# SURVIVAL AND DISPERSAL OF MALE LONG-BILLED MARSH WRENS

By JARED VERNER

From 16 June to 4 August 1967, 264 Long-billed Marsh Wrens (*Telmatodytes palustris*) were individually color banded at Turnbull National Wildlife Refuge, 15 miles south of Spokane, Spokane Co., Washington. During the summer of 1968, all lakes on the refuge and most of the large lakes off the refuge within a 10-mile radius of the refuge center were carefully and completely censused in an effort to locate as many as possible of the banded birds that had returned. Suitable marshes are widespread within this 10-mile radius, and they extend beyond it in all directions except east and northeast. Systematic efforts were made to totally census only males; females are too secretive to permit an effective total count.

## RESULTS

*Survival.* Table 1 summarizes results of the banding and subsequent census. Upper and lower Turnbull Lakes, which normally support large wren populations, had none at the time of census because they had previously been drained. Only 13 (17.1 percent) of 76 adult males banded in 1967 were relocated in 1968. If half (91) of the wrens banded as nestlings or fledglings in 1967 were males, the 10 first-year males relocated in 1968 represented an 11.0 percent return.

The tarsi of 48 males were not seen clearly enough to determine whether or not they carried bands. Assuming the same percentage of those to be banded as determined for males whose tarsi were seen clearly, one additional male banded as an adult and one banded as a nestling should have been among those whose tarsi were not observed. Adjusting survival rates with these additions gives 18.4 percent survival among males banded as adults and 12.1 percent among males banded as nestlings or fledglings. Comparison with banding returns of other species indicates that adult survival suggested here is unusually low, while survival of first-year males is high. Most studies of yearling survival, however, have not involved exhaustive censuses of vast areas of suitable habitat. Many authors state that low yearling returns are likely explained by dispersal.

*Dispersal.* Mean distance between 1967 and 1968 breeding territories of adult males, measuring between territory centers and rounding to the nearest 10 m, was 386 m (range = 0-3353, N = 13, SE = 63). Five of the 13 adults held the same territory in 1967 and 1968, and two others held sites in 1968 adjacent to those held in 1967. Only one established a territory on a different lake in 1968.

Mean distance between rearing territories and first breeding territories among the yearlings was 1951 m (range = 180-4090,

N = 10, SE = 423). Only one of the ten yearlings established its first breeding territory on the same lake on which it was reared. The observed differences in mean dispersal distances between adult and yearling males are statistically significant ($t = 3.17$; $0.01 > P > 0.001$) and are in agreement with similar results available in the literature for a wide variety of bird species (e.g., see Low, 1934; Kendeigh and Baldwin, 1937; Nice, 1937; Kendeigh, 1941; Stoner, 1941; Farner, 1945; Allen and Nice, 1952; and Perrins, 1963). The same phenomenon is reported among small mammals (see Howard, 1960).

## DISCUSSION

*Survival.* Based on earlier studies (Verner, 1965) of nesting success in this population, observed survival rates are inadequate to maintain the population of Long-billed Marsh Wrens at Turnbull Refuge. While the population there may, indeed, be declining, any one or a combination of several possible factors could account for the apparently low survival rate.

Some banded individuals may have been missed during the census. I believe this to be only of minor importance here, since the census was conducted with great care. Males' territories were readily discovered by the presence of the numerous nests used in courting, and males typically sang and approached intruders in their territories or could easily be induced to do so by an observer. Loss of bands would also reduce observed survival rates below actual survival rates. Since most males wore bands on both legs, both would have to have lost their bands in order that a previously banded individual would be classified unbanded. This likelihood is remote. Moreover, five banded birds were retaken in 1968 and found to carry complete and correct color patterns in reference to their aluminum band numbers.

If wrens dispersed beyond the range of the census, the actual survival rate may have been higher than that observed here. Short dispersal distances determined for males banded as adults, coupled with similar observations for numerous other species studied by other workers, speak strongly against dispersal of any adult male beyond the 10-mile radius of the census area. The fact that the census area had a radius nearly four times the length of the longest recorded dispersal of any yearling male suggests that long-distance dispersal among that group is also not likely a significant factor affecting the observed survival rate. There is no reason to assume that one portion of the yearling population should confine its dispersal to within 4100 meters, that another portion would disperse to distances of at least 17,600 meters, but that none would occupy the hiatus between (but see Johnstone, 1956).

