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Author(s): Thomas G. Marr and Ralph J. Raitt

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ANNUAL VARIATIONS IN PATTERNS OF  
REPRODUCTION OF THE CACTUS WREN  
(*CAMPYLORHYNCHUS BRUNNEICAPILLUS*)

THOMAS G. MARR AND RALPH J. RAITT

**Abstract.**—The breeding ecology of the Cactus Wren was studied during three years. Significant differences in clutch size, breeding success, and the timing of clutch initiation were observed between years. The differences are related to annual differences in the abundance and emergence of the major food of nestlings. Long-term temperature patterns were analyzed for predictability and show that, on the average, Cactus Wrens initiated clutches during a period when high temperatures predicted favorable temperatures for the period when they would be feeding nestlings. Several factors that appear to affect clutch initiation in the Cactus Wren are discussed.

Responses of clutch size in birds during years of increased abundance of food are variable among species (Anderson, 1977; Sealy, 1980). Likewise, the onset of breeding of birds in arid or semiarid areas (reviewed by Serventy, 1971) shows interspecific variation in the degree of flexibility in relation to environmental variation. Some species in Australia are nearly completely opportunistic (Marshall, 1959; Williams, 1979), while some in southwestern Africa are regular (Moreau, 1950; Immelmann, 1967). Marshall (1963) described patterns of regularity of breeding among some species of Sonoran Desert birds, but in general little has been published concerning the breeding periodicity of birds in arid areas of North America.

The Cactus Wren (*Campylorhynchus brunneicapillus*) is a common resident in the deserts of southwestern North America south to central Mexico, where it occupies a variety of xeric habitats (Anderson and Anderson, 1973). Aspects of its natural history, ecology, and physiology have been studied extensively in southern Arizona (Bailey, 1922; Ricklefs, 1966, 1975; Ricklefs and Hainsworth, 1968a, 1968b, 1969; Anderson and Anderson, 1973). However, it has received little or no attention elsewhere in its range.

During our study of the Cactus Wren in southern New Mexico, 1978-1980, we had the opportunity to study their responses to widely different abundances and different dates of emergence of band-winged grasshoppers (Oedipodinae, *Trimerotropis*). In all years, these grasshoppers were the principal food of nestlings. Of 306 feeding trips to nestlings, only 5% were with food other than *Trimerotropis* (Marr, 1981). As discussed below, we believe that much of the variation that we observed in the breeding ecology of the Cactus Wren was a result of marked differences in abundance and emergence dates of *Trimerotropis*. *Trimerotropis* is a ground-mimicking genus and is a true desert-adapted grasshopper (Otte and Joern, 1975). Adults overwinter in the soil and emerge in the spring after a warming trend over several days. *Trimerotropis* normally feeds on annual plants, and population fluctuations are probably a result of rainfall differences and the resultant annual plant crop differences (Otte and Joern, 1975). The abundance and distribution of annual plants during spring and early summer in the Chihuahuan Desert

are related to the amount of rainfall during the previous October and November (Whitson et al., in press).

In view of the apparent coupling of various environmental factors (e.g., fall precipitation, temperature during spring) that modify important variables in the nesting ecology of the Cactus Wren (e.g., food supply, onset of breeding) we compared long-term weather patterns to patterns during our study. The results of the comparison are used to interpret the annual differences observed in 1) the timing of first clutches, 2) the size and success of first clutches and 3) abundance of grasshoppers.

**STUDY SITE AND METHODS.**—The area selected for the study consisted of several sites 8-16 km east of Las Cruces, Dona Ana Co., New Mexico, at an elevation of about 1500 m. It lies on a broad alluvial slope (bajada) dissected by numerous shallow watercourses (arroyos) that are dry most of the time and that drain the west slope of the Organ Mts. The vegetation is typical Chihuahuan Desert scrub, dominated by low shrubs providing a generally open and patchy aspect. Density and stature of shrubs and herbs are greatest on the edges of the several arroyos. Soils, topography, climate and vegetation are similar to those described in some detail by Raitt and Maze, (1968).

The study was conducted during the breeding seasons of 1978, 1979, and 1980 (primarily April through July). We attempted to locate all breeding territories of pairs of Cactus Wrens within 150 m of an 8-km strip of unpaved, narrow road through the study area. We visited an arbitrarily chosen subset of territories at frequent intervals beginning in early April of each year to determine sizes and dates of first clutches. Once nests with clutches of eggs were found on particular territories, those territories were visited at least every 4 days until eggs hatched, to determine when the eggs were laid and the ages of nestlings.

