BEHAVIOR OF YOUNG CACTUS WRENS AND CURVE-BILLED THRASHERS

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WHILE studying the growth of nestling Cactus Wrens (*Campylorhynchus brunneicapillus*) and Curve-billed Thrashers (*Toxostoma curvirostre*) near Tucson, Arizona, during the late spring and summer of 1964, I made incidental observations on their behavior. A nestling of each species was removed to be raised in an artificial environment. The wren was 12 days old, the thrasher, 9. Both birds, but especially the wren, were somewhat retarded in physical growth (weight) prior to their removal from the nests. A retardation of their behavioral development may have been associated with this, but no behavioral abnormalities were observed.

The birds were kept together in my room in a small cardboard carton with "nests" made of cloth-lined pint-sized containers. Other than keeping them indoors, I made no attempt to restrain them, even after they could fly. Both birds were handled regularly and became extremely tame. Most of my observations were made when the birds were placed on a large flat table for feeding. Horsemeat proved to be quite satisfactory. Other observations were made on nestlings which were being weighed daily in the field.

In the Sonora Desert of the Tucson region, this wren and thrasher are two of the most conspicuous passerines and are usually associated with each other. In my study area, both use cholla cacti (*Opuntia* spp.) for nesting. Certainly the greatest difference between the environments of the nestlings of the two species, disregarding parental behavior, is the construction of the nest, the wren's being an enclosed structure with a side entrance, the thrasher's, open (Fig. 1).

NESTLING BEHAVIOR

The nature of behavior and the amount of activity are limited by physical capabilities. The weakness of the newly hatched bird is reflected in its assumption of a nonalert attitude (the "embryonic position") in the nest, and little activity. Early nestling behavior, and its change with increase in size and strength, has been described for the Cactus Wren by Anderson and Anderson (1961) and for the Curve-billed Thrasher by Rand (1941), and will not be stressed in this paper.

Feather preening and picking at disintegrating feather sheaths, as well as wing-stretching and exercising during the last few days of nestling life, are certainly related to the physical development of the nestling. The time of fledging must also reflect the attainment of a critical level of physical capabilities of the young bird.

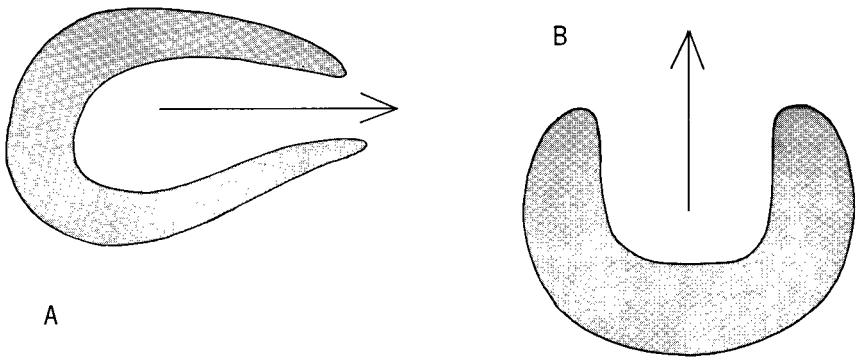

FIG. 1. Idealized cross sections of the nests of (a) the Cactus Wren and (b) the Curve-billed Thrasher. The arrows indicate the direction of parent–nestling interaction.

Many features of nestling behavior demonstrate adaptation to nest form.

Begging.—In Figure 1, the direction of the interaction between the nestling and the parent is indicated by an arrow. As would be expected, the nestling thrasher begs vertically with full extension of the legs, body, and neck. The wren assumes a horizontal, almost crouched, position, stretching the neck forward. The difference in direction, when both were placed on a flat table, was striking. Loud, high-pitched cries accompany the begging of both.

If food is presented to the wren from above, the bird will maintain the horizontal body position and direct only its head upwards. Conversely, if food is presented to the thrasher from the side, the nestling will still stretch upwards with its legs and body, directing only its head, with some difficulty, towards the food.

