

BREEDING BIOLOGY OF THE LONG-BILLED MARSH WREN

BY JARED VERNER

Although much of the life history of the Long-billed Marsh Wren (*Telmatodytes palustris*) has been described (see especially Welter, 1935; Bent, 1948; and Kale, MS), most aspects have not been quantified adequately to permit analysis of geographical variation between populations. Such variation often leads to insights into the ecology of a species which would otherwise be impossible. This paper presents comparative data on birds from two populations in Washington State, one (*T. p. paludicola*) at Seattle, the other (*T. p. plesius*) at Turnbull National Wildlife Refuge, 15 miles south of Spokane and 225 miles due east of Seattle (fig. 1). Other aspects of this study are treated elsewhere (Verner, 1964; also MS, 1963).

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the numerous helpful suggestions and criticisms of Drs. Frank Richardson and Gordon H. Orians throughout the course of this study. Dr. R. C. Snyder kindly read the manuscript. Many colleagues assisted with field work and were helpful in discussions of the data; in this regard I would especially like to thank T. H. Frazzetta, M. E. Kriebel, K. P. Mauzey, E. R. Pianka, C. C. Smith, L. W. Spring, and M. F. Willson. My wife, Marlene, processed many of the raw field data and was responsible for lettering most of the figures. Working facilities were provided by the Department of Zoology, University of Washington, and financial assistance was provided by National Science Foundation predoctoral fellowships (1960-1963).

STUDY AREAS

At Seattle, two marshes (Red, 6.3 acres, and Blue, 3.3 acres) in the University of Washington Arboretum were studied in 1961. These were destroyed early in 1962 by a bridge construction project; so a nearby marsh (Yellow, 3.2 acres) was studied in 1962. These were all extensive patches of cattail (*Typha latifolia*) with scattered small stands of bulrush (*Scirpus acutus*) in the Blue and Yellow marshes (see fig. 5). Portions of these same two marshes that were based on a floating mat of roots and decaying plant materials remained free of standing water in spite of fluctuations in surrounding water level. Those portions of the marshes that did not float were mostly without standing water during fall and early winter, but by late winter Lake Washington (level controlled at canal locks) began to rise and flood into the marshes. Maximum depth in the marshes reached 12 to 18 inches in places by late April both years and remained constant until late June. Mid-August found the marshes again without standing water, and it was possible to move about them in street shoes.

At Turnbull, observations were concentrated on a 0.5-acre marsh at Blackhorse Lake with less intense observations on a 1.0-acre marsh at Beaver Pond (fig. 1). These, in contrast to the extensive marsh patches at Seattle, were narrow pond-margin strips and lenses of cattail and bulrush, the latter forming a more dominant part of the habitat than at Seattle. Lake water was supplied by spring runoff supplemented by springs. All marshes had standing water by mid-March, but evaporation left most marshes without standing water by late July. The water level at Beaver Pond dropped 16.5 inches from April 1 to July 31 in 1962, while that at Blackhorse Lake dropped 18.0 inches during the same period.

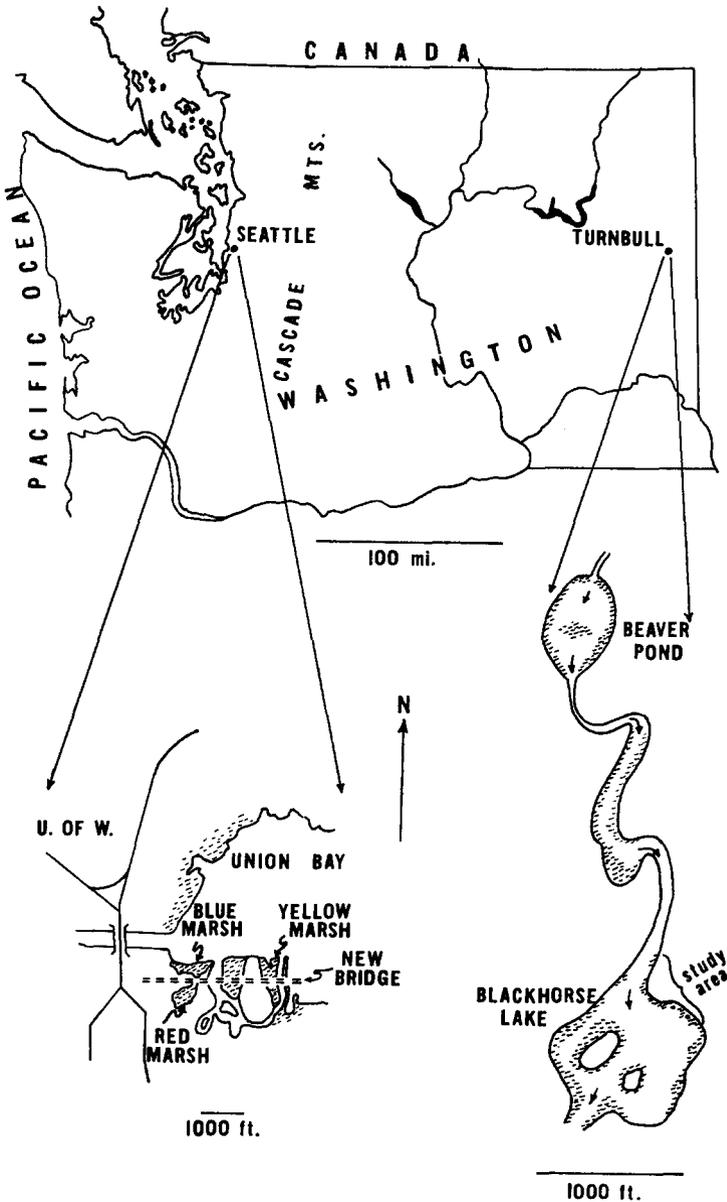


Fig. 1. Map of Washington State with study locations indicated and enlarged below.

METHODS

At Seattle most observations were carried out from January through August in 1961 and 1962. At Turnbull, visits were made approximately bi-weekly, usually for two days at a time, from late March through July in 1962. All marshes were mapped by plane table and several hundred maps of each were printed for use in the field;

surface areas were determined by planimeter. Routine investigations of territories were made regularly to obtain data on the progress of nest cycles, and limited observations were made from blinds near nests during laying, incubation, and nestling periods. Over 100 hours of data on incubation rhythms were obtained with an automatic recorder placed at nest apertures. Finally, several hundred hours of recorded observations were made from towers located strategically in relation to territories of wrens.

To facilitate recognition of individual birds, in 1961, 13 of 19 adult males, 10 of 15 adult females, and 61 of 71 young fledged in the Red and Blue marshes were individually color banded. In addition, one unbanded female was readily identified by a spot with missing feathers on her right flank, and a second female was identified by having more cinnamon plumage than any other bird in the population. The destruction of these marshes led to a very poor return of birds the following year, since it was necessary to change study areas. Only one bird banded in 1961 appeared in the Yellow Marsh in 1962, although the Yellow Marsh was less than a quarter of a mile from the Red and Blue marshes. In 1962, 5 of 10 adult males, 9 of 12 adult females, and 34 of 40 young fledged in the Yellow Marsh were color banded. Of these, only two males and three females were observed in 1963; neither of the males survived the breeding season, and no young of the previous season was seen in 1963. At Turnbull only one female was color banded. Substantial evidence from the Seattle population indicates that males remain on the same territory throughout the breeding season. When a male disappeared, it was usually easy to determine whether a neighbor or a newcomer occupied his territory.

LIFE HISTORY

NONBREEDING SEASON

In Seattle, with its maritime climate, ice rarely forms in the marshes and the wren population is resident. In contrast, Turnbull is in a region of continental climate where lakes and ponds are normally frozen over for long periods between late November and late February. Thus the Turnbull population is migratory.

During the nonbreeding season, the Seattle wrens spend nearly all their time foraging, resting, and performing preening and other comfort actions. Although songs have been heard during every month of the year, singing is at a minimum from September through December. Juveniles can regularly be heard in subsong from late June into October, but full adult song is rare after the early part of August, and song rates begin to decrease noticeably as early as the first half of July, depending upon environmental conditions. Full song begins again in late winter (January, if the weather is warmer than normal), increasing during late February and early March.

In 1962, Turnbull wrens returned during the second half of March, and full song was apparently reached then or very shortly thereafter. Welter (1935) reported that marsh wrens at Ithaca, New York, returned early in May and showed full song and territorial activity within a day or two.

