

LIFE HISTORY OF THE CACTUS WREN Part IV: DEVELOPMENT OF NESTLINGS

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In our earlier papers on a life history study of the Cactus Wren (*Campylorhynchus brunneicapillus*) in the vicinity of Tucson, Arizona (1957, 1959, and 1960) we discussed the environment, winter activities, roosting nests, song, territorial establishment, pair formation, and the nesting cycle up to the time at which the young leave the nest. The present paper describes the nestling growth and development from the time of hatching to the time of fledging.

GROWTH OF NESTLINGS

The following data were obtained from five nests, two in 1940, one in 1941, and two in 1958. The nest studied in 1941 was the first brood of the year; the others were first and second broods. Nests near our home on Kleindale Road, northeast of Tucson, Arizona, were visited once a day, usually between 5:00 p.m. and 6:00 p.m. All the nestlings were removed at the same time and taken into our house, where they were examined and weighed to a tenth of a gram. Immediately thereafter they were replaced in their nest. If the adult birds observed us, they made little protest unless the young squealed. Sometimes they must have been entirely unaware of our intrusion, for they were not seen at all at this time. Our interruption in their feeding routine seems unimportant so far as weight of the nestlings is concerned. In the following accounts, the nestlings are considered to be a day old on the evening of the day after hatching. Although this introduces a possible error of an additional 12 hours, the actual error is probably much less. Some eggs hatch in the course of the afternoon.

The descriptions which follow roughly represent averages of individual variations in development. Although the sequence of feather development appears to be the same in these nestlings, the time at which changes occur may vary as much as 48 hours.

Age 0 days.—At hatching, the eggshell is cut in a ragged line almost exactly around the equator. The separated halves may adhere for a brief time to the extended head and the swollen abdomen. When freed from the shell, the nestling is still wet; the down sticks close to the skin in irregular streaks. Later, when it dries, the down becomes whitish and fluffy. It varies in length from 4 to 8.5 mm. and is present in tufts in the capital, spinal, humeral, alar, femoral, crural, and ventral tracts (fig. 1). There is considerable individual variation in quantity of down in members of the same brood. The bare crown is usually surrounded by a ring of down that extends backward from the forehead, passing above the eyes to cross the occiput. Sometimes this circle is incomplete. There is a dense tuft in the dorsal region and usually a smaller one in the pelvic region, just above the oil gland protuberance. From one to five small tufts have been found on the humeral tract, and as many as seven in the alar region; as many as eight have been seen in a row in the femoral region. Fewer tufts are present on the front and back of the crural tract. There are from one to three small tufts on each side of the lower abdomen; otherwise the ventral tract is bare. Sometimes the skin of the cervical, dorsal, and crural areas appears wrinkled.

Saunders (1956:122) has assumed that the presence of natal down on only the capital and dorsal tracts is a character of the wren family, but his observations were limited to only two species, the House Wren (*Troglodytes aëdon*) and the Long-billed Marsh Wren (*Telmatodytes palustris*). This assumption proves invalid when the Cactus Wren is considered.

The bill is pink, above and below; the swollen edges are yellow from the angle of the mouth to a point about halfway along the length of the bill. Near the end of the slightly shorter upper mandible the egg-tooth projects upward as a tiny, light-colored, sharp point, less than 0.5 mm. long. The closed eyes appear as large slate-gray bulbs with a suggestion of a slit in the lower, paler portion of the surface. The mouth lining is orange-red.

Age 1 day.—Very little change, except for a slight darkening of the skin.