Lateral movement.—While in the nest, thrashers have very little freedom of lateral movement, whereas nestling wrens, when large enough, crawl out to the opening of the nest to meet the parent with the food, and then crawl back into the safety of the nest cavity after being fed. This is possibly the basis of the wren's much greater "exploratory" activity and movement when placed on a tabletop, and also the "backup" behavior (described by Anderson and Anderson (1961) as a fright response). After being fed, the wren would often back up, with as much agility as in forward movement. If it backed into any object within a few inches, such as my hand placed on the table, the wren would not hesitate to snuggle up against it. In this case, the behavior could not be attributed to fright, and may be directly related to the wren's manner of crawling back into the nest cavity. Satisfaction of hunger, or fright, would serve to initiate the response. During the backup, the wren often backed off the tabletop and so apparently did not rely on vision to

determine its course. In one instance when I did not catch it, one leg was injured enough so that the other was favored for a couple of days. Such manner of movement could be of value only if there is always something to back into, the nest cavity.

Defecation.—The manner of defecation of the thrasher and wren was strikingly different. In both cases, the parents remove the feces when present, after they have fed the young. Thus, it is essential that the parents be aware of the presence of fecal sacs in the nest. The nestling Cactus Wren defecates only immediately after being fed. Its position when defecating is not markedly different from that when begging, but it is accompanied by an unmistakable shaking of the body. Whether this is a necessary accompaniment to the physical act of defecation, or is a secondarily adapted "signal," could not be determined, but it did serve as adequate warning to me. I did not determine, in the field, whether nestling wrens face the nest opening or the nest cavity while defecating. It would seem at first thought that the latter position would make the task of finding and removing the feces easier for the parent. However, the presence of several well-grown nestlings in the neck of the nest at the same time leaves no room for turning around, and the young bird must face the opening to be fed. It is likely that the wrens are always facing the nest opening when in the neck of the nest and so the "signaling" behavior may have developed for the purpose of advertising the defecation which the parent could not otherwise observe.

The thrasher's cup-shaped nest is deep, and when defecating, the nestling raises its posterior as high as possible, making the fecal sac readily visible from above. This action was invariably displayed on the flat tabletop in the absence of a nest rim. When the nestling is large enough, it can defecate onto the nest rim, making the fecal sac conspicuous without the parent's having to observe the defecation. Towards the end of its "nestling" period, the hand-raised thrasher frequently defecated between feedings. Body-shaking did not accompany defecation in the thrasher as it did in the wren.

Exercises.—The form of the nest also affects the manner of wing- and leg-stretching which commences several days prior to normal fledging. The nestling thrasher is not confined in a vertical direction and the hand-reared bird exhibited three general exercises: (a) stretching the leg and wing on one side far back, (b) standing up, stretching both legs, and (c) the previous exercise combined with wing-flapping.

The young wren's stretching behavior seems to have adapted to the extreme confinement of the nest. The only exercise observed was a peculiar wing-stretching which involved lowering and moving posteriorly the wrist of the wing and spreading the primary feathers over the back. Thus, the exercise was accomplished without using additional space.

BEHAVIORAL CHANGES

Begging.—As early as the 15th day, the thrasher would beg towards a food source, rather than in a primarily vertical direction. Beginning on the 20th day, it would wait until I had presented food before begging, now without strong vocalization and stretching, and occasionally accompanied by a quivering of the wings.

By the 18th day, the wren begged with its head drawn back instead of extended, and also quivered its wings. Begging was still accompanied by strong vocalizations. After the 23rd day, the wren would beg only when presented with food.

The wren from the 17th day, and the thrasher from the 15th day, occasionally begged towards the other bird. After the 21st day, attempts to place food in the begging wren's mouth often elicited a *refusal behavior.* The wren drew its head back and turned it rapidly to the side, usually ejecting the food from its mouth. The bird then had to be force-fed. Rand reported similar behavior in young thrashers after the 30th day. After the 20th day, when food was presented on the palm of my hand, the thrasher would often gape or beg at the food.

