

LIFE HISTORY OF THE CACTUS WREN
Part VI: COMPETITION AND SURVIVAL

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In the concluding part of our study of the Cactus Wren (see earlier papers, 1957-1962), *Campylorhynchus brunneicapillus*, we are concerned with the effects of the physical environment upon the wrens, their conflicts with other birds, the enemies they faced, and finally the survival of the Cactus Wrens in our limited area of research.

PHYSICAL ENVIRONMENT

From 1939 to 1961 the temperature maxima recorded at the University of Arizona weather station, about three miles southeast of our home in Tucson, ranged from 110° to 115°F. The extreme minimum was 16°F., in January, 1949. These records may vary considerably, especially in winter, from those in the Kleindale Road study area. At night, the cold air from the upper elevations of the adjacent Santa Catalina Mountains moves down into the Rillito Valley trough, often producing frosts in our neighborhood, while the slightly higher portions of the city escape. These extremes in temperature must be well within the limits of tolerance of the Cactus Wren. In other localities of their extensive range, they maintain themselves under even higher and lower temperatures.

The microclimate of the Cactus Wren's environment is markedly different from the picture given by the standard weather information. Only when the wrens perched at a four foot height in shade, were they subjected to the official temperatures. On clear mornings, in January, the ground surface temperature at sunrise might be several degrees lower than the standard air temperature; by 3:00 p.m., when the air temperature had reached 84°F., the ground temperature had risen to 101°F. More striking variations occur in midsummer. At an air temperature of 106°F. we have observed a ground temperature of 146°F. in the sun. The temperature was measured by means of a Weston metallic thermometer, its stainless steel tube placed horizontally upon the surface of the sandy ground. The errors introduced by the reflection from the bright metal tube, and its exposure to air circulation, are on the negative side. Undoubtedly, the actual temperature was higher. Shreve (1951:14) reported rock surface temperatures in the Sonoran Desert of from 150° to 160°F.

The Cactus Wrens obtained relief from the midday summer sun by seeking the shade of bushes and trees. In their search for food on the ground, they visited open spaces for only short periods of time or avoided them altogether. We once frightened a family of wrens from the shade of our house; they returned as soon as we were out of sight. In summer wrens frequently move slowly on the shady ground or in the lower branches of a mesquite tree, holding their bills open a quarter of an inch, as though panting, while they peer into the tangle of shrubbery for food. At the same time they lift their wings slightly to air their bodies.

The use of a covered breeding nest that obstructs the direct rays of the sun is of considerable advantage to the Cactus Wrens. If the roof of the nest completely shades the nest cavity, and if the walls are sufficiently porous to permit air circulation, the temperature of the inside of the nest approaches the standard shade temperature. At two breeding nests, checked on June 29 and July 12, respectively, we found the shade temperature and the interior nest temperature to be identical, 105°F. in the first, and 106°F. in the second. Another nest, with a thinly latticed roof, which the sun was able to penetrate, was checked on May 25, and found to be 112°F. inside, when the shade

temperature was 107°F. The inside of a nest of dense construction would probably reach a still higher temperature, the temperature of the solid wall mass.

There is a fascinating problem in physiology here which is yet to be thoroughly studied. Other desert birds, notably Curve-billed Thrashers (*Toxostoma curvirostre*), Mourning Doves (*Zenaidura macroura*), and House Finches (*Carpodacus mexicanus*) build open nests and often incubate their eggs while sitting under direct sunlight. Mourning Doves do not change places in the heat of the day, but Curve-billed Thrashers alternate in incubation. The female Cactus Wren leaves her eggs periodically to obtain food for herself. We do not know if she can withstand direct sunlight upon her back during incubation, but, in any event, her eggs could probably not be left uncovered for ten or fifteen minutes in the midday sun of June or July without suffering injury.

Some apparent discomfort has been observed at nests on hot summer evenings. Fledglings sometimes roost in the vestibule of their nest, with their bills pointing outward, instead of crowding into the interior. Occasionally adults, evidently hesitant, will stand or sit at the entrance of the nest for some time after dark before moving inside.

One would expect water requirements of wrens to be high under these conditions. In the normal desert habitat, pools of water are seldom available for any useful length of time. On our lot we provided a steady supply of water in a bird bath saucer, sunk in the lawn. Drinking by adult wrens from this pool became noticeable in September, increasing to a high in December and January. We have very few records of drinking by adult wrens in July and August. Evidently the insect food obtainable in the winter months does not have a sufficiently high water content to satisfy the needs of the wrens. With the coming of spring, the rainfall usually dropped to zero, but the winter annual plants, now bloomed in more or less profusion, supporting fresh succulent insects. As the days grew warmer the insect population increased, and the wrens seldom came to drink. Strangely, in August we have numerous observations of drinking by immature wrens.

The time at which a Cactus Wren retires to its roosting nest is evidently governed by the light intensity. As daylength increased, the wrens followed sunset closely. To some extent, weather conditions, such as cloud cover and rainfall, influenced the time. We have records in March of wrens going to roost on cloudy evenings as early as eight minutes before sunset. Rain at roosting time may also induce early roosting. Temperature seems to have little effect. Generally, from December to April, both sexes are in their nests by five minutes after sunset. We have some evidence that females retire earlier than their mates in the winter and spring; later in the year we find no constant difference between the two. While incubation was in progress, little change in roosting time could be observed. When feeding of nestlings began, retirement occurred later, sometimes from eleven to sixteen minutes after sunset.