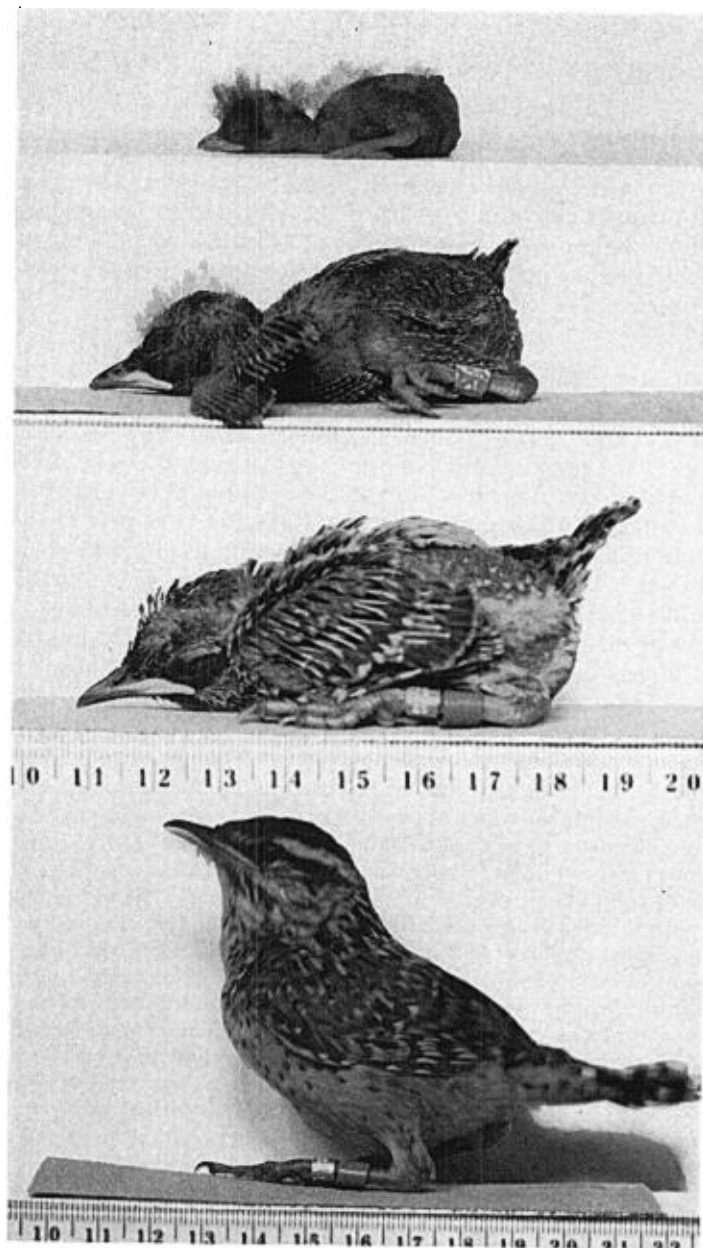


Fig. 1. Nestling of Cactus Wren. From top to bottom, age 0 days, age 7 days, age 11 days, age 18 days.

Age 2 days.—The mouth lining changes to orange-yellow; the crown becomes darker, a dull reddish color, with small, indistinct specks in the skin. A dark streak has appeared along the center of the manus, and small dark specks can be seen on the forearm. In the caudal tract tiny bristles indicate where the tail feathers will appear. The skin of the spinal and ventral tracts is darker and all tufts of down are gray.

Age 3 days.—The bill is now pinkish brown; the eye-slit, still closed, has become more prominent, and the crown, now dark, reddish black, appears wrinkled and speckled. In the alar region which is also darker, the primary and secondary bristles are visible. A dark area can be seen just anterior to the feather germs of the caudal tract. The skin of the cervical tract is darker than previously. Faint spots can be seen on each side of the ventral region.

Age 4 days.—The bill has become light brown, but the swollen edges are still yellow. As the head grows larger, the eyeballs protrude less and their eyelids appear almost black. On some nestlings the eye-slit is cracking open very slightly. Two-thirds of the outer surface of the forearm and manus is now blackish and the primary and secondary bristles are 0.5 mm. long. A dark area has appeared under the skin of the humeral tract. The dark caudal area is more prominent, and all of the spinal tract is darker and dotted. In the ventral region the light sheaths beneath the skin outline the entire tract; the axillary branch can be seen for the first time.

