TERRITORIES, MULTIPLE NEST BUILDING, AND POLYGYNY IN THE LONG-BILLED MARSH WREN

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THE problem of natural selection for polygyny in a bird species with a 1:1 sex ratio has received considerable attention in earlier papers (Verner, 1963, 1964; Verner and Willson, 1966). Briefly it is argued that for polgyny to evolve when unmated males are available, females pairing with males that are already mated must realize a higher reproductive output than they could attain paired with an unmated male, despite receiving less assistance in the care of their offspring. This implies more suitable conditions for breeding in the territory of the chosen male. An examination of various features of the territories of male Long-billed Marsh Wrens (*Telmatodytes palustris*) in a population at Seattle, Washington, revealed two features, total territory size and area of territory with standing water, that correlated highly with the pairing success of the males. The amount of territory with standing water very likely affects the abundance of wren food in the territory. Similar attempts to clarify relationships between pairing success and territorial features of male Long-billed Marsh Wrens at Turnbull National Wildlife Refuge were unsuccessful, possibly because the Turnbull sample was too small.

In the course of investigating the response of male wrens to playback of recorded songs within their territories at Turnbull Refuge during the summer of 1967, we made detailed measurements of the territories, their component vegetation, distribution of nests, and the number of females and the conditions of their nests. These data provide the basis for a further analysis of the possible factors influencing the pairing success of male Long-billed Marsh Wrens at Turnbull Refuge.

The refuge lies 15 miles south of Spokane, Washington, in the geologic formation of the channeled scablands. Most of the uplands are covered with open pine (*Pinus ponderosa*) forests. More than 15,000 acres and 80 separate lakes of various sizes lie within the refuge boundaries. Most of the lakes are fringed with cattail (*Typha latifolia*) and bulrush (*Scirpus validus*) marshes that provide breeding habitat for a large population of Long-billed Marsh Wrens. A complete census of all lakes on the refuge in 1968 revealed 625 territorial males. Our studies in 1967 were conducted on the following lakes: Kepple, Beaver, Blackhorse, Windmill, Ice, Middle Pine, Lower Pine, West Tritt, Little Isaacson, Big Isaacson, Little McDowell, and Big McDowell.

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METHODS

We investigated a total of 80 males, their territories, and nesting cycles in 1967. Each territory was mapped in detail by plane table and a 30-m steel tape for precise measurements of boundaries, nest locations, and bulrush and cattail distributions. All areas were later measured with a planimeter. The boundaries of marsh wren territories, in contrast to those of most other species of birds, can be determined readily. The lake delimits one side, the shore another, and the boundaries between the ends of adjacent territories can be determined in several ways: (1) Males can be chased to the ends of their territories, where they double back around the observer; the boundary can then be confirmed by driving the neighboring male to it. (2) Neighboring males can sometimes be attracted to the presumed boundary by an imitated alarm call ("squeak") where they then engage in boundary dispute flights over the actual boundary. (3) Near the ends of their territories males commonly leave sections without courting nests; hence relatively long sections without nests, sandwiched between long sections with nests, indicate the approximate location of a boundary. (4) Territory boundaries commonly coincide with breaks in the vegetation where the open lake reaches the shore. The longer the interruption in marsh vegetation, the more likely it is to be a boundary between territories. We generally used a combination of the above methods to determine a boundary, but every case included either (1) or (2).

Marsh wren nests are also easily found. Prior to mapping, all nests within each territory were located, tagged with red tags numbered consecutively, and their condition and contents recorded. Each nest was then plotted accurately on the map. As most territories were examined before the males had finished building nests for the year, each territory was searched completely for nests a second time after nest building ceased.

Immediately after the playback session with each male, a swath was trampled within his territory, a mist net was placed in the cleared lane, and the male was netted and individually color-banded. Of the 80 males utilized in the study, 76 were banded, 2 were collected for gonadal examination, and only 2 were neither banded nor collected.

