

LIFE HISTORY OF THE CACTUS WREN

Part II: THE BEGINNING OF NESTING

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This is the second part of a life history study of the Cactus Wren (*Campylorhynchus brunneicapillus*). Most of the field observations were made in the vicinity of Tucson, Arizona. In Part I (Condor, 1957) we discussed the environment, winter activities, roosting nests, song, territorial establishment, and pair formation. This second part deals chiefly with the beginning of the breeding cycle of the local population of wrens. Our studies are still in progress, and, since Part I was written, additional Cactus Wrens have been trapped and color-banded.

THE BREEDING TERRITORY

The appearance of the dominant creosote bush (*Larrea tridentata*) south of Rillito Creek changed very little from 1930 to 1957. The growth of this shrub is normally slow, and its age is difficult to determine. According to Shreve (1951:157) its age probably "greatly exceeds 100 years." Many of the creosote bushes in the area in 1930 were old, with dead, dry, drooping outer branches. Small seedlings were very scarce; they had evidently been crowded out long ago. If there had ever been successional stages leading to this climax community, the remnants of these stages were gone. Although portions of an abandoned irrigation ditch were present in 1930, there is no evidence that the water had been used in the vicinity of Kleindale Road. The ditch merely crossed the area. It seems safe to assume that the creosote bush association had been here for at least 50 years; it was probably here when the first Spaniards arrived in the sixteenth century.

A small invasion of cholla cacti into the creosote bush area was evidently relatively recent. In 1930 these plants were widely spaced. They occupied a strip of land approximately one-half mile long by one-tenth mile wide, immediately south of the Rillito streamside fringe of mesquite and catclaw. There was no tendency toward colonialism, such as occurs in mature stands. No large, dead or dying chollas, with basal circlets of new, young seedlings were present. The invasion could have begun with the introduction of cattle into the area by the early settlers. Cattle are well-known disseminators of cholla cacti. The spiny joints of the jumping cholla are easily detached when an animal brushes against the shrub. These joints cling to the hide and are often transported long distances before falling to the ground. There they germinate readily. Some of the cane chollas may have been introduced by rodents. Round-tailed ground squirrels (*Citellus tereticaudus*) and antelope squirrels (*Citellus harrisii*) were common in the vicinity in 1930. Both of these species have been observed carrying cholla fruits. The nearest extensive cholla community is on the north side of the Rillito, at the foot of the bajadas of the Santa Catalina Mountains.

Cactus Wrens do not inhabit a pure creosote bush association, for it has no nesting sites. Evidently the wrens extended their range southward across the Rillito at the time the cholla cacti became large enough to live in. Judging from the rate of cholla growth in lot 7, this occupation probably occurred no earlier than 1915.

The number of breeding territories in the neighborhood each year, including those contiguous to the Kleindale Road study area (fig. 1), varied from one to five. The local area about our home has been arbitrarily numbered territory I, regardless of the pair of wrens which inhabited it. Beginning in 1939 we noted that the two, one-acre lots east of Edith Street (fig. 1) were occupied consistently by another pair of wrens. These wrens had probably been there, unnoticed, for some years before. The lots were fenced, and

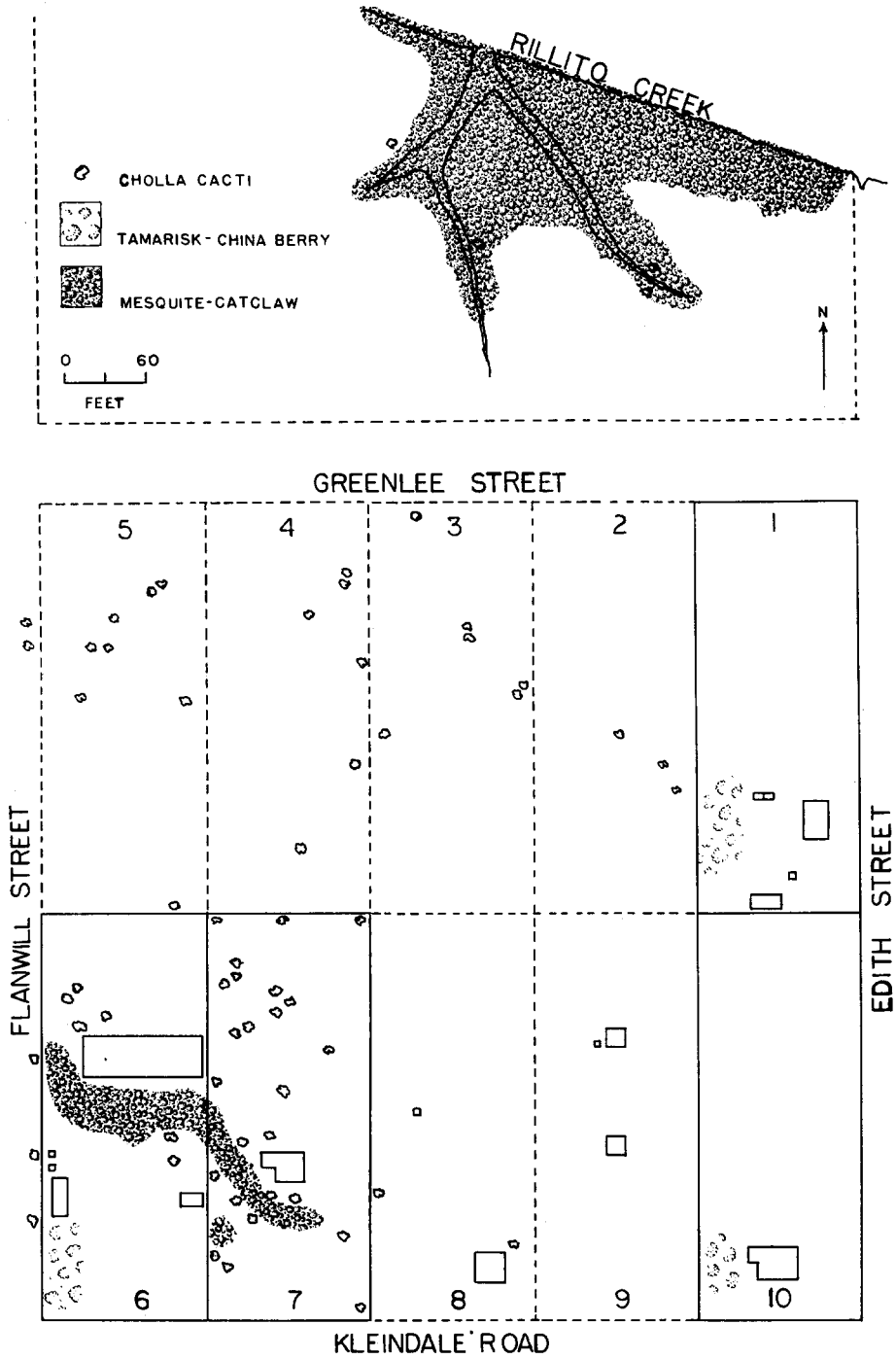


Fig. 1. Kleindale Road study area in 1941. Solid lines indicate fences; dashed lines lot boundaries. Creosote bush association covered all unshaded areas except streets.

the original vegetation was undisturbed. Under such favorable conditions, it is not surprising that Cactus Wrens have occupied this eastern territory (number II) to the present time. It was not always practicable to explore and define the other territories thoroughly. We could determine the location of the common boundaries with fair accuracy, but the extent of these territories could only be estimated. Our early incomplete records

