NESTING MORTALITY AND HABITAT SELECTION BY MARSH WRENS

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ABSTRACT.—We identified mortality factors for Marsh Wrens (*Cistothorus palustris*) at two study sites and related them to the choice made by males and females between sites. More nests were successful and more young were fledged at Site 2, which had significantly denser vegetation and deeper water than Site 1. Both males and females settled at Site 2 in densities higher than predicted by chance, although they settled synchronously at the two sites. This suggests that Marsh Wrens select breeding habitat to increase their nesting success. *Received 23 October 1986, accepted 11 March 1987.*

SELECTION of breeding habitat should be based largely on the relative importance of features that affect offspring mortality. Individuals may not always make optimal habitat choices, however, because mortality patterns may be difficult to predict at the time of settlement (Wittenberger 1981). Thus, the decisions an animal makes may depend on the availability of cues useful in predicting future events.

Predation is considered to be one of the most important sources of egg and nestling mortality in Temperate Zone marshes (Orians 1961, Kale 1965, Willson 1966, Ricklefs 1969, Robertson 1972, Howe 1976, Richter 1984, Bancroft 1986). Colonial nesting, common in many marsh-nesting icterids (e.g. Orians 1961, Willson 1966, Bancroft 1986), may reduce predation through group vigilance and mobbing. In species where the costs of group living are greater than the benefits, however, the best strategy may be to select a habitat that is relatively safe from predators.

If mortality factors are predictable, individuals should select habitat to reduce potential nesting losses. If individuals are making optimal choices with regard to habitat, then the best habitat should be settled first by both males and females, and there should be more individuals of both sexes in the preferred area.

Marsh Wrens (*Cistothorus palustris*) are small, insectivorous passerines found in marshes throughout most of North America. Males in most populations are polygynous, although the number of polygynous males varies within populations (Verner 1963, Kale 1965). Harems of two or three females are most common. Both male and female Marsh Wrens destroy the eggs and nestlings of conspecifics (Picman 1977a) and other marsh-nesting passerines (Orians and Willson 1964, Burt 1970, Picman 1977b). We examined the habitat preferences of Marsh Wrens by comparing their breeding success and settlement patterns in two marsh sites.

METHODS

Study sites.—Our study was conducted between 1 May and 17 July 1983–1985 in two marsh sites in Delta, Manitoba. Site 1 was a homogeneous cattail (*Typha* spp.) marsh approximately 7.8 ha in area. Site 2 was more heterogeneous, with phragmites (*Phragmites australis*) and cattails along the edges and bulrush (*Scirpus acutus*) and cattail patches around two central ponds. We used 6.1 ha in 1983. In 1984 we increased the size of this site to 7.9 ha. Because of the ponds and the presence of a Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) colony, there were 4.0 ha of suitable breeding habitat available at Site 2 in 1983 and 6.2 ha available in 1984 and 1985. The study sites were separated by 1 km of grassland.

Habitat characteristics.—Each site was divided into a grid of 20 × 20 m squares, marked by 2-m-high wooden stakes. Vegetation quality and water depth were measured throughout the study sites in 1983 and 1984. Point samples, 50 cm in diameter, were made at each grid stake at the time males were settling. Information on vegetation height, vegetation density, and water depth was collected at each sample point. Vegetation height and water depth were measured using a 2-m-high vertical stake marked at 5-cm intervals. Vegetation density was estimated using a 50-cm horizontal bar placed 100 cm up on the vertical height stick. The bar was painted with 20 evenly spaced red circles each 1 cm in diameter. A relative measure of vegetation density was estimated by counting the number

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TABLE 1. Percentage of males in each mating class for Sites 1 and 2 in 1983–1985. Sample sizes are given in parentheses.

	Site 1	Site 2
Bachelor	11.3 (7)	4.9 (3)
Monogamous	47.5 (28)	41.0 (25)
Bigamous	37.3 (22)	42.6 (26)
Trigamous	3.4 (2)	11.5 (7)

TABLE 2. Mean ± SD clutch size, number hatched from all nests, number fledged from all nests, number fledged from successful nests, and nestling mass for Sites 1 and 2. Data from 1983–1985 combined. A Mann-Whitney *U*-test was used to test for differences between sites. Sample sizes are given in parentheses.