Knowledge of the normal duration of the various stages of the nesting cycle in this species, coupled with the knowledge that a female normally remains mated to the same male throughout one breeding season, permitted us to extrapolate the probable date of initiation of each breeding nest. As the field work was not begun until early June, many females had already completed one nesting cycle. Nests from which young have fledged are readily identified by their large opening and the accumulation of feather scales in the nest bottom. We assume that females involved in a nesting cycle at the time of the study were also responsible for those cycles evidenced by nests from which young had fledged.

To evaluate pairing success, we assume that the most successful males are those that attract the most mates; so males are ranked 0, 1, and 2 to indicate bachelor, monogamous, and bigamous status respectively.

Additional observations in 1968 provided further insight into the possible significance of habitat quality as a factor in the mating system of the marsh wren. For the following reasons the 1968 data were mainly qualitative: June of 1968 was given wholly to playback studies with the hope that territorial measurements could be conducted in July, but a prolonged drought of near record proportions in eastern Washington dropped lake levels about 18 inches below normal. The cattail stands around most lakes had little or no water even by mid-June, and many wren territories in such stands were abandoned. Bulrush normally grows in deeper water than does cattail, and most stands of bulrush still had water at least a few inches deep. Those wrens whose territories adjoined or contained sufficient bulrush simply moved into it exclusively or nearly so. Those whose territories contained only cattail sought suitable habitat elsewhere. On Thirty-acre Lake we found three territories late in June in spots known to hold no wrens in previous years. The males on those territories had built very few nests, suggesting recent occupancy, probably from abandoned cattail territories on other lakes. Similar evidence of late occupancy was noted in other bulrush stands throughout the refuge in July. Because of this evident instability of males in territorial locations, we were able to map only eight territories with confidence. These territories were known to be occupied by wrens in early May, when the sites were visited briefly, and continuously from mid-June through July.

RESULTS

Number of nests.—The 80 males whose territories were mapped began a total of 1,966 nests and completed 1,761 of them. By estimating the per cent completion of the 205 uncompleted nests to the nearest 10 per cent, we computed the number of complete equivalent nests each male built (Table 1).

The number of nests built per male in 1968 appeared to be lower than that in 1967, but the prevalence of males changing territories in mid-season, 1968, certainly confused the picture. In 1968 we counted the nests in the eight territories known to be occupied throughout the season. In all eight cases the occupying males had territorial boundaries identical to those determined for the same eight territories in 1967, a fact apparently attributable to vegetational discontinuities in most instances. Only one of the eight males in 1968 had occupied the same territory in 1967. Although no significant difference was evident between the means of nests completed in the eight territories in the 2 years ($t = 0.84$, $P > 0.10$), the 1968 mean (19.9) was considerably lower than that (25.3) in 1967.

TABLE 1

NEST BUILDING ACTIVITIES OF BACHELOR, MONOGAMOUS, AND BIGAMOUS MALE LONG-BILLED MARSH WRENS, 1967

Males	No.	Mean no. nest sites	Mean no. nests completed	Mean no. incomplete nests	Mean no. of equivalent complete nests
Bachelor	13	19.8	17.4	2.5	18.3
Range		10–25	5–25	0–8	6.4–25.9
Monogamous	47	24.7	22.1	2.7	23.0
Range		14–45	12–41	0–8	12.9–42.2
Bigamous	20	27.3	24.9	2.4	25.6
Range		16–50	15–44	0–7	15.4–46.1
Total	80	24.6	22.0	2.6	22.9
Range		10–50	5–44	0–8	6.4–46.1

TABLE 2

NEST COVER TYPES COMPARED WITH AMOUNT OF COVER TYPES AVAILABLE IN TERRITORIES

Males		Cattail	Bulrush	Mixed
Bachelor	Cover (m^2)	3,084 (45.9)[1]	2,935 (43.7)[1]	699 (10.4)[1]
($N = 13$)	No. nests	115 (44.6)	108 (41.9)	35 (13.6)
Monogamous	Cover (m^2)	10,688 (35.4)	11,863 (39.3)	7,614 (25.3)
($N = 47$)	No. nests	533 (47.5)	287 (24.7)	323 (27.8)
	Brood nests	32 (50.8)	18 (28.6)	13 (20.6)
Bigamous	Cover (m^2)	7,226 (52.7)	3,212 (23.4)	3,270 (23.9)
($N = 20$)	No. nests	325 (59.7)	81 (14.8)	139 (25.5)
	Brood nests	36 (62.1)	9 (15.9)	13 (22.4)
Total	Cover (m^2)	21,008 (41.5)	18,008 (35.6)	11,583 (22.9)
($N = 80$)	No. nests	993 (50.5)	476 (24.2)	497 (25.3)
	Brood nests	68 (56.2)	27 (22.3)	26 (21.5)

[1] Percentages shown in parentheses.