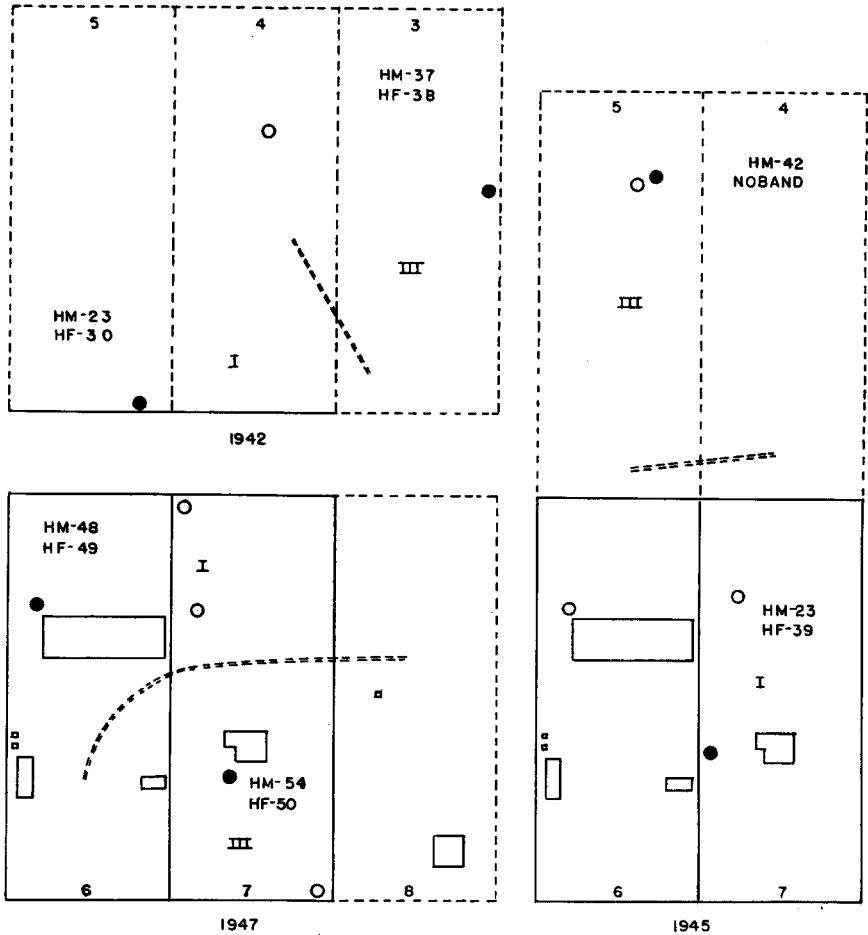


Fig. 2. Local territories of Cactus Wrens in 1942, 1945, and 1947. Lots and boundaries as in fig. 1; open circles = roosting nests; solid circles = breeding nests; double dashed lines = assumed territorial boundaries.

show that a pair of wrens nested in lot 6 in 1932, in lot 7 in 1933, in lot 8 in 1934, in lot 6 in 1935, in lot 7 in 1936, and in lot 6 in 1939. We lack nesting data for 1930, 1931, and 1937, but the wrens were present and undoubtedly bred in the area.

In the course of the next eight years, beginning in 1940, the number of territories varied as follows: 3 in 1940, 2 in 1941, 5 in 1942, 2 in 1943, 4 in 1944, 3 in 1945, 2 in 1946, and 4 in 1947. In only three of these years, 1942, 1945, and 1947, did territory I suffer encroachment from an adjacent pair of Cactus Wrens. This additional territory we have designated number III for each of these years, although its location changed each year (fig. 2). In the other five years territory I was maintained at its usual ten-acre

dimensions. The northern peripheral territories were actually marginal in value. They did not contain enough cholla cacti for expansion of nesting facilities. In addition, the chollas were smaller. The hinterland included the dense, brushy creek border and sandy, unsuitable bed of the creek. Nevertheless, this area apparently provided room, even if only temporarily, for surplus individuals from other territories.

After 1947, the territorial fluctuations smoothed out. The destruction, by a sand and gravel company, of all the vegetation on the river bank, eliminated this habitat entirely. Finally, territory I, our main study area, also suffered severely. Half of its cholla cacti were lost when lots 2, 3, 4, and 5 were scraped clean of all plant life. Only territory II, east of Edith Street remained intact. The available nesting sites in cholla cacti in territory I were now restricted to lots 6 and 7. From 1948 to 1958 only one pair of Cactus Wrens was able to hold its own in this territory. In spite of these many adverse changes, the population, small to be sure, maintained itself in the Kleindale Road area for the past 27 years. If the few remaining cholla cacti are not destroyed, the wrens will probably cling to this habitat indefinitely.

DEFENSE OF TERRITORY

Up to 1947 the territorial boundaries were so far distant from our house in lot 7, that we never saw or suspected that boundaries were actually defended after the territory was occupied. It appeared to us that no defense was necessary, once the breeding season began. Other territories were far removed; the breeding nest of the Edith Street pair in territory II was at least 600 feet from the nest in territory I. The area utilized by the local pair was probably the maximum it needed. We occasionally heard the scratchy *scri* note connected with disputes. Adults sometimes used it in evening squabbles at roosting nests, and also in their early spring pre-nesting activities. The division of the ten-acre block into two territories in 1942 and 1945 was not a drastic alteration. The newcomers in the northern part of the area obtained the less desirable portions of the tract. The breeding nest of territory III in 1942 was approximately 310 feet from that in territory I; in 1945 it was 435 feet away.

Defense of territory is a somewhat misleading, elastic concept. Defense occurs, of course, but in our studies it was always accompanied by a compromise. Each of the three annual intrusions brought about the annexation of a portion of the original territory. What would have happened, had a third or a fourth pair attempted to move in, is uncertain. There must be a limit beyond which a Cactus Wren refuses to give up any more land. This limit may have been reached in 1947, when the breeding nests of territories I and III were only 180 feet apart. Boundary disputes became very frequent; they began in the spring, and they continued through the entire year and even into the following spring. It seems incredible that we could have missed these conspicuous, noisy disputes before. We can only assume that they occurred infrequently because of the greater separation of the breeding nests.

In the early part of 1947 we observed nothing that indicated that a change in the local distribution was in progress. HM-48 and HF-49, whose roosting nests were in the rear third of lot 7, seemed to be in complete possession of the ten-acre block. Then, suddenly, on February 19, we discovered that another pair of Cactus Wrens had occupied the southern portions of lots 6, 7, and 8. (We trapped and banded them later, and numbered them HM-54 and HF-50.) They were building a new nest, number 19C, in a cholla 12 feet southwest of our front porch. The female, at least, of this pair probably came from territory II, for she returned to that area nightly, until she had built a new roosting nest, number 8P, in lot 8. If any quarrel or fight occurred over the annexation of this considerable portion of the original territory, we failed to observe it. As often

happened, when we became aware of a change in the situation, it was already an accomplished fact. It should be noted that in this instance there were no roosting nests in the land that was given up to the invaders. Had there been roosting nests, the outcome might have been different.

After his retreat northward, singing was heard more frequently from HM-48. The new male, HM-54, busy at nest building, was not at first as vigorous a singer as HM-48. Most of his singing was done while at work, at or in the vicinity of his nest. Later he found time to give rebuttal to HM-48, chiefly from stations in the trees in the southern portion of lot 7, and from the electric wires along Kleindale Road. On March 22 we observed the first indication of a definite boundary between the new territory III and the old territory I. It began at the west fence of lot 7 (fig. 2). HM-54 and HF-50 moved slowly eastward across our lot almost to the east fence. A few feet to the north, HM-48 travelled parallel to them. No singing was heard and there was no obvious antagonism in their actions. They refrained from intermingling and they moved quietly. Then the first two flew southward; HM-48 continued foraging eastward into the middle of lot 8.