Age 5 days.—All the original down is still present. The bill is light brown at the tip and paler around the nostrils. The glint of the eyeball can be seen through a slit now open for about 1 mm. Light-colored sheaths are now apparent under the skin of the femoral and crural tracts. Most of the outer wing surface is blackish; the sheaths of the primaries, secondaries, and their coverts have pierced through the skin. The humeral sheaths are still beneath the skin. A dark semicircle has appeared anterior to the light-colored papilla of the oil-gland. The points of the sheaths in the entire spinal and ventral areas are visible beneath the skin.

Age 6 days.—The egg-tooth has now become almost microscopic; in some nestlings it is entirely gone, but a small bump will remain for at least a week. The eye-slit is open 1.5 mm.; the width of the opening is so slight that it is improbable that the bird can see effectively. Growth has continued in the primaries, secondaries, their coverts, and the alula. The sheaths are breaking through the skin in the spinal area. In some nestlings sheaths have emerged in the ventral and crural tracts.

Age 7 days.—The tip of the bill has become a darker brown, and the mandibles appear equal in length. Some vision may be possible now, for the eye-slits have opened to 2 mm. and the area between them is oval in shape. The lids are movable, opening and closing the small oval. On the capital tract the sheaths have erupted through the skin on the forehead, crown, and nape. They have likewise emerged in all the remaining tracts (fig. 1). The dorsal tract has fanned out. There are three rows of closely spaced sheaths on each side of the abdomen; at the axillary branch of the ventral tract, seven rows are visible. Widely scattered sheaths are present on the breast between the ventral tracts, and a denser growth is apparent on the chin.

Age 8 days.—The tips of the sheaths are breaking open, showing small light-colored, fuzzy tufts at the ends of the primaries, secondaries, and some of their coverts, and on the feathers of the dorsal, femoral, crural, and caudal tracts. Down is still present.

Age 9 days.—The eye-slit opening appears as an oval about 3 mm. in length. In the ventral region the axillary sheaths are the first to burst at the ends. The upper mandible has lengthened.

Age 10 days.—The eye opening is now almost round and the lids open and close more frequently; rows of sheaths are evident on the eyelids. A whitening of the superciliary sheaths is apparent. Sheaths cover half of the ear opening. Most of the sheaths of the ventral area, except those on the chin, have burst at the ends. The ends of the secondaries are now fan-shaped and about 3 mm. wide.

Age 11 days.—The eyes are now open wide. Sheaths of the nape and the superciliary stripe have begun to open; sheaths of the greater primary coverts have burst. All other tracts show further widening of the fan-shaped ends of the feathers as the sheaths continue breaking (fig. 1).

Age 12 days.—Most of the bill, with the exception of the edges, is now darker in color. The sheaths of the entire capital tract are bursting. All of the upper part of the body appears rather well covered when the bird is crouching. The ventral tracts have broadened, leaving a narrow open strip down the middle. Sheaths cover almost the entire ear opening; the chin and throat feathers are still in their sheaths. Down is still present.

Age 13 days.—The capital tract now appears smooth with new, brown feathers, and the white of the superciliary stripe is prominent. Bristly sheaths are still evident at the base of the bill. The wings cover almost all of the dorsal ateria; a small apron of feathers conceals the oil gland. Natal down can still be seen above and posterior to the eyes and on the humeral and dorsal tracts.

Age 14 days.—The bill is dark on top with lighter nostrils; its edges are yellow. The eyelids

appear fringed with slender sheaths. When the nestling is at rest, all the dorsal surface appears feathered, and the tips of the wings reach as far back as the oil gland. Only the central abdomen is bare.

Age 15 days.—The primaries and secondaries are out of their sheaths for about half their length. Disintegration of the sheaths of the body feathers is so extensive that the broken pieces fall like chaff when a nestling is handled.