Stacked nests.—Occasionally, two nests were supported by the same stalks of marsh vegetation, with the upper nest normally resting on the lower. In one case two pairs of stacked nests were bound together, side by side, into a virtual four-nest apartment. Only 39 (2 per cent) of all nests were stacked in this manner. Of these, 31 (79.5 per cent) were supported by cattails, 5 (12.8 per cent) by bulrush, and 3 (7.7 per cent) by mixed cattail and bulrush. A significantly greater proportion of the stacked nests was placed in cattails than would be predicted from the percentage of all nests placed in cattails ($\chi^2 = 34.00$; $P < 0.001$).

Bachelor males built 6 (15.4 per cent) of the pairs of stacked nests, monogamous males 20 (51.3 per cent), and bigamous males 13 (33.3 per cent). Each of the above groups of males constructed their proportionate share of stacked nests in comparison with the percentages of all nests built by each group ($\chi^2 = 2.47$; $0.50 > P > 0.20$), indicating that all three groups are equally likely to stack nests.

Nest cover preference.—Table 2 compares the percentages of nests supported by cattail, bulrush, and mixed cattail-bulrush with the percentages of each of the three types of cover available. Chi-square tests (Table 3) indicate that both monogamous and bigamous males used cattails for nest support significantly more often than would be predicted from the per cent of cattail available in their territories. Bachelor males, on the other hand, showed no such selective preference for nesting cover. Similar results are evident for supporting cover of brood nests, which are selected by females, of both monogamous and bigamous males. No significant difference existed between nesting cover of courting nests and breeding nests.

An insignificant ($P > 0.20$) negative correlation ($r = -0.101$) was found between total nest sites and the amount of pure cattail stand in the

TABLE 3

Chi-square Tests of Nest Cover Preference[1]

Males		Cattail vs. bulrush	Cattail vs. bulrush vs. mixed	Brood nests[2]
Bachelor (N = 13)	Total nests	$\chi^2 = 1.08$ $0.50 > P > 0.20$	$\chi^2 = 0.08$ $0.98 > P > 0.95$	
Monogamous (N = 47)	Total nests	$\chi^2 = 9.98$ $0.01 > P > 0.001$	$\chi^2 = 10.38$ $0.01 > P > 0.001$	$\chi^2 = 0.93$ $0.50 > P > 0.20$
	Brood nests	$\chi^2 = 9.61$ $0.01 > P > 0.001$	$\chi^2 = 10.48$ $0.01 > P > 0.001$	
Bigamous (N = 20)	Total nests	$\chi^2 = 4.09$ $0.05 > P > 0.02$	$\chi^2 = 4.20$ $0.20 > P > 0.10$	$\chi^2 = 0.73$ $0.80 > P > 0.50$
	Brood nests	$\chi^2 = 4.35$ $0.05 > P > 0.02$	$\chi^2 = 5.29$ $0.10 > P > 0.05$	

[1] Percentages of nests placed in each cover type are compared to the percentages of the various cover types available in territories (see Table 2).

[2] Brood nest cover is compared with total nest cover only in cattail and bulrush.

territory and an insignificant ($P > 0.20$) positive correlation ($r = +0.111$) between total nest sites and area of pure bulrush. On the other hand the correlation ($r = +0.330$) between area of mixed cattail and bulrush stand in the territory and the total number of nests sites was highly significant ($0.01 > P > 0.001$). The correlation ($r = +0.200$) between total territory size and number of nests sites was not significant ($0.08 > P > 0.07$).