Eggs were laid in nest 6AJ by HF-49 about March 15. HF-50, after various difficulties, appropriated her mate's roosting nest, 19C, and laid her first egg on March 26. In the course of the next three weeks we noted no further activities along the boundary. Apparently the chores of nest-building, incubation, and later, the feeding of nestlings confined the birds more to the vicinity of their nests. Our attention, also, was focused more upon the readily visible and accessible breeding nest in our front yard. We may have missed some of the events farther north. In April we occasionally heard the scratchy call note from that direction. On the evening of April 23, HM-48 and HF-49 brought their fledglings into lot 7 and put them to bed in nest 22H, the former roosting nest of HM-48. In December this nest had belonged to HF-49. Nest 22H was only 130 feet north of nest 19C. Boundary disputes were now noted frequently. In fact, these disputes took place with such regularity, that we suspect they were of daily occurrence until February 29 of the following year, when HM-54 disappeared. We observed 13 of these disputes in October, 8 in November—a normally quiet month—and 6 in December. We probably missed many more, for our time for observation was limited in the fall.

The invisible boundary line between the two territories was best observed in lot 7, where most of the disputes occurred. It was a bare strip of ground, less than ten feet wide, that extended across the lot between the widely spaced creosote bushes. To the Cactus Wrens it may have been better defined by the conspicuous landmarks along its length, such as cholla cacti. At the west fence the "line" entered a chicken yard and curved abruptly southward between the house and garage in the front of lot 6. In lot 8 it seemed to vanish at the middle of the lot. There were no territorial singing stations close to the boundary line. Such stations were frequently as much as 100 to 300 feet distant. A song at the boundary itself was usually the signal for action.

The north pair, HM-48 and HF-49, had the best view of the boundary. Our house, situated between the breeding nest of HM-54 and HF-50 and the boundary, obstructed the view of the south pair of wrens. Consequently most disputes began when the north pair discovered what appeared to be an impending invasion into its territory. First we heard a song or two from the rear of lot 7. Immediately thereafter came a series of scratchy *scri* notes, as HM-48 and HF-49 flew southward to the "line." As they landed on the ground opposite HM-54 and HF-50, the *scri* calls increased in number; evidently these calls were uttered by both pairs. Short songs were interspersed by both of the males and females, while the four wrens moved either eastward or westward, in parallel lines, each pair carefully avoiding contact with the other. The group seldom travelled over 15 to 20 feet before it reversed its direction and moved back. Occasionally one of

the wrens fluffed out its feathers, lowered and spread its tail, and then turned its body in a quarter or half circle. Sometimes it moved sideways, its toes pointing toward the boundary, its head facing in the direction of movement. Frequently the dispute ended after a minute or two of this stereotyped ritual. Then the wrens separated and retreated to the more distant parts of their territories (fig. 3). A few times we noted that several disputes occurred in quick succession, about 50 feet apart, as the wrens moved across lot 7 into lot 8.

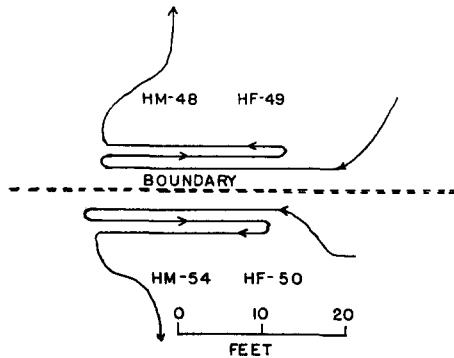


Fig. 3. Paths travelled by Cactus Wrens during a boundary dispute on July 13, 1947.

Now and then the excitement of the ritual increased to the point of breaking out into active chasing and fighting. A chase was always short. If HM-54 chased HM-48 north for four or five feet, the latter quickly turned about and chased his opponent back. Thus it went, like a miniature seesaw battle, neither side venturing into the other's domain. A male chased male or female, and was in turn driven back by male or female. Those who gave ground were threatened; those who turned and fought were apparently acknowledged the winners for the moment. Physical combat, when it occurred, was vigorous and vicious. As two wrens came to blows, they rose upward into the air for a foot or more, facing each other, pecking and fluttering until they dropped to the ground again. There they sometimes squirmed in a tangled heap, as they grasped a foot or a wing with their bills and claws. Then they often squealed in pain or fright before they were able to break apart and return to their former positions at the edge of the boundary. In a few minutes the battle was over. It always ended in a draw.

Although the fledglings of the first brood could not at first have been aware of the invisible boundary, they nevertheless observed it with remarkable consistency. No doubt their close association with their parents for the purpose of obtaining food kept them for a month or so in their proper territory. Only on a few occasions did these immature wrens stray across the boundary. On May 25, HM-54 chased a fledgling from territory I northward, when it appeared on our rear lawn. On July 16, juvenile H-51, of territory III, now entirely independent of its parents, was intercepted on the boundary by HF-49, who climbed on top of the crouching, immature wren and pecked it. The other wrens which had gathered in the course of this dispute remained aloof.

By the middle of July both families were taking part in these disputes. At first the fledglings stayed in the background, apparently attracted only from curiosity. Later they followed their parents about in the ritual. We feel certain that these young, inexperienced wrens often precipitated the quarrels at the boundary. They revealed their presence there by the noisy, practiced imitation of all the adult sounds. At close quarters

they were more aggressive. While the adults were usually content to leave the dispute on a vocal level, the immature wrens often dashed forward to attack. The result was always an increase in excitement. Once when HM-48 was being followed by his fledgling, the male reversed his direction so abruptly that he stepped on the neck of the other and ran over it. By midsummer most of the immature Cactus Wrens had disappeared. H-52 of territory III remained until December and often participated in the autumn disputes. The lone survivor of territory I, which was not banded, was also present. Up to November we identified from four to five wrens in every dispute.

Displacement or irrelevant behavior was of frequent occurrence toward the end of each of these boundary disputes. The indeterminate outcome of the conflicts resulted in the wrens running about and picking up nest materials such as chicken feathers and grass stems. Then, as the quarrel ended, the materials were carried to their roosting nests. Rarely, following a dispute, other species of birds were threatened. For example, on July 1, HM-54 sang from the crossarm of the electric pole on Kleindale Road, just south of lot 7. HM-48 answered from the northeast. Suddenly both wrens began uttering the *scri* note. HM-54 flew north about 200 feet to a small pole in lot 8, which was near the territorial boundary. At once HM-48 arrived from the north and landed on the pole, forcing the other to fly down. Then the wrens faced each other on the ground, five feet apart, and moved slowly eastward, while they uttered the *scri* note. HM-48 appeared more nervous. He tried to pull loose some of the dry grasses near him, but failed. HM-54 then abandoned the "line" and returned to his pole on Kleindale Road, where he found that a male Pyrrhuloxia (*Pyrrhuloxia sinuata*) had taken over his singing station. While the Pyrrhuloxia sang, HM-54 moved closer and closer until the former became alarmed and flew, and the wren then flew down. Shortly afterward, a Gila Woodpecker (*Centurus uropygialis*) lit on the side of the crossarm and uttered its peculiar, sharp, rolling note. HM-54 came flying back at once. He twisted and turned, retreated and advanced, and gradually edged closer. Suddenly he dashed directly toward the woodpecker. The latter backed up to the pole and spread its wings in a defensive or aggressive gesture and then climbed back upon the crossarm. Again the wren fidgeted closer. This time the woodpecker gave up and flew. Normally a Pyrrhuloxia is ignored and a Gila Woodpecker is deferred to.

Extensive trespassing upon the others' territory was seldom observed. The north pair of wrens occasionally visited the rear lawn with its feeding table and bird bath, but only when the owners were absent. HM-54 once explored the north end of lots 6 and 7, deep into territory I, and scanned the horizon from a high perch. Since he refrained from singing, he was unnoticed and unchallenged. HF-50, who accompanied him, was more timid and ventured only half as far. That this boundary line was very real was demonstrated on July 10. At the conclusion of a dispute, HM-48 and HF-49 flew north to the fence of lot 7 and buzzed at a cat that was slowly walking by. HM-54, HF-50, and their offspring H-51, attracted by the danger sounds, flew north into cholla number 3, which was about 25 feet inside of territory I. They perched there quietly, evidently watching and listening, but apparently reluctant to advance and take part in the mobbing of the cat. Soon, however, HF-49 left the cat and returned. She flew directly to cholla 3. The south pair retreated at once to its territory, leaving H-51, who was, perhaps, not so aware of its trespassing. Then HF-49 flew toward the juvenal wren. The latter quickly joined its parents and all was quiet again.

