WHY ARE NESTING MARSH WRENS AND YELLOW-HEADED BLACKBIRDS SPATIALLY SEGREGATED?

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ABSTRACT.—The activity centers of Marsh Wrens (*Cistothorus palustris*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) are spatially segregated. This segregation may occur because (1) one species excludes the other or (2) the two species prefer different habitats. These hypotheses were tested by documenting changes in the size and location of Marsh Wren territories throughout the breeding season, and by the removal of conesting Yellow-headed Blackbirds. The expansion of Marsh Wren territories into blackbird breeding areas after both the natural departure and the removal of blackbirds best supports the explanation based on the active exclusion of Marsh Wrens by Yellow-headed Blackbirds. *Received 8 February 1985, accepted 21 August 1985.*

ECONOMIC defensibility of resources (Brown 1964) necessary for reproduction should favor the evolution of breeding territories in birds. Resources are defended most often against conspecifics because these individuals are generally more similar in their requirements than heterospecifics. However, territories also may be defended against individuals of closely related species and morphologically or ecologically similar species (e.g. Cody 1969, Reed 1982). Of particular interest are incidences of interspecific aggression and territoriality between markedly dissimilar species (Willson 1967; Verner 1975; Picman 1980, 1982).

Marsh Wrens (*Cistothorus palustris*) puncture eggs and kill nestlings of other marsh-nesting passerines (Orians and Willson 1964, Burt 1970, Picman 1977, Bump 1983). Aggressive interactions have been noted between Marsh Wrens and Swamp Sparrows (*Melospiza georgiana*; Willson 1967), Song Sparrows (*M. melodia*; Willson 1967), Red-winged Blackbirds (*Agelaius phoeniceus*; Orians and Willson 1964, Willson 1967, Picman 1983), and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*; Orians and Willson 1964, Verner 1975, Bump 1983). Previous evidence suggests that egg pecking has evolved primarily as a means of reducing competition and not of obtaining food (Picman 1984). Marsh Wren nest locations and feeding areas are often spatially segregated from other co-occurring passerines (Willson 1967, Verner 1975, Picman 1980).

The most intensive studies have concentrated on interactions between Marsh Wrens and Red-winged Blackbirds (Nero 1956, Burt 1970, Runyan 1979, Picman 1980). Yellow-headed Blackbirds also nest in marshes, and limited evidence suggests that yellow-heads may force compression of Marsh Wren territories (Orians and Willson 1964, Verner 1975).

Spatial segregation between Marsh Wrens and Yellow-headed Blackbirds can be explained by the following hypotheses. (1) One species excludes the other from mutually preferred habitat, either directly through behavioral interactions (interference competition) or indirectly through resource depletion (exploitation competition) (Ricklefs 1979). (2) Each species prefers a different habitat. These hypotheses make the following predictions. First, if one species excludes the other, then the removal of the dominant species should result in the movement of the subordinate species into that area. This expansion should not occur in areas inhabited only by the subordinate species. If, however, spatial segregation results from differences in habitat preference, then both species should remain in the same area throughout the breeding season, regardless of the presence or absence of the other species, and barring any major seasonal changes in the habitat. Alternatively, if one species actively excludes the other, then aggressive interactions should be observed between them. The absence of aggressive interactions would support the explanation based on indirect exclusion.

The purpose of our study was to determine which hypothesis best explains spatial segregation between Marsh Wrens and Yellow-

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TABLE 1. Dates of sampling periods for 1983 and 1984 and the maximum number of Yellow-headed Blackbird nests active during those intervals at Site 2.

Year	Period	Date	No. (%) of active yellow-head nests
1983	1	22 May to 5 June	197 (87%)
	2	5-19 June	131 (58%)
	3	19 June to 3 July	19 (8.4%)
	4	3-15 July	5 (2.2%)
1984	1	24 May to 7 June	194 (88%)
	2	7-21 June	180 (82%)
	3	21 June to 5 July	14 (6.4%)
	4	5-17 July	2 (0.9%)

headed Blackbirds. Two types of data were collected to test the above predictions: (1) descriptive data on interactions between the species and on seasonal changes of wren territories in one area with and another area without yellow-heads; and (2) experimental data on the responses of Marsh Wrens to the removal of nesting yellow-heads.