While quantitative data for 1968 are unavailable for similar analyses of nest-cover preference, our observations point decisively and uniformly in one direction. Males exploited cattail for nest cover most commonly, so long as the cattail still had standing water around the bases of the stalks. As soon as the cattail stands dried out, the birds exploited bulrush stands exclusively for nesting cover. Probably over 90 per cent of the nests built after mid-June were supported by bulrush.

TABLE 4

Numbers and Cover Types of Nests Left Incomplete by Bachelors, Monogamists, and Bigamists

Males		Cattail	Bulrush	Mixed	Total
Bachelor	Incomplete nests	7 (21.9)[1]	21 (65.6)[1]	4 (12.5)[1]	32
(N = 13)	% of all bachelors' nests	6.1	19.4	11.4	12.4
	Mean stage of completion	3.0	3.7	4.3	3.6
Monogamous	Incomplete nests	63 (50.0)	36 (28.6)	27 (21.4)	126
(N = 47)	% of all monogamists' nests	11.4	12.5	8.4	10.9
	Mean stage of completion	3.9	2.9	3.9	3.6
Bigamous	Incomplete nests	31 (66.0)	8 (17.0)	8 (17.0)	47
(N = 20)	% of all bigamists' nests	9.5	9.9	5.8	8.8
	Mean stage of completion	3.4	2.5	3.5	3.3
Total	Incomplete nests	101 (49.3)	65 (31.7)	39 (19.0)	205
(N = 80)	% of all males' nests	10.2	13.7	7.8	10.4
	Mean stage of completion	3.7	3.1	4.0	3.5

[1] Percentages shown in parentheses.

TABLE 5

MEAN AREAS OF TERRITORIES AND THEIR COMPONENT VEGETATION IN $m^2 \pm 2$ STANDARD ERRORS[1]

	Bachelor	Monogamous	Bigamous
Total area	516.8 ± 183.0	642.3 ± 89.9	685.3 ± 169.0
Cattail	237.2 ± 199.4	227.4 ± 68.3	361.3 ± 120.7
Bulrush	225.8 ± 143.3	252.4 ± 92.7	160.6 ± 120.8
Mixed	53.8 ± 25.0	162.0 ± 52.4	163.5 ± 103.3
Other	0.0	0.4 ± 0.6	0.0

[1] Pure stands of cattail and bulrush, mixed stands of cattail and bulrush, and other.

Incomplete nests.—Table 4 summarizes the numbers of nests left incomplete by bachelors, monogamists, and bigamists in cattail, bulrush, and mixed stands. No significant difference is evident in the total numbers of nests left incomplete by males of the three categories. Student's *t*-tests further indicate that no significant differences existed between the mean stages of completion of incomplete nests placed in cattail, bulrush, or mixed stands by males of any category, although bachelors left a significantly higher percentage of nests incomplete in bulrush than predicted from the percentage of their total nest sites in bulrush ($\chi^2 = 25.08$; $P < 0.001$). This was not true of monogamists ($\chi^2 = 3.50$; $0.20 > P > 0.10$) and bigamists ($\chi^2 = 4.66$; $0.10 > P > 0.09$).

Territories.—Results presented in Table 5 show territories in 1967 were slightly larger than those found in 1962 (mean = 450 m^2, Verner, 1965), although the sample size was considerably smaller in the earlier study. Moreover, that study was confined to Beaver and a portion of Blackhorse Lakes. Although Table 5 indicates an increase in mean territory size from bachelors to monogamists to bigamists, the individual variability in territory size is so great that the observed differences are not statistically significant (bachelors vs. bigamists—$t = 1.35$; $0.20 > P > 0.10$). Moreover, no significant correlation exists between total territory size and male pairing success ($r = 0.153$; $P > 0.10$).

Mating system.—Previous studies of adult sex ratios in the Long-billed Marsh Wren (Verner, 1964) indicated no significant deviation from 1:1, and yet polygny was found to be common. Those results are confirmed by the present study, in which sample size was substantially larger than previously. Of the total of 80 males studied, 13 remained bachelors throughout the breeding season, 47 never obtained more than one mate at a time, and 20 had two mates simultaneously at least part of the time. This indicates a ratio of 80 males to 87 females (1.00:1.09), which does not differ significantly from unity ($\chi^2 = 0.61$; $0.50 > P > 0.20$). The fact that some bigamous males were not bigamous throughout the season suggests that some females changed mates, so the population probably contained fewer than 87 females. During the playback studies we exploited 17 males that were bachelors at the time of playback, 51 that were monogamists, and 12 that were bigamists. These figures suggest a ratio of 80 males to only 75 females (1.07:1.00).