SYNOPSIS OF BREEDING CHRONOLOGIES

In figures 2, 3, and 4 the breeding chronologies of the various males and females included in this study are presented for Seattle, in 1961, Seattle in 1962, and Turnbull in 1962, respectively. Breeding cycles are represented by variously marked horizontal bars (see key, fig. 3), successive cycles of the same pair following in direct line.

In 16 cases of renesting by the same banded female in the same season, 13 (81

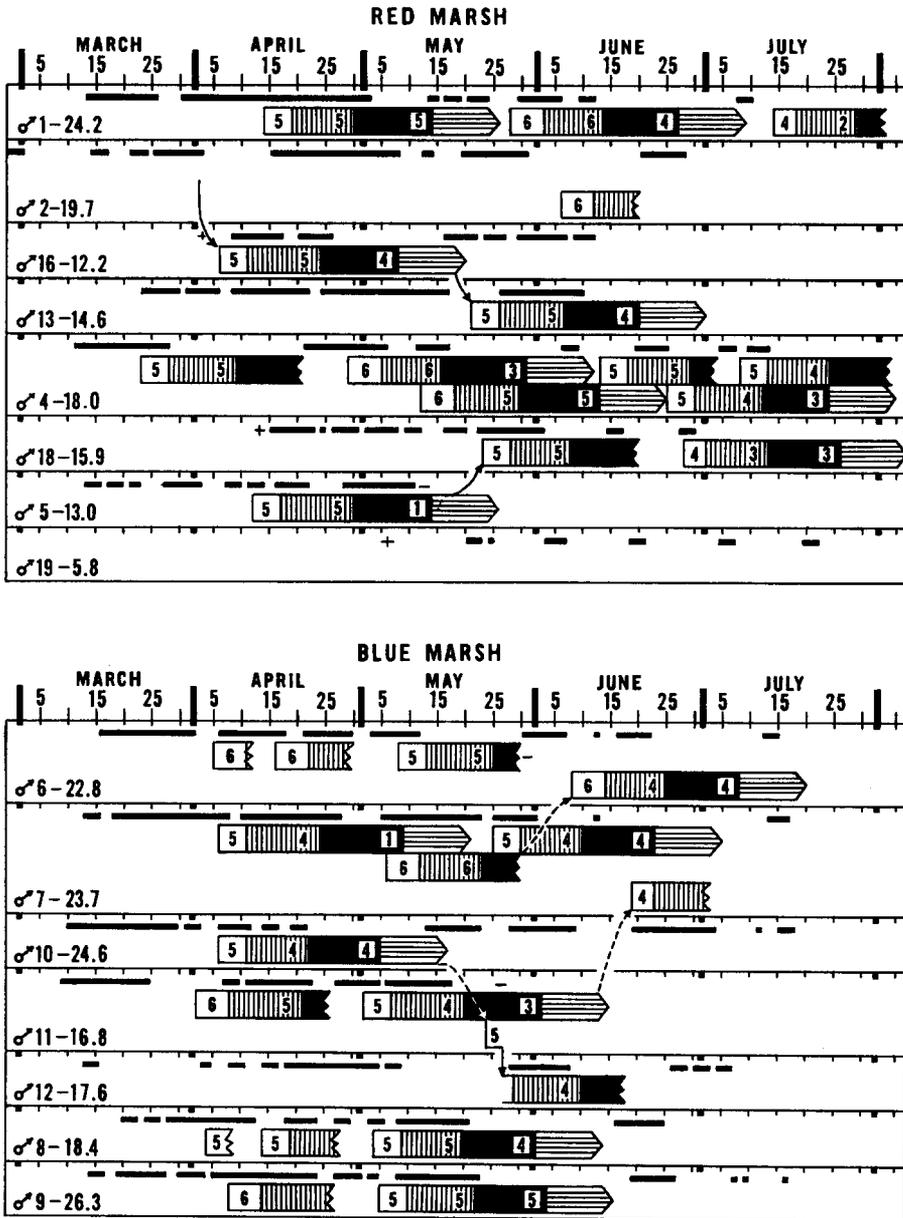


Fig. 2. Breeding chronologies of pairs of marsh wrens in Seattle in 1961; key with figure 3.

per cent) remained with their original mate and three (19 per cent) changed mates while their original one still lived. With unbanded females, it was usually possible to trace their probable choice of mates for reneating simply by the timing of nest cycles. It was therefore possible to reconstruct the various pair bonds even among unbanded individuals with a high degree of accuracy. Altogether, probably only 9 (23 per cent)

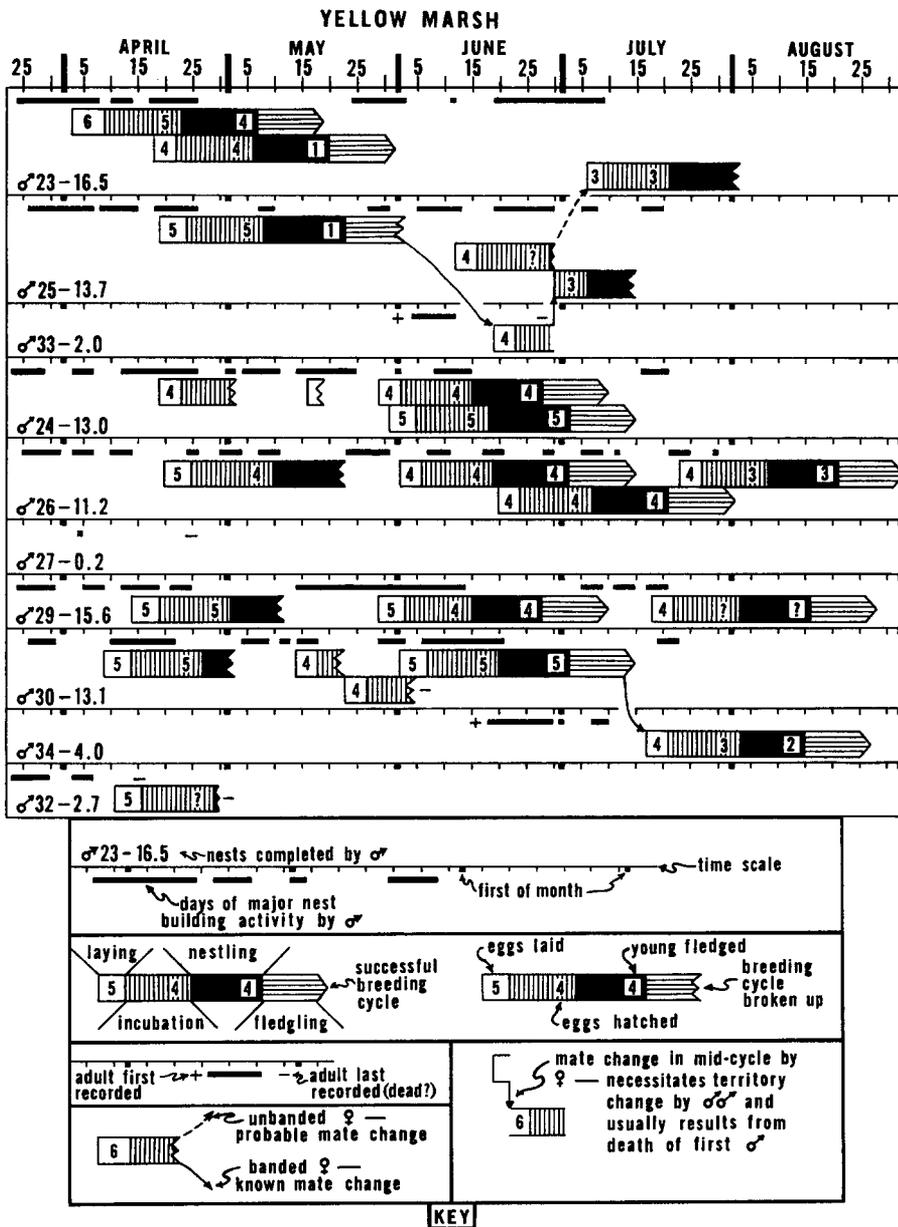


Fig. 3. Breeding chronologies of pairs in Seattle in 1962; key below.

of 39 renestings by females in the same season involved mate changes while the original mate still lived. From 45 to 50 days are required to complete one cycle and start a second. Females at Seattle can, without mishaps, rear three broods in a season, whereas females at Turnbull are apparently limited to two.