By the end of May 1978 it was apparent that wrens were selecting *Trimerotropis* to feed nestlings older than 2-3 days. Therefore, at that time we initiated flush-count transects 100 m long to obtain an index of abundance of those grasshoppers. In 1979 and 1980 we began flush-counts in early April to detect the emergence and abundance of grasshoppers during the period when wrens laid first clutches, and continued them throughout most of the breeding season. The observer walked along marked 100-m lines, counting all *Trimerotropis* that flushed from within 1 m. Approximately weekly, we randomly selected two territories, in each of which we sampled along five lines. Daily maximum and minimum air temperature records for Las Cruces were obtained from the Department of Experimental Statistics, New Mexico State University. We analyzed records for 1 March - 28 August (representing a period approximately 1 mo. before and after the normal breeding season of the Cactus Wren) for the 30 years 1931-1960.

The temperature data were analyzed following Myers and Pitelka (1979), using a statistic,  $d_{n,j}$ , based on the difference between  $t_{i,j}$ , the daily mean temperature on day  $i$  during year  $j$  and  $\bar{t}_i$ , the average daily mean temperature for day  $j$  over a number of years:

$$d_{n,j} = \sum_i^n (t_{i,j} - \bar{t}_i)$$

Thus,  $d_{n,j}$ , represents the cumulative deviation from the long-term daily mean temperatures during year  $j$  from day  $i$  through day  $n$ . We computed  $d_{n,j}$  for daily mean temperatures during the 30-yr period. We also computed 1) the variance among years in temperatures for each 14-day period, and 2) correlation coefficients between average mean temperatures of different 14-day periods during the part of the year we were interested in (Myers and Pitelka, 1979).

**GRASSHOPPER ABUNDANCE AND WEATHER PATTERNS.**—Fig. 1a shows striking differences in the relative abundance of *Trimerotropis* among years. The amount of rainfall during October and November was strikingly different among years (Table 1); the amount in 1978 was the highest ever recorded in over 100 years of records and it produced a magnificent bloom of annuals during the spring and early summer of 1979. For the two years in which flush counts were initiated early in the breeding season (1979, 1980), there

