

BEHAVIORAL ONTOGENY OF THE MOCKINGBIRD

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THE reconstruction of behavioral phylogenies stems mainly from comparisons among existing animals since behavior leaves almost no fossil record. These comparisons seldom include ontogenetic development. This paper describes the development of behavior in the Mockingbird (*Mimus polyglottos*) and incorporates this ontogeny into Nice's (1962) useful scheme of five stages based on the age of first appearance of behavior patterns and on dominant behaviors. The Mockingbird ontogeny is also