Age 16 to 17 days.—Feathers cover the entire body with the exception of the lower abdomen. There is an indistinct center line in the ventral region, but all apteria are rapidly being concealed by the spreading feathers. The iris is pale grayish or yellowish. It will be weeks before it darkens and finally becomes red. No further examinations were attempted because of the risk of premature departure of the wrens from their nest, but a photograph was taken at the age of 18 days (fig. 1).

BEHAVIOR OF NESTLINGS

Age 0 days.—The nestling appears very weak and is unable to right itself, although it moves about when handled. Occasionally a bird of this age defecates. The head trembles when the bill is opened wide. The legs are too weak to serve for bracing or for grasping. When the bird is not disturbed, the head rests upon the large abdomen. The small pink body becomes cold quickly.

Age 1 day.—Weakness is still very apparent, but the wren struggles longer in an effort to right itself. It assumes the embryonic position when resting and becomes noticeably cold when left exposed for a short time.

Age 2 days.—More strength is evident as the nestling struggles to turn upright. When suddenly touched, it responds by moving. Sharp *peep* notes are occasionally heard, especially during handling.

Age 3 days.—Although strength has increased, the nestling still rests in the embryonic position.

Age 4 days.—The nestling becomes cold quickly. It can lie flat on its chin, abdomen and tarsi, but now and then it drops its chin upon its abdomen. One nestling could stand on its horizontal tarsi, using its bowed wings for braces, while it opened its bill. Gaping has become more frequent, while peeping is variable. Some nestlings are exceedingly vocal, others silent.

Age 5 days.—By this time there is much individual variation in restlessness. Some nestlings lie quietly, grasping one's hand with their claws; others lie flat and try to crawl forward, using both wings and feet. It is difficult for them to remain upright. The head trembles on the outstretched neck.

Age 6 days.—Temperature regulation must be at least partly effective now, for the nestlings cool off much less rapidly. Their activity has increased considerably. They are harder to remove from their nest; they grasp the lining with their claws and hold on. The righting reaction takes place with less difficulty. When placed on its belly on a smooth table, a nestling tried frantically to obtain a foothold by "swimming" with its wings and legs. It showed no fright.

Age 7 days.—Peeping notes are heard frequently when the wrens are taken from their nest. Their bodies feel very warm. When handled or held, most of their efforts were directed toward assuming a head-up position.

Age 8 days.—The nestlings try to crawl away, but no real fright is apparent. This may be merely an attempt to attain a more comfortable situation, away from an annoyance.

Age 9 days.—Strength has now increased to a point where the nestlings crawl and climb so vigorously that they must be placed in a box for weighing. They climb with outstretched necks and grasp with their claws, but they cannot yet perch on one's finger. If the hand holding them is dropped suddenly, they raise their wings and tail instinctively to balance. After we tumbled three of them back into their nest, they righted themselves at once so that they faced the opening, their chins resting upon the edge of the nest cavity.

Age 10 days.—Fear reactions are not yet evident. The nestlings are stronger and can perch on one's finger, but they have difficulty in balancing. They have begun to turn their heads slightly in order to peer around at nearby objects.

Age 11 days.—At this time the first signs of fright are apparent in some of the nestlings. They exhibit the "back-up" posture, in which the head is lowered with the bill held horizontal; then the middle and posterior end of the body are humped up while the wings and tail are lifted as the nestling tries to back up in the palm of one's hand. Defecation before and after weighing becomes more frequent. Some squealed loudly when we tried to remove them from their nest; they were packed down

like sardines, perhaps in an effort to hide, and were difficult to grasp without pinching. When they were replaced in the nest vestibule, they crawled back into the cavity at once.

Age 12 days.—Crouching and withdrawing, as in fear, at sudden movements are increasing now; so also, is the effort to climb out of the hand, usually upward, in attempts to escape. They are not yet able to stand on their toes, but rest on their horizontal tarsi. If rolled on their backs, they struggle fiercely to right themselves.