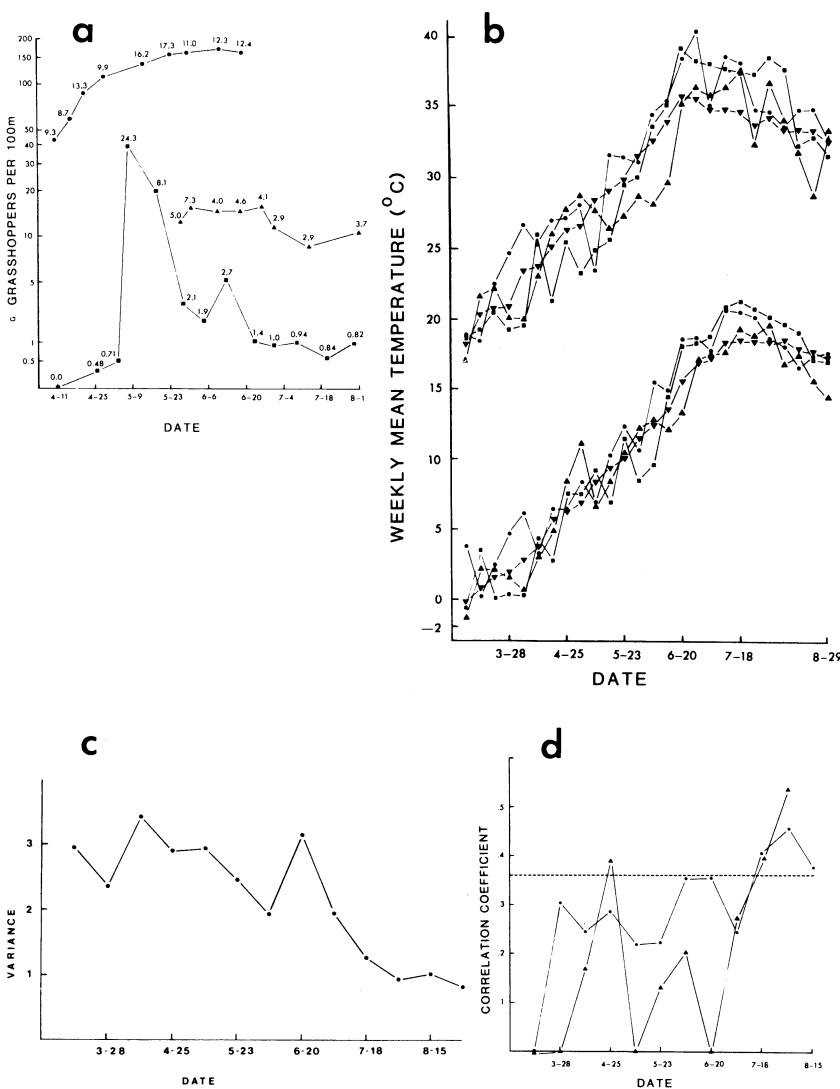


FIG. 1a.—Grasshopper flush counts for 1978 (triangles), 1979 (circles), and 1980 (squares). Each point represents the mean of 10 100-m transects; the standard deviation is listed above each point. 1b, Weekly mean maximum (upper set of points) and minimum (lower set of points) air temperatures for 1978 (circles), 1979 (triangles), 1980 (squares), and the 30-yr averages (inverted triangles). 1c, Among-year variance in average temperature (°C) during different 14-d periods. 1d, Spearman rank correlation coefficients between 14-d periods; period t and t+1 (circles) and period t and t+2 (triangles). The horizontal dashed line represents the 0.05 significance level based on a t-test (two-tailed) of the correlation coefficients.

also were differences in the timing of the major emergence of grasshoppers; in 1979 they were abundant by 11 April, whereas in 1980 they were not abundant until early May (Fig. 1a).

TABLE 1.—Fall precipitation (mm) for 1977-1979, Las Cruces, New Mexico.

Year	Aug.	Sept.	Oct.	Nov.	Dec.	Total for year
1977	164.5	53.3	31.5	2.0	6.1	224.8
1978	66.0	75.9	47.2	65.8	19.6	376.9
1979	125.0	12.5	0	0	30.0	238.0

The progression of maximum and minimum temperatures differed among years (Fig. 1b). In both 1978 and 1979 there were sustained rises in temperatures above the 30-yr mean in late March and early April; this was particularly striking in 1978 when the cumulative deviation for the 2-wk period before 28 March was +35 C°. In 1980, sustained rises in temperatures did not occur until late April, which coincided with the emergence of grasshoppers (Fig. 1a). Because the grasshoppers respond to a warming trend over several days, we assume that they emerged in early April of 1978; however, we cannot be certain because flush counts were not initiated until late May. The reason for the large decline in grasshopper abundance in late May 1980 is unclear, but it probably was related to the failure of their food supply; there was almost no growth of annuals, and perennial plants were dehydrated at that time and remained so throughout most of the summer (Paul Kemp, pers. comm.).

**CLUTCH SIZE, BROOD SIZE, AND NESTING SUCCESS OF WRENS.**—Data on first clutches (Table 2) show that the largest mean clutch size occurred in 1979, the year when grasshopper abundance was also highest (Fig. 1a) and when grasshoppers had emerged before the first clutch was laid. The smallest mean clutch size occurred in 1978 when grasshopper abundance was considerably lower than in 1979 and when grasshoppers presumably had emerged before the first clutch was laid. The intermediate mean clutch size occurred in 1980, when all first clutches were laid before grasshoppers had emerged.

Mean brood size in 1980 was the smallest among years, rather than intermediate (Table 3). Overall nesting success was similar in 1978 and 1979 but was very low in 1980 (Table 4). There were two types of failure during 1980: only 41% of the eggs hatched (7 out of 17 pairs abandoned entire clutches while other pairs hatched only part of their clutches) and only 68% of the eggs that hatched produced fledglings (two broods of four starved). Hatching failure occurred in the first two weeks of May when record low nocturnal temperatures occurred. The only pair successfully to fledge a brood of four in 1980 laid its clutch approximately 12 days earlier than the median date and 9 days earlier than any other pair. Their eggs hatched on 27 and 28

TABLE 2.—Size of first clutches of Cactus Wrens. All years were significantly different from each other, 0.005<P<0.01; Chi-square contingency tests.