THE FUNCTION OF TERRITORY

The Cactus Wren's territory belongs in type A of Nice (1941:458) in which the territory is used for mating and nesting and as a feeding ground for the young. In addition,

the territory is retained, with some relaxation of defense, throughout the winter as a feeding and roosting area. We found it to be primarily the property of the male; the female's rights were only secondary. Although she assisted in the defense of the territory, she did so, vigorously and successfully, only when her mate was present. Without a partner, she was apparently incapable of defending her territory against usurpation by another pair. This was very evident in 1945, when the male of territory I was lost. The pair of Cactus Wrens in the adjacent territory III expanded its activities at once into the entire block, with complete disregard for the presence of the widowed female. She offered no resistance, and she later disappeared.

The problem of the critical function and significance of the Cactus Wren's territory remains unsolved. Territorialism is readily demonstrated, and its various elements are easily discerned. We do not know, however, exactly how this form of behavior serves the species. Certain advantages accrue from it, but these advantages are also obtained in some degree by other species through other means. In her survey of territory Nice (1941:470) stated that "The chief function of territory is defense—defense of the individual, the pair, the nest and young. In many cases it also serves to bring the pair together and to strengthen the bond between them."

The maintenance of a territorial boundary in Cactus Wrens did, of course, prevent intrusion and possible interference from other wrens. The question arises, would there have been interference in nest building, egg-laying, incubation, and feeding of nestlings if no defended boundary existed? In this connection we must point out that most of the boundary disputes occurred after the nestlings of the first brood were fledged. One must conclude that the Cactus Wrens were so busy raising a family that no time was available for quarrels over a territorial boundary. Somehow, that boundary during the early part of the nesting period, was tacitly accepted by both pairs.

There seems little doubt that territorialism assists in pair formation by bringing the sexes together. Yet, all that is required here is that the male make himself conspicuous. This could be accomplished, just as successfully, in a common feeding and nesting area. It appears more probable that territorialism is most useful in maintaining the pair bond, for the restriction of the female to the vicinity of one male must surely be of pairing value.

Territorial behavior in the Kleindale Road area limited the number of pairs that occupied the ten-acre tract. Here, too, the problem is left unsolved. Although competition reduced the size of the territories in 1947, nothing is known of what would have happened had there been more Cactus Wrens drawing upon the limited food supply and nesting sites. If Cactus Wrens acquired and defended territories in order to reserve an adequate food supply, then these territories should be larger in the winter months, when insects are less numerous. This appears to be the case; but the wren population per territory also increased so that nothing was gained until the late winter environmental attrition had removed the surplus offspring.

Perhaps the simplest way of regarding this troublesome problem of the function of territory is to postulate like Wheeler (Nice, 1941:468) that the basic instinct of self-preservation is equivalent to dominance. It manifests itself not only in the individual's defense of itself, but also in an inherent attitude of dominance toward individuals of its own species. This dominance can best be expressed by the male Cactus Wren by maintaining ownership of the small area in which it feeds and sleeps. The female's self-assertion appears to be weaker. Our banding operations were not of sufficient extent to determine if the female held a territory of her own before she found a mate. She probably defends her roosting area against other females. The orderly sequence of the nesting cycle, the perpetuation of the species, and the basic food resources are assured by the

male's intolerance of other wrens at this time. The female contributes to a successful cycle by making sure she has no distracting competitors in her habitat.

BREEDING NEST

It was seldom that all of the roosting nests, including those occupied by the adults, in the months of November and December, remained intact until the breeding nest was started in the spring. The instability of the Cactus Wrens' nest situation must, at least to the wrens, have been most disturbing. To the observers who tried to follow the course of the winter activities of the wrens, it was next to maddening. Nothing seemed to be permanent or settled. Following is a summary of some of the winter to spring nesting sequences (for most of these nest locations see part I, page 280, figure 4).

1938-1939.—HM-1 roosted in nest 28A, and HF-2 roosted in 27A. The only other roosting nest, 5F in lot 7, was destroyed in February. The breeding nest, 28B, was placed in cholla 28, about two feet from the male's roosting nest. This was 140 feet from the female's winter nest.

1939-1940.—Both adults roosted in cholla 6 near Flanwill Street, HM-1 in nest 6J and HF-2 in nest 6I. Just before nest 6J fell to the ground in the latter part of November, HM-1 had rebuilt an old nest, 6H, in which he continued to roost. It is hard to believe that the wren anticipated the loss of nest 6J; the nest, when it began slipping downward into a vertical position, may have caused difficulty in entry or discomfort in roosting. By the middle of January, the remaining roosting nest, 4C in lot 7, had been damaged. The breeding nest, 6M, was constructed almost midway between the two roosting nests in cholla 6.

1940-1941.—The death of HM-1 in 1940 and the disappearance of HF-2 in January of 1941 created considerable uncertainty. Most of the rather numerous roosting nests were in lot 6; their tenants were not known. The breeding nest 35B of the new pair of Cactus Wrens, HM-23 and HF-22, was located 300 feet north of cholla 6 in lot 5, close to Flanwill Street. This was the first breeding nest discovered in the northern tier of lots along Greenlee Street since our studies began in 1932. Whether our persistent efforts, sometimes unsuccessful, to capture the wrens in lot 6 for banding purposes proved to be annoying, or whether the new pair preferred the more open surroundings of the northern portion of the tract, is hard to determine. Later observations lead us to believe that the Cactus Wrens are not easily driven away by ordinary human activities.

1941-1942.—Although seven banded wrens were present during the winter, they had only four roosting nests available at the beginning of 1942; all others had been destroyed. When the wrens paired up in the spring and selected their territories, new roosting nests were built near the breeding nest location. HM-37 and HF-38 settled in lots 2 and 3 and built their breeding nest in lot 3; HM-23 and HF-30 chose the south end of lot 5.

1943-1944.—At the beginning of 1944, cholla 6 contained four roosting nests; HM-23 and HF-39 had occupied two of them during the preceding months. On January 6, three of these nests were completely destroyed. HF-39 remained in nest 6W, but this nest, too, was found destroyed on the 15th, and the female began another nest, 6AA, in the same cholla. Eight days later, it also was torn apart. Then the male, which had probably been roosting on the west side of Flanwill Street since the first part of the month, began building nest 6AB, which later became the breeding nest. Another nest, 6Y, was rebuilt also, we believe, by HF-39. In spite of the destruction of four roosting nests and the replacement nest 6AA, the pair of Cactus Wrens succeeded in building their breeding nest in the same cholla.

1944-1945.—Again cholla 6 provided a roosting nest location for a female, HF-39.

Another nest close by, for some reason, was left vacant. The male, HM-23, roosted in lot 7. Suddenly on January 6, the female began building a new nest, 14C, in lot 7. This nest was abandoned before it was completed. Then on January 21 she started nest 23F in earnest and had it practically finished on the 25th. Now her nest was only eight feet from the roosting nest of the male in cholla 22. Two days later, both adults began the task of completing the first nest, 14C. This became the breeding nest. Meanwhile HM-42, which roosted in lot 6 during the latter part of 1944, was forced to find another location when his cholla was cut down on January 14. (It would doubtless soon have been driven out of territory I, anyway.) It moved north into lot 5, where a breeding nest and a roosting nest were built.

1946-1947.—The roosting nests of HM-48 and HF-49 were about 50 feet apart at the north end of lot 7. On December 27, the male's nest was found to be torn apart. Another nest blew down. The female began building nest 19C, south of our house in lot 7, on January 21. She did not finish it and evidently continued to roost in her old nest. A month later two "noband" wrens moved in; one of them took over nest 19C and added more material. HM-48 and HF-49 retreated to the north and west. On March 8, the female was roosting in a new nest in cholla 6, 6AJ. It became the breeding nest. The male was discovered roosting in the female's old nest in lot 7.