METHODS

Study sites.—The descriptive study was conducted from 22 May to 16 July 1983 and 24 May to 17 July 1984 in two marsh sites in Delta, Manitoba, Canada. Site 1 was a relatively dry, homogeneous cattail (*Typha* spp.) marsh, approximately 6 ha in area, that supported 13 Marsh Wren territories in 1984. In addition, 2 pairs of Common Yellowthroats (*Geothlypis trichas*) and 3 pairs of Red-winged Blackbirds nested along the drier edges of this site. Site 2 was 4 ha in area and consisted of phragmites (*Phragmites australis*) and cattails along the edges, and bulrush (*Scirpus* sp.) and cattail patches surrounding two central ponds. In 1983 this marsh contained 67 Yellow-headed Blackbird and 6 Marsh Wren territories; in 1984, there were 63 yellow-head and 10 Marsh Wren territories. No other passerines nested in this area. The vegetation at both study sites became denser as the season progressed (i.e. with the growth of new vegetation). However, water depth and the composition and distribution of vegetation within each site remained constant. Both sites were divided into a grid of 20 × 20-m squares, marked by 2-m-high wooden stakes. Water depth was measured at each stake using a 100-cm-high stick divided into 5-cm intervals. The experimental study was conducted from 31 May to 11 June 1984 at a third site in Delta. This site was approximately 1.5 ha in size and composed of a relatively homogeneous cattail stand surrounding a small pond. The area contained 21 yellow-head and 4 Marsh Wren territories.

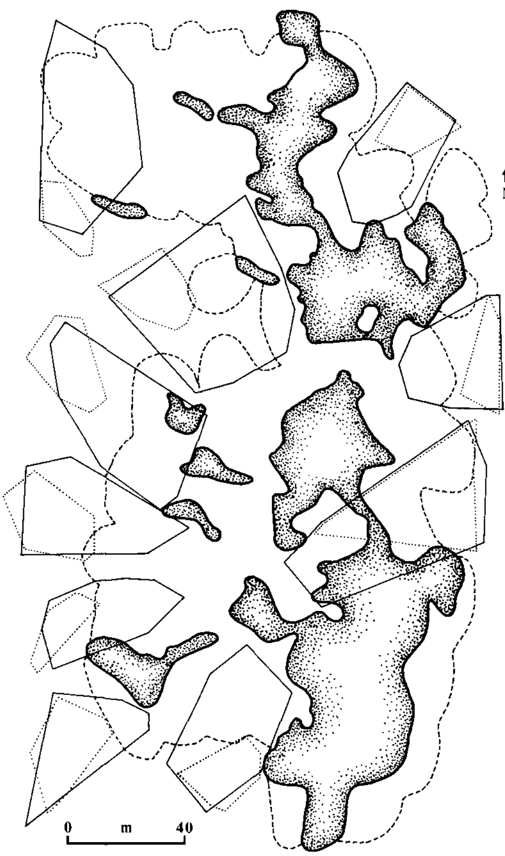

Fig. 1. Map of Marsh Wren territories at Site 2 for Period 2 when yellow-heads were present (dotted lines) and Period 3 when yellow-heads were absent (solid lines), 1984. Shaded areas represent water. The boundary of the yellow-head colony is represented by a dashed line. Results were similar for 1983.

Territory movements.—Male yellow-heads in the Delta area arrive approximately three weeks before male Marsh Wrens (pers. obs.). Yellow-head males were captured and marked individually with colored leg bands. Territory boundaries were mapped by plotting song perches and flight paths of individual males on a map of the study site. Each male was observed for a 30-min interval twice a week throughout the breeding season.

Twenty-six of 29 male Marsh Wrens were trapped and marked. Territory boundaries were mapped on a weekly basis throughout the study period by observing the movements of individual males during 1-h intervals in 1983 and 30-min intervals in 1984. Song perches, courtship nests (Verner 1963), and flight paths were plotted on maps of the study sites for each interval. Territory areas were calculated by the minimum convex polygon method for four 2-week in-

TABLE 2. Mean water depth (cm, ± SD) measured in Marsh Wren and Yellow-headed Blackbird territories at Site 2 in 1983 and 1984 and mean water depth in Marsh Wren territories at Site 1 in 1984.