Since the timing of many events represented in figures 2, 3, and 4 was interpolated



Fig. 4. Breeding chronologies of pairs at Turnbull in 1962; key with figure 3.

or extrapolated, the figures must not be construed as perfectly accurate records of each case. Estimates of incubation periods and other phases of the breeding cycle are given later and are based on those cases for which accurate observations were available. The figures do, however, provide a rapid means of appreciating relation-

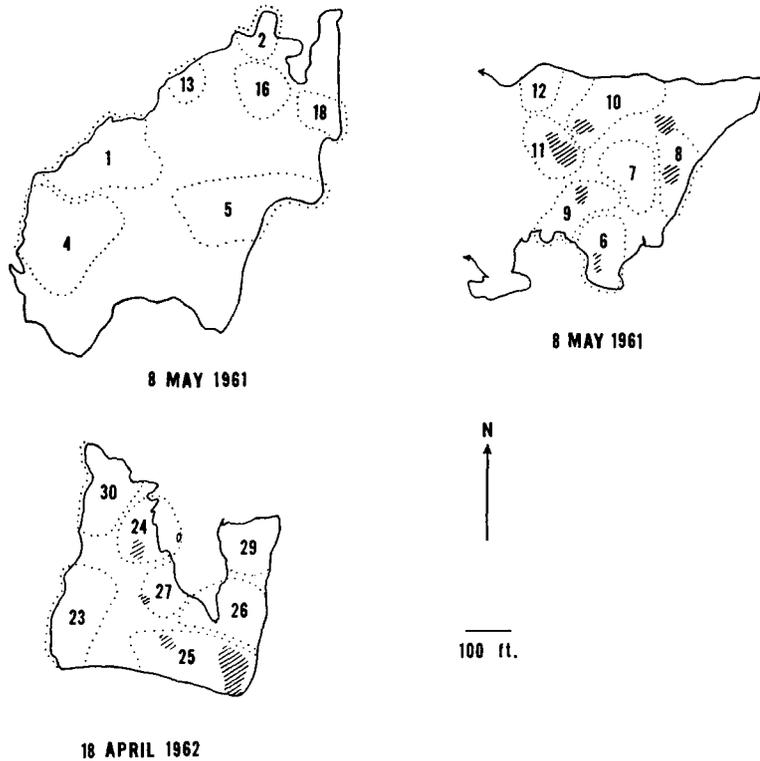


Fig. 5. Representative territorial maps of Red Marsh (upper left), Blue Marsh (upper right), and Yellow Marsh (below). Territories are outlined by dotted lines; males are designated by number. Shaded areas of Blue and Yellow marshes indicate bulrush stands.

ships in timing among the activities of different pairs in this study. Attention is called, for instance, to the high degree of synchrony in the initiation of nest construction by males in each of the various study plots.

TERRITORY

Wrens at Seattle apparently maintain rather ill-defined territories during the nonbreeding season. In late winter, concurrent with a gradual increase in song rates and conspicuousness, males decrease the area over which they range, and breeding territories become fairly well defined by late February. Boundary disputes are most frequent before nest construction begins and drop off sharply thereafter, song apparently serving effectively to maintain territories. Many territorial boundaries were not contiguous with those of other wrens (fig. 5), making boundary determination more difficult. Through daily observations, however, I was aware of the extent of each male's foraging activities and was thus able to plot territories on the maps. Occasionally adults foraged off their territories, especially in undefended locations, although both sexes normally remained within the territories. Females occasionally drove intruders out, especially juveniles later in the breeding season.

At Turnbull, territorial limits were largely determined by the distribution of marsh

TABLE 1
MEAN TERRITORY SIZE (SQ. FT.) IN THE DIFFERENT STUDY AREAS*

Location	Mean	Range	N
Red Marsh	18,200 \pm 2200	2600 - 38,700	26
Blue Marsh	13,500 \pm 252	7400 - 23,700	27
Yellow Marsh	14,700 \pm 281	4500 - 25,800	29
Blackhorse Lake	4500 \pm 315	1800 - 7900	26
Beaver Pond	5200 \pm 316	2500 - 9600	34

* Territories were measured on four occasions in each Seattle marsh, seven times at Blackhorse Lake, and five times at Beaver Pond. Consequently the same males' territory may enter into the calculations a number of times, but the boundaries were rarely the same each time.

vegetation, and birds utilized all of the areas they occupied. Consequently, territorial boundaries were more easily determined and there were fewer seasonal shifts in boundaries there than at Seattle. Designations of territories at Seattle correspond most closely to the "maximum territory" of Odum and Kuenzler (1955), while at Turnbull the "maximum" and "utilized" territories were the same. Since work at Turnbull's Beaver Pond was limited to bi-weekly examination of nests, the precise divisions between territories were not ascertained, and indications of territory size are not as accurate as those for Blackhorse Lake. Approximate territorial sizes are presented in table 1 and selected territorial organizations in figure 5.

NEST CONSTRUCTION

Probably the best-known fact of the biology of this species is that males build a number of nests that are never used for breeding purposes. Nests are domed ellipsoids about 7 inches from top to bottom, outside, and 5 inches from side to side, outside; the single opening is usually just above the equator but frequently displaced nearer the top. Breeding nests differ from nonbreeding nests in having a substantial lining. Welter (1935) presents photographs of sagittal sections through both types of nests. Nests are usually placed in cattails (preferably in stands of moderate density), but occasionally they are placed in bulrushes. Wrens in a colony located in a dense stand of emergent *Spiraea douglasii* near Kirkland, Washington, placed their nests in the *Spiraea*, no cattails being available. Nest heights (from marsh floor to bottom of nest), measured to the nearest inch, are summarized in table 2. Nest height was in direct relation to the height of supporting cover so that it increased

TABLE 2
MEAN NEST HEIGHT IN INCHES IN DIFFERENT STUDY AREAS

Location	Nonbreeding nests	Breeding nests
Seattle, 1961	37.4 \pm 0.62	36.5 \pm 2.04
	23 - 77	20 - 77
	N = 260	N = 33
Seattle, 1962	31.4 \pm 1.35	30.0 \pm 2.97
	13 - 60	14 - 70
	N = 70	N = 21
Turnbull, 1962	35.6 \pm 0.88	33.3 \pm 2.32
	13 - 73	12 - 55
	N = 218	N = 27

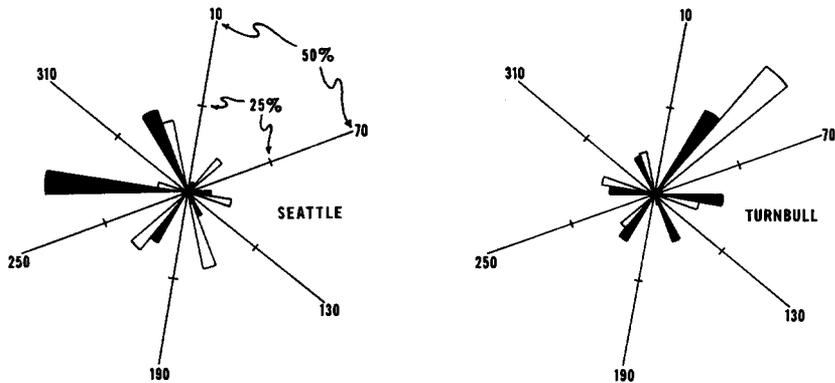


Fig. 6. Orientation of nest apertures at Seattle and Turnbull. Solid wedges indicate percentages of courting nests and open wedges indicate percentages of breeding nests oriented in each sixth of the compass.

steadily during the season after new plant growth rose above the collapsed plant stems of the previous season. Nest materials usually consisted of cattail parts, the shell being of interlaced strips of dead cattail leaves obtained in a soaked condition from the marsh floor. Into this shell, down plucked from cattail heads was incorporated. Lining materials were gathered principally by females by peeling dry strips from dead cattail stalks. Feathers of various species were also used in the lining. Wrens nesting in bulrushes used bulrush stems to construct their nests, and those nesting in the *Spiraea* thicket used grasses.

Three nonbreeding nests found in cattails were carefully teased apart in water and found to contain an average of 100 (62–175) pieces of down and 476 (346–596) strips of cattail leaves with a mean length, measured to the nearest 0.5 inch, of 5.9 ± 0.13 inches (0.5–25.0; $N = 853$). Mean dry weight of nonbreeding nests was 21.6 ± 0.59 gm. (16.1–29.8; $N = 28$), weighed to the nearest 0.1 gm.

The report that male wrens occasionally fill a nest cavity with cattail down (Higman and Larrison, 1951) is probably erroneous. In every case of a down-filled nest it was found that a single bumble bee (*Bombus californicus*) had made a nest within. The down was probably brought in by the bee.

