities during the fourth. The trial continued with a second series of sample periods beginning at least 8 min after the first playback ended, performed in the same manner as the first series, but with a different species' playback tape (Marsh Wren or alternate).

Playbacks were initiated only when a male was present on the territory; females were not always present. Thus, *male responses* include cases when the female was absent, when she was present but did not approach, and when the male approached aggressively before the female approached. *Female responses* include cases when the male did not approach, and when the female approached aggressively before the male approached. Therefore, a playback might yield only a male response, only a female response, both male and female responses (i.e., both present, neither approached), or neither male nor female response (e.g., approach by male followed by flight over the speaker by female). Since a trial consisted of one pair of playbacks, it is not always possible to make paired comparisons within trials because one playback may have yielded a male response while the other gave a female response. Responses are classified as either an aggressive approach or not aggressive. Aggressive approaches were the most characteristic aggressive response by Yellow-headed Blackbirds to playbacks and consisted of flights over

TABLE 2. Comparison of male Yellow-headed Blackbird responses to playbacks according to the order in which playbacks were presented. Only trials in which Yellow-headed Blackbird behavior qualified as male responses during both Marsh Wren and alternate playbacks are included. A = alternate playback presented first; B = Marsh Wren playback presented first. AA = aggressive approach, NA = not aggressive. MW = Marsh Wren, SS = Song Sparrow, YT = Common Yellowthroat, YHB = Yellow-headed Blackbird.

Order of playback	Trial comparisons											
	MW vs. SS				MW vs. YT				MW vs. YHB			
	AA	NA	AA	NA	AA	NA	AA	NA	AA	NA	AA	NA
A	4	17	0	21	3	14	0	17	5	18	4	19
B	4	14	0	18	9	14	3	20	5	23	4	24
	NS[a]		NS[a]		NS[a]		NS[a]		NS[a]		NS[a]	

[a] df = 1, $P > 0.10$, Fisher's exact test.

or landing within 3 m of the speaker. In the absence of aggressive approach yellowhead responses are classified as not aggressive; this includes behaviors either not directed toward the speaker (perch changes, leaving the territory, sexual chasing, foraging, vocalizing, etc.), nor behaviors directed toward the speaker but presumably of lesser intensity than aggressive approaches (tail flicks; *check* or *pit* calls; sleeked alert posturing; approaching the speaker, but not within 3 m; etc.). Only aggressive approaches are counted as aggressive responses to playbacks and, when there was a flight toward the speaker, only the first bird of the pair to approach the speaker was scored for that test.

Marsh Wren activity was monitored by the number of wren songs given per minute within 25 m of the speaker to determine whether changes in wren song rates might bias yellowhead responses to playbacks. Marsh Wrens respond to Marsh Wren playbacks by being quiet and secretive during the first 2 or 3 min of playback; they then fly to a nearby perch where they steadily increase their song rate to significantly above normal (J. Verner, pers. comm.). Thus, it is unlikely that singing wrens would interfere with blackbird responses to playbacks.

Data were analyzed using Chi-square and Wilcoxon's matched-pairs signed-ranks tests (tied scores disregarded).

RESULTS

Wrens destroyed eggs in four of the five Yellow-headed Blackbird nests presented to them. The fifth nest was approached by a Marsh Wren, but the eggs were not disturbed. I also saw a Marsh Wren enter and destroy eggs in a Yellow-headed Blackbird nest as I was placing the speaker beside the nest in preparation for a playback. Two 8-mm films showed wrens reaching into the nest and then, lifting their heads, moving moist mandibles as if drinking egg contents; however, little appeared to be consumed at the nest. After sampling the eggs' contents, wrens disappeared into the marsh for one to several minutes carrying eggs. Wrens removed the second egg in the same way and also carried away portions of egg yolk without the shell. The wren that did not sample the eggs' contents dropped both eggs within 4 m of the nest. After two jabs the first egg rolled down the side of the nest into the water, and the second was dropped in flight en route to a perch where the wren sang loudly.

Large portions of egg shells were removed, but small shell chips and smeared yolk were often left in the nest. One wren sang while he destroyed eggs, but all others were silent at the nest.