The observed time at which the sun was entirely below the horizon in the Kleindale Road study area seemed to be from four to eleven minutes earlier than the official astronomical sunset. This was obviously because of the ragged, irregular profile of the Tucson Mountains at the western horizon. As the sun moved northward sunset followed the saw-tooth outline. For a short time we recorded the light intensities in the evening by means of a General Electric photographic exposure meter. This meter was calibrated in foot candles, its scale reading from 0 to 75. (Later when we obtained a slip-on multiplier, its range could be increased to 750 foot candles.) We realize that considerable error could be introduced in our measurements, for the locations of the light meter varied from time to time, the sky was not always uniformly bright and clear, and too few readings were taken for them to be truly representative of daily, seasonal, and climatic vari-

ations. Nevertheless, certain patterns are evident. Sixteen readings were recorded of the roosting time of a male Cactus Wren, from December 26 to March 25. On seven of these evenings the pointer of the meter went off scale at 75 foot candles. From subsequent observations we estimate the true values to be from 120 to 140 foot candles. The remaining nine readings ranged from 34 to 70 foot candles; the average was 54 foot candles. This would indicate that roosting usually occurred very close to the standard sunset time, or a little before. Actually the wrens retired shortly after they observed that the sun in our neighborhood had sunk below the horizon. Movement toward the roosting area usually began before sunset, at a fairly high value of light intensity. Cactus Wrens which roosted on our lot, or the adjacent lot to the west often approached their nests in the evening from the east or northeast. They moved toward the sun, facing it.

We have defined awakening time as the time at which the wren leaves its nest in the morning. Singing by the male usually occurs immediately thereafter. Our few records of awakening have been combined with the more numerous records of first morning song, for a total of 27, in the first four months of the year. Male wrens left their nests and sang on the average 29.6 minutes before they saw the sun rise. Incubating females were tardier, sometimes remaining in their nest until just before sunrise. As with sunset, the variation in the time of sunrise followed the slope of the mountains on the horizon. The standard sunrise occurred about ten minutes before the sun appeared over the Rincon Mountains. Only eight foot candle readings are available in the foregoing tabulations. They range from a (estimated) low of 0.5 to a high of 7, with an average of 2.6. Apparently the Cactus Wren retires when the light intensity is 20 times as great as it is in the morning awakening period. Fatigue may be a factor contributing to early retirement, but it is difficult to prove. At night in the nest, the bird's eyes may grow accustomed to darkness, permitting profitable activity at a lower light intensity in the twilight before sunrise. Not to be ignored in this discussion are the songs of the other desert birds. Curve-billed Thrashers and House Finches habitually began singing earlier than the Cactus Wrens. If there were no sounds to awaken the wrens, hunger of course would eventually bring them forth in search of food.

Windstorms occasionally blew down poorly placed or flimsily constructed nests in the cane cholla (*Opuntia spinosior*). Heavy, prolonged rains water-logged the older nests until they slipped from their supports and fell to the ground. Jumping chollas (*Opuntia fulgida*), far more spiny and intricately branched, held nests tightly and securely. Heavy rains also thoroughly soaked the Cactus Wrens, turning them into bedraggled tramps. Wrens seldom realized that they could find dry shelter under eaves and patio roofs, or even in their own roosting nests.

INTERSPECIFIC RELATIONSHIPS

Few conflicts could be detected between the Cactus Wrens and the varying numbers of migrants that arrived in the fall to remain for the winter. Brewer Sparrows (*Spizella breweri*), White-crowned Sparrows (*Zonotrichia leucophrys*), and Lark Buntings (*Calamospiza melanocorys*), all seed eaters, made inroads on the available food supply, but apparently there was enough food for all. Some of these birds roosted in cholla cacti in which the wrens had roosting nests. By retiring later than the wrens, they avoided detection and possible interference. Wintering Mockingbirds (*Mimus polyglottos*) and Phainopeplas (*Phainopepla nitens*) fed regularly, undisturbed, on the mistletoe berries (*Phoradendron californicum*) in our large mesquite tree.

Transients from the adjacent Rillito Creek streamside vegetation, such as Brown Towhees (*Pipilo fuscus*), Rock Wrens (*Salpinctes obsoletus*), and even Cardinals

(*Richmondia cardinalis*), were occasionally chased, but not very far. A Western Kingbird (*Tyrannus verticalis*) which had built a nest on the wire bracket of a light pole, located near a wren's breeding nest, prevented the wren from using the pole as a singing station. On February 24, 1957, we saw a male wren singing from the tall television antenna in our neighbor's lot. A few feet away a male Pyrrhuloxia (*Pyrrhuloxia sinuata*) alternated with his vigorous, whistled song. Singing Mockingbirds and Cardinals were not molested. Cardinals which brought their fledglings into our vicinity were once observed chasing several immature wrens from a mesquite tree.

The species which nested commonly in the same area as the Cactus Wren were the Mourning Dove, Inca Dove (*Scardafella inca*), Curve-billed Thrasher, House Sparrow (*Passer domesticus*), and House Finch. The Inca Dove and House Sparrow, both doorway birds, are not found in the usual habitat of Cactus Wrens. More accurately, one could say that the Cactus Wrens had remained here until their marginal area had become semi-domesticated. The desert, except for small patches like those in our back lot, gradually disappeared as the human population moved northward to the bank of Rillito Creek.

Mourning Doves, which had seldom nested in our area before, have become more numerous in the past ten years. Freedom from disturbance, and our constantly filled pool of fresh water, no doubt contribute to their desire to stay. They nested commonly in cholla cacti, often directly upon an old Cactus Wren's nest. There never was a serious question of ownership. At the approach of a wren, the incubating Mourning Dove raised up threateningly. That was enough; the wren backed up and left. In the spring of 1961, when the Cactus Wrens left our lot to breed in adjacent lots, three pairs of Mourning Doves moved in. In all they made fourteen nesting attempts that year, lasting from February to September. Twelve of the nests were in cholla cacti. Some of these nests were used over and over again, thus reducing the competition for new sites. About half of the nesting attempts were successful. So far as we could observe, none of the losses of eggs or nestlings or the desertions could be attributed to conflicts with the Cactus Wrens.