The orientation of nest apertures is summarized in figure 6. Using the Chi square to approximate a multinomial distribution indicates that the orientations of nonbreeding nests both at Turnbull and Seattle and the breeding nests at Turnbull differ significantly from random ($P < 0.002$ in each case). The possible biological significance of these nonrandom orientations is uncertain at this point.

In 1961, two Seattle males started building nests on February 22 and 27, respectively. The earlier nest was completed but the male was accidentally killed in a mouse trap. The second was brought to half-completion before the male suspended building operations until the remainder of the male population began to build between March 9 and 20 (mean in Red Marsh, March 13; in Blue Marsh, March 14). In 1962, nest construction did not begin until March 23, and by March 26 all males, with a single notable exception that began on April 4 (Male 27, fig. 3), were actively building nests. At Turnbull, building was underway by April 1 at Blackhorse and some other lakes, while it began later at Beaver Pond. Average dates of first con-

TABLE 3
NESTS COMPLETED PER MALE, INCLUDING ONLY THOSE MALES THAT
WERE PRESENT THROUGHOUT BREEDING SEASON

Location	Mean	Range	N
Seattle, 1961	21.0 \pm 1.21	14.6 - 26.3	10
Seattle, 1962	13.9 \pm 0.78	11.2 - 16.5	6
Turnbull, 1962	22.3 \pm 1.64	15.5 - 32.2	10

struction were April 8 at Blackhorse and April 14 at Beaver. One male (no. 4) at Blackhorse spent most of the first three weeks in April establishing a territory by starting first at the zone of contact between two established territories and gradually usurping a portion of one of them. His building activity was thus delayed until April 19.

Nest construction was arbitrarily divided into nine stages, each requiring approximately an equivalent amount of material to complete, and an assessment of the rate of construction was thus derived. Material in incomplete nests could be estimated and equated to fractions of a complete nest. In this way it was possible to calculate the number of equivalent complete nests built by each male (table 3). Figures in table 3 are based only on males that were present throughout the nest building period; complete equivalent nests of all males, regardless of the length of their occupation, are indicated in figures 2, 3, and 4. Adjustments were made on the assumption that females built 26 per cent of the shell of breeding nests early in the season (see beyond).

Welter (1935:19) reported that males near Ithaca, New York, built an average of five or six nests "during the rearing of the first brood," with ten being exceptional. On June 20, 1962, I examined four territories of marsh wrens at North Spencer Marsh (one of Welter's study areas), about 12 miles south of Ithaca, finding an average of 7.0 completed nests per male. The breeding season was just starting, and only one territory contained an active breeding nest (six warm eggs). Since Welter did not specify how many nests were completed by the end of the season, the number may run well over ten per male.

Kale (MS) reported a range of 3 to 27 nests per male in wrens of the Georgia salt marshes (mean 12.3 in 1958, 11.9 in 1959). The range suggests that males not present during the full season were included; the number of nests completed by males remaining the full season was probably greater.

Figure 7 illustrates the rates at which nests were constructed per male in each of the areas on a semi-monthly basis. In contrast to Welter's (1935) observations of marsh wrens in New York and Minnesota, males in Washington continue to build throughout the breeding season. Data from the Red and Blue marshes were combined to give an estimate for Seattle in 1961, and data from Blackhorse and Beaver were combined to estimate the rates at Turnbull in 1962. Occasionally nests were completed in less than one day, although usually about three days were taken. During several intervals, males, especially at Turnbull, completed one nest every three days or less, thus completing five or more nests in a 15- to 16-day period.

The mean time actually spent building a single nonbreeding nest (558 minutes or 9.3 hours) was estimated from knowledge of the mean number of pieces of down and strips per nest (see preceding discussion) and the mean time required to collect, transport, and incorporate each piece into a nest (table 4). The differences in time spent

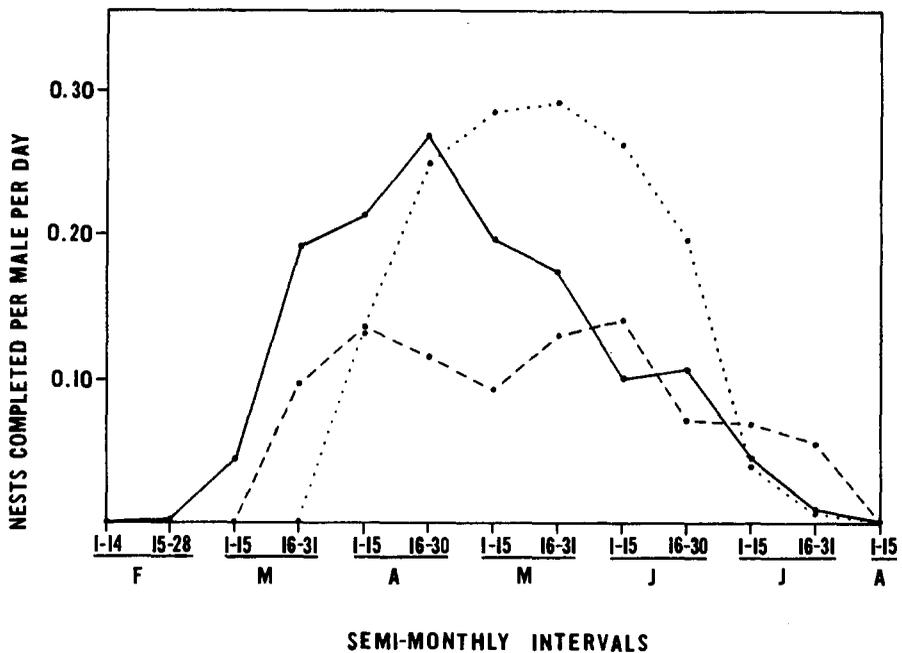


Fig. 7. Mean semi-monthly nest-building rates of males throughout the season in each area: Seattle, 1961, solid line; Seattle, 1962, dashed line; Turnbull, 1962, dotted line.

placing materials between males at Seattle and those of Turnbull (about 6–8 seconds longer by Seattle males) were significant ($0.001 < P < 0.01$, Student's t test) for strips but not for down ($0.2 < P < 0.3$); although a larger sample size may reveal the latter difference to be significant as well. Seattle wrens use nonbreeding nests for winter shelter but Turnbull wrens, being migratory, do not. Extra time spent at the nest by Seattle males may thus be an adaptation to weave a more substantial structure better able to withstand the winter. Comparable data were not obtained on the lining of nests by females.

Observers have long puzzled over the function of multiple nest building by males of this species. Welter (1935) suggested that multiple nests provide an outlet for excess sexual energies prior to the time of pair formation, apparently basing his conclusion on the doubtful observation that males stopped building after they were paired. It has been known for years that male House Wrens (*Troglodytes aedon*) may build several nests or place nesting material in more than one cavity (Kendeigh, 1941); and the same is true of the European Wren (*Troglodytes troglodytes*) as found by Kluijver, *et al.* (1940), Armstrong (1955), and others. Moreover, evidence indicates that nests of these wrens serve in courtship, males leading prospective females to them and displaying nearby. The same behavior occurs in the marsh wren, indicating that multiple nests function importantly in the courtship process.

Gilliard (1956) was apparently the first to suggest that multiple nests of the marsh wren might serve in courtship, arriving at this conclusion through consideration of the courting behavior of bower birds. In bower birds there is an inverse correlation between the elaborateness of bowers and the elaborateness of the plumage of the

TABLE 4
NEST BUILDING ACTIVITIES*

Location	Mean time gathering, carrying, and placing (min.)		Mean time placing (sec.)		Mean distance materials carried (ft.)	
	Strips	Down	Strips	Down	Strips	Down
Seattle	0.94 ± 0.01	0.90 ± 0.03	37.3 ± 2.03	35.2 ± 2.58	10.9 ± 0.74	29.3 ± 1.94
	0.25 - 2.50	0.25 - 2.50	7.8 - 113.3	6.1 - 128.3	2 - 70	1 - 180
	N = 403	N = 304	N = 130	N = 94	N = 204	N = 292
Turnbull	0.75 ± 0.01	0.68 ± 0.02	29.1 ± 2.30	29.3 ± 3.87	10.4 ± 0.69	21.8 ± 2.28
	0.25 - 2.00	0.25 - 1.25	4.1 - 117.3	8.9 - 80.5	3 - 68	3 - 80
	N = 275	N = 105	N = 98	N = 24	N = 149	N = 64

* Total time gathering, carrying, and placing materials was recorded to the nearest quarter of a minute; time placing was recorded to the nearest 0.1 second; distance carried was estimated to the nearest foot from 1 to 15 feet and to the nearest five feet at distances greater than 15 feet.

males that built them. Gilliard postulates that there may have been a shift in releasers associated with courtship from characters of the males to their courting structures, and he further suggests that something analogous may have taken place in marsh wrens. I agree; moreover, the same probably applies to the House Wren, European Wren, and Short-billed Marsh Wren (*Cistothorus platensis*). It is probably significant in this connection that the polygamous wrens are the only North American passerines reported to be regularly polygamous that are not also sexually dimorphic in plumage characters, although meadowlarks are only slightly dimorphic.