Year	Number of nests	Clutch Size				Mean (S.D.)
		2	3	4	5	
1978	11	1	9	1		3.0 (0.45)
1979	14	1	2	4	7	4.2 (0.97)
1980	17		7	10		3.6 (0.51)

TABLE 3.—Size of first broods of *Cactus Wrens*. All years were significantly different from each other,  $0.002 < P < 0.016$ ; Chi-square contingency tests.

Year	Number of nests	Brood Size					Mean (S.D.)
		1	2	3	4	5	
1978	11		1	9	1		3.0 (0.45)
1979	14		1	3	3	7	4.1 (1.0)
1980	10	3	2	2	3		2.5 (1.3)

April, which happened to coincide with the emergence of grasshoppers, and the young fledged during the precipitous decline in grasshopper abundance (Fig. 1a).

We weighed four 5-day-old nestlings of one of the two pairs that hatched complete clutches of four in 1980 and in which the nestlings later starved. Their body masses (mean = 8.75 g, s.d. = 0.64) were considerably below the average reported for 20 5-day-old nestlings (mean = 14.0 g) by Anderson and Anderson (1973). Of the remainder of the pairs that hatched eggs, only those with broods of three or fewer (Table 3) successfully fledged young. Cactus Wrens did not renest after grasshopper abundance declined early in 1980, indicating that alternate food sources were not available.

Ricklefs (1965) described two general strategies for adjusting brood size to accommodate food supply: evaluation and brood reduction, which are not mutually exclusive. In the evaluation strategy the female is capable of evaluating the food supply just prior to laying and modifies its clutch size accordingly (Ricklefs, 1965). The brood reduction strategy is most likely to occur in birds in environments in which the accuracy of evaluation is low, or, in the words of Ricklefs (1965:509): "Brood reduction should be expected in any species whose average food availability while feeding young shows temporal fluctuation without corresponding variation in clutch size." The Cactus Wren clearly shows variation in clutch size both within and among years (Anderson and Anderson, 1973; this study) and is, therefore, predicted not to have adopted the strategy of brood reduction. Starvation of nestlings occurred only in two pairs in 1980. However, they were the only pairs to hatch complete clutches (four) in that year. In clutches of four or fewer, eggs of Cactus Wrens generally hatch over two days and size variation among nestlings is not noticeable. Thus parents may be unable to determine which young it would be advantageous to selectively feed under conditions of limited food. Based on this small sample, it appears as if the Cactus Wren has not adopted the strategy of brood reduction. The evidence from 1978 and 1979 strongly indicates that the Cactus Wren is capable of evaluating the

TABLE 4.—Overall nesting success of *Cactus Wrens*. Fledging success was calculated from those eggs that hatched and thus reflects losses due to predation and starvation.

Year	Number of nests	Number of eggs	Hatching success (%)	Fledging success (%)
1978	11	33	100	100
1979	14	59	98	90
1980	17	61	41	28

TABLE 5.—Timing of first completed clutches of Cactus Wrens.

Year	Number of nests	Median date	Range of dates
1978	11	9 May	2 April-1 June
1979	14	15 May	10 April-29 May
1980	17	25 April	13 April-29 April
Total	47	2 May	2 April-1 June

food supply, and that it adjusts its clutch size to accomodate prevailing food supplies.

**ONSET OF BREEDING.**—The average date among years of first completed clutches was 2 May (Table 5). If it takes about 7 days to develop ova in the Cactus Wren (Anderson and Anderson, 1973), then most wrens started developing eggs in the last week of April. However, in both 1978 and 1979 there was considerable variation within the population with regard to the timing of first clutches (Table 5). In 1978, they were laid over a 5-wk period, and in 1979, over a 7-wk period. However, in 1980, 15 of 17 pairs laid first clutches within a 1-wk period.

Anderson and Anderson (1973) found similar variation among years with regard to the degree of synchrony of laying in the Cactus Wren in southern Arizona. During their 6-yr study, the range of laying of first clutches varied from 7 to 47 days, with a mean of 28.1 days. Thus, two separate questions need to be addressed. One is why do wrens, on the average, start developing eggs in the last week of April? The other is why is there a high degree of synchrony among pairs in some years and not in other years?