Although a direct competitor for nesting sites in cholla cacti, the Inca Dove appeared to have little difficulty in maintaining its hold in the vicinity. Nesting success has been summarized through 1947 (Anderson and Anderson, 1948). We observed few conflicts with the Cactus Wrens. Two doves, which began building a nest in a small cholla, abandoned the attempt when they were chased several times by a male wren. We once saw a wren drive away a dove that had landed on a roosting nest. At other times they fared much better. Twice the Inca Doves succeeded in fledging their broods from nests which they had constructed only a few feet from a breeding nest of a Cactus Wren in the same cholla. The pyracantha bush at our front door, in 1961, contained an Inca Dove's nest and two roosting nests of the Cactus Wren. At least one of the latter was occupied.

The Cactus Wren's distribution in southern Arizona coincides in large part with that of the permanent resident Curve-billed Thrasher. At least one pair of these thrashers was always present in our study area in northeast Tucson. They occupied a territory approximately the same size as that of the Cactus Wren. The spines of the cholla cacti presented no obstacles to them; they roosted exclusively in these cacti, and always chose them for their nest sites. As in the wrens, if a second pair crowded in, the territory of the first pair shrank to accommodate the newcomer at the margin.

Conflicts between the two species occurred frequently, and in many instances these conflicts seemed to be purposeful. At other times the behavior of the thrashers appeared erratic, confusing and unpredictable. While feeding on the ground, the Cactus Wrens

always gave way at the approach of the larger thrasher. No wren ever engaged in actual physical combat to retain its food supply. A short threatening run of a thrasher toward a wren sufficed; we never observed a thrasher attempt to drive a wren out of the thrasher's territory.

Fewer conflicts were noted at roosting time, for the Cactus Wrens retired early into their nests, usually at least ten minutes before the thrashers retired. The latter often roosted regularly in the same chollas, sometimes only a foot or two from the wren's nest. No objections were raised by the wrens. Occasionally one appeared at the entrance of its roosting nest to investigate some disturbing noise made by a thrasher as it settled down for the night on a nearby twig. Satisfied that no threat was intended, the wren crept back into its nest. Although the thrashers must have been aware that the roosting nests were occupied, they attempted no interference at these times.

In the course of the breeding season, both species vigorously defended their own breeding nests. Thrashers chased wrens and wrens chased thrashers whenever the need arose; each was successful in defense in all the conflicts that we observed. Neither species damaged or destroyed the other's breeding nest at this time. When fledglings appeared, the clashes became more numerous. The Cactus Wrens did not hesitate to attack the fledgling thrashers that strayed into their vicinity. Not only did they chase them; they pecked them frequently, usually on the head; and the ensuing squeals brought the adults rapidly into a furious combat that raged from cholla to cholla until the thrashers retreated to a proper distance. Fledgling Cactus Wrens seemed to be more active and wary of danger; they seldom precipitated a conflict with the thrashers. Each species successfully defended its own young in its territory.

By far the most obvious evidence of conflict was the persistent destruction of the roosting nests of the Cactus Wren by the Curve-billed Thrashers. We first observed this puzzling, erratic behavior in the winter of 1932 (Anderson, 1934). Before this, we had attributed the occasional damaged nests to the depredations of the small boys who roamed the neighborhood. Since then, however, we have caught the thrashers in the act so frequently that there is no longer any doubt that they were responsible for almost all of the destruction. Edwards (1919:66) reported that "on the Mohave and Colorado deserts, and particularly the Mexican deserts, the large desert wood rats and ground squirrels cause the destruction of many nests." The type of nest, whether breeding or roosting nest, was not mentioned; neither was any actual proof offered that mammals were involved. Wood rats (*Neotoma* sp.) were absent in our study area, but ground squirrels (*Citellus tereticaudus*), antelope squirrels (*Citellus harrisi*), and Merriam kangaroo rats (*Dipodomys merriami*) inhabited the tract at the beginning. Later they vanished, perhaps because of the numerous cats in the neighborhood. We see no reason why any of these species should destroy a nest that presents no difficulty in entering. Furthermore, roosting nests do not contain eggs. Nevertheless, the nest destruction in our vicinity continued year after year even after the rodents disappeared.

The pattern of nest destruction was nearly always the same; only the extent of the damage varied. Usually the thrasher began at the entrance of the roosting nest. It tore out, bit by bit, as much of the vestibule grasses as its bill would hold; then it dropped the pieces to its right and left. The whole operation suggested the alternate side strokes with which the thrasher digs into the ground in searching for food, but the movements were slower and more deliberate. Now and then it had to brace its feet to pull. Next went the roof of the nest, followed by the miscellaneous trash of the nest cavity, such as cotton, feathers, lint, and scraps of paper. As previously reported (Anderson and Anderson, 1957:285) the nests were often of flimsy construction; they could be torn

apart with little effort. In every case the appearance of the destroyed nest was typical: only a ragged cup remained. Sometimes only part of a nest was torn out, indicating, perhaps, that the thrasher had been interrupted or disturbed at its work.

These acts of destruction were not particular idiosyncrasies of any one individual thrasher. From 1940 to 1961 we trapped and color-banded most of our resident thrashers, a total of 30 individuals, and found that all of them acted alike. Both males and females destroyed the roosting nests of the Cactus Wrens that had been built in the territory of the thrashers.