Other functions served by nonbreeding nests are: (1) Roosting at night by adults; (2) secondary shelters for fledglings after the breeding nest has been abandoned; (3) winter shelters for birds in the Seattle population.

COURTSHIP AND PAIR BOND

Briefly, courtship occurs in the following manner. After establishing a breeding territory the male begins building "courting" nests which are usually grouped in a small area subsequently referred to as a courting center. The number of nests per center ranges from one partial to four or five (occasionally more) complete nests. Males unsuccessful in attracting a mate may suspend building for a brief period but shortly resume building in the same or another area. As the season advances more courting centers are built, often overlapping others and making it impossible to define separate centers or to say with certainty how many nests constitute an average center.

Most songs are delivered from the courting center and little foraging is done there. Conversely, little singing is done in the major foraging areas. When a prospective female approaches a male's territory, he immediately flies toward her, delivering a rapid volley of songs with his tail cocked—often appearing to touch his nape. If the female enters the male's territory, he flies toward his courting center, the female sometimes following. At the center, the female examines and often enters one nest after another, being escorted to each by the male. One female was seen to visit the territories of three males within a period of ten minutes, but only in one territory did courtship proceed to the stage of nest examination. The male practically ceases singing during courtship, resorting instead to display. Courtship feeding was not observed.

After a female selects a male, she either selects one of his courting nests for breeding and lines it, the male rarely helping, or she initiates a new nest, which is con-

structed chiefly by the male. Welter (1935) reported that females regularly built the breeding nest, but I have observed only five females participating in construction of nests prior to lining. In those five cases, males made 74 per cent of 229 observed trips with nesting material. All five cases involved first breeding nests of the season. In later nesting attempts females usually, and perhaps always, accept one of the courting nests if the first breeding cycle has been even half completed.

After a male acquires a mate, he shifts to another part of his territory, either a day or two before laying begins or shortly thereafter, and starts building a new courting center from which he advertises for additional mates. Song rate did not decline during this period (Verner, 1963). All males in both populations behaved in this manner, indicating that all attempt to become polygamous, but not all are successful. I refer here to the simultaneous maintenance of more than one pair bond.

Welter (1935) reported 30 per cent polygamy among males in the New York and Minnesota areas, whereas Kale (MS) found only two to three per cent of the males at Sapelo Island, Georgia, to be polygamous. In the present study, the Red Marsh had 12.5 per cent polygamous males, the Blue Marsh had 30 per cent, the Yellow Marsh had 50 per cent, Blackhorse Lake had 50 per cent, and Beaver Pond had 50 per cent. In Seattle no male had more than two mates concurrently, while at Turnbull one male had three. The adaptive significance of polygamy is considered elsewhere (Verner, 1964).

LAYING

Laying began fairly synchronously in the various populations (see figures 2, 3, and 4), with about a three-week delay between the mean date of first nest construction by males and the mean date of first egg deposition. Eggs were invariably deposited at a rate of one per day, in the early morning hours only (Welter, 1935; Kale, MS), until a clutch was completed. At two nests during laying, eggs were removed daily, leaving one egg in the nest. In both cases, a normal-sized clutch was laid and then abandoned.

TABLE 5
CLUTCH SIZES

Location	Mean	Range	N
Seattle, 1961	5.2 ± 0.11	4 - 6	32
Seattle, 1962	4.4 ± 0.14	3 - 6	22
Turnbull, 1962	6.0 ± 0.19	4 - 8	25

Subsequent relaying began six days after desertion in one case and five days after desertion in the other. These two cases suggest that the marsh wren is a determinate layer, corresponding to the observations of Armstrong (1955) and Chappell (1948) on the European Wren; although Armstrong cites one report indicating that the European Wren is an indeterminate layer. More experiments are desirable.

Clutch sizes are summarized in tables 5 and 6. Clutches at Turnbull were significantly larger than those at Seattle in either year ($P < 0.01$ in both cases, Student's *t* test), and clutches at Seattle were significantly larger ($P < 0.01$) in 1961 than in 1962.

During the laying period, males spent most of their time away from the breeding nest at a new courting center. Copulation was apparently very infrequent, being observed only three times in over 40 hours of recorded observations of males during the period it could reasonably be expected to occur. The observed times were: 2:35

TABLE 6
SEASONAL VARIATIONS IN MEAN CLUTCH SIZE*

Location	March	April	May	June	July
Seattle, 1961	5.0 (1)	5.4 (11)	5.3 (12)	5.0 (6)	4.5 (2)
Seattle, 1962		4.9 (8)	4.3 (4)	4.3 (6)	3.8 (4)
Turnbull, 1962		6.0 (3)	6.5 (13)	5.6 (8)	4.0 (1)

* Number is given in parentheses below means.

p.m., April 14, 1962 (three days prior to laying); 8:36 p.m., May 9, 1961 (second day of laying); and 10:26 a.m., June 9, 1961 (second day of laying). Copulation in each case occurred within three feet of the breeding nest, apparently upon solicitation by the female.

INCUBATION

Incubation was performed solely by the female. No male was seen to enter a breeding nest in over 87 hours of recorded observations of males at that time. Furthermore, only females develop a brood patch. Eight full days' (7304 minutes or about 122 hours) records of incubation rhythm were obtained by automatic recorders placed at the nest entrance. The mean attentive period, with time recorded to the nearest minute, was 8.1 ± 0.14 minutes (1-20; N = 462) in duration, and the mean inattentive period was 7.7 ± 0.13 minutes (1-26; N = 466) in duration. The difference between means is significant ($0.02 < P < 0.05$).

The mean duration of attentive and inattentive periods varies throughout the day (fig. 8) in such a way as to suggest that the mean time spent on the eggs decreases with increasing ambient temperature, while the reverse is true of the time off the eggs. However, numerous other factors, such as light intensity, sky condition, wind, and age of eggs, appear to influence incubation rhythm. The data are inadequate properly to assess the role of each of these, and the pattern displayed in figure 8 is certainly the net result of a number of environmental influences.

Incubation periods are summarized in table 7. The trend toward shortening the period as the season advanced has been observed in many other species and has been suggested to result from improving foraging conditions permitting more time on the eggs or from variations in the time incubation is begun (see Armstrong, 1955, for discussion). Increasing temperatures, reducing the rate of heat loss from unattended eggs must be important as well.

The usual method of calculating incubation periods—from the laying of the last

TABLE 7
MEAN INCUBATION PERIODS (DAYS)*

Location	April	May	June	July
Seattle, 1961	15.75 (4)	14.50 (6)	14.00 (3)	14.83 (3)
Seattle, 1962	16.45 (5)		15.50 (1)	13.25 (1)

* Number is given in parentheses below means.