Both of the newcomers worked on nest 19C in February, but the nest was damaged by a Curve-billed Thrasher. Nest 8P in lot 8, about 100 feet east of 19C, was started. Work continued on nest 19C, and it was occupied at night by the male. The female HF-50 (now banded) worked on nest 8P and roosted in it until March 18, when the nest was destroyed. The following day, the male began work on nest 15C in the southeast corner of lot 7. Then both adults joined in finishing nest 19C, which had now become the female's roosting nest. The male spent the nights at least as far east as Edith Street. On March 22, the pair shifted their labors to nest 15C; then they went to work again on nest 19C. This finally became their breeding nest.

1947-1948.—The division of the tract into two territories was maintained throughout the winter. For the third time in our studies a male and a female Cactus Wren of territory I roosted in the ever-popular cholla 6. HM-48 roosted first in nest 6AN; when it fell to the ground, he built nest 67B at the west edge of lot 6, 45 feet southwest of cholla 6. Then at the end of December he began work on nest 6AO. The roosting nests of HM-54 and HF-50 in territory III remained in good condition up to the time the male disappeared about February 28. The north pair of Cactus Wrens then took over the entire area. HF-49 began work on nest 23J in the north third of lot 7 on March 1. Two weeks later it was torn apart; only one good nest remained in cholla 6—6AK, the female's roosting nest. HM-48 built himself another roosting nest in cholla 67. Finally, unexpectedly, HF-49 laid her eggs in nest 6AK.

1956-1957.—Six Cactus Wrens, four of which were banded, were present in November and December of 1956. When the situation "stabilized" in January, after six nests were damaged or destroyed, only two wrens, HM-70 and HF-71, were left in possession of the territory. On January 21, HF-71 began construction of nest 21C, about 40 feet north of our house and roosted in it. The male roosted in nest 17G in the southwest part of lot 7. This nest was soon destroyed; another was begun, and it, too, was torn. Some repairs were attempted, but again the thrashers damaged it. Then the male, apparently without opposition, began to carry nest material to the female's nest 21C. The female started another nest, 21D, a few feet away from her former nest. The Curve-billed Thrashers now turned their destructive activities upon the new location. The female wren held on, roosting regularly in nest 21D, although it had been torn at least three times. At last, on January 26, she gave up and began a new nest, 94B, in the northeast

corner of lot 7. Then on February 8, we discovered that the breeding nest, 93B, was being constructed in a cholla near the west fence of lot 6, some 320 feet southwest of her last roosting nest, and 180 feet from the male's roosting nest.

From the foregoing accounts it might be conjectured that the selection of a nest site was not always a matter of a simple choice of a favorable location. Could the competitive thrasher be a determining factor? Such a supposition, we believe, is wrong, for the Curve-billed Thrashers did not destroy the breeding nests of the Cactus Wrens, so far as we could observe. It was the unattended, unprotected roosting nests that suffered. Once a breeding nest was begun, the presence of the Cactus Wrens at the nest seemed to be sufficient to deter the thrashers from their depredations at that particular point. There are some exceptional events, very difficult to explain adequately, in this connection that will be related later. In a few cases, too, it was not always possible to determine, because of the lateness of the season, if a newly begun nest, that was destroyed had been intended to serve as a breeding nest or a roosting nest.

We had no better success in observing the beginning of the first breeding nest of the season than we had in seeing the beginning of the roosting nests. The choice of a particular site, however, was probably made by the female. Sometimes, early in the year, we found a pair of Cactus Wrens prowling through the branches of a cholla cactus, apparently examining it for a suitable nest location, instead of searching the spiny joints for insect food. Occasionally the male would be carrying a grass stem in his bill as he followed his mate or moved from one side of her to the other. Usually his movements were far from deliberate; he appeared excited and eager and jumped from twig to twig with quick, abrupt twists of the body. Then with outstretched neck he peered into the tangle of branches while he held the nest material. Some of the rapid movements reminded one of the courting behavior of the ever-present male English Sparrows, but the elaborate posturing and noisy sounds were absent. The inspection of the cholla always ended while we were present in the departure of the wrens to another portion of the tract.

The events of the spring of 1947, previously mentioned, suggest that the female makes the final choice of a nest site, and it is sometimes at the expense of the male. The destruction of HF-50's roosting nest 8P (possibly also her intended breeding nest), on March 18, was followed quickly by her appropriation of the male's partly finished nest 19C. Then, when HM-54 built another roosting nest, 15C, for himself, he also assisted his mate in the completion of her nest. Suddenly, for no apparent reason, at least to us, the female began carrying material to the male's new roosting nest. Finally both wrens went back to work on nest 19C. It is possible that at first HF-50 felt that she was being disturbed too often, since her nest was so close to our house. The male's nest in the southeast corner of lot 7 was farther away, but it had disadvantages, too. The Kleindale Road traffic was only a few feet away.

It would be easy, but certainly misleadingly anthropomorphic, to say that this was a perfectly matched pair of Cactus Wrens that worked together for the common good, at least after the female took possession of the male's roosting nest. The behavior of the male suggests a different explanation. He did not appear eager to be displaced from his roosting nest; in fact, one received an impression of reluctance. On March 19, the day after the loss of the female's nest, HM-54 was observed at the entrance of 19C. He uttered a peculiar whining sound as though he were disturbed; then he sang. Soon afterward both wrens were inside the nest. The same painful, whining sound was heard again. HM-54 was first to come out of the nest. By midmorning, the male was busily constructing his new roosting nest, 15C. Possibly the presence of the female in his nest was an indication that he must give it up. The next day, although both adults worked energetically on nest 19C, apparently without friction, the male continued to utter this

squeal. Several times we observed that he entered the nest without nest material and squealed inside. When he came out, he usually sang once on the doorstep. At 6:20 p.m., when HF-50 arrived in the cholla, HM-54 quickly slipped into the nest. The female looked in but did not attempt to enter. The male soon came out, for it was still too early to retire for the night. Twenty minutes later, when both wrens flew to the nest, HF-50 was the first to enter. The male peered into the nest for several moments; then he left. On March 21 the same behavior was noted, except that the male followed his mate inside. He remained there only a short while, before flying east to roost. Nest 15C was not occupied as a roost until the following night. We had never heard this squeal before, and have very few records of its occurrence in later years. It would appear to be an utterance of protest from the male, mild to be sure, for no quarrel ensued as the female dispossessed the male of his roosting nest. We heard this protest only when the female was near or in the male's nest at the beginning of the breeding season. In some way the male may have sensed that the nest was to become a breeding nest. Here we tread upon dangerous ground. We do not know how the male is led to help in the construction of a breeding nest, nor do we know how he distinguishes this nest from the recently-built roosting nests. We have observed that the usual protest upon eviction from a roosting nest is an angry sputter of *scri* calls, sometimes followed by a brief fight. The loser buzzes as it retreats to find another roosting place. The squeal was not noted at nest 15C, which the male had just begun. Perhaps the attachment to a newly begun nest is not as firm as that to a long-occupied one.

We believe that when the breeding season begins, the period of complete male dominance is over. The female, evidently by means of increased aggressiveness, is able to determine to some extent the course of her own affairs. She can and does at times select her own breeding nest site for the first brood.

Both sexes constructed the first breeding nest of the year. Under normal, unhurried and undisturbed conditions, the division of labor was probably nearly equal. It was not unusual to observe the male and female arriving at the nest at the same time with bills full of nest material. Sometimes, before the roof was in place, they would enter side by side and deposit the grasses upon the floor, or poke them into the thin, rising walls of the nest cavity. The first one to finish left through the open top. Later, after the roof and vestibule were outlined, only one could enter at a time. Occasionally both birds would be working inside, but usually at this stage of construction the visits appeared to be so timed that no waiting was necessary at the entrance.