Banding of young birds in 1967 did not begin until 23 June, yet young wrens were fledging at Turnbull Refuge by mid-May. In a study of dispersal of young Great Tits (*Parus major*) by Dhondt and Huble (1968), "lower recovery-rate for late young near the

TABLE 1. BANDING AND SUBSEQUENT CENSUS OF LONG-BILLED MARSH WRENS AT TURNBULL NATIONAL WILDLIFE REFUGE AND VICINITY

| Lakes | Banding, 1967 | | | | Band returns and census, 1968 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Ad. ♂♂ | Ad. ♀♀ | Nestl. | Fledgl. | Yearling ♂♂ | Older ♂♂ | Unbanded ♂♂ | Other* ♂♂ | Total ♂♂ | Unbanded** ♀♀ |
| Long | | | | | 0 | 0 | 22 | 0 | 22 | 17 |
| Mann | | | | | 0 | 0 | 0 | 1 | 1 | 0 |
| Railroad*** | | | | | 0 | 0 | 3 | 0 | 3 | 0 |
| Reeves | | | | | 0 | 0 | 12 | 2 | 14 | 12 |
| Roberts | | | | | 0 | 0 | 7 | 0 | 7 | 4 |
| Thirty-acre | | | | | 0 | 0 | 17 | 4 | 21 | 3 |
| East Tritt | | | | | 0 | 0 | 29 | 0 | 29 | 14 |
| Lower Turnbull | | | | | 0 | 0 | 0 | 0 | 0 | 0 |
| Upper Turnbull | | | | | 0 | 0 | 0 | 0 | 0 | 0 |
| Winslow | | | | | 0 | 0 | 3 | 1 | 4 | 0 |
| Amber**** | | | | | 0 | 0 | 4 | 0 | 4 | 0 |
| Badger**** | | | | | 0 | 0 | 15 | 1 | 16 | 6 |
| Chapman | | | | | 0 | 0 | 0 | 0 | 0 | 0 |
| Philleo | | | | | 0 | 0 | 17 | 1 | 18 | 4 |
| Williams**** | | | | | 0 | 0 | 4 | 1 | 5 | 2 |
| TOTALS | 76 | 6 | 177 | 5 | 10 | 13 | 597 | 48 | 668 | 211 |

* "Other" designates males known to be present but whose tarsi could not be clearly enough observed to determine if bands were present.
** Numbers of unbanded females indicated refer to those positively known not to be wearing bands.
*** Consist of two or more small ponds in a restricted area.
**** Census incomplete.

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|---|---|---|---|---|---|---|---|---|---|---|
| | Ad. ♂♂ | Ad. ♀♀ | Nestl. | Fledgl. | Yearling ♂♂ | Older ♂♂ | Unbanded ♂♂ | Other* ♂♂ | Total ♂♂ | Unbanded** ♀♀ |
| Beaver | 2 | 1 | 4 | 0 | 0 | 0 | 3 | 1 | 4 | 0 |
| Blackhorse | 21 | 0 | 77 | 0 | 0 | 4 | 14 | 2 | 20 | 0 |
| Blackhorse Channel | 1 | 0 | 0 | 0 | 1 | 1 | 17 | 4 | 23 | 0 |
| Ice | 1 | 0 | 4 | 0 | 0 | 0 | 2 | 0 | 2 | 0 |
| Big Isaacson | 2 | 0 | 0 | 0 | 1 | 0 | 18 | 3 | 22 | 4 |
| Little Isaacson | 2 | 0 | 5 | 0 | 0 | 0 | 5 | 1 | 6 | 1 |
| Kepple | 5 | 2 | 3 | 1 | 0 | 1 | 17 | 1 | 19 | 0 |
| Big McDowell | 19 | 1 | 33 | 3 | 3 | 4 | 44 | 9 | 60 | 15 |
| Little McDowell | 6 | 0 | 18 | 0 | 0 | 1 | 8 | 2 | 11 | 1 |
| Lower Pine | 8 | 1 | 9 | 1 | 4 | 1 | 36 | 5 | 46 | 1 |
| Middle Pine | 2 | 0 | 5 | 0 | 1 | 0 | 5 | 0 | 6 | 0 |
| West Tritt | 6 | 1 | 12 | 0 | 0 | 1 | 126 | 0 | 127 | 27 |
| Windmill | 1 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Little Blackhorse | ..... | | | | 0 | 0 | 1 | 0 | 1 | 0 |
| Lower Blackhorse | ..... | | | | 0 | 0 | 4 | 0 | 4 | 0 |
| Campbell | ..... | | | | 0 | 0 | 99 | 6 | 105 | 72 |
| Cossalman*** | ..... | | | | 0 | 0 | 46 | 1 | 47 | 10 |
| Findley*** | ..... | | | | 0 | 0 | 0 | 0 | 0 | 0 |
| Hale*** | ..... | | | | 0 | 0 | 8 | 1 | 9 | 6 |
| Lasher*** | ..... | | | | 0 | 0 | 11 | 1 | 12 | 12 |