We recorded approximately 200 instances of total or partial destruction of Cactus Wrens' nests in our study area from 1932 to 1961. There are many gaps in this record; the actual total of nests damaged must have been considerably greater. Damaged roosting nests numbered 160; damaged secondary nests numbered 11. The thrashers did not attack breeding nests while they were in use. After the young had fledged, however, they tore apart 18 of these nests. In addition, eight nests which had been abandoned following unsuccessful nestings, suffered similar damage. Nests were not always completely destroyed in the initial attack; 25 nests were damaged twice, 7 nests 3 times, 4 nests 4 times, and one nest 7 times, before the destruction ceased.

We found the nest destruction to be unpredictably erratic. Sometimes a roosting nest would remain undisturbed for weeks or even months; another nest would be ripped apart as soon as it was completed; others were damaged while under construction. Particularly vulnerable were the unoccupied nests in the chollas in which thrashers roosted. If a thrasher roosted beneath such a nest, it finally tore it open at the bottom. The destruction decreased to a minimum in the breeding season from February to May. It increased in June and then continued at a rate two to four times as high throughout the summer and autumn until January. Although there appeared to be a definite increase in territorial assertion in the fall of the year, as exemplified in this orgy of nest destruction, the wrens were not otherwise molested.

Despite the evident importance of the roosting nests, the Cactus Wrens never defended them against the attacks from the thrashers. We saw disputes occasionally among the wrens themselves for possession of a nest at roosting time, usually when the fledglings approached independence, and now and then we noted that they even went so far as to eject one of their own kind that had usurped a nest. It seems incredible that the wrens could be unaware of the nest destruction. They foraged regularly in the vicinity when it occurred and they must have witnessed an act so conspicuous; yet, at no time did we see one oppose the thrasher, or utter a *tek* or *buzz* note in protest. Furthermore, after the departure of the thrasher, the wren ignored the damaged nest.

Not until evening did the disturbing picture of destruction confront the wrens; then it apparently took them by surprise. When one landed on the doorstep, it stood upright in actual bewilderment. Then it leaned forward as though to enter, but it could find no opening, for the nest was now a ragged, shallow saucer. Sometimes it gave up the attempt and flew away in search of a vacant nest. If all were occupied, it returned and tried again to enter. Finally, after considerable moving about and *buzz*-ing in frustration it settled down into the untidy floor of feathers and hid its head in the fluffy mass, its back exposed to the sky. Fledglings and immature wrens continued to roost in such nests until the structure flattened, fell apart, or otherwise became uninhabitable. Adults might occupy the nest for as long as a week; then they constructed new nests for roosting. The owner seldom endeavored to repair a damaged nest. If the nest was under construction at the time it was damaged, it was sometimes repaired, provided the damage was not extensive. Frequently the first attack was only the beginning, for the thrasher

returned in a day or two to finish the job. Eventually the nest was abandoned. Later, a new tenant often added material and made an effort to install a new roof.

The Curve-billed Thrashers made no use of the nests which they destroyed. Rarely, an adult or a fledgling could be found roosting on the floor of an abandoned wren's nest, but as a rule, they chose the horizontal branches of the chollas, close to the main trunk. In the winter months thrashers often carried small twigs to their roosting chollas to be fashioned into a loose platform on which they sometimes roosted. Later this platform might become the breeding nest.

The distance between nests of the two species in the area ranged from an unbelievable three feet to a comfortable 480 feet. Nests with first clutches averaged 177 feet apart; nests with second clutches averaged 118 feet apart. The only two nests with third clutches were 210 and 120 feet, respectively, from nests of Cactus Wrens with third clutches. Nest sites chosen, of course, depended upon the availability of the cholla cacti, and these were very irregularly spaced.

The three-foot separation of nests occurred in 1960. Unfortunately these nests were in cholla number 67, at the edge of Flanwill Street, completely hidden from our view by the shrubbery and buildings on the intervening lot. We obtained no details of any of the conflicts there. The first egg of the Cactus Wren was laid about April 13; that of the Curve-billed Thrasher was laid about April 30. Both species fledged successfully; the wrens fledged about May 21 and the thrashers about May 29. Apparently the Cactus Wrens recognized the dangerous situation, for they made no attempt to lead their fledglings to roost in the old breeding nest. Instead they chose another nest at a safe distance in our front yard.

Dates of first eggs laid in our vicinity varied considerably. Now and then the two species laid at almost the same time; in some years the wrens were first; in others the thrashers were first. The young fledged sufficiently close together to be in competition for food. Generally, in a given season, the Cactus Wrens attempted to raise a greater number of broods. In addition, their clutches averaged larger. In 12 of the 22 years from 1939 to 1960 we have reasonably complete nesting data on both species. The Cactus Wrens fledged 82 young from 27 successful broods, with an average of 6.83 per year; the thrashers fledged 51 young from 25 successful broods, with an average of 4.75 per year. In spite of their lower productivity, the thrashers maintained their relative numbers in the study area. It is extremely difficult to draw any safe conclusion here, for we really know very little of the dispersal into adjacent territories or of the immigration of outside members of the two species into our area. We suspect that it was the outsiders that filled in the gaps occasioned by local losses of birds. The depredations of the thrashers seemed to have little effect upon the size of the wren population; it remained stable also.

Both Huey (1942:368) and Hensley (1954:200) have mentioned the competition for nest sites of these two species in the Organ Pipe Cactus National Monument in southwestern Arizona. The former reported that "their choice habitat amongst the cholla cactus was occupied commonly by Palmer Thrashers and the competition appeared to be too much for the wrens." However, he gave no figures on relative abundance or observations on definite conflicts. Hensley likewise stressed the competition, saying that "the denser more luxuriant chollas were usually taken by the thrashers which needed considerable protection for their nests." Our studies have not yet proven that thrashers need denser chollas or more protection for their nests than the other birds in the area. On our lot Curve-billed Thrashers nested frequently in the cane cholla, a cholla of open structure. The mere fact that a thrasher chooses a particular cholla for

its nest does not seem to be sufficient proof that a conflict occurred which resulted in a Cactus Wren being forced to accept an "inferior" location. In an undisturbed habitat many dense chollas are not occupied by either wrens or thrashers. The thrashers avoided some competition by using the same nest two or more times for breeding purposes.