At first we supposed that two Cactus Wrens working together could build a nest twice as rapidly as one could working alone. This, however, does not appear to be the case, for the inattentive periods were often long and irregular. The rate of construction was probably set by the female. When she left her nest building, the male followed her; and the urgency with which she worked was, no doubt, dictated by the nearness of the egg-laying stage. There are so many variables that more data would be desirable here. If we average the number of visits to the roosting nest 23A (Condor, 1957:284) for the three active working periods, we get one visit for each 0.80, 0.88, and 1.1 minutes respectively, or roughly one visit every 0.9 minute. Any faster rate of delivery of materials would leave very little time for their placement in the nest. At breeding nest 28B, in 1939, two wrens working together made 10 visits in 28.5 minutes; then beginning 15 minutes later, they made 11 visits in 20 minutes, the average being one visit in 2.8 and 1.8 minutes. The breeding nest 19C of 1947, observed for 40 minutes, revealed 26 visits with nest material, an average of 1.5 minutes between visits. These averages of elapsed time between visits for two wrens working together are approximately twice as great as for the one wren working alone on its roosting nest. The work at roosting nest 23A was observed

early in the forenoon in August; breeding nest 28B was watched at noon and 19C in midmorning, both in March. Although nest construction proceeded more rapidly early in the morning, the breeding nest rate did not equal or exceed the roosting nest rate.

No satisfactory method could be found for determining when the first breeding nest of the year was completed, because the installation of nest material usually continued up to the time the first egg was laid. In some instances this period of time was not what one could call a normal one. Loss of mates, nest destruction, unfavorable weather conditions possibly, and many human disturbances complicated the picture until we have such extremes as 5 to 41 days from the time of beginning of nest construction to the laying of the first egg (fig. 4). The average time in the Kleindale Road tract for the 13

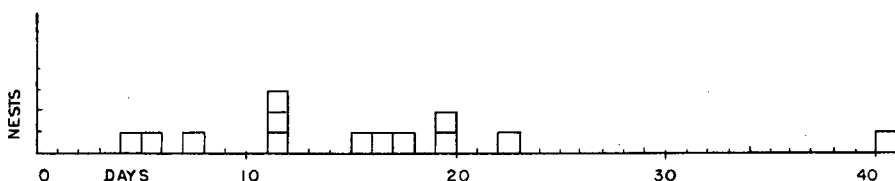


Fig. 4. Time (estimated) from start of construction of first brood nest of Cactus Wren to laying of first egg. Data are for 13 years.

years in which we have sufficient data is 16.1 days. If we ignore the abnormal high of 41 days our average is 14 days. Since visits to the Santa Rita Experimental Range, south of Tucson, could usually be made only at weekly intervals, exact data on nest building was not obtained. At least seven of the breeding nests in that area, however, required more than 15 days in construction.

We have only one good observation on the length of time it takes for the growth of the ovum in the Cactus Wren. On May 29, 1958, we discovered that the three, three-day-old nestlings in nest 25H were gone. Two days later the adults were at work on another nest and the first egg was laid either on June 4 or 5. Nice (1943:210-211) states that "the start of nest building in the Song Sparrow roughly corresponds with the rapid growth of the ovum which normally begins 5 days before the egg is laid." The basis for the latter part of this statement is her observation that after the loss of a set of eggs, the next egg is laid 5 days later. The interval of 5 days in the Song Sparrow and 6 to 7 days in the Cactus Wren occurred not at the beginning of the breeding season, but later, when the female's reproductive condition must have been in an advanced stage of readiness. Our Cactus Wrens, on the average, began their first nests at least a week before the beginning of the 6 to 7 day period of rapid egg development.

Since the Song Sparrow nest is built entirely by the female (Nice, 1937:94), the stimulus for the initiation of nest building probably arises from her own physiological condition. Although the situation in regard to the Cactus Wren is complicated with more variations in behavior, it seems likely that the female normally installs the first nest material when she is ready to begin her first brood of the year. The male then assists in the construction as long as the female is present. A few exceptions to this sequence have been noted in the summaries of winter nests. The female does occasionally take over a nest which the male has built for a roosting place. This can occur because of nest destruction, or perhaps from a sudden development of favorable environmental stimuli that makes egg-laying urgent. The variation most difficult to account for is the one in which the female laid her eggs in her own roosting nest. This did not occur often, and in one case the roosting nest was new. It may actually have been intended for a breeding nest. Some nests in neighbors' lots were difficult to watch; we may have missed the work of

the male. For her later broods a female did not need to build a nest. The nest was already waiting for her; it had been constructed by the male while she incubated.

Copulation has been observed as early as 18 days before the first egg was laid. It continues up to at least the laying of the eggs. We have a record of a 40-day interval, but in this instance the wrens experienced difficulties in their nest building, and they were doubtless delayed. This is also our earliest record; it occurred on January 12, 1957. In the extremely early nesting of January 2, 1958, copulation must have taken place in December, even before the female's selection of a breeding nest site.

The female indicated her readiness, from an elevated perch, by crouching low and singing a rapid series of *rar rar rar rar rar* notes several times. The tone appeared to be at a somewhat higher pitch than that of the normal song. Her bill pointed slightly upward, and she fluttered or quivered her wings. The male responded by flying to her quickly. Sometimes he spread his tail upon arriving, as he might do in the customary recognition display. Then he, too, fluttered his wings, just before he mounted the female to make momentary contact. Sometimes he hopped beneath or to the side of her first, in evident excitement. After completing the act, they usually perched quietly a few moments before flying to the ground; but at one observation the male pecked the female on the head. She did not move. Then he pecked her twice more before she left him. We have only one record of the female flying to the male. This occurred when the male was singing, and he stopped at once when she crouched and fluttered her wings.

THE START OF LAYING

We had hoped in the course of this study that a sufficiently large sample of data on the time of the laying of the first egg could be accumulated to enable us to place the results on a statistical basis. This hope proved futile, for seldom was more than one territory available and accessible in the Kleindale Road vicinity during any one year. In addition, the variations in the time of laying from year to year proved to be very great. Had we been content to work on the life history of the Cactus Wren for only a year or two, these variations would have remained undetected, with most of the difficult problems happily unnoticed.

In table 1 will be found the estimated date of the first egg of the year in the Kleindale Road area from 1934 to 1958. There are three years missing, 1937, 1949 and 1951, in which no data were obtained. Although one sample per year is obviously inadequate for any generalization, there are two interesting and suggestive years in the table. In 1942 there were three territories (fig. 2, the Edith Street territory not shown). The date of the first egg was the same in two of them, and only three days later in the third. There were two accessible territories in 1947, with the egg-laying dates eleven days apart. Had it not been for the destruction of HF-50's first breeding nest in this year, the dates would probably have been closer together. We think the possibility is present that many of the dates in the table may be the normal ones and should be considered as the time at which a larger population would have begun to lay. If this be true, then some explanation will have to be devised to account for the yearly variations.