Age 13 days.—The head movements are more noticeable and blinking is frequent, as the nestling observes its surroundings.

Age 14 days.—Escape attempts are the rule now. The nestlings crawl ahead, apparently blindly, regardless of obstacles, evidently unable to judge distance or depth. They will crawl to the edge of a table and fall to the floor, happily without injury. Their legs are still weak, but they can travel rapidly on a carpet where a good foothold can be obtained. If a hand is placed in front of the nestling, it climbs over it, falls, and then continues on its way until it finds a dark corner in which to hide. Peeping notes are still heard during the examination. One nestling protested loudly while it was held in the palm of the hand, perhaps at some unexpected movement close by.

Age 15 days.—Rapid peering movements of the head are frequent now, and attempts to escape, assisted by fluttering of the wings, occur. The birds may try to stand on their toes, but usually they settle down on heels and tarsi.

Age 16 days.—Restraint of the nestlings is difficult now, for they are able to run on their toes, and they even attempt to fly a few feet if inadvertently released. All struggled vigorously, grasping at anything within reach as they kicked and churned in trying to turn upright. When finally quieted, they held their bills upward at an angle. One uttered a begging note when it heard a squeaking sound.

Age 17 days.—The begging note, *dzuþ*, was heard from three nestlings on this day. It was uttered several times when a wren was placed on the floor alone. One hears this note frequently in the course of the last week of undisturbed nestling life. Its occurrence while being examined would indicate that this nestling was not alarmed at the time.

Age 18 days.—The wren which was photographed in 1941 (fig. 1) uttered a lively *dzip* note frequently while being set up for its picture. Apparently it was not afraid as long as we did not touch it or move suddenly when near it. On being returned to its nest, however, it escaped and flew a distance of about 15 feet to a small bush. Here it remained and permitted us to pick it up again. As soon as it was placed in the nest entrance it crawled inside and vanished in the dark, crowded cavity.

On the 19th day, at nest 27B, we pulled out the five nestlings, one by one. Two escaped at once, the first flying a distance of 30 feet, the second 75 feet, accompanied by a noisy, frantic, adult wren. This nestling took refuge at the foot of a creosote bush, and, by running to the opposite side of the bush whenever we approached, frustrated all our attempts to catch it. We replaced the remaining three nestlings in their nest and abandoned any further efforts to photograph them. On the following day at 6:00 p.m. the nest was vacant.

The progressive increase in escape reactions after the age of 10 days was very pronounced in all the wrens that we examined. Our regular visits, begun on the day of hatching, did not eliminate these escape reactions. In the course of the examination each nestling was handled for an average of five minutes; the total time out of the nest for the entire brood did not exceed 30 minutes. It is difficult to see how these brief periods could have had much effect in altering the normal behavior of the nestlings. Our observations agree with those of Banks (1959:101) on the White-crowned Sparrow (*Zonotrichia leucophrys*) and are sharply at variance with those of King (1955:160-161) whose study of the Traill Flycatcher (*Empidonax traillii*) indicated that escape reactions did not appear under the routine of daily visits. It is worth noting that the enclosed, covered cavity of the Cactus Wren's nest provides the nestlings with a place in which to hide. Even as late as the 18th day, the nestlings crawled rapidly into the interior and sought safety by concealing themselves from our view. Had these nestlings been in an open nest, it is highly probable that they would have "exploded" into flight several days

TABLE 1
MEAN DAILY WEIGHTS OF NESTLINGS

Age	Sample size	Mean	Range	Age	Sample size	Mean	Range
0	20	3.4	2.6-4.1	9	20	25.1	19.8-27.2
1	20	4.9	3.6-6.3	10	20	26.9	21.9-29.3
2	20	6.7	5.5-8.1	11	20	28.4	24.0-31.3
3	20	8.9	7.4-10.4	12	20	29.5	26.3-33.5
4	20	11.5	9.5-13.5	13	20	29.9	27.0-33.2
5	20	14.0	12.4-16.4	14	20	30.2	26.5-33.7
6	19	16.9	15.4-19.0	15	19	30.0	26.2-34.5
7	19	20.9	17.8-22.0	16	16	30.0	27.3-33.2
8	18	23.1	19.5-24.8	17	9	31.3	28.8-34.2

earlier when we touched them. Premature fledging is, we believe, in most instances actually an escape reaction caused by fright or some threatening disturbance.