	Site 1	Site 2	*Z*	*P*
Clutch size	5.8 ± 0.8 (79)	5.6 ± 0.8 (96)	−1.03	>0.10
Hatched from all nests	2.9 ± 2.8 (83)	3.9 ± 2.2 (94)	1.41	>0.10
Fledged from all nests	2.3 ± 2.6 (81)	3.4 ± 3.4 (95)	2.63	<0.02
Fledged from successful nests	5.1 ± 1.2 (37)	4.5 ± 1.3 (71)	−2.38	<0.02
Nestling mass (g)	8.9 ± 1.6 (118)	8.3 ± 1.7 (187)	−3.51	<0.02

of dots that were totally clear of vegetation from a distance of 2 m. The higher the density measure, therefore, the sparser the vegetation.

Breeding biology.—Eighty-nine of the 121 males used in the study were trapped and marked individually with colored leg bands. Female wrens were not marked. Territory boundaries were mapped weekly throughout the study period by observing the movements of males during 1-h observation periods in 1983 and 30-min observation periods in 1984 and 1985. Song perches and flight paths were plotted on maps of the study sites. The area of each territory was determined with an Apple Graphics Tablet.

All nests were mapped and checked twice a week and their contents noted. Clutch size was based on complete clutches only. Each nest was marked with a numbered tag placed approximately 3 m north of the nest. If clutches were incomplete when found, the initiation date was estimated (Kale 1965). A nest was considered depredated by a mammal if the opening was enlarged (we used this characteristic until nestlings were 8 days old) or the nest dislodged from the supporting vegetation. Depredation by Marsh Wrens was assumed if eggs were discovered with holes and nest contents were missing, but the nest was intact. Nests were considered abandoned if clutches were complete and the eggs in the nest were cold.

When Marsh Wrens kill older nestlings (>8 days) they generally peck the nestling and then remove it from the nest (Picman 1977a, Leonard pers. obs.). We assumed that an older nestling had fallen from a nest (as opposed to having been removed by a Marsh Wren) if it was found below the nest with no apparent wound. Younger nestlings found below the nest were considered to have been killed by Marsh Wrens. We considered a nestling to have starved if it was found dead in the nest with no apparent injuries. We could not identify cases where a nestling had died in the nest from starvation and then was removed from the nesting area by an adult. In these cases losses were attributed to unknown causes. We assumed that nestlings had fledged if they were absent from the nest at 12 or more days of age. If nestlings were gone from the nest before this stage and we were unable to locate them in the general vicinity, we assumed the nest had been depredated. Chick mortality after fledging was not assessed directly. Because nestling mass has been correlated with postfledging success (Perrins 1965, Lack 1966), however, all nestlings were weighed 8 days after hatch.

A territory was considered settled if there was a male present in the area for 3 consecutive days. Male pairing success was determined by the maximum number of simultaneously active nests within each territory. Female pairing date was estimated from the date of the first egg, and female reproductive success was measured as the number of young fledged. A nest was considered successful if it fledged at least one young. Data for each year were analyzed separately and pooled if the results between years were similar. Thus, unless stated otherwise, results are based on the combined data. All means are ±1 SD.

RESULTS

Population size and habitat characteristics.—Site 1 supported 14 male Marsh Wrens in 1983, 19 in 1984, and 28 in 1985. Site 2 supported 17, 22, and 21 males in 1983, 1984, and 1985. Site 2 also supported 67 Yellow-headed Blackbird territories in 1983 and 63 territories in 1984 and 1985.

Vegetation was significantly denser (Site 1: 15.3 ± 5.2 dots/20, $n = 355$; Site 2: 6.8 ± 6.3 dots/20, $n = 183$) and higher (Site 1: 12.1 ± 11.7 cm, $n = 297$; Site 2: 28.9 ± 13.9 cm, $n = 180$) and the water deeper (Site 1: 91.9 ± 26.6 cm, $n = 324$; Site 2: 132.1 ± 36.3 cm, $n = 196$) at Site 2 than at Site 1 (Student t-test, $P < 0.001$ in all cases).