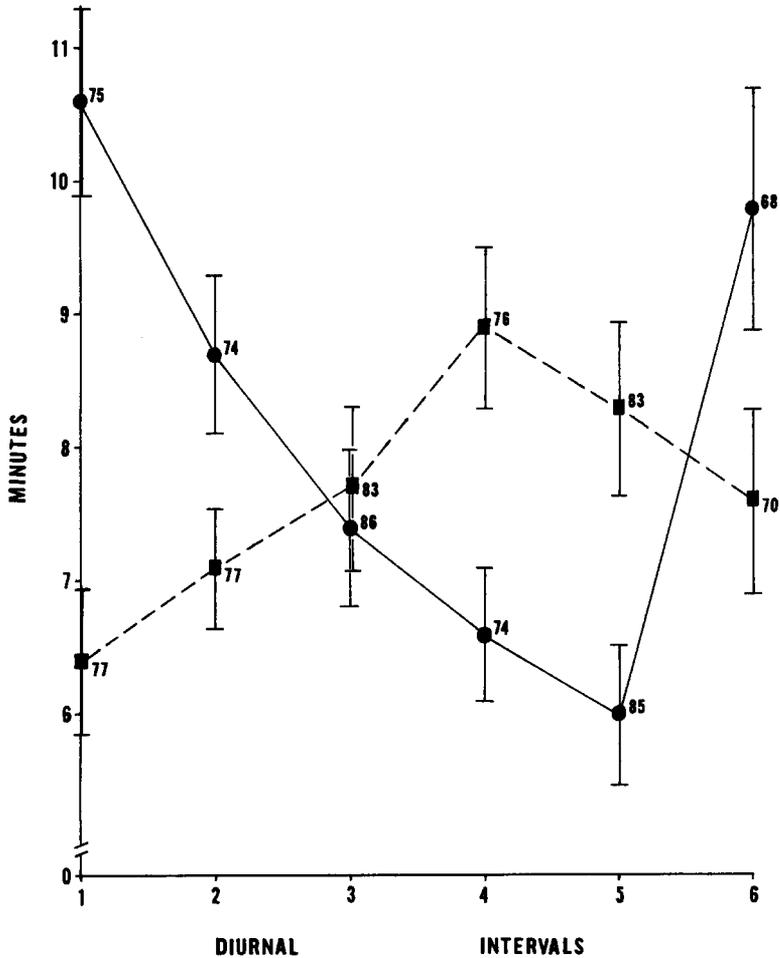


Fig. 8. Diurnal variation in mean duration of attentive (circles) bouts during incubation, with two standard errors marked on each side of mean. The value of N is entered by each mean. The daily active period has been divided into six equal intervals.

egg to the hatching of the last young—has been employed here. In addition, during 1961 all eggs in most nests were numbered in the order in which they were laid, and the order of hatching was established in as many cases as possible. Without exception, eggs hatched in the order in which they were laid, there being a difference of from 1.5 to 2.5 days between the hatching of the first and last eggs. This indicates that incubation commences before laying is completed, a fact borne out by direct observations.

The male continues to advertise for additional females while the first female incubates and, if he is successful in forming a second pair bond, he will strive for a third in a new courting center until young in his first nest demand too much of his time. This was true at Seattle, but not at Turnbull, where males do not feed young of early nests. Males were never observed to feed the incubating female.

TABLE 8
FEEDING RATES DURING NESTLING PERIOD, SEATTLE, 1961

Approximate age of oldest young in days	Feedings per young per hour					
	Male	Morning Female	Total	Male	Afternoon Female	Total
1	0.0	0.4	0.4	0.0	1.7	1.7
2	0.8	1.1	1.9	0.0	4.8	4.8
3	0.8	0.3	1.1	—	—	—
4	0.0	2.6	2.6	0.4	1.1	1.5
5	1.4	2.4	3.8	0.8	1.3	2.1
6	—	—	—	1.3	2.1	3.4
7	1.6	2.1	3.7	1.8	1.8	3.6
8	—	—	—	0.2	1.8	2.0
9	—	—	—	—	—	—
10	0.5	5.8	6.3	1.0	3.8	4.8
11	—	—	—	2.3	3.8	6.1
12	1.2	2.8	4.0	3.0	3.3	6.3
13	1.1	5.3	6.4	2.8	4.1	6.9
14	1.5	3.0	4.5	—	—	—
15	0.0	7.0	7.0	—	—	—
Mean	0.8	3.0	3.8	1.2	2.7	3.9
Per cent	21	79		31	69	

NESTLING PERIOD

When the eggs hatch, the shell fragments are removed from the nest by the female; one piece bearing the egg number was found 112 feet from the nest. Hatching, from the time pipping was begun to complete freedom of the young from the shell, took from 9 to 40 hours. There was no apparent tendency for eggs to hatch at a particular time of day.

The female brings food to the first young within a few hours of hatching, but males were not observed carrying food to nestlings until the oldest was about two days old. At Turnbull, males did not feed young early in the season but did so at the end. Table 8 presents data on feeding rates, and although only 35.8 hours of observations at eight nests are represented in the tabulation, it does indicate a general trend of increasing feeding rate with increasing age of young. The significance of feeding rates is difficult to interpret because biomass brought per trip is less during the early part of the nestling period than later. Moreover, evidence from other species indicates there may be a difference between sexes as to the amount of food transported per trip (references in Nice, 1943).

Adults arriving at the nest present food to the young and leave immediately, except on those occasions when the female (never the male) remains to brood. This occurs regularly until the young are 7 to 8 days old. The average time at the nest during feeding visits (when fecal material not removed) was 3.0 ± 0.26 seconds (1.0–6.3; $N = 27$) for the male and 2.9 ± 0.27 seconds (1.2–9.6; $N = 34$) for the female. When fecal sacs were removed, the time was 7.1 ± 3.03 seconds (2.3–12.7; $N = 3$) for the male and 5.8 ± 1.19 seconds (1.8–9.1; $N = 5$) for the female. Time was recorded to the nearest 0.1 second with a 10-second stopwatch from the time the adult arrived at the nest until it left. Extra time was required to remove fecal sacs early in the period because the adults had to search the nest cavity for them. Later

they had to wait while the young reversed its position to defecate toward the nest opening, sacs being taken directly as they were defecated, before they touched the nest. Females, but never males, were seen eating the sacs. This occurred only until the oldest young was about two days old. After the young were 11 to 12 days old they defecated over the edge of the nest; the adults periodically searched for and removed this material from below the nest opening.

In Seattle, males usually ceased singing and nest building almost entirely during this period, although different males varied considerably in these respects, and the same male occasionally differed between two cycles in the same season. In sharp contrast, males at Turnbull continued singing and nest building until the end of the season, a difference undoubtedly related to the different roles of males in parental care.

FLEDGLING PERIOD

When young birds normally leave the nest is difficult to determine, as young of many species leave earlier than normal when the nest is disturbed (see Skutch, 1945). Occasionally 11- to 12-day-old young left the nest when banded, but an undisturbed nest often contained young 15 or 16 days old. I felt that young were normally ready to leave the nest when the oldest was 14 days old; and although they were not expert fliers at that age, I considered them fledglings. Fledglings frequently roosted in the breeding nest for several nights or took up quarters as a brood in one of the male's courting nests.

When the male helps feed the fledglings, the family may remain together as a single group, or part of the brood may follow the male while the remainder follows the female in a separate group. Adults rarely call while feeding the fledglings, simply returning near the area where the last feeding took place. The young approach the parent with loud begging calls which attract those young too far away to see the parent. In this way the group is maintained and the parent can largely determine its movements. Limited observations indicate that the group is led away from the roosting nest during the morning (farther as the young age) and back to it in the evening.

Females, and normally males at Seattle, continued to feed the fledglings for 12 or more days. The oldest young observed receiving food from its parents was about 27 days old (about 13 to 14 days out of the nest), but one young was observed a great distance from the breeding nest, alone, and apparently completely independent at 23 days of age. Most broods remained close to the breeding nest until completely independent, at which time small groups of juveniles, combined from various nests, moved throughout the marsh.

As the young aged and became progressively more independent, the males' rates of singing and nest building once again increased. Frequently males resumed nest building by the fifth day after the young left the nest, and in a few cases they built during most or all of the fledgling period. This probably depended largely upon foraging conditions at the time and upon the number of young successfully fledged. At Turnbull the males' singing and nest building activities continued throughout the fledgling period, as described for the nestling period.

DISCUSSION

INITIATION OF THE BREEDING SEASON

Marshall (1949, 1954, and 1961) has emphasized that, although gonadal devel-

opment of birds in the temperate zone is influenced by changes in photoperiod, numerous other features of the immediate environment also exert some control over gametogenesis and hence result in the final timing of reproduction. He concludes (1961:332) that the most important of these "may be appropriate nesting materials, a safe nesting site, mild weather, and an abundance of the food on which the young are traditionally fed."

If all portions of a habitat became equally suitable for occupation by breeding birds at the same time, migrants should settle in all portions at the same rate. On the other hand, if different portions developed suitable conditions at different rates, these should either be occupied by migrants at different rates, or breeding chronology should vary among the areas, or both. Marked differences were observed in the times various events in the breeding cycle of the marsh wrens were initiated at the various lakes at Turnbull. Events at Beaver Pond lagged behind those at Blackhorse Lake by several days (13 in the case of first eggs), yet the two areas were located less than half a mile apart on the same drainage (fig. 1).