	Site 2		Site 1
	1983	1984	1984
Marsh Wren	23.0 ± 10.9 $n = 28$	17.0 ± 11.6 $n = 26$	8.98 ± 5.42 $n = 76$
Yellow-head	39.2 ± 8.9 $n = 35$	33.9 ± 9.7 $n = 60$	
Statistical comparison	$t = 6.31$ $P < 0.001$	$t = 7.63$ $P < 0.001$	

tervals. These intervals represent two periods with respect to yellow-heads (Table 1): when yellow-heads were present in the study area (Periods 1 and 2) and when yellow-heads were essentially absent (Periods 3 and 4). Although there were no yellow-heads at Site 1, territory sizes for the same intervals were recorded as controls.

Behavioral interactions.—Behavioral interactions between Marsh Wrens and yellow-heads were recorded during time-budget studies. In 1983 a maximum of 4 territorial male wrens/day were observed for 1 h each. In 1984 8 males/day were observed for 30 min each. The observation period for both years was between 0530 and 0930, corresponding to the birds' most active period (pers. obs.). The duration, type, and number of separate interactions were recorded for each period. Any of the following activities was considered to be an interaction: (1) a chase involving individuals of the two species, (2) a yellow-head flying directly to a wren perched high in the vegetation, and (3) a yellow-head perched directly above a wren that had been chased down into the vegetation.

Removal experiment.—A project conducted by A. Isabelle involving the removal of yellow-heads gave us an opportunity to directly test our predictions. Individual yellow-head territories in the removal area were located as described above, and Marsh Wren territory boundaries were determined by flushing (Wiens 1969). Thirteen of 21 male yellow-heads and all active yellow-head nests were removed on 31 May and 1 June 1984. Further abandonment in the following two days left a total of 3 active yellow-head territories at this third site. Marsh Wren territories were mapped 1 day before and 10 days after the yellow-head removal.

RESULTS

Most Yellow-headed Blackbirds in Delta Marsh established territories before the first male wrens arrived. They finished breeding and left the marsh at least two months before the Marsh Wrens (only 2.2% of all yellow-head nests were active in Period 4 in 1983 and 0.9% in 1984). Marsh Wren and yellow-head territories did not overlap except for one case in 1983 and one in 1984. Yellow-heads at Site 2 defended territories surrounding the central ponds, whereas Marsh Wrens established territories along the edges of the marsh (Fig. 1). The water was significantly higher in yellow-head territories than in Marsh Wren territories at Site 2 in both 1983 and 1984 (Table 2). Water depth measured at Site 1 in 1984 was significantly lower than water depth measured in the Marsh Wren territories at Site 2 in 1984 (Table 2; $t = -3.59$, $P < 0.001$).

Territory movements.—There were no significant differences among the four periods (randomized block ANOVA; $F = 1.23$; df = 3, 26; $P > 0.10$) in the territory sizes of Marsh Wrens nesting at Site 1 (Fig. 2). There were, however, significant differences in territory sizes across the season at Site 2 [randomized block ANOVA; $F = 13.2$; df = 3, 15; $P < 0.001$ for 1983 (Fig. 3); $F = 9.03$; df = 3, 27; $P < 0.001$ for 1984 (Fig. 4)]. Marsh Wren territories increased in size following the departure of yellow-heads (Figs. 3 and 4). This increase in territory size was directed into areas formerly occupied by yellow-heads (Fig. 1), and toward the deeper portions of the marsh.

Behavioral interactions.—During 72 sampling periods (49.2 h) in 1983, we observed 31 interactions, totaling 18 min, between Yellow-headed Blackbirds and Marsh Wrens. This included wrens with territories that overlapped with yellow-head territories ($n = 2$). In 1984 there were 32 interactions, totaling 17.2 min, during 82 sampling periods (38.8 h). These interactions involved the arrival of either male (in 36/63 cases where sex was noted) or female (in 23/63 cases where sex was noted) yellow-heads at a Marsh Wren singing perch, followed by a dive by the wren into the vegetation. The yellow-heads chased individual wrens into the