From notes on 189 active yellowhead nests visited more than once in Benson marshes, eggs in at least 10 (5%) appear to have been destroyed by Marsh Wrens. I saw a wren destroy one clutch of yellowhead eggs. Marsh Wrens were seen within 25 m of all 9 Yellow-headed Blackbird nests that contained egg shells with small holes or narrow tears and with contents either partially or not consumed, suggesting destruction by Marsh Wrens. Marsh Wrens apparently attacked and removed young nestlings as well. In a marsh where I did not monitor nest success, I found two young Yellow-headed Blackbird nestlings below a nest. One chick, still alive, hung by its neck between the leaves at the base of the cattail supporting the nest. The other chick was dead in the water and had four needle-like puncture wounds in the head. A Marsh Wren, presumably responsible for the condition of the nestlings, sang 5 m from the nest. I found no convincing evidence that Marsh Wrens had attacked nestlings from other yellowhead nests.

Yellowheads occasionally perched within 5 m of a singing Marsh Wren and initially seemed not to notice him, but suddenly plunged headfirst at the wren. Wrens quickly escaped into dense vegetation when yellowheads flew at them, and I never saw a blackbird actually capture or strike a Marsh Wren. Yellowheads, unable to maneuver in the dense vegetation,

TABLE 3. Comparison of male Yellow-headed Blackbird responses to the speaker during pre-playback and playback sample periods.

	Yellow-headed Blackbird response		
Sample periods	Aggressive approach	Not aggressive	χ^2
Marsh Wren			
Pre-playback	5	131	20.5*
Playback	30	106	
Song Sparrow			
Pre-playback	1	44	1.0^{NS}
Playback	0	45	
Common Yellowthroat			
Pre-playback	2	42	0.2^{NS}
Playback	3	41	

* df = 1, $P < 0.0005$.
NS df = 1, $P > 0.10$.

climbed around on the matted cattails and bulrushes in attempting to follow the Marsh Wrens. At Benson, I estimated a ratio of 41 male : 64 female yellowheads. Using the sex ratio to approximate an expected frequency of chases by males and females, I saw male yellowheads chase wrens significantly more often than I saw females chase them ($\chi^2 = 16.0$, df = 1, $P < 0.0005$). I observed 41 chases by male yellowheads and 16 by females from 10 May to 24 June 1981, with 25 chases on 10 May. It is noteworthy that 23 of these chases were directed toward one Marsh Wren by two pairs of neighboring yellowheads. The territory of one pair had only one nest without eggs (laying began 11 May), and the other territory had two nests, one without eggs (laying began between 11 and 13 May) and another with four eggs.

Yearling yellowheads also chased Marsh Wrens. As early as 10 May I saw an adult male together with a yearling female (Crawford and Hohman 1978), presumably mated, repeatedly chasing a Marsh Wren. On 5 June I saw two yearling males chasing Marsh Wrens and singing, as female yellowheads flew over the area. They did not establish territories.

Except in one instance, yellowheads did not lunge headfirst at the speaker playing Marsh Wren songs the way they responded to live Marsh Wrens. Instead, they often flew to and hovered over the speaker, sometimes landing 1 to 2 m from it. During four playbacks male yellowheads from other territories also were attracted to Marsh Wren playbacks, and in three cases the residents ignored the songs and defended their territories against conspecific intruders. In the fourth case the resident male flew over and landed beside the speaker, and a neighboring male flew toward the playback and onto the territory but did not approach the resident male.

Male yellowheads did not respond aggressively to Song Sparrow or to Common Yellowthroat playbacks (Table 3). They responded more strongly to Marsh Wren playbacks than to playbacks of either Song Sparrow or Common Yellowthroat (Table 4). Sample sizes were too small for a similar comparison using female responses, so results of that test are inconclusive.

The proportion of aggressive approaches by male yellowheads to Marsh Wren playbacks did not change with the stage of the nests (Table 5). Marsh Wren playbacks beside nests with eggs elicited a significantly greater proportion of aggressive approaches by females than did playbacks beside prelaying nests. Females defended nestlings considerably less often than they defended eggs, although this difference was not significant.

The frequency of songs given by Marsh Wrens within 25 m of the speaker did not change significantly between pre-playback and playback observations (song rate: $z = 0.686$, $n = 25$, 2-tailed $P = 0.493$, Wilcoxon's signed rank test), and wrens were seen approaching the speaker during only two playbacks of wren song. Thus, Marsh Wren responses probably did not confound yellowhead responses to playbacks.