TABLE 3. Percentage of all Marsh Wrens (n) lost to various mortality factors for Sites 1 and 2, 1983–1985 combined.

Mortality agent	Site 1	Site 2	Both
Mammalian predation	33.3 (24)	11.1 (8)	44.4 (32)
Marsh Wren predation	12.5 (9)	11.1 (8)	23.6 (17)
Weather	5.6 (4)	5.6 (4)	11.2 (8)
Nest abandonment	5.6 (4)	2.7 (2)	8.3 (6)
Unknown	5.6 (4)	6.9 (5)	12.5 (9)

Pairing and reproductive success.—Harem sizes were significantly larger at Site 2 (1.60 ± 0.76 females/male, $n = 59$) than at Site 1 (1.32 ± 0.73 females/male, $n = 61$; Mann-Whitney U-test, $Z = 2.3$, $P = 0.01$). Fifty-four percent of males at Site 2 were polygynous vs. 41% at Site 1 (Table 1). In addition, 7 of 9 cases of trigamy were at Site 2, while 7 of 10 bachelors were at Site 1 (Table 1). The total number of young fledged per male was also significantly higher at Site 2 than at Site 1 (Mann-Whitney U-test, $Z = 2.45$, $P < 0.02$). Clutch size and the number of eggs hatched from all nests (successful and unsuccessful nests combined) did not differ significantly between sites (Table 2). When successful (nests that fledged at least 1 young) and unsuccessful nests were considered together, however, significantly more young fledged per nest at Site 2 (Table 2). These results, presumably, were because more nests were successful at Site 2 (80.7%, 67/83) than at Site 1 (40.4%, 38/94; $\chi^2 = 21.1$, df = 1, $P < 0.005$). When only successful nests were considered, there were more young fledged per nest at Site 1 than at Site 2 (Table 2). In addition, 8-day-old nestlings at Site 1 were significantly heavier than nestlings at Site 2 (Table 2).

TABLE 4. Number of nests (%) with partial losses and the apparent causes for Sites 1 and 2 from 1983–1985 combined. Some nests lost eggs to more than one source.

Losses	Site 1	Site 2	Both
Successful nests	38	67	105
Partial loss	17 (44.7)	44 (65.7)	61 (58.1)
Unhatched eggs	10 (58.8)	43 (97.7)	53 (86.8)
Eggs to Marsh Wrens	4 (23.5)	5 (11.4)	9 (14.8)
Nestlings to Marsh Wrens	1 (5.8)	5 (11.4)	6 (9.8)
Starvation	0 (0.0)	3 (6.8)	3 (4.9)
Fallen nestlings	1 (5.8)	1 (2.3)	2 (3.2)
Losses unknown	2 (11.8)	2 (4.5)	4 (6.6)

Nesting losses.—During the 3 yr of this study 68% (49/72) of all unsuccessful nests were lost to predators. Forty-six percent (33/72) of these nests were at Site 1 and 22% (16/72) at Site 2. At Site 1 most nests were lost to mammals, although Marsh Wrens were responsible for some losses (Table 3). At Site 2 mammals and Marsh Wrens had a similar impact. The remaining losses were attributed to a heavy wind storm in 1985 and female abandonment (Table 3). Most (79.9%, 373/468) mortality occurred during the egg stage. Egg predation accounted for 50.4% (188/373) of all egg mortality and 40.2% (188/468) of the total egg and nestling mortality. Depredation at the nestling stage accounted for 84.2% (80/95) of nestling mortality and 15.5% (80/468) of total mortality.

Forty-five percent (17/38) of successful nests at Site 1 and 65.7% (44/67) of nests at Site 2 suffered partial brood loss (Table 4). At both sites most losses were due to unhatched eggs, although some losses were attributed to Marsh Wrens (Table 4).