At present, in the light of our still inadequate knowledge, the Curve-billed Thrasher appears to be a poor competitor. Hensley's figures (*op. cit.*:195) on population density actually indicate that the Cactus Wrens were more abundant than the thrashers in each of the three areas he studied. However, it is possible that the thrasher requires a larger territory, and that its lower population density is a direct result of its own intraspecific territorial aggressiveness.

House Sparrows lived in our neighborhood during the entire period of our study. They offered a good opportunity to observe the impact of an introduced species on the resident desert birds. The food supply had to be shared; the sparrows found abundant insect food in the upper parts of the mesquite trees in the summer months. The wrens searched the lower part, gathering their food from the trunk and larger branches. Both species foraged on the ground.

House Sparrows avoided the cholla cacti; the adults could not be induced to land or perch on the spiny joints, or on roosting nests in these shrubs, even if we placed food there. A few of their inexperienced fledglings flew into chollas and became impaled on the spines and died. Obviously, we observed no competition for cholla nesting sites. The sparrows built their nests under the eaves of small buildings, or occasionally in catclaw bushes (*Acacia greggii*). An abandoned Cactus Wren's nest in a catclaw bush was appropriated by House Sparrows with no apparent difficulty. Another nest, in a large pyracantha shrub, was similarly occupied, but later the wrens took possession again. Chasing was seldom observed.

At other times more serious conflicts occurred. Our next door neighbor reported that in April, 1942, a Cactus Wren entered a nest of a House Sparrow and removed at least one of the eggs, despite the spirited attack of the owners. The Cactus Wrens' young had been fledged eleven days earlier, and their presence in the vicinity may have contributed to the defensive raid. On March 27, 1954, we saw a male wren raid the House Sparrow nest in our back yard bird box. This bird box had been installed as a control to enable us to compare nesting dates. House Sparrows occupied it regularly year after year, both for roosting and for breeding purposes, with no violent interference. At this particular time, the female wren had been found dead in her nest, a short distance away, a few days before. In his efforts to obtain a new mate, the male sang from every point in the territory, moving about vigorously, apparently challenging the world. We found a dead House Sparrow nestling on the ground that morning. Soon afterward, we examined the nest box; it contained only one egg. That afternoon we saw the male wren fly to the nest box and perch in the hole while he looked inside. Then he pulled out a feather. Half a dozen House Sparrows now gathered around, excitedly uttering their alarm notes. One flew at the wren and both tumbled to the ground, fighting furiously. The wren drove the sparrow aside and returned to the box. Soon it came out with the egg in its bill. It flew to the ground, dropping the egg; then it pecked it once. Amid the clamor of the sparrows, the wren again returned to the nest, evidently to explore it further. When he left the box, he again fought with the sparrows.

In the course of the next half hour the wren entered the box three more times. Once he sang from the top of the bird box, immediately engaging in a fight with a male House Sparrow. They fought in mid-air, three feet above the ground, the sparrow holding the upper position. Finally they dropped into a creosote bush, the sparrow two feet above

the wren, chattering violently, but refusing to budge. The wren then left, apparently the loser in the brief battle. Later, however, he visited the box again to pull out a feather, which he dropped to the ground; then he chased a sparrow. This done, he flew northward and sang. In a few moments, a male sparrow returned to its perch on the box. On the following day, the wren again removed a feather from the nest. This time he carried it to his secondary nest. The loss of his mate, the complete break in the breeding pattern, and the frantic effort to secure his territory may have been responsible for the extreme and unusual aggressive behavior.

In late summer the House Sparrows gathered in flocks and extended their feeding activities into adjacent areas. Large numbers roosted in the ornamental bushes in the vicinity. In general, they filled a niche within the Cactus Wren territory that was not used by the wrens.

House Finches were present in our vicinity at least as far back as 1934. They roosted usually in cholla cacti, sometimes beneath roosting nests of Cactus Wrens, sometimes in old open nests, or even near breeding nests. They were chased occasionally at roosting time if the wren happened to find the House Finch already in the cholla. They built their nests in chollas in March and April, in direct competition with the wrens. In fact, we gained the impression that they chose only the sites that the wrens permitted them to have. We recorded nesting attempts in most of the years from 1934 to 1946. Five of these were successful; in two of the years, two pairs succeeded in fledging young. While House Finches were seen frequently in the vicinity in the course of the past five years, we observed no further nesting attempts. Harassment usually consisted in chasing House Finches that carried nest materials. Once we saw a wren fly to a partly completed House Finch nest and tear loose some of the soft lining. Singing, interspersed with *scri* sounds, preceded this attack. At another time we observed a wren seize an egg in an abandoned House Finch nest. It flew with it to the ground and broke it.

Verdins (*Auriparus flaviceps*) did not breed in our study area. A single bird usually appeared in July or August and built a roosting nest in the large mesquite tree, or in the catclaw or pyracantha bushes. They encountered no interference, either while nest building or while foraging in the territory, so far as we could observe. However, immature wrens in search of a roosting nest, sometimes forced their way into these nests, distorting and damaging them so severely that the Verdins abandoned them.

ENEMIES

The most dangerous predator in our vicinity was the house cat. We wondered at times how the birds could hold on at all, for almost every home had a cat that prowled at will. Feathers, chiefly from Cactus Wrens, were a common sight along the fences. Small boys with BB guns took their toll also. Snakes rarely visited our lot, and no losses could be attributed to them. Occasional Sparrow Hawks (*Falco sparverius*) did not attack the wrens; accipiters were absent.