Defecation.—Noticeable changes in defecation took place in the thrasher and the wren at 18 and 21 days, respectively. As "nestlings," their feces were large and enclosed in a fecal sac; defecation occurred after feeding (except as mentioned for the thrasher during the latter part of the nestling period) and in the wren was accompanied by a conspicuous behavioral "signal." After the time when fledging would have occurred in the wild, feces were smaller and not enclosed in a sac. The wren's "signal" behavior also disappeared and the thrasher no longer raised its posterior.

Roosting.—Adult and fledged Cactus Wrens use roosting nests for passing the night, but the fledged thrasher roosts perched in the cholla cactus. On the 18th and subsequent nights, the thrasher slept perched on the rim of its artificial nest.

New behavior.—On the 17th day the wren began head-scratching, on the 21st day was cocking its tail in an adult manner, on the 23rd day began exploratory pecking, and on the 24th, bathing (without water) and bill-wiping motions. For the thrasher, bill-wiping was first noticed on the 16th day, tail-cocking on the 18th, pecking on the 20th, and head-scratching on the 22nd.

Pecking activities were seemingly acquired simultaneously in the two birds. They began pecking on the same date and would peck objects together. When one would start pecking, the other would also become interested in this activity. Other than this and the mutual begging described above, the only other interaction witnessed between the two birds was that the wren often

TABLE 1

THE ONSET OF BEHAVIORAL FEATURES AND CHANGES

	Days after hatching												
	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Cactus Wren														
Begging:														
Towards thrasher						x								
Flexibility							x							
Only with food												x		
Defecation change										x				
Chatter syllable							x							
Adult chatter										x				
Refusal behavior										x				
Pecking												x		
Preening				x										
Stretching						x								
Tail-cocking										x				
Head-scratching						x								
Bill-wiping													x	
Bathing													x	
Weak flight											x			
Curve-billed Thrasher														
Begging:														
Towards wren				x										
Flexibility				x										
Only with food									x					
Defecation change							x							
Chirp note					x									
Adult song phrase							x							
Roosting							x							
Pecking									x					
Preening		x												
Stretching				x										
Tail-cocking							x							
Head-scratching											x			
Bill-wiping					x									
Weak flight							x							

Behavioral features and changes are listed in the left column and an (x) is placed under the day by which these changes were first observed. First weak flight is given as a reference to physical development. The normal time of fledging is indicated by the vertical line. See text for details.

snuggled up beside the thrasher while in the box; the thrasher paid little attention to this.

Vocalizations.—On the early morning of the 22nd day, the wren gave a typical adult chatter for the first time. For several days it had constantly been using single syllables of this phrase. On the morning of the 18th day,

and at subsequent times, the thrasher uttered a short warbled and liquid phrase similar to that which adults often gave when I was weighing their young in the field. By this time, the thrasher also occasionally used a "chirp" note.

The onset of the behavioral changes observed in the wren and the thrasher are compared in Table 1.

DISCUSSION

One must be careful in drawing conclusions from behavioral studies on hand-raised birds. The environment of the hand-raised bird is artificial and may elicit responses at incorrect times and in false context, thus leading to misinterpretation. A comparison of my observations with those of Rand (1941) on artificially raised thrashers shows that while the behavior patterns correspond closely, they were often initiated at different ages. Some of the discrepancy may be due to observational errors, but the environments were undoubtedly dissimilar in any number of ways as Rand raised his thrashers with a "minimum" of human contact in large outdoor cages, each containing several birds. The variation may partly be due to the absence of parent birds, whose behavior must act to stabilize the environment of the young and give direction to their behavioral development.