We gradually came to believe that for a given species in a uniform habitat, the approximate date of physiological readiness for breeding is probably in part determined genetically in that it is the result of centuries of selection for response to regular, periodic, seasonal changes. In a desert environment the supply of insects and spiders must be rather low by the end of the colder months. Theoretically the egg laying should be so timed that sufficient food is available for the young when the eggs are hatched. If they are hatched too early, they may suffer for want of the proper food; if they are

Table 1

Date of First Egg with Summary of Data on Temperature and Rainfall

Year	Date first egg laid	Average of mean temperatures 7 days before laying	Average of mean temperatures 14 days before laying	Rainfall from October 1 to date of first egg
1934	March 21	65.5	64.6	3.65
1935	March 23	56.1	53.8	7.68
1936	March 1	56.0	55.1	5.01
1938	March 14	60.7	58.4	2.83
1939	March 16	59.3	55.4	3.01
1940	Feb. 20	49.0	48.5	2.08
1941	Feb. 24	59.0	58.6	8.14
1942	March 7, 7, 10	53.7	53.5	5.39
1943	March 20	58.0	57.1	2.44
1944	Feb. 20	47.7	48.6	1.81
1945	Feb. 8	53.0	50.5	5.21
1946	March 13	58.7	57.2	4.35
1947	March 15, 26	53.1	53.3	2.37
1948	March 13	53.0	50.4	3.81
1950	March 1	58.7	60.0	3.21
1952	March 3	55.1	52.9	5.37
1953	March 23	61.7	62.0	4.84
1954	Feb. 25	57.0	57.1	1.21
1955	March 12	64.4	59.5	2.18
1956	March 7	58.8	56.9	2.60
1957	Feb. 21	62.5	63.7	3.05
1958	Jan. 2	54.4	54.4	3.89

hatched much later, the time for additional broods is shortened. The dependence of this food supply upon a proper interrelationship of temperature and precipitation must be apparent. Without winter rains, the plants and their accompanying insects will not develop, even though temperatures are favorable. Rainfall without a sustained increase in temperature is likewise inadequate for growth.

In table 1 we have included the average of the mean daily temperatures ($^{\circ}$ F.) for the seven days preceding and the fourteen days preceding the laying of the first egg of the year. These intervals correspond to the presumed time for the rapid development of the ovum and the time required to build the breeding nest, respectively. The temperatures are taken from the University of Arizona weather recording station situated about three miles southwest of our study area. The range of variation is slight; it is 17.8° for the 7 days, with extremes of 47.7° and 65.5° ; it is 16.1° for the 14 days, with extremes of 48.5° and 64.6° . There are 15 and 17 of these 22 layings in the 50° to 60° interval, respectively. Early layings were not necessarily at the lowest mean temperatures. Fifteen of our dates are in March. Early nestings, we believe, can usually be explained by favorable environmental conditions. Rather difficult to account for is the fact that three females laid earlier in the second year that we had them under observation than they did in the first; possibly they were birds only one-year of age when first observed. HF-2 laid her first egg on March 16, 1939; the next year she laid on February 20. HF-49 laid her first egg on March 15, 1947; in 1948 she laid on March 13; there are no data for 1949, but in 1950 she laid on March 1. HF-71 laid her first egg of 1957 on February 21; the following year she laid on January 2.

In 13 of the 22 years, laying began after a steady rise in mean temperatures of sev-

eral days duration. In most of the other years a period of above normal temperatures preceded the laying. These temperatures were, of course, preceded by a climb, which may have provided the stimulus toward nest building. The early laying of February 21, 1957, occurred near the bottom of a temperature decline of 6 days, but the previous peak, after a 9-day climb, had reached the unusual extreme of 72°. The still earlier record of January 2, 1958, occurred after a 3-week period of above normal temperatures, some of which were as much as 10° above the average for Tucson at this time of year. In 1940 and 1944, the start of laying was at temperatures below normal, but in both these instances an above-normal peak occurred about 2 to 3 weeks previously.

The effect of rainfall in the Kleindale Road area is far more difficult to interpret. If we tabulate the precipitation from October 1 to the date of the first egg (table 1), we obtain 3.65 inches for 1934 and 7.68 inches for 1935, 2.08 inches for 1940 and 8.14 inches for 1941, with the corresponding egg dates on March 21 and 23, and February 20 and 24. There is no evidence here that laying is postponed in periods of low rainfall until mean temperatures are higher or that total quantity of rainfall, by itself, influences the time of laying. Normal rainfall in October, November, and December, accompanied by mild temperatures, initiated and accelerated the growth of winter annuals to a very striking degree. For instance, filaree (*Erodium cicutarium*) and bladder-pod mustard (*Lesquerella gordonii*) which usually begin flowering in the first part of February, were in bloom in the last week in December, 1957, and their first shoots were observed as early as the second half of October. Another mustard (*Sisymbrium irio*) and a grass (*Schismus barbatus*) appeared in November. On January 2, 1958, the first Cactus Wren egg was laid. Whether this was the result of mild temperatures, or the combination of mild temperatures, rainfall, and new fresh vegetation, we cannot determine. Mesquites, creosote bushes, and chollas varied considerably in their time of flowering, but their growth could hardly have had any influence on early egg laying, for nesting was always well under way by the time these larger plants were flowering.

Earlier we have tried to show that our population of Cactus Wrens was composed of immigrants from the neighboring population north of Rillito Creek. The two populations should normally begin laying, if our supposition of genetic similarity is correct, at about the same time. In fact, the entire Tucson mesa, although exhibiting considerable variations in vegetational aspect, is rather uniform in winter temperatures and rainfall. On Kleindale Road, close to the Rillito Creek trough, the winter nighttime temperatures were lower than those on the mesa. We should expect little difference in time of egg laying anywhere in the area. Here again we are plagued with insufficient data for a proper comparison. Working with estimated dates, we have in 1941 the first egg on March 2, at a point one-fourth of a mile northwest of our home, still on the south side of the Rillito. The first egg in the home area was on February 24. Seven miles to the southeast, the first egg was laid on March 6. In 1955, 3 miles to the east, along the edge of the foothills of the Santa Catalina Mountains, bordering the Rillito, eggs were laid on March 30 and April 2; in our area it was on March 12. A few more data are at hand from the Saguaro National Monument, 11 miles to the southeast of our home. In 1954, the first egg was laid on March 17, estimated from information furnished by Hal Harrison; on Kleindale Road we have February 25. In 1956 we estimated the first egg was laid on March 23 as compared with March 7 in our area; in 1958 the first egg was laid on February 16 in one nest and February 26 in another, compared with January 2 in our lot. In the same year we estimated that an immature Cactus Wren collected by Allan R. Phillips 17½ miles southeast of Tucson came from an egg laid about February 20. Evidently the southeastward population was also influenced by the mild winter. We have but few egg dates from residential parts of Tucson: March 8, and possibly February 22, 1956, esti-

mated from data given to us by John Chalk, and March 12, 1954, by Allan R. Phillips. While we realize that our data are meager and that some of the estimates could be wrong by as much as plus or minus five days, we are faced with the peculiar fact that egg laying took place later in all the adjacent areas than it did in our small ten-acre study tract. The available information suggests that egg laying begins earlier in and close to cities. Much more work, however, is necessary on this phase of the Cactus Wren's behavior before definite conclusions can be drawn.

It is interesting to consider the effect on the Cactus Wren of living in the vicinity of human activities. We have stated (Condor, 1957:276) that we purposely left our lot as much as possible in its original condition. This is not strictly true, for our occupation of the land effected numerous drastic changes. Most of the chollas and creosote bushes were left undisturbed. However, space was taken over by buildings; a fence was constructed that excluded cattle, and also to a considerable extent rabbits. Although the vegetation now received protection, the ground cover gradually changed from native plants to the introduced mustards and grasses. (This change was not confined to our lot alone; it was general in the vicinity.) Native diurnal rodents became scarce; the antelope squirrel disappeared completely and the round-tailed ground squirrel left, but returned irregularly. Numerous cats from our neighbors roamed the tract, in spite of the presence of our dog. House mice obtained a foothold in adjacent chicken houses. Snakes were few, because people and their automobiles disturbed them. English Sparrows moved in quickly and took up residence under the eaves of neighboring garages. As the spreading subdivisions expanded nearer, the inevitable gangs of small boys increased; and they prowled the Rillito banks with their deadly BB guns. Our ornamental shrubs and trees grew in number and size. No doubt various new insects multiplied far more abundantly and probably earlier in these well-watered ornamental shrub areas than in the dry sandy expanses among the creosote bushes. Perhaps it is these insects that are the key to the early nestings.