In all three years, all individuals started laying following sharp rises in daytime temperatures over 3-4 consecutive days. Thus, a period of rising temperatures is associated with egg-laying in the Cactus Wren early in the breeding season. Among-year variance in temperature is greatest in that period (Fig. 1c). Temperature has direct influences on the Cactus Wren. They feed nestlings most actively during early morning hours to avoid heat stress (Marr, 1981). Below-normal temperatures disrupt schedules of feeding of nestlings that have not attained thermoregulatory capabilities, because females must spend more time brooding, at the expense of time for feeding of nestlings (Marr, 1981). Therefore, it would be advantageous to a Cactus Wren to initiate its clutch at a time that would correctly anticipate favorable temperature when young nestlings are to be fed.

Spearman rank correlation coefficients were computed between deviations from the long-term means for different 14-day periods, in particular between periods  $t$  and  $t+1$ , and periods  $t$  and  $t+2$ . Computed in this manner, the correlation coefficients represent the degree to which deviations during period  $t$  predict similar deviations during period  $t+1$  or  $t+2$  (Myers and Pitelka, 1979). If a Cactus Wren, with an incubation period of about 16 days; initiated its clutch during the period  $t$ , the  $t+2$  period would coincide with the hatching of eggs and the feeding of young nestlings. Figure 1d shows that the only period during the breeding season in which deviations during period  $t$  were significantly correlated ( $p < 0.05$ ) with deviations dur-

ing period  $t+2$  is the 14-day period ending on 25 April ( $t$ ) with the 14-day period ending 23 May ( $t+2$ ). The median date for first completed clutches for the three years of our study was 2 May and in each year there were rises above the normal temperatures during the 14-day period before 25 April. Thus, on the average, Cactus Wrens initiated clutches during a period when high temperatures predicted favorable temperatures for the period when they would be feeding nestlings.

The problem remains of explaining the underlying basic for the between-year variation in synchrony within the population in taking advantage of the favorable prediction. All pairs of Cactus Wrens that we studied had established territories by the beginning of April. We found no evidence that differences in clutch initiation were related to particular site differences; i.e., some sites had territories in which birds started early in one year and late in the other. The most salient difference between the year of high synchrony (1980) and the years of low synchrony (1978, 1979) was the absence and presence, respectively, of grasshoppers at the time of clutch initiation. In 1979 grasshoppers were certainly very abundant on the study site before the initiation of clutches, and in 1978 they presumably were also. In 1980, all wrens laid eggs before grasshoppers were abundant and most started developing ova before grasshoppers had emerged. Anderson and Anderson (1973) reported similar results for the Cactus Wren in southern Arizona: the year of their study in which wrens were most highly synchronized was one when the growth of annual plants was poor, and the least synchrony occurred in a year when there was an abundant growth of annuals and their associated insects. Walsberg (1977) found a similar relationship between spring insect blooms and blooms of annual plants in a desert habitat in southwestern California. Thus, the state of the vegetation and associated insects appear to be important in determining the degree of synchrony in populations of the Cactus Wren.

The origin of the individual variation exhibited in two years of this study and in certain years of that of Anderson and Anderson (1973) may be explained by the variation in success in 1980. Favorable conditions were predicted by early rising temperatures and most pairs responded at the proper time. However, the prediction failed and the only pair successfully to fledge a complete clutch laid its clutch 9 days earlier than any other pair. Thus, the prediction may work on the average but atypical years may be sufficiently frequent to produce variation within the population.

The explanation for the apparent relation of failure of expression of such variation to low food abundance early in the season, as in 1980, is not obvious. All that we can offer by way of explanation is a speculative hypothesis. The state of the vegetation and insects may be useful in predicting the probability of interspecific competition from migrant and other late-breeding insectivores. Such species as the Western Kingbird (*Tyrannus verticalis*) and Loggerhead Shrike (*Lanius ludovicianus*) begin to nest in late May in the same area and they also feed grasshoppers to their nestlings (Raitt and Pimm, 1976). If the early spring vegetation is poor and no information concerning food supply is available, as in 1980, the likelihood of significant interspecific competition later in the season would be high. Under such conditions it may be especially advantageous to all Cactus Wrens to breed as early as possible.



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Address of authors: Dept. of Biology, New Mexico State Univ., Las Cruces, NM 88003. (Present address of T. G. Marr: Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ 85721).