No attempt was made to obtain quantitative measures of differences between these two sites, although it was easily seen that Beaver Pond supported denser stands of marsh vegetation than Blackhorse Lake. That denseness of vegetation influences the amount of light striking the marsh floor and consequently production at that level is certain. Whether or not this is a critical factor in the present case is unknown. Casual observations in other marshes at Turnbull revealed similar differences in the time nesting was initiated at different sites. One of the earliest sites occupied, that at the north end of Lower Turnbull Lake, was an extensive stand of bulrush, which collapsed more completely than the cattails, thus allowing more light to penetrate to the water surface. This area, however, also had shallower water than most so it may have warmed sooner. In any event, it seems likely that differences in the time of maximum food production were important in determining the order in which breeding commenced at these various marshes.

At Seattle, nest building in February by two males in 1961 was probably brought on by favorable time and energy budgets resulting from temperatures higher than normal during the preceding month. In 1962, earliest nest building was not until March 23, and most males were busy constructing by March 26. This delay was most likely the result of two abnormally cold periods, one in late January, the other in late February and early March (fig. 9). That temperature influenced the start of nest building was further supported by the fact that in 1963 nests were begun on March 1, following one of the warmest Februaries on record in Seattle. At Turnbull, males had begun building probably as early as March 18, 1963, since some had at least two completed nests by the 26th (M. F. Willson, *in litt.*).

First laying followed first nest construction by 11, 14, 22, 24, and 26 days in the five areas studied in 1961 and 1962. In 1963 the first egg in the Yellow Marsh was not deposited until 39 days after first nest construction; the intervening period was characterized by abandonment of several lined nests by most females in the population, indicating that conditions were fluctuating about a threshold of suitability and that this had the effect of alternately stimulating and inhibiting female gonadal activity. Even the nest building activity of the males waxed and waned with changes in the weather during this period in March; a similar effect was observed in males during late April and most of May in 1962 (see beyond).

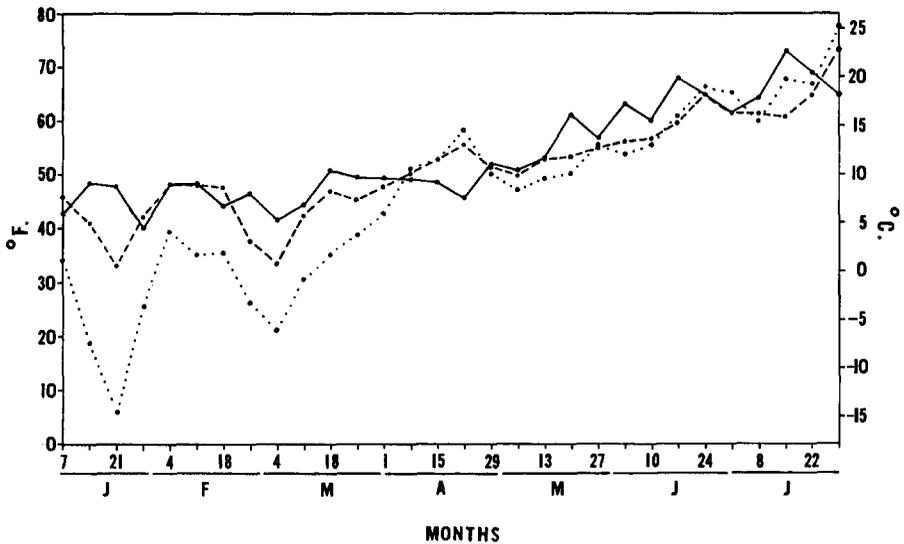


Fig. 9. Temperatures in the different study areas; each point represents the average of the median temperatures for each of the previous seven days: Seattle, 1961, solid line; Seattle, 1962, dashed line; Turnbull, 1962, dotted line. Data for Seattle were taken at a United States Weather Station three miles from the marshes; those for Turnbull were taken at a station 15 miles distant (Spokane); incomplete temperature records taken at Turnbull correspond very closely to those recorded at Spokane.

PROGRESS OF BREEDING SEASONS

There are a number of reasons for believing that conditions for nesting marsh wrens in Seattle were better in 1961 than in 1962. Breeding began later in 1962; mean clutch size in 1962 (4.4) was significantly lower than that in 1961 (5.2); incubation periods were generally longer in 1962, and the average time to complete one cycle and start another was longer in 1962. Males in 1962 built only 68 per cent as many nests as males in 1961. These differences were probably related primarily to food supply of the birds as this was affected by weather.

Abnormally low temperatures in early 1962 (see fig. 9) may have resulted in heavy losses among invertebrates, the effects of which could have been felt for a considerable period. Gibb (1960) demonstrated a direct relationship between the lowest late winter level reached by invertebrate food species of tits and goldcrests in an English Scots pine plantation and the mean temperature from January through March. It is possible that the food supply of the wrens at Seattle may have been affected adversely even to the end of July by the early low temperatures. This being the case, the whole season would be expected to be retarded, but this would not explain the facts that both clutch size and nest building rate began to decline in late April in 1962. The latter situation is complicated by the fact that late April temperatures averaged lower in 1961 than in 1962, yet clutch size did not decrease and nest building rate increased in late April of 1961.

Since nest building was largely inhibited when males had young to feed, it is possible that the reduction in building rates in 1962 was the result of more males having parental responsibilities at that time. Considering the period from April 23

to May 31, and including all days during which there were nestlings or fledglings (to the 12th day out of the nest) in a male's territory, males in 1961 averaged 12.8 days with dependent young, while those in 1962 averaged 15.3. This difference seems insufficient to account for the differences in building rates if other factors were roughly comparable in the two years. Moreover, there is still the problem of changes in clutch size.

Another possible explanation of the situation is that many of the food species of the wrens may require a certain minimum photoperiod or a time of increasing photoperiods to break diapause. After the photoperiodic requirements are reached, temperature might inhibit emergence until it reaches a certain minimum level or summates in a particular way. The number of studies of factors breaking diapause is not large (reviews by Andrewartha, 1952; Cloudsley-Thompson, 1961; and Beck, 1963), but Beck writes: "Emergence from winter diapause has been shown to be a photoperiodic response in a few instances. . . . Undoubtedly more will be found as more species are investigated. We must, of course, realize from the outset that photoperiod does not act in isolation; other ecological factors are always involved . . . moisture and temperature are probably the most important."

If the photoperiodic requirements were met by late March or early April, it is possible that the rapid increase in temperature during the first half of April, 1962, caused many organisms to emerge. A subsequent drop in temperature may then have had a disastrous effect on these organisms and resulted in extensive reduction of wren food. It may be, however, that the drop in temperature was not critical but that foliage development had been slowed by the generally lower temperatures before April in 1962 so that there was not adequate forage or cover for the emerging animals. By May 6, 1961, cattail growth in the Red Marsh had reached six feet and in the Blue Marsh about three feet. By that date in 1962, growth was generally less than 18 inches high. A third possibility is that high mid-April temperatures may actually have killed many organisms in diapause, since "many insects in a state of diapause die when exposed to temperatures that might normally be expected to favour development." (Cloudsley-Thompson, 1961:98).

CLUTCH SIZE

Lack (1947; 1948) has admirably presented the case for adjustment of clutch size to maximize production in relation to food availability. The validity of his argument has been shown in those species for which adequate data on clutch size, fledging success, juvenile survival, and food supply are now available; inadequate knowledge of any one of these points might lead to a different conclusion. These cases emphasize that it is not wise to estimate subjectively a species' food supply and arrive at the conclusion that it is not limiting.

MacArthur (1961) has recently revived the hypothesis that reproductive rates may be selected in response to inevitable mortality rates, stating that "if, due to severe climate and the hazards of longer migration, mortality is always greater at high latitudes, then so must clutch size be higher." That this cannot, however, operate as an ultimate factor (in the usage of Baker, 1938; Lack, 1954; Marshall, 1961, and others) in determining reproductive rates is clear when one considers that selection will favor those phenotypes that leave the most offspring, even if this results in overpopulation (Lack, 1954). The very fact that species can persist where they do, which is the truism of the argument for mortality as an ultimate factor, means that there is adequate food for them to rear their young.

Johnston's (1954) data on increasing clutch size of montane populations of the Song Sparrow (*Melospiza melodia*) in relation to coastal ones have been cited to support the view that mortality can be an ultimate factor in the evolution of reproductive rates (MacArthur, 1961; Hoffmann, 1958), but this is not justified for three reasons. First, no measurements of food supply were taken. Second, the montane birds began breeding considerably later than coastal birds, so the mean daily photoperiod during the season of young in the mountains was longer than that on the coast. Finally, there were no data to support the primary assumption that the montane form suffered greater mortality than the coastal ones.