birth-place was found, but the recovery-rate from all places for early and late young is remarkably similar." Dhondt and Huble believe, therefore, that late-hatched young disperse farther than do those hatched earlier in the year. For reasons suggested in the previous paragraph, this possibility is not likely involved in the present study. On the other hand, earlier hatched young probably have a better chance to survive than do those hatched later, as shown in the Pied Flycatcher (*Muscicapa hypoleuca*) by Campbell (reviewed by Lack, 1966, p. 107). Consequently, the sample reported here probably exhibited lower survival than average for all yearlings together.

Some yearling males may not establish territories and would thus not be censused. Kendeigh and Baldwin (1937) estimated, for example, that 23.4 percent of yearling male House Wrens (*Troglodytes aedon*) do not establish territories.

Finally, banded birds may sustain higher mortality, as a direct result of their bands, than that incurred by the unbanded segment of a population. This possibility cannot be eliminated here. It could be tested in a more extensive study by comparing survival rates among groups of birds receiving different numbers of bands.

*Dispersal.* Of the various hypotheses advanced to explain observed differences in dispersal distances of different age classes, some cannot be properly evaluated before many more data are available on a wide variety of species. Some hypotheses, however, can probably be adequately negated even in the absence of such extensive data. For example, it is commonly held that young males disperse further than adults because their parents actively evict them from the home territory. Howard (1960) suggests that available information on small mammals does not support this view.

Since among many bird species the facts indicate that territories of yearling males are generally distributed throughout a breeding population, the hypothesis requires the assumption that fathers resist their own sons as neighbors more than they do the sons of other males. I cannot accept this as sound application of the principles of natural selection. Moreover, the hypothesis requires that adults either (1) drive their young long distances from their rearing points, where the young subsequently establish breeding territories, or (2) that adult males have the capacity to recognize their own sons a year later and that they then execute territorial defense maneuvers against their sons of a magnitude never executed against non-relatives. I have been unable to find references of any kind to support either of these two alternatives. I believe, instead, that we must seek a solution on the premise that for some reason yearling males that establish territories near those in which they were reared leave fewer offspring than do those that establish farther away.

The suggestions that yearlings are less precise in their homing abilities than are adults may provide a proximate explanation to the phenomenon under consideration, at least among migratory

species, but it cannot be regarded as an adequate ultimate (evolutionary) explanation. Variations in homing ability among yearlings would eventually lead to evolution of yearlings that homed accurately to areas near their rearing places, if yearlings that established territories in such places produced more surviving offspring than those less precise in their homing ability.

The suggestion that different dispersal distances exhibited by birds of different age and sex function to reduce inbreeding (Lincoln, 1934; Kendeigh, 1941) is worth further consideration. In addition to requiring that yearlings disperse different distances than do adults, such a function would also require that yearling females disperse different distances than do yearling males, which some data indicate to be true (e.g., Low, 1934; Nice, 1937; Kendeigh, 1941; Dhondt and Huble, 1968). On the other hand, reduction of inbreeding would not require that adult females show less site fidelity than do adult males, yet this phenomenon is probably widespread among birds (e.g., von Haartman, 1949; Berger and Radabaugh, 1968; and many references cited above). This does not negate the inbreeding hypothesis, but some other explanation would have to account for lower site fidelity among adult females than among adult males.

## SUMMARY

Returns of banded male Long-billed Marsh Wrens at Turnbull National Wildlife Refuge, as determined by careful census, indicate 18.4 percent survival among banded adults and 12.1 percent survival among banded young between 1967 and 1968. Observed survival rates are insufficient to provide population replacement, and several factors are suggested that may have resulted in observed survival rates being lower than actual.

Mean distance between 1967 and 1968 breeding territories of adult males was 386 m. That between hatching and first breeding territories of yearlings was 1951 m. The difference is significant ($0.01 < P < 0.001$). Two commonly held explanations of the difference between dispersal distances of adults and first-year birds, viz. (1) that young breed some distance from their rearing site because they are evicted by their parents, and (2) that they do so because their homing abilities are less precise than those of adults, are rejected as being in conflict with the principles of natural selection. The suggestion that age differences in dispersal distance function to reduce inbreeding merits further consideration.

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*Dept. of Biological Sciences, Central Washington State College, Ellensburg, Washington 98926*

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