In spite of drawbacks, this method has important advantages. The ease of observation, and familiarity obtainable with hand-raised birds, is not possible in the field. Further, because subtle behavior patterns and changes are out of natural context, the artificial environment tends to emphasize some of them.

There are several factors which appear to limit and direct the behavioral development of the young bird: (1) physical development, (2) environment, (3) energy requirements, and (4) the goal: mature adult behavior.

Physical development.—Whereas growth is essentially continuous, the passing of certain critical points marks off phases of behavior. Feather-preening and exercising have already been mentioned. The opening of the eyes might be correlated with the restriction of indiscriminate begging of the nestling.

The termination of the nestling period is ultimately determined by survival probabilities in and out of the nest, and should be regarded as a behavioral change, or complex of such changes, occuring with the attainment of a level of development dependent on the nest type and the physical capabilities of the nestling.

Environment.—The nest form determines the direction of begging and the manner of defecation, restricts the amount and nature of exercising in the Cactus Wren, and may also affect the motility of the nestling.

The abandonment of the nest environment is reflected in the abrupt change

in defecation behavior and the adoption of a new roosting behavior in the thrasher. New behavior, such as pecking and tail-cocking, not useful to the bird until out of the nest, develops at this time.

The nest serves as the focal point for the breeding activities of the parent bird and, with its abandonment, the parents and young associate as a family. Whereas nestlings are physically confined by the nest, the family must be held together by behavioral means. Vocalizations are used by the young to indicate their presence and position. Both the wren and the thrasher had developed "location notes" (the chirp note of the thrasher and the single chatter syllable of the wren) by the time either would have been ready to fledge.

Energy requirements.—The growth curves of the thrasher and the wren are sigmoid in shape and thus the rate of growth, and hence the required input of energy, is highest during the middle of the growing period and tails off toward both ends. It is possible that while the growth rate is increasing and the parents are becoming increasingly taxed, the energy resources of the young are directed primarily to growth, and behavior is limited to begging and defecation. During this period (the *competitive phase*) nestlings compete with each other for food by begging with extreme extension towards the feeding parent (Ricklefs, 1965). With the passing of the maximum growth rate, a *noncompetitive phase* ensues and continues until the bird becomes independent. Begging becomes flexible in direction and pronounced stretching is absent.

Mature behavior.—After the onset of the noncompetitive phase more time and energy are diverted towards such mature behavior as awareness, behavioral flexibility, and learning. The young bird begins to acquire a greater consciousness of its surroundings as indicated by head movements, and its repertory of behavioral responses broadens (cf. mutual begging). Fear reactions, such as crouching in the nest and escape attempts when being handled, appear fairly late in the nestling period.

Some of Rand's observations suggest that species recognition may take place after the onset of the noncompetitive phase. Rand mentioned that thrashers taken from the nest when 14–15 days old learned to beg, whereas birds taken on the 18th day never begged and had to be force-fed. This suggests that birds taken on the 18th day had identified themselves with thrashers and would not accept food from other sources. Begging during earlier stages of nestling development appears to be a generalized response to many types of stimuli. Either the young nestling is not capable of distinguishing, for example, man from its own parents, or the distinction carries no significance.

Ability to recognize species would enable the fledgling to distinguish its

parents from possible predatory animals. Recognition would also be expected to play an invaluable role in family association and the development or learning of specific mature behavior.

The relationship of the parent to young during the early nestling stage is so simple (i.e., the transfer of food and protection from weather) that even the crudest, or most restricted, level of recognition will suffice. After fledging, the nature of the parent–fledgling relationship becomes spatially more varied and behaviorally more complex. At this time the young bird must have a better defined conception of the characteristics of its species.