TABLE 4. Response by Yellow-headed Blackbirds to playbacks of Marsh Wren songs compared with their responses to Song Sparrow and Common Yellowthroat playbacks. Only trials in which a similar response category resulted from both Marsh Wren and alternate playbacks within a trial are included.

	Male responses			Female responses	
Playback comparison	Aggressive approach	Not aggressive	χ^2	Aggressive approach	Not aggressive
Marsh Wren	8	31		3	6
vs.			8.91*		
Song Sparrow	0	39		1	8
Marsh Wren	12	28		4	9
vs.			6.65*		
Common Yellowthroat	3	37		3	10

* df = 1, $P < 0.01$.

TABLE 5. Responses by Yellow-headed Blackbirds to playbacks of Marsh Wren songs presented beside Yellow-headed Blackbird nests at various nesting stages (playbacks at prenesting stage broadcast from territory center).

	Male responses			Female responses		
Nest stage	Aggressive approach	Not aggressive	χ^2	Aggressive approach	Not aggressive	χ^2
Prenesting	6	18		—	—	
Prelaying	8	36	0.44^{NS}	2	12	
Eggs	7	22	0.38^{NS}	16	14	6.02^{*}
Nestlings	9	30	0.01^{NS}	4	11	2.88^{a}

^{NS} df = 1, $P > 0.10$.
* df = 1, $P < 0.025$.
^{a} df = 1, $0.10 < P < 0.05$.

DISCUSSION

Marsh Wrens destroyed and removed eggs from Yellow-headed Blackbird nests. In four of five cases Marsh Wrens punctured eggs, gave every appearance of sampling egg contents, and then promptly disappeared into the marsh with the eggs. Allen (1914) and Monnett (cited in Picman 1977) also reported seeing Marsh Wrens sample Red-winged Blackbird egg contents, but Picman (1977) found only 1 instance in 35 observations of egg destruction in which a Marsh Wren seemed to eat something from a broken egg. Picman also found that Marsh Wrens attacked Red-winged Blackbird nestlings, and he suggested that such behavior may be common. Marsh Wrens also appear to peck nestlings of Yellow-headed Blackbirds, but of 189 nests monitored at Benson I found no evidence that this had occurred. Nevertheless, Marsh Wrens were implicated in the destruction of eggs in at least 10 of those 189 nests.

Yellow-headed Blackbirds responded to playbacks of Marsh Wren songs (Table 3), yet qualitatively these responses were different from observed reactions to live Marsh Wrens. Since Marsh Wren songs contain a broad spectrum of frequencies and sharp discontinuities, they are probably easy for yellowheads to localize, but visual cues are likely to be important releasers for actual chases. The lack of a visual target may explain why yellowheads failed to lunge at the speaker during playbacks of Marsh Wren songs.

Why yellowheads did not approach aggressively during more than 60% of the Marsh Wren broadcasts beside nests with eggs (Table 5) is puzzling. Natural selection is expected to encourage behaviors that minimize an individual's projected costs and maximize its reproductive success. The cost to yellowheads responding aggressively to Marsh Wrens near nests with contents vulnerable to wren destruction is probably minimal. Adult yellowheads chasing Marsh Wrens do not incur the risk of injury associated with responses to predators such as raptors or terrestrial mammals. Time spent chasing wrens represented only a small fraction of the time devoted to attracting females, so males chasing wrens were not expected to attract fewer females than males that did not attack Marsh Wrens. Neither can chasing Marsh Wrens be considered an important energetic consideration for males, since they vigorously chased females and male intruders without hesitation and wren chases were relatively infrequent. Also, by responding to Marsh Wrens near vulnerable nests males did not commit themselves to future investment in those nests. Benefits were potentially great in terms of reproductive success for males that attacked Marsh Wrens threatening their eggs or nestlings. Adult yellowheads inevitably won direct confrontations with Marsh Wrens. If a parent responded in time, the probability of clutch survival was substantially increased, presumably increasing the individual's reproductive success as well.