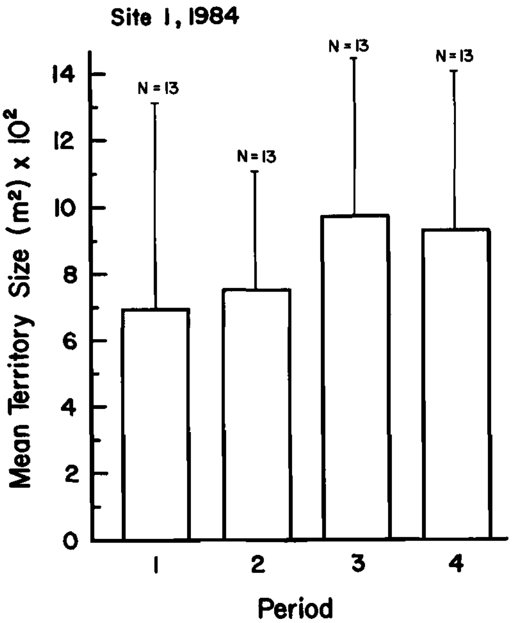

Fig. 2. Mean territory sizes (±SD) for Marsh Wrens at Site 1 during Periods 1-4, 1984.

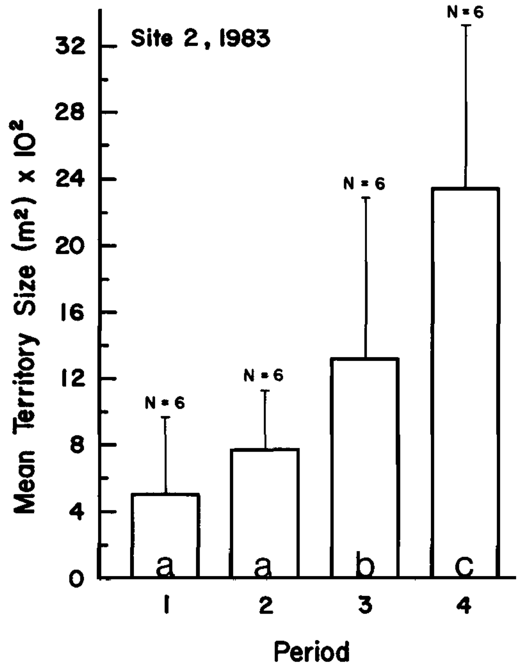

Fig. 3. Mean territory sizes (±SD) for Marsh Wrens at Site 2 during Periods 1-4, 1983. Significant differences between means, as determined by a Student-Newman-Keuls Multiple Range Test ($P = 0.05$), are represented by different letters (i.e. bar "b" is significantly different from bar "c").

vegetation in 10 of 31 altercations in 1983 and 10 of 32 in 1984. In the remainder of the interactions the yellow-heads remained perched above the wrens. Yellow-heads never ignored wrens that were present either in or near their territories.

Removal experiment.—Marsh Wren and yellow-head territories were mutually exclusive at the removal-experiment site. Yellow-heads formed territories around the pond, while Marsh Wrens were located near the edges of the marsh.

In the 10-day period following the removal of yellow-head males, all Marsh Wren territories ($n = 4$) increased in size. The mean size of these territories more than doubled (mean territory size ± SD before yellow-head removal = 231.1 ± 73.3 m; after = 585.8 ± 259.9 m). Presumably because of the small sample size, this difference was not significant (paired t-test, $t = 1.31$, $P > 0.05$). As at Site 2, territories expanded in the direction of the formerly occupied yellow-head territories. In addition, after the yellow-head removal 2 wrens moved into this area and formed territories in areas previously inhabited by yellow-heads. There was no significant change in territory size nor were there any newly arrived wrens at Sites 1 and 2 during this time.

DISCUSSION

In both the descriptive and the experimental studies, increases in Marsh Wren territory size coincided with the departure or removal of Yellow-headed Blackbirds. Wrens expanded their territories into areas formerly occupied by yellow-heads. Territory size did not change significantly in a control area that did not contain yellow-heads. Yellow-heads also actively chased and harassed Marsh Wrens whenever they were encountered. Our results best support the hypothesis that the spatial segregation of Marsh Wrens and yellow-heads is a result of direct interactions between these passerines.

Verner (1975) reported that yellow-heads both chase wrens and destroy wren eggs and nests. The almost tenfold size advantage of the yellow-heads may facilitate these behaviors. Furthermore, the earlier arrival of the yellow-heads should help them exclude Marsh Wrens because (1) the yellow-heads should be more familiar with the area they are defending, and (2) interactions with conspecifics should be reduced because male yellow-heads already have acquired territories and females.