Male and female settlement.—The first male Marsh Wrens were observed in the study area on 10 May 1983, 7 May 1984, and 1 May 1985. The first female wrens arrived approximately 1 week after the arrival of the first male. Male wrens settled at Site 2 more often than expected by chance ($\chi^2 = 3.48$, df = 1, $P < 0.05$). However, this difference was not significant in 2 of 3 yr. Females settled at Site 2 significantly more often than predicted by chance ($\chi^2 = 33.2$, df = 1, $P < 0.0005$), and this difference was significant in each year. Both males and females settled at the two sites simultaneously, although proportionally more males and females settled at Site 2 per day. Return rates of adult males and yearlings were low. Ten percent (2/19) of marked males returned to Site 1 and 9% (2/22) to Site 2 in 1984. Seven percent (2/28) returned to Site 1 in 1985, but no marked males were observed at Site 2 that year. With one exception, returning males settled either on or within 100 m of their previous territories. Return rates of yearlings were extremely low. Only 1 of 540 banded nestlings was observed in the study area. This yearling male held two different territories in succession at Site 2 in the 1985 season. The first was approximately 140 m from his natal territory and the second was within 40 m.

DISCUSSION

In general, male Marsh Wrens showed a weak preference for Site 2, although they settled at the two sites in numbers predicted by chance in 1984 and 1985. Female wrens consistently settled in higher densities at Site 2. Both males and females settled at the two sites simultaneously. Thus, there appears to be a preference by both sexes for the site where male pairing success and female success for each nesting attempt were highest. The timing of settlement is contrary to predictions, however, if all individuals made optimal habitat choices.

Predation is an important mortality factor for marsh-nesting passerines (Orians 1961, Willson 1966, Ricklefs 1969, Robertson 1972, Holm 1973, Caccamise 1976, Clark and Wilson 1981, Bancroft 1986), including Marsh Wrens (Welter 1935, Kale 1965). Predation by mammals was the main source of nesting mortality for this population of Marsh Wrens, and the impact was greatest at Site 1. Tall, dense vegetation and deep water may provide protection from mammalian predators (Goddard and Board 1967, Holm 1973, Hoogland and Sherman 1976, Collias and Collias 1984, Richter 1984). We found proportionally more successful nests at Site 2, the site with denser vegetation and deeper water. Also, within each site, successful nests were in significantly denser vegetation and deeper water than unsuccessful nests. Thus, dense vegetation and deep water may make Site 2 a safer habitat.

Male Marsh Wrens that acquire territories at Site 2 increase their chances of mating polygynously and in fledging more young than males at Site 1. In general, males displayed a preference for Site 2. The two sites were settled simultaneously, however, so some individuals apparently settled at Site 1 before Site 2 was filled. There are several possible explanations for this settlement pattern: return rates between years are low, so individuals may not respond to local conditions (Lenington 1980, Cody 1985); males may be unable to assess habitat differences early in the season (Wittenberger 1981); and individuals may be prevented from settling by other males (Fretwell and Lucas 1969).

Despite the general preference by females for Site 2, the timing of settlement suggests that some individuals settled at the less preferred site unnecessarily. The explanations proposed to explain male settlement patterns should also apply to females. In addition, females at Site 1 fledged more young per successful nest, and these young were heavier than at Site 2. Fledging mass has been correlated positively with postfledging survival in some species (Perrins 1965, Lack 1966, von Haartman 1971). If this correlation holds for Marsh Wrens, nestlings from Site 1 may be more likely to survive than those from Site 2. Thus, some females may opt to increase the number or quality of young, while others may attempt to increase their chances of having a successful nest.

When examining female settlement patterns, one must separate mate selection from habitat selection. We found no relationship between male quality and female choice in this population (Leonard 1986, Leonard and Picman MS). This suggests that females probably rely on features of the habitat when selecting a nesting area.

Both male and female Marsh Wrens preferred to settle in the habitat that increased their pairing and reproductive success per nesting attempt, respectively. When the timing of settlement is considered, however, some individuals apparently did not settle as predicted. The reason for this is unclear but may be related to the ability of individuals to assess different habitats and the fitness options available.

ACKNOWLEDGMENTS

We thank Drs. P. Weatherhead and D. Hickey for valuable suggestions throughout this study. A. Horn and K. Teather critically reviewed the manuscript, and Dr. J. Verner and an anonymous referee made many constructive comments. We are especially grateful to J. Geggie and H. den Haan for their assistance in the field. This study was part of a Ph.D. project funded by a Canadian National Sportsmen's Fund Award and a NSERC operating grant to J.P. and a University of Ottawa scholarship and a NSERC postgraduate scholarship to M.L.

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