Cats, Roadrunners (*Geococcyx californianus*), and snakes, even dead snakes, excited the wrens as soon as they were discovered in the territory. Uttering the *buzz* danger note persistently, the wrens gathered around the intruder and followed it as it moved away. House Sparrows joined the group and chimed in with their warning calls. Evidently enemy discrimination was accurate, for our small brown dog was completely ignored as he roamed the yard.

Shrikes (*Lanius ludovicianus*) nested in the Rillito Creek bottomlands a quarter of a mile away. Now and then they appeared in our neighborhood. So far as we could determine, they never molested the wrens. No warning *tek* or *buzz* note greeted them

to indicate to us that they were considered to be enemies, and no mobbing occurred. Yet, they were never permitted to remain very long. The moment a shrike arrived on a bush, post, or electric wire, a wren flew toward it, usually stopping about ten feet away. They eyed each other; then the wren moved closer with a fidgety, threatening motion. At three feet or so the shrike seemed undecided. Finally it retreated a short distance. Then the wren repeated the maneuver. Sometimes it had to fly directly at the shrike to emphasize its threat. The shrike did not always give way. When it fought back, the wren retreated. Back and forth they fenced, the wren never giving up, the shrike retreating a little more each time.

One evening just before roosting time, such a seesaw battle lasted for fifteen minutes, in and out of the creosote bushes and around them on the ground. The shrike climbed and twisted its way through the branches; the wren darted faster in a circle until it was hounding the other again. As it grew darker the shrike departed without having made contact with the wren. The latter then retired into its nest.

SURVIVAL

We banded three-fourths of our adult Cactus Wrens in the period from late September to March. How many, if any, of these were birds that had been fledged here the preceding spring, is not known. It was usually safe to assume that if a banded wren had not been seen in the area for a month or so, it would never be seen again. Returns after such an absence were negligible. As a rule, our Cactus Wren population appeared to maintain itself by additions from other territories. The length of time that banded adult wrens remained in our area is shown in figure 1. The age given is a minimum; some wrens may have been at least a year old when first banded; others may have been birds

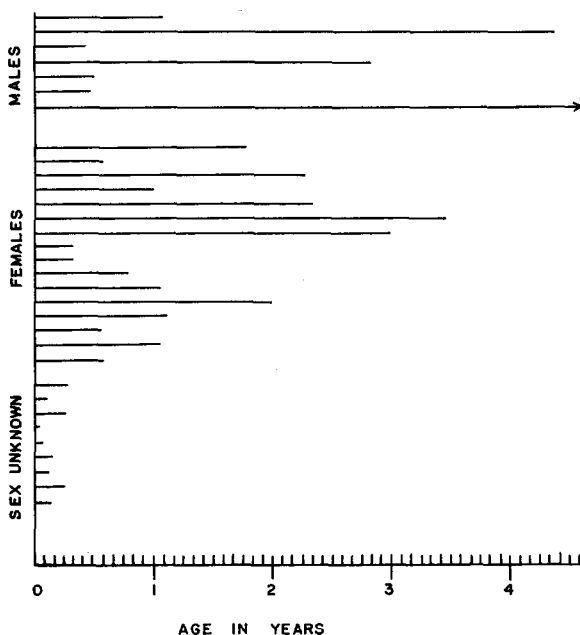


Fig. 1. Length of time that adult Cactus Wrens (*Campylorhynchus brunnei-capillus*), banded from 1939 to 1962, remained in the Kleindale Road study area. HM-73 (arrow-tipped line) was still alive on January 31, 1962.

of the year, just over their postjuvinal molt. HM-73, our patriarch, banded on July 7, 1957, was still present at the end of January, 1962. He was then at least five years old. HM-23, runner-up, was banded on January 19, 1941. He was last seen on May 24, 1945. The average age of the seven banded adult males is 737 days; the average age of the sixteen females is 493 days.

We know that many of our wrens were killed by cats. Some apparently died from natural causes. We found four adult wrens dead in their nests. Three of these were in roosting nests; the fourth was a female with eggs just hatching. Such cases may not be uncommon, for we have several similar records in other localities. Six other wrens were found dead on the ground beneath their nests. Four were adults and two were immature wrens. In two of these instances, the nests were damaged, but there is no direct evidence that thrashers killed the wrens. It seems more probable that the nests were attacked after the thrasher discovered that they were not defended. Three other wrens were found dead in the yard; the cause of death is unknown.

We wish to correct an error which crept into one of our previous papers (1957:355) where we reported that "none of the female nestlings, or the few immature wrens from adjacent territories, which we banded, remained to breed the following year." Three immature Cactus Wrens, two females and a male, of unknown origin, succeeded in maintaining themselves in our study area. HF-22, banded September 8, 1940, was molting when banded, and her age is somewhat in doubt. However, we believe this wren was probably the same immature wren that had been seen in the territory for some time before. On February 27, 1941, we found her incubating three eggs in nest 35B. She was last seen on March 3; on the following day we discovered that her nest had been destroyed by boys. HF-30, banded on May 18, 1941, laid her first egg in nest 7E on March 7, 1942. Her four nestlings were fledged successfully on April 17. In May she was incubating her second clutch in nest 6T; the young were fledged in June. She was last seen on October 11, 1942. HM-66, an immature male, banded July 25, 1954, was last seen on July 16, 1956, after having stayed for two breeding seasons. A nestling, HM-42, banded on April 23, 1944, fledged on May 4. This male was the only nestling out of 55 banded ones, from 1939 to 1961, that remained until the following breeding season. He was last seen on January 20, 1946.