Siglin and Weller (1963) similarly noted that "responses of Yellow-headed Blackbirds to models [of predators] were considerably more variable and of lower intensity than those of Red-winged Blackbirds," and "attacks were a common response of redwings but were rare among yellowheads." It is possible that the predators represented by models to evoke aggressive responses from yellowheads were too rare to have selected for strong responses from yellowheads or, as in the case of raptors that are mobbed almost exclusively in flight yet have been represented by perched study skins (Siglin and Weller 1963), the models have not incorporated effective releasers.

Only male Marsh Wrens sing (Bent 1954); however, male and female adult and immature Marsh Wrens peck blackbird eggs (Picman 1977). Verner (1965) found Marsh Wrens already fledged in early May when yellowheads began nesting, and it is likely that immature wrens are encountered at least occasionally by nesting yellowheads. Thus, Yellow-headed Blackbirds should exclude not only vocal male Marsh Wrens but also females and immatures, which are usually silent and move quietly through a marsh. Visual cues may be stronger releasers for aggressive responses than vocal cues because not all wrens sing, yet all pose a potential threat to blackbird clutches.

Male yellowheads responded aggressively to Marsh Wren playbacks, but not to broadcast Song Sparrow or Common Yellowthroat songs (Table 4), indicating that males discriminated among song stimuli. Male aggressiveness did not fluctuate with the vulnerability of nest contents, but female responses did (Table 5). It remains unclear whether females differentiated among playbacks of Song Sparrow or Common Yellowthroat and Marsh Wren. Nevertheless, the pattern of their responses to broadcast Marsh Wren songs suggests that females responded to wrens by defending eggs more than nestlings. A model of nest defense based solely on the mean amount of future reproductive success for progeny of a given age and sex predicts that yellowhead responses will continually increase through the nesting stages. Patterson et al. (1980) showed that such a model must incorporate the biological relevance of the stimulus, so that responses to an egg predator will be stronger during the egg stage than at other stages. The pattern of female yellowhead responses to Marsh Wren songs best reflects the response to an egg predator. Thus, it appears that females recognized Marsh Wrens primarily as egg predators and responded to Marsh Wren playbacks accordingly.

Female yellowheads nesting near Marsh Wrens probably do not defend their nests effectively by themselves (Rutberg and Rohwer 1980), so male yellowheads are an important component in nest defense against predators such as Marsh Wrens. Although males responded infrequently to playbacks of wren songs presented beside nests, I observed more chases of live Marsh Wrens by male yellowheads than by females, and this is consistent with Verner's (1975) data. This simply could reflect the broader surveillance by males since they appeared to be more conscious than females of conspecifics flying over their territories. Thus, males probably were more aggressive toward wrens than playback experiments might imply.

Trivers (1972) emphasized that sexual selection rarely favors similar male and female reproductive strategies. It is clear that male and female Yellow-headed Blackbirds had different roles in their defense against Marsh Wrens. In responding to Marsh Wrens, females defended nests against egg predators; whereas males, in a more general way, defended their territories. Excluding Marsh Wrens from a territory may enhance territory quality. Males might then attract more females and sire more offspring than males not excluding wrens.

Females were absent from their territories during 15 of the 97 playbacks beside nests with eggs, presumably foraging on an abundance of insects in alfalfa fields adjacent to the marshes. The time spent off territories by females with eggs probably reflects a compromise between the threat of clutch loss by predators and the threat of starvation. Willson and Orians (1963) and Willson (1966) reported that, in the colonies they studied, starvation was the major cause of yellowhead nestling mortality. Orians (1980:29) found that the presence of carp (*Cyprinus carpio*) in lakes severely reduced the emergence of odonates, on which yellowheads specialize for food, and he presented evidence that carp infestations can devastate yellowhead breeding attempts. Carp were abundant in all Benson marshes, and yellowheads often left their territories to feed in agricultural crops on adjacent uplands, very likely in response to poor food availability on territories. Thus, females may have been forced to leave their territories to forage in spite of a real threat to their clutches by Marsh Wrens.