Previous studies (Orians and Willson 1964, Catchpole 1978, Cody 1978) indicate that species may be interspecifically territorial because they compete for limiting resources. Marsh Wrens and yellow-heads potentially could compete for food or suitable nest sites (Verner 1975). Yellow-heads at Delta Marsh forage away from their territories (Andre Isabelle pers. comm.), and thus competition for food seems unlikely. However, Marsh Wrens forage on their territories and, although they may not compete directly with yellow-heads for food, they are excluded from high-quality feeding sites along the water's edge (see Orians 1980).

Nest sites protected from predators [i.e. in the deeper, central portions of the marsh (Horn 1968, Hoogland and Sherman 1976, Richter 1984)] may be limited. Marsh Wrens at Site 1, the drier site, suffered higher predation rates than those at Site 2 [50% (14/28) were depredated at Site 1 and 19% (7/37) at Site 2]. Yellow-heads with nests in the central part of the colony had fewer nest losses due to predators and higher overall nesting success than individuals that nested in the drier peripheral areas (Andre Isabelle pers. comm.). Therefore, yellow-heads may increase their fitness by defending nest sites in the deeper parts of the marsh.

Intense interference competition between Marsh Wrens and Yellow-headed Blackbirds is suggested by the nest-destroying behavior of Marsh Wrens. At Site 2, 50.4% of all active yellow-head nests were depredated in 1983 and 35% in 1984. The proportion of losses due to Marsh Wrens could not be assessed directly. However, there was a significant correlation between the number of depredated yellow-head nests and the distance to the nearest active Marsh Wren nest ($r = -0.90$, $P < 0.025$; Andre Isabelle pers. comm.). Only 15% of the yellow-heads in 1983 and 23% of the yellow-heads in 1984 renested. Therefore, the nest-destroying behavior of the wrens may drive many yellow-heads from the marsh and increase the wrens' access to optimal foraging grounds and nesting sites.

If yellow-heads chase Marsh Wrens to exclude them from mutually preferred habitat, as we have argued, then the observed segregation could be a result of interference competition (Ricklefs 1979). However, if yellow-heads chase Marsh Wrens to prevent the destruction of yellow-head eggs and young, then the segregation may also be the result of exploitation competition (Ricklefs 1979). That is, yellow-heads may be more effective competitors, depleting resources so that they are unavailable to wrens. In this case, interference competition and exploitation competition need not be mutually exclusive. Unfortunately, our data do not allow us to rule out exploitation competition as a viable hypothesis. However, this explanation is weakened by the evidence for interference competition and by the fact that Marsh Wrens quickly moved into yellow-head territories after yellow-heads left or were removed, suggesting that resources were not depleted.

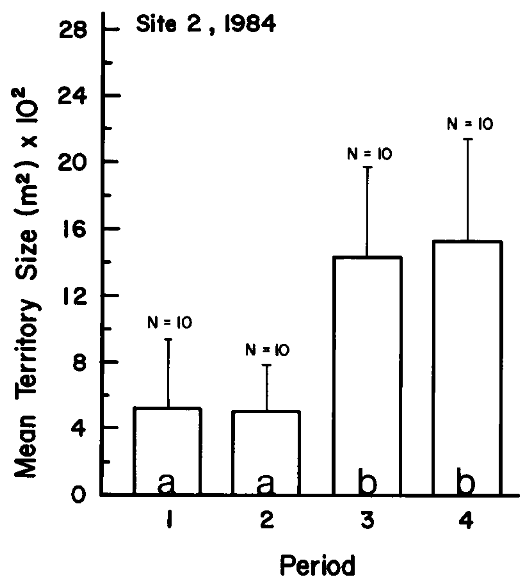

Fig. 4. Mean territory sizes (±SD) for Marsh Wrens at Site 2 during Periods 1–4, 1984. Significant differences between means, as determined by a Student-Newman-Keuls Multiple Range Test ($P = 0.05$), are represented by different letters (i.e. bar "a" is significantly different from bar "b").

Our data suggest that yellow-heads exclude Marsh Wrens from high-quality feeding and nesting sites. Because the spatial segregation between these species appears to result from aggressive interactions (i.e. interference competition), we suggest that this is a case of interspecific territoriality. In addition, the compression of Marsh Wren territories by yellow-heads may lower wren pairing success. Thus, the behavioral interactions between these species may influence not only their spatial distributions, but also their reproductive strategies.

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