A small number of the breeding nests was inaccessible; they could not be examined without destroying a large portion of the chollas in which they were placed. Others could not be visited at the proper time. Consequently all nestlings in our vicinity did not receive bands. It is just possible that the percentage of fledglings that survived to breed in our area would be slightly greater if one knew the origin of those wrens which we did not succeed in banding until late autumn or winter.

Survival of banded nestlings, after fledging, is shown in figure 2. To obtain the actual age, the average age of 20 nestling days should be added to the lines in the chart. Ten of the 55 fledglings could not be found after their first day out of their nests; in 45 days, 41 of the 55 had disappeared. Scattered piles of feathers near fences gave evidence that house cats had been responsible for many of these losses. About half of the 55 fledglings had probably attained a fair degree of independence in their search for food and may have dispersed into surrounding territory. Their fate is unknown; we could not explore the neighboring residential blocks with any success. However, it is doubtful if many of these fledglings survived. Spare roosting nests were not available in the immediate vicinity; and in most of the residential lots there were no cacti in which to build nests. Furthermore, the fledglings had not yet reached the nest-building age. Four of our banded nestlings, after reaching an average age of seven months, disappeared at the end of December.

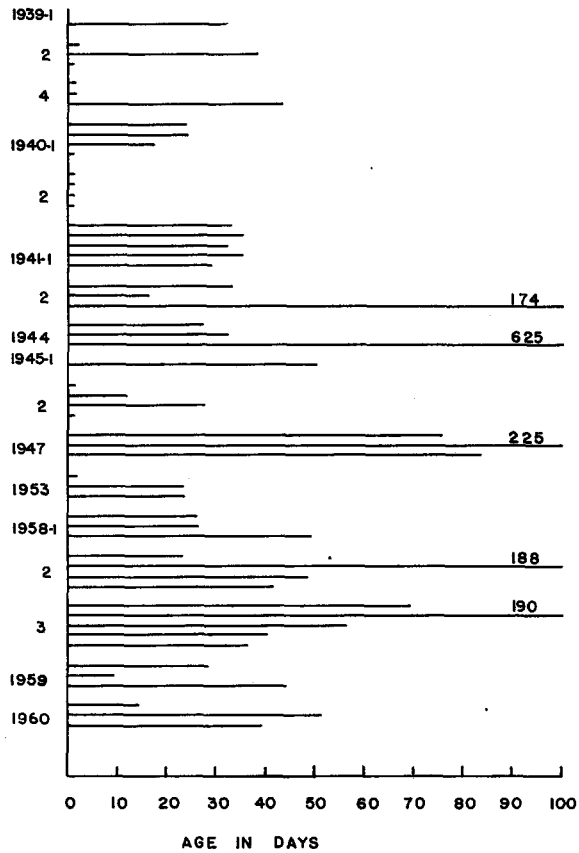


Fig. 2. Survival, in days after fledging, of banded nestlings of the Cactus Wren in the Kleindale Road study area. Off scale values are indicated by numerals at the right. Numerals at left side, 1, 2, 3, 4, indicate broods.

We have no evidence to support the theory that dispersal of first-year birds is of a genetic nature (Johnston, 1961). The problem in the Cactus Wren appears complicated by the territoriality of this extremely sedentary species. Once established, the adult wren remains in its chosen territory for life; it mates for life. Dispersal of the immature birds must occur, either voluntarily or involuntarily. There is simply no space available for the young Cactus Wren in this situation where the aggressive behavior of the dominant adult pair excludes all others of its own species. It seems illogical to attribute to the immature Cactus Wren an hereditary tendency to dispersal when its dispersal may be entirely involuntary. Immature wrens assist their parents in boundary disputes in the summer and autumn, but eventually they leave. No data are available to indicate whether their dispersal distances follow a normal probability curve or a bimodal one, or any type of curve for that matter. Dispersal in the autumn usually implies the abandonment of a completed, comfortable roosting nest. Such a serious dislocation of routine could only be caused by force, or by repeated disturbances at roosting time. Dispersal immediately upon the attainment of independence must certainly occur in a period of familial instability. The weaning process imposes a strain. A sufficient number of im-

mature wrens have wandered into our neighborhood in the late spring to establish the fact that early dispersal does occur. Sometimes these wrens found roosting nests and remained a while, but as long as an adult exercised control, their stay was temporary. Most of our data so far in this restricted area indicate that immature wrens endeavor to remain in the place of their origin, but few succeed.

REPLACEMENT OF MATES

We have two chronological sequences of approximately five years each, 1941 to 1945, and 1957 to 1961, inclusive, of mated pairs of Cactus Wrens (fig. 3), on our re-

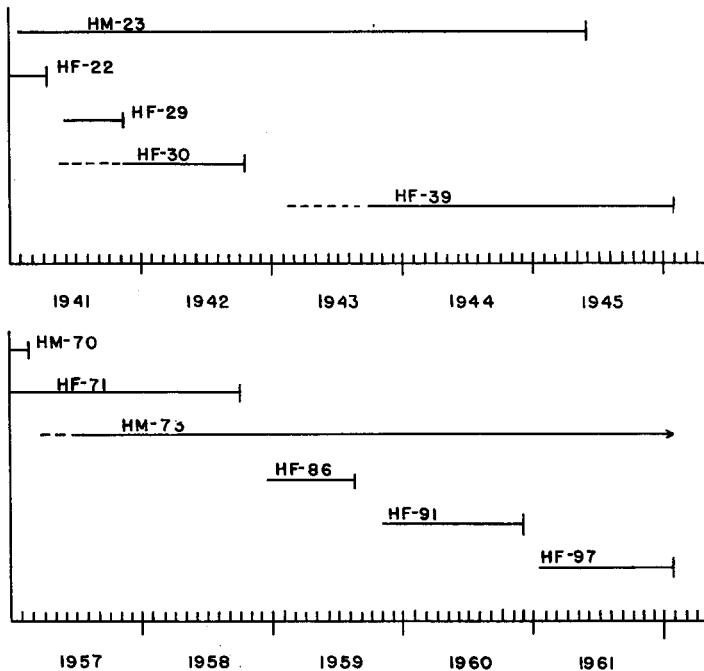


Fig. 3. Sequence of replacements of mates in Cactus Wrens in the Kleindale Road study area. Heavy line indicates banded wren was present; dashed line, present but not banded; arrow-tipped line, wren still alive on January 31, 1962; vertical line, last seen.