Studies of interspecific aggressive responses to songs (non-mimics) have focused on species that use resources in similar ways and for which interspecific aggression probably reduces competition (Gill and Lanyon 1964, Cody 1969, Gorton 1977, Catchpole 1978, Reed 1982). Yellowheads and Marsh Wrens may compete for food when marsh insect production is low, but female yellowhead responses to broadcast Marsh Wren songs on yellowhead territories appear to be nest defense against an egg predator rather than against a competitor for food, although these are not exclusive alternatives. It is reasonable to expect prey (yellowheads) to respond "appropriately" to the acoustical signals of their predators (Marsh Wrens) if those signals are given with regularity. Support for this view comes from this study, and from Rowe and Owings (1978), who demonstrated that California Ground Squirrels (*Spermophilus beecheyi*) can extract information leading to changes in the squirrels' behavior from the rattling sounds of Northern Pacific Rattlesnakes (*Crotalus viridis oreganus*).

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LITERATURE CITED

ALLEN, A. A. 1914. The Red-winged Blackbird: a study in the ecology of a cattail marsh. Abstr. Proc. Linn. Soc. N.Y., Nos. 24–25, 1911–1913, p. 43–128.

BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers and their allies. U.S. Nat. Mus. Bull. 195:1–475.

BURT, D. E. 1970. Habitat selection and species interactions of some marsh passerines. M.Sc.thesis, Iowa State University, Ames.

CATCHPOLE, C. K. 1978. Interspecific territorialism and competition in *Acrocephalus* warblers as revealed by playback experiments in areas of sympatry and allopatry. Anim. Behav. 26:1072–1080.

CODY, M. L. 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. Condor 71:222–239.

CRAWFORD, R. D., AND W. L. HOHMAN. 1978. A method for aging female Yellow-headed Blackbirds. Bird-Banding 49:201–207.

GILL, F. B., AND W. E. LANYON. 1964. Experiments on species discrimination in Blue-winged Warblers. Auk 17:658–663.

GORTON, R. E., JR. 1977. Territorial interactions in sympatric Song Sparrow and Bewick's Wren populations. Auk 94:701–708.

MARLER, P. 1959. Development in the study of animal communication, p. 150–206. *In* P. R. Bell [ed.], Darwin's biological work. Cambridge Univ. Press, Cambridge, England.

NERO, R. W. 1956. A behavior study of the Red-winged Blackbird. II. Territoriality. Wilson Bull. 68:129–150.

ORIANS, G. H. 1980. Some adaptations of marsh-nesting blackbirds. Princeton Univ. Press, Princeton, NJ.

ORIANS, G. H., AND M. F. WILLSON. 1964. Interspecific territories of birds. Ecology 45:736–745.

PATTERSON, L., L. PETRINOVICH, AND D. K. JAMES. 1980. Reproductive value and appropriateness of response to predators by White-crowned Sparrows. Behav. Ecol. Sociobiol. 7:227–231.

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

PICMAN, J. 1980. Impact of Marsh Wrens on reproductive strategy of Red-winged Blackbirds. Can. J. Zool. 58:337–350.

PICMAN, J. 1982. Impact of Red-winged Blackbirds on singing activities of Long-billed Marsh Wrens. Can. J. Zool. 60:1683–1689.

REED, T. M. 1982. Interspecific territoriality in the Chaffinch and Great Tit on islands and the mainland of Scotland: playback and removal experiments. Anim. Behav. 30:171–181.

ROWE, M. P., AND D. H. OWINGS. 1978. The meaning of the sound of rattling by rattlesnakes to California Ground Squirrels. Behaviour 66:252–267.

RUTBERG, A. T., AND S. ROHWER. 1980. Breeding strategies of male Yellow-headed Blackbirds: results of a removal experiment. Auk 97:619–622.

SIGLIN, R. J., AND M. W. WELLER. 1963. Comparative nest defense behavior of four species of marsh birds. Condor 65:432–437.

TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 136–179. *In* B. G. Campbell [ed.], Sexual selection and the descent of man, 1871–1971. Aldine Press, Chicago.

VERNER, J. 1965. Breeding biology of the Long-billed Marsh Wren. Condor 67:6–30.

VERNER, J. 1975. Interspecific aggression between Yellow-headed Blackbirds and Long-billed Marsh Wrens. Condor 77:329–331.

WILLSON, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. Ecol. Monogr. 36:51–77.

WILLSON, M. F., AND G. H. ORIANS. 1963. Comparative ecology of Red-winged and Yellow-headed blackbirds during the breeding season. Proc. XVI Int. Congr. Zool. 3:342–346.