Herbert Brown (1888:116) reported that "nesting was well under way" in the Tucson region on March 13, 1885; Scott (1888:162) said that eggs are laid as early as March 20 in the Santa Catalina region. Brandt (1951:679) stated that fresh eggs could be found in the desert about Tucson as early as March 15, "but the peak of season is not until a month later; while over in the high country at 5000 feet, near where the San Pedro River crosses the Mexican line, I found a nest with 4 fresh eggs on June 21, 1944." We have purposely omitted the listing of nesting records from other states, because they are too scattered and they lack important data. The practice followed for many years in Bent's "Life Histories of North American Birds" of recording the length of the egg-laying season, and then attempting to establish the most frequent period is misleading. For instance, in the case of the Cactus Wren (Bent, 1948:231) we have: "Egg dates.—Arizona: 82 records, March 10 to August 6; 40 records, April 21 to May 25, indicating the height of the season." In a multi-brooded species the "height of the season" is actually the first brood. Later records must pertain to second or more broods. Furthermore, it is inconceivable to us that a given population subjected to the same environmental factors would respond with such irregularity as is indicated by egg dates from March 10 to April 21. These extreme dates must come from different populations or from first and second broods.

As we pass on to larger areas in Arizona the confusion increases. If we attempt to correlate nesting with temperature, then elevation must be taken into account, for the range of the Cactus Wren extends from near sea level at Yuma to the lower edge of the Upper Sonoran Life-zone in the eastern part of the state. Are eggs laid earlier at lower elevations where the temperatures rise earlier in the season? Not necessarily, for the

rainfall in Arizona is directly proportional to elevation; and rainfall is necessary to produce the spring annuals and abundant insects. Hensley (MS) gives the date of March 10, 1949, for the first egg of the Cactus Wren in the Organ Pipe Cactus National Monument in southwestern Arizona. The area which he studied is slightly lower in elevation than Tucson, but the mean temperatures for the first three months in the year are slightly higher. The annual precipitation is about 3 inches less. Unfortunately, we do not have any nesting from Tucson for 1949 for comparison.

Through the courtesy of the late Fred M. Dille we have available the field note book of George F. Breninger, who collected eggs in the Phoenix region of Arizona from 1896 to 1905. The elevation of Phoenix is about 1200 feet; the mean temperatures are higher than those in Tucson, and the average annual precipitation is similar to that in parts of the Organ Pipe Cactus National Monument. In five of the years the data are fairly complete, although the condition of the eggs was not always recorded. The dates on which the first complete sets of eggs were collected are as follows: March 10, 1896, March 8, 1897, March 11, 1898, March 21, 1899, and February 21, 1901. Most of the subsequent sets collected were in the month of March, and some of these later sets were catalogued as advanced in incubation. The habitat is not described, but nests were found in mesquites, "thorn bush," ironwood, palo verde, and "thorn tree"; a few were in cacti. These dates are, of course, subject to the same errors as those in Bent's "Life Histories." They are not dates of first eggs laid, but dates when eggs were collected. It is to be noted that none of these dates are in April. In contrast to these old records, we have a letter from Ruth M. Crockett, of Phoenix, reporting that in 1952 nestlings were being fed on February 3, near Squaw Peak. The young in another nest were fledged about February 23. We estimate that the first of these eggs was laid about January 13. The nest locations were described as on the edge of a residential area, and "the vegetation was unusually lush from recent rains."

There has been little in the foregoing extensive summaries to support the supposition that the time of egg laying is genetically controlled for a given population. Some evidence, we believe, has been presented to show that most of the records in Arizona occur in the month of March, regardless of elevation, and that earlier egg laying takes place under favorable circumstances. This was the status of our studies up to the beginning of 1953. In order to examine a larger population of Cactus Wrens we now turned most of our attention to the Santa Rita Experimental Range, a large desert tract situated about 35 miles south of Tucson, Arizona. Here we discovered to our great surprise, that in a 60-acre study area, not one pair of Cactus Wrens laid their first eggs before April 16. This occurred not only in 1953, but also in 1954, 1955, and 1956. We discontinued our studies in 1956, but we returned in 1958 to see if the mild winter with the early nesting in the Tucson area was also reflected upon the range population. To our satisfaction it was; we estimated the date of the first egg to be on March 29, 1958. Evidently there is a distinct population of Cactus Wrens on the Santa Rita range, whose time of egg laying seems to be genetically controlled to occur a month later than that on the Tucson mesa. Our efforts to determine the cause of the late nesting have so far been largely futile.

SUMMARY

The invasion of the cholla cacti into the creosote bush association of the Kleindale Road area of Tucson, Arizona, appears to have been relatively recent. When these cacti became large enough to furnish nest sites, the Cactus Wrens probably moved in from the foothills on the north bank of the Rillito. This may have occurred about 1915.

Breeding territories each year varied from one to five, including those bordering the study tract. Destruction of the habitat resulted in only one territory within the ten-acre area from 1948 to 1958. Encroachment upon the territory by other Cactus Wrens resulted in defensive behavior, but a compromise was reached by giving up some of the original land to the newcomers. The "boundary line" was well defined in 1947, when the two breeding nests were only 180 feet apart.

Disputes were frequent in 1947, after the young were fledged in territory I, and they continued until the end of February, 1948. Singing stations were not on the "boundary," but some distance inside. Disputes occurred when one pair or the other detected what appeared to be an intrusion upon its territory. Both pairs then faced each other along the "line" and moved slowly in parallel lines. Short songs and the scratchy territorial sounds were uttered by both males and females, as they proceeded for 15 to 20 feet, after which they turned and retraced their steps. Threatening postures, such as fluffing out feathers and spreading the tail were noted. Sometimes short chases and brief fights took place back and forth, but the "line" still held, and the battle was over in a minute or two. Then both pairs retreated. Fledglings participated in the disputes and often apparently precipitated the quarrels by straying across the "boundary." Displacement behavior was evident as the Cactus Wrens ran about, picking up nest material at the end of the dispute. Occasionally displacement activity consisted of threatening other species such as Gila Woodpeckers and Pyrrhuloxias which happened to be near at the time of the dispute.

The Cactus Wren's territory is used for mating, nesting, and feeding ground for the young, and it is also retained as a roosting area for the remainder of the year. The female defended this territory only when her mate was present. Although the maintenance of a territory provided freedom from interference in the nesting cycle, the duties of nesting seemed to leave little time for boundary disputes. Territorialism probably assisted in maintaining the pair-bond; it limited, too, the number of pairs in the tract.

The basic instinct of self-preservation appears to manifest itself in an attitude of dominance, which in turn is expressed by maintaining ownership of a feeding and sleeping area.

The autumn roosting nests seldom remained intact until the next year's breeding nest was begun. Nest destruction and change of nests were frequent. Curve-billed Thrashers destroyed roosting nests but not breeding nests.

The female probably chose the breeding nest site for the first brood, and the male then assisted her in the nest construction.

Average time from beginning of construction to the laying of the first egg was about 14 days. After the failure of a nesting attempt, the next egg was laid in 6 to 7 days. Copulation occurred as early as 18 days before the eggs were laid; the female always invited it and indicated her readiness by crouching, singing, and quivering her wings.

Human activities encroaching upon the Cactus Wren's habitat generally favored the wrens; more food probably became available and, as long as the cholla cacti and the nests were protected, the wrens remained to breed.

Variation in time of the laying of the first egg was great. The date for breeding readiness probably has some genetic basis for a given population; it is subject to modification by important environmental deviations from the normal. Most of the layings in the Kleindale Road area occurred after a rise in temperature, or at above normal temperatures. In Arizona, below 3000 feet elevation, the first egg is usually laid in March. Early nestings occurred after mild winters with rainfall adequate for new spring plant growth. Estimated dates for the first egg are given for 22 years in the Kleindale Road area. In

about two-thirds of these years the layings occurred when the average of the mean temperatures for the preceding seven days was between 50° and 60°. Delays in nesting are attributed to failure to find a mate in time, loss of mate, or nest destruction. Rainfall by itself was not a factor inducing laying.

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