WEIGHTS

The lightest weight recorded on the day of hatching, 2.6 grams, was that of H-75. This nestling was hatched sometime between 9:30 a.m. and 5:00 p.m. It could hardly have been many hours old, for its down was still wet. The greatest weight, 4.1 grams, was that of H-17, but it may have been as much as 24 hours old. It hatched in the course of the night and probably received considerable food before we weighed it at 5:40 p.m. the following day.

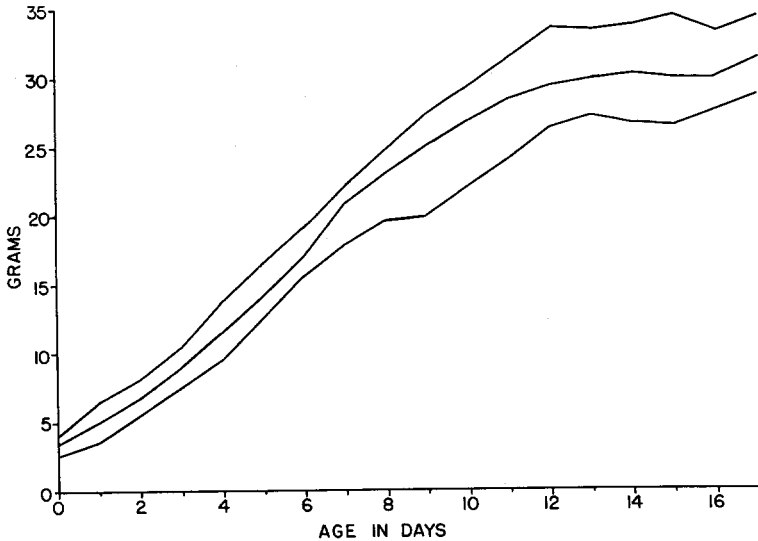


Fig. 2. Mean daily weights in grams of nestlings of the Cactus Wren. Upper and lower curves indicate range of variation.

Table 1 shows the mean daily weights of the nestlings from five nests. The variation for a given age is considerable, but the overlap is least during the first week of nestling life. Later, the use of weight for the determination of age becomes very unreliable; a nestling weighing 30 grams could be from 11 to 17 days old.

The daily increment of weight is fairly uniform up to the 11th day (fig. 2). Then the curve of mean weight flattens and soon falls in the characteristic manner reported

in a number of other species. Before the birds fledge, the curve has begun to rise again. The cause of this leveling off and decrease in the daily weight gained has been a subject of much speculation. It would seem to be a problem for the physiologist, for although many variables could be involved, we need first to know the food requirements for body and feather growth and the energy consumed in temperature regulation at the ambient temperatures normally experienced by the nestlings. Without these quantitative data, solution of the problem seems impossible. Changes in availability of food or rate of feeding, the latter stemming from an assumed temporary parental exhaustion, are difficult to prove. The loss of weight is consistent in practically all of our nestlings in the five broods. Considerable feather growth has already occurred by the 11th day, but more occurs in the course of the next five days, so that by the time the bird leaves the nest its short tail is the only disproportionate appearing element. A small loss of weight takes place from disintegration of feather sheaths.

Weights at time of fledging could not be obtained, but they were probably about 32 grams.