Skutch (1949) suggested that clutch sizes of tropical passerines may not be as large as the parent birds could rear with greatest success with available food sources. His evidence in support of this contention, although mainly circumstantial, is good (but see Snow and Snow, 1963). The interesting point is made that nest predation may be considerably higher in tropical than in temperate regions, so that smaller clutches could be an adaptation to reduce the noise of hungry young as well as the number of trips made to the nest by the adults, thus reducing the probability of predation. In the present study, however, predation was not heavy. Only 15 of 81 (18.5 per cent) nests were believed to have been destroyed by predators, and at least three and probably eight of those were definitely made more vulnerable by my repeated visits and consequent trail blazing to them. Clutches of wrens in this study are therefore believed to be ultimately controlled by food supply, comparative data between Seattle and Turnbull supporting this view.

The significantly larger clutch sizes of wrens at Turnbull, if food supply controls clutch size, points to a higher productivity there. No measurements were made of food supply but other evidence is available to support the conclusion. Population density of wrens at Turnbull was much greater than that at Seattle. Daily temperature extremes at Turnbull were consistently greater than those at Seattle, and it has been shown that the growth rate of insects is increased by increasing the difference between temperature extremes, even if the mean is unchanged (see Allee, et al., 1949:110). It was noted, however, that wrens at Turnbull were able to maintain greater periods of activity on about the same foraging time as Seattle birds (Verner, MS) even before maximum temperatures at Turnbull exceeded those at Seattle. Thus thermal differences cannot account for the whole difference in productivity between these areas.

Dr. W. T. Edmondson has pointed out to me that lakes of eastern Washington are generally far richer in nutrients and hence in plankton than those of western Washington. Studies of the concentration of zooplankton in eastern Washington lakes (Anderson, Comita, and Engstrom-Heg, 1955; Edmondson, Comita, and Anderson, 1962) indicate that organisms there reach much greater peak densities than organisms of comparable size in Lake Washington, at Seattle (Comita, MS; Edmondson, Comita, and Anderson, 1962). Comita's (MS) data on the copepods, *Diaptomus sicilis* from Lake Lenore (eastern Washington) and *Diaptomus ashlandi* from Lake Washington, indicate that *sicilis* reaches densities about five times that of *ashlandi*. Although wrens probably do not feed directly on the plankton, it is probably important to them via the food web, and the fact that productivity among those species is greater in eastern than western Washington may result in a comparable difference between food species of wrens.

Care must be exercised in assuming that differences in primary productivity between two habitats will be reflected by proportional differences in clutch sizes.

TABLE 9
FLEDGING SUCCESS AT DIFFERENT TIMES OF THE BREEDING SEASON AT SEATTLE, 1961 AND 1962*

Laying period	Clutches	Eggs	Nestlings	Fledglings	Fledging success (per cent)
1961					
April 5-14	4	20	20	15	75.0
May 1-28	7	38	35	29	76.3
June 5-28	4	20	16	15	75.0
Total	15	78	71	59	75.6
1962					
April 3-19	3	15	14	6	40.0
May 29-June 2	5	23	22	22	95.7
June 20-July 23	4	15	13	12	80.0
Total	12	53	49	40	75.5

* Only nests from which at least one young fledged have been included; nests were eliminated if the investigator appeared to have caused lowered fledging success.

The density of breeding marsh wrens at Sapelo Island, Georgia (Kale, MS), was, on a comparable basis, about four times that at Turnbull, indicating a much higher productivity in the Georgia marshes. Clutch size at Georgia, however, was smaller (4.6) than that at Turnbull, comparing more closely with that at Seattle; but nest predation, principally by rice rats (*Oryzomys palustris*), raccoons (*Procyon lotor*), and mink (*Mustela vison*), was very high in the Georgia wrens. It is possible that this population has had its clutch size ultimately determined by predation according to the hypothesis of Skutch (1949). Before food can be eliminated as the ultimate factor in the Georgia case, however, quantitative measurements of the average size of food items brought to the young must be made and compared with the abundance of these organisms in the environment.

In those species in which clutch size is ultimately adjusted to food supply, there are usually ways to adapt to changing conditions; that is, there are proximate factors influencing the numbers of eggs laid in different circumstances. Since the critical period from the standpoint of food supply is during the nestling and fledgling stages, any phenomenon occurring at the time of laying and correlated with food levels during the period of young would have great adaptive value as a proximate factor controlling clutch size. In this way, clutches could be adjusted on the basis of a "prediction" of future conditions. Proximate factors controlling clutch size have been studied in few species (review in Lack, 1954), but it seems to be generally indicated that these are immediate habitat conditions, such as food supply or condition of foliage, rather than major features of the total environment, such as temperature or photoperiod.

In the marsh wrens at Seattle there is evidence that clutch size is proximally controlled by conditions at the time of laying, probably food supply, although weather factors cannot be ruled out. During 1961, weather conditions were more nearly normal and there were no prolonged periods of low temperature after breeding by the wrens was underway. Food species of wrens probably responded normally. Thus predictability of future foraging conditions should have been nearly constant and the wrens should have had about the same probability of accurate adjustment throughout the season. Table 9, in fact, demonstrates that fledging success remained fairly

constant. During 1962, however, extreme weather fluctuations, with resultant effects on food supply, should have resulted in variations in predication and, hence, in fledging success. There was a marked reduction in fledging success in nests with eggs laid early in April, when existing conditions were favorable, but having young during late April and early May, after conditions had deteriorated. Those clutches laid in May, during the period of unfavorable weather (therefore smaller clutches), had young in June after the weather had improved considerably. These nests had 95.7 per cent fledging success, and males were not helping to feed the young. Finally, clutches laid from late June on, after conditions had stabilized, had 80.0 per cent success, comparing favorably with that throughout the season of 1961. Although sample sizes do not permit statistical treatment, the data agree well with other observations and are believed to be biologically significant. Had the birds been able to predict conditions at the time young would be fed, April clutches should have been smaller and late May clutches larger in 1962. It is interesting to note that total fledging success at Seattle was essentially the same in 1961 and 1962.

SUMMARY

This report on the Long-billed Marsh Wren (*Telmatodytes palustris*) is based on studies in two separate and racially distinct populations in Washington State, one at Seattle, the other at Turnbull National Wildlife Refuge near Spokane. Wrens at Seattle are resident, but the wrens at Turnbull are migratory, returning to the breeding area in March. Territories at Seattle averaged about 15,000 square feet (2600 to 38,700), whereas territories at Turnbull averaged only about 5000 square feet (1800 to 9600). Males in both populations built many nests (mean per male: Seattle, 1961, 21.0; Seattle, 1962, 13.9; Turnbull, 1962, 22.3), most of which were not used for breeding. Building continued throughout the breeding season, males at times completing five or more nests in a 15-day period. These nests function importantly in courtship, males directing prospective mates to them and displaying near each as the female examines it. Females usually lay in a nest built largely or wholly (except lining) by the male. After the first breeding nest is underway, a male builds more nests in another part of his territory and advertises for additional mates. Males are polygamous, although not all succeed in acquiring more than one mate.

Laying occurs daily, early in the morning, until the clutch is completed. Clutches averaged 5.2 (Seattle, 1961), 4.4 (Seattle, 1962), and 6.0 (Turnbull, 1962). All differences were statistically significant. The female incubated alone, and the male did not feed her during this period. Attentive periods on the eggs averaged 8.1 minutes; inattentive ones averaged 7.7 minutes. Incubation periods averaged 15.1 days and showed a tendency to decrease as the season progressed. Both sexes at Seattle assisted with care of nestlings and fledglings, but males at Turnbull did so only with the last brood of the season. Each young was fed an average of 3.8 times per hour in the morning and 3.9 times per hour in the afternoon; the number of feedings per hour increased with age of the young.

Evidence was cited that initiation of breeding activities was influenced by the suitability of the habitat and by weather conditions. Onset of various activities varied considerably in different localities at Turnbull, even though the localities were close together, indicating that subtle differences between two areas can affect the rate of development of conditions suitable for breeding wrens.

Clutch size in these two populations is believed to be ultimately controlled by food supply. Clutches at Turnbull were significantly larger than those at Seattle

(the two areas are at the same latitude), and evidence is presented in support of the conclusion that productivity is greater at Turnbull. Data on fledging success indicate that proximate control of clutch size is based on conditions at the time of laying. Clutches laid during good weather that led to young during bad weather suffered heavy losses; in the reverse situation a higher than normal success was realized.

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Department of Zoology, University of Washington, Seattle, Washington, March 16, 1964. (Present address: Department of Zoology, University of California, Berkeley, California.)