Coefficients of correlation between male pairing success and the various parameters of their territories and behavior were calculated. A negative correlation ($r = -0.219$) between pairing success and percentage bulrush in the territory is probably significant ($P = 0.051$), thus refuting an earlier suggestion (Verner, 1965) of a possible positive correlation between these factors. A highly significant correlation ($r = 0.289$, $0.01 > P > 0.001$) existed between pairing success and total nest sites in males' territories. All other correlations between male pairing success and territorial parameters (area of pure cattail, area of pure bulrush, area of mixed cattail and bulrush, total area, per cent pure cattail, and per cent mixed cattail and bulrush) were statistically insignificant. Additional evidence suggests that other territorial parameters may be of importance in a male's pairing success.

One of the eight territories examined during both 1967 and 1968 was used by the same (color-banded) male both years; he was a bachelor in 1967 and a monogamist in 1968. The three territories held by bigamists in 1967 were also held by bigamists (but different individuals) in 1968, while the four held by monogamists in 1967 were held by monogamists (also all different individuals) in 1968. We emphasize that the boundaries of all these territories were, as nearly as we could determine, identical in both years.

Along the north shore of Blackhorse Lake one spot was known to contain a monogamist in 1962, 1967, and 1968, although the territory boundaries were not exactly coincident all 3 years. On the other hand a nearby marsh segment held two monogamists and one trigamist in 1962, two bigamists in 1967, and two monogamists in 1968.

Further evidence that male pairing success is related in some way to the habitat is provided by the fact that males have greater pairing success on some lakes than on others. In 1967, for example, mean pairing success of males on Kepple Lake was 1.60; it was 1.38 on Lower Pine Lake, 1.13 on Blackhorse, 1.11 on Little McDowell, 1.00 on Big McDowell, and 0.83 on West Tritt.

DISCUSSION

Attempts to correlate various territorial parameters with male pairing success were disappointing. The possible significance of bulrush in territories, in our opinion, still requires further study. The wrens clearly preferred cattail as nest cover in 1967, a factor that supports the probable negative correlation between male pairing success and per cent bulrush in the territory. From this we conclude that natural selection favors those males with a tendency to establish territories in exclusively or predominantly cattail stands. On the other hand the fact that no significant correlation existed between the absolute amount of pure bulrush stand in a male's territory and his pairing success suggests that the correlation with per cent bulrush may not be real. Moreover the fact that low water level in 1968 forced males to exploit bulrush stands almost exclusively after May brings a new focus on the possible value of bulrush to the birds. Preliminary studies indicate that aquatic invertebrates comprise a major part of the wren's diet. As bulrush typically grows in deeper water than cattail, only the bulrush stands could have provided this important source of food for the wrens in June and July of 1968. Certainly in that year, at least, selection favored those males whose territories contained some bulrush because they were less likely to be forced to abandon their territories in mid-season and run the risks of establishing new territories elsewhere. It is now clear that cattail is the preferred nesting cover only if it has standing water. The importance of water could be in protection of the nest from predation and/or provision of a highly important food source.

Certainly other territorial parameters could influence a male's pairing success, but they are probably much more subtle and difficult to measure than those parameters considered here. While we cannot attach profound significance to the limited number of comparisons of pairing success of males on eight territories in 2 successive years, nonetheless, the fact that bigamy and monogamy appeared to be related to sites rather than to males is consistent with the hypothesis that a male's pairing success is related to the habitat he occupies. The fact that mean pairing success varies from lake to lake also supports this view. While no data obtained to date conflict with this hypothesis, this does not necessarily mean that characteristics of the male are not also important. It seems likely that the most vigorous, or successful, males are those best able to discriminate and defend the most suitable habitats. Any characteristics of the males that were correlated with their ability to locate and defend superior territories could serve to attract mates and have the same ultimate effect that female discrimination of the habitat itself would have.