GROWTH OF WING AND TAIL

Measurements of wing, tail, culmen, and tarsus were taken at the time the nestlings were weighed. The last two measurements proved to be so unreliable that they were discarded. Without feathers for a starting point, the culmen became indefinite; the

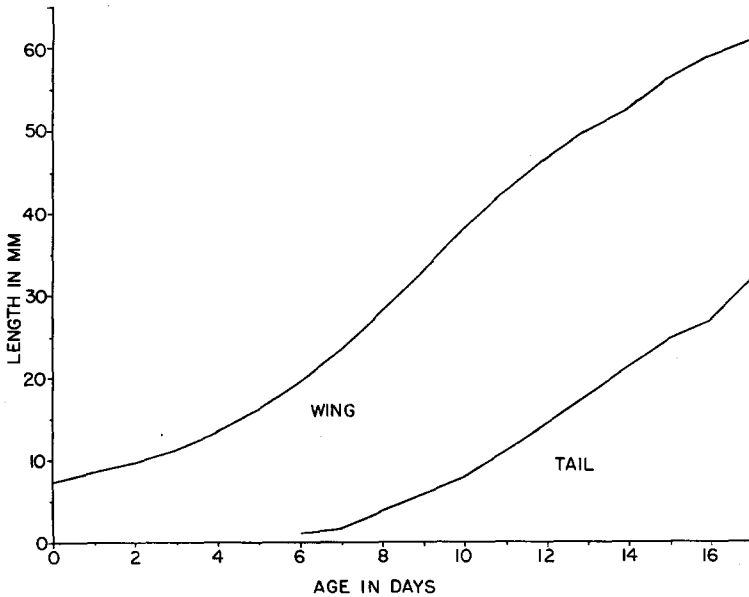


Fig. 3. Mean daily length of wing and tail of nestlings of the Cactus Wren.

tarsus in the live bird could not be held steady long enough for a satisfactory measurement. The mean daily growth of wing and tail is shown in figure 3. Up to the fifth day the rate of growth of the bare manus is rather slow. Then, when the remiges have broken through, the rate of growth of the combined manus and primaries rises rapidly to a fairly constant value and does not begin to drop until after the 13th day. By the 17th day the rate has decreased to one-half the maximum rate. At the time of fledging the

wing is probably 75 per cent of the adult wing length. The tail feathers appear to maintain a more steady rate of increase, at least up to the 17th day, when they have attained 50 per cent of the adult tail length. Both the wings and the tail at the time of fledging are of sufficient size and strength to sustain flight, with fair control, for a considerable distance.

SUMMARY

Nestlings from five nests of the Cactus Wren (*Campylorhynchus brunneicapillus*) at Tucson, Arizona, were removed daily for observation, weighing, and measurements.

At hatching, down in varying amounts is present on the capital, spinal, humeral, alar, femoral, crural, and ventral tracts. By the age of 5 days, the sheaths of the primaries, secondaries, and their coverts have pierced the skin; at 7 days of age the sheaths in all the tracts are out. In another day they have begun breaking open at the ends. The eye-slit opens at the age of 5 days but widens so slowly that vision is probably not effective for several additional days. At the time of hatching the upper mandible is shorter than the lower; by the fifth day they appear equal and at 9 days of age the upper is longer.

Sharp *peep* notes have been heard on the second day, and frequently thereafter for several days, but by fledging time this note has changed to the normal begging *dzip*. Strength increases rapidly; at 4 days the nestlings can rest on their tarsi, while their wings are used for braces. Fear reactions, such as backing up, when an object is suddenly placed before them, were not observed until 11 days old. By 14 days escape attempts were the rule. At the age of 6 days, temperature regulation apparently becomes effective.

The lowest weight on the day of hatching was 2.6 grams. Gain in weight is fairly uniform at first. By the 12th day the curve of mean weight becomes flatter, in the manner typical for many other species of birds. Just before fledging another gain is recorded.

The growth of the wings was slow up to the 5th day, at which time the sheaths pierced through the skin. Then the rate increased with the increments to sheath length until the 13th day, after which the rate dropped again. The tail feathers maintained a steady rate of increase.

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