One might easily imagine that a fledged bird which had not learned recognition might be prone to confusion. Possibly the "juvenile defense behavior" described by Rand in which the young thrashers drew back their heads, opened their bills wide, and spread their wings slightly is an example of such confusion. This behavior lasted for a period of 2 weeks or so and was given towards a ring-tailed cat, a juvenile Gila Woodpecker, and occasionally to an extended hand and to small objects placed quickly in front of a bird. That the "juvenile defense" is solely a defense behavior seems unlikely since prior to its onset, and later when the fledgling is beginning to attain independence, the normal response to unfamiliar or menacing objects is to flee. During the period of the "juvenile defense" there must be another factor acting to produce the observed response. The desire to obtain food is a likely possibility. The attraction of an object as a potential food source could produce a behavior which is neither solely a begging or solely a fleeing response, but a combination of the two. When the young bird becomes self-feeding, the urge to beg gives way to the fleeing response and the "juvenile defense" disappears. Such behavior would not be expected from a bird which had learned species recognition, but Rand does not mention whether the behavior was observed in birds removed at 18 days.

In other species, nestlings may exhibit a similar behavior towards their parents, involving a withdrawal of the head, gaping, and spreading or quivering of the wings. This suggests two other possibilities for the "juvenile defense." First, it may be a modification of the begging response as a mechanism of, or due to interaction with, species recognition learning. One could postulate that the behavior stimulates complementary behavior on the part of the parent which facilitates species recognition. More likely, the juvenile defense may be a submissive behavior. Gaping and forward movements are major components of both aggressive action of adults and begging behavior of nestlings. It is possible that these components must be abandoned or modified when the young leave the nest and take on an adult appearance so that the parent may readily distinguish begging from aggressive behavior.

TABLE 2

NESTLING DEVELOPMENT SCHEME

Physical development	Environment	Energy requirement	Mature behavior
Hatching			
Weak, blind	Nest phase:	Competitive phase:	
Indiscriminate begging		Energy devoted to growth, behavioral responses few and simple	
Eyes open	Behavior modified by nest form		
		Peak energy requirement	
Feather preening		Noncompetitive phase:	Awareness
Exercising		More energy diverted to behavior	Signs of fear Species recognition
Weak flight, fledging behavioral complex			
Bird becoming adult in appearance and physical capabilities	Family association:		Development of feeding behavior and specific adult behavior
	Adult environment modified by parents		
	Independence		
	Adult environment		

Table 2 summarizes the progress of development as outlined in the discussion.

SUMMARY

A Curve-billed Thrasher and a Cactus Wren were taken from their nests at 9 and 12 days, respectively, and raised in an artificial environment. They retained behavioral features obviously adapted to the nest types of their own species.

Most of the behavioral features of the nestlings underwent one or more changes which were tentatively related to (1) changes in environment associated with fledging, or (2) to a possible shift from increasing to decreasing energy requirements of the nestlings. It

was proposed that while energy requirements for growth are increasing (the *competitive phase*), little energy is allocated towards elaborate behavior. The beginning of the *non-competitive phase*, when the requirements of growth are decreasing, allows the nestling to divert energy resources towards the development of adult behavior.

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NOTE ADDED IN PROOF: Recent studies on nestling Red-winged Blackbirds and Barn Swallows indicate that energy requirements for maintenance and temperature regulation are considerably greater than for growth. Because the former are related to weight and the development of thermoregulation rather than the rate of growth, they do not decrease at any time, but reach a plateau approximately when the nestling has reached its maximum size. When the young bird leaves the nest, its energy requirements will increase still further due to added activity and the abandonment of the insulative qualities of the nest. The increased demands are critical until the young bird becomes self-feeding and presumably capable of gathering more than enough food for its own requirements.

In view of these considerations, a causal relationship between changes in nestling behavior and changes in total energy requirement is highly questionable. More likely, new and more flexible behavior is by way of preparation for fledging which will place the young in a new situation. In the Red-winged Blackbird, a species with a short nestling period (10–11 days), new behavioral features (awareness, flexible begging behavior, fear reactions and changes in vocalizations, roosting behavior and defecation) occur at about 8 days, when energy requirements are still increasing.

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