search area. In these years the males survived considerably longer than their mates. Data on other years are incomplete. HM-48, banded August 11, 1946, was last seen on June 4, 1949; HF-49, his mate, banded on December 28, 1946, was last seen on May 27, 1950.

In those years when a single pair of Cactus Wrens occupied the entire ten acre block in the vicinity of our home, the loss of a male in the course of the breeding season was not often immediately apparent. One had to be alert to observe the vacancy; and, if we did not watch for colored bands each day, the event was missed, for a new unmated male usually moved into the territory at once. The cessation of song appeared to be a signal that space was available. Our first indication that something had gone wrong was the discovery that a noband wren was singing instead of a familiar banded one.

We experienced less difficulty in following the changes when crowding constricted

the territories into smaller units. Upon the absence of a rebuttal territorial song, the adjacent pair of wrens quickly invaded and occupied the vacant territory. When this happened in late February, 1948, the widowed female retreated, probably to the edge of the territory and returned in the evening to slip quietly into her roosting nest. A month later, she vanished; then, after an absence of about 22 months, she reappeared with a new mate and attempted to build a breeding nest. Before the nest was completed, she vanished again.

In April, 1940, HF-2 was incubating four eggs when her mate died. The new mate, which arrived at once, had little to do until the nestlings required food; then he assisted in feeding the brood. Once we saw him feed his mate. After the loss of the fledglings, the pair moved eastward, out of the territory.

Females were not always readily replaced, especially after the beginning of the breeding season. On March 21, 1954, when the female had died in her nest, the male began singing vigorously and frequently. Day after day he continued; once he even sang in flight. Six days later he raided a nest box occupied by House Sparrows, as we reported earlier under "Interspecific Relationships." At one singing station, on March 28, at the far corner of the territory, we counted 166 songs in 25 minutes. These were uttered without interruption. In the interval from 8:20 a.m. to 9:26 a.m. he sang 274 songs. Finally, on April 4, a new female appeared. The male attempted copulation the same day. Singing decreased noticeably thereafter, but the territorial aggressiveness did not stop. When we examined the sparrow nest box on April 6, two of the newly laid eggs were missing.

The exact time that replacements occurred in the course of the early winter months could not be determined. The pair bond now became too inconspicuous, and the presence of other wrens in the territory contributed to the difficulty of observing such events.

THE FUTURE

Cactus Wrens are hardy, adaptable, aggressive birds that will probably be able to maintain themselves in limited numbers within the residential sections of the rapidly expanding cities of our southwest. If given a few ornamental chollas, they remain. In Tucson, the wrens can now be found nesting in olive, eucalyptus, and palm trees. Some years ago Milam Cater (personal communication) was successful in attracting them to bird boxes at his home. If House Sparrows could be kept from usurping these substitute nest sites, we feel that the Cactus Wren can become established as a dooryard bird. It is an interesting species with only one disappointing attribute—its so-called song.

SUMMARY

Cactus Wrens avoided the extreme high summer ground temperatures by seeking shade. In hot weather they opened their bills slightly and raised their wings to permit freer air circulation. Water drinking by adult wrens occurred chiefly in the fall and winter months. Immature wrens drank in the summer months.

Daytime nest temperatures varied with the thickness of the nest roof. Thin-walled nests were hot, for the sun shone through; shaded, ventilated nests approached the standard air temperature.

The Cactus Wrens retired at a light intensity about twenty times as great as the intensity when they left the nest in the morning.

There were no important conflicts between the migrant and transient species of birds and the wrens. Mourning Doves and Inca Doves nested in the cholla cacti without interference from the wrens. House Finches were harassed at times but they succeeded in raising young.

Curve-billed Thrashers nested in chollas, evidently competing for nest sites. Conflicts were numerous; each species, however, was successful in defending its own breeding nest and young. Thrashers frequently destroyed the roosting nests of the wrens; they also destroyed breeding nests after they had been abandoned or had become roosting nests. Most of the destruction took place from late summer to January. The wrens did not defend their roosting nests.

Nests of the two species were spaced from 3 to 480 feet apart. The Curve-billed Thrasher appeared to be a poor competitor. While it held its own in our territory, its productivity was lower than that of the wrens. Generally, the Cactus Wrens laid larger clutches and attempted more broods in a season. They succeeded in raising more young.

The most dangerous predator was the house cat. Cats, Roadrunners, and snakes were "mobbed" and followed by the wrens until they left. Shrikes, although apparently innocuous, were harassed whenever they appeared.

The average age of 7 males was 737 days; 16 females averaged 493 days. Some wrens were found dead in their roosting nests.

Forty-one out of 55 banded nestlings had disappeared at the end of 45 days after fledging. Three immature wrens, two females and a male, succeeded in maintaining themselves until the following breeding season. Hostility, as in weaning, probably forced the remainder out.

Mates were usually replaced rapidly after a loss. There seemed to be an adequate outside supply waiting to be called.

Cactus Wrens will probably hold on as dooryard birds in the rapidly growing cities of the southwestern desert.

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