The highly significant correlation between pairing success and total nest sites prompted as complete an analysis of the various aspects of nest building behavior as our present data would permit. This correlation is of especial interest in view of the important role of nests in the courting behavior of male wrens. Failure to discover a similar correlation in earlier studies (Verner, 1964) is attributable to two factors: (1) Sample sizes were too small. (2) Males in the Seattle population, in contrast to those at Turnbull Refuge, regularly fed their young; consequently, the males with greatest pairing success spent the greatest amount of time feeding young and had the least time for building nests. If anything, one would predict a negative correlation between number of nests and male pairing success at Seattle, but the small sample size precludes adequate analysis.

The importance of total nest sites can be interpreted in at least two ways. First, the number of nests is of direct importance, and it is the total number of nests that prospecting females assess. This could serve as an index to the male's vigor, which is of importance in the survival of the female's offspring. Limited evidence is available to refute this interpretation. In the Seattle population the first males to obtain mates commonly had completed fewer nests by the time they were paired than had males that paired later (Verner, 1964). At Turnbull Refuge it was not unusual to find mated males that had as few as two or three nests. Experimental manipulation of the number of nests in the territories of a large sample of male wrens could be employed to explore this possibility.

Second, the number of nests could be of indirect importance, simply being correlated with another factor that is of prime importance to females. Those males whose territories provide the richest food supply would require the least amount of time to forage and would thus have more time to build nests. The females might directly assess the suitability of a territory for foraging. The apparent reduction in nest building rate of male wrens in 1968, compared with 1967, may have been a direct result of the drying of the marshes and its impact on the availability of aquatic food sources. For example we repeatedly found that stomachs of wrens collected from nearly dry sections of cattail contained principally plant materials, while those of wrens collected in areas with ample standing water contained principally insects. Further evidence on the importance of food supply to male nest building activities was provided by a prolonged period of abnormally cold, wet weather during the middle of the usual peak of nest building activity at Seattle in 1962 (see Verner, 1965). This period saw a substantial decline in nest building by male wrens. It is our belief that less food was available during that period and/or that the wrens needed more food to maintain themselves. Either would have required more time for foraging and left less time for nest building. We believe the most promising hypothesis, still unexplored, to explain the observed differences in pairing success of male Long-billed Marsh Wrens is that females somehow assess the availability of food among the territories of different males, and that this has a profound effect on their choice of nesting sites.

In addition to the correlation between pairing success and total nest sites, other statistically significant differences in the nest building behavior of bachelors, monogamists, and bigamists warrant comment. First, monogamous and bigamous males showed a significant preference for cattail as supporting cover for their nests; bachelors showed no such preference. Second, only bachelors left a significantly higher percentage of their bulrush nests incomplete than was predicted from the percentage of their nests placed in bulrush. These results are consistent with the possibility that experience plays a role in the selection of nesting cover by male wrens. Perhaps they must learn that cattail stalks provide stronger support for nests and that nests are less likely to slip down cattail stalks than they are to slip down bulrush stems. It follows that bachelors may usually be first-year males that have not yet learned many important facets of efficient marsh exploitation, including the best nesting cover.

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SUMMARY

Detailed analyses of the territories, nest building activities, and pairing success of 80 male Long-billed Marsh Wrens were conducted at Turnbull National Wildlife Refuge during the summer of 1967. Eight of the same territories were examined again during the summer of 1968. The wrens were polygynous in spite of a 1:1 sex ratio, confirming earlier studies. Male pairing success could not be clearly shown to be correlated significantly with any territorial parameter measured. Significant differences in the nest building behavior of bachelor males, compared to that of monogamous and bigamous males, suggest that learning may be important in the development of the male's efficient exploitation of the marsh. If this be true, first-year males may be less successful in attracting mates than older males. A significant correlation found between male pairing success and total nest sites may simply be a spurious correlation resulting from the fact that females select mates on the basis of the density of food within their territories, and those males with greater food densities require less time for foraging and so have more time for nest construction. Other evidence is also consistent with the hypothesis that differences in food availability between territories are of prime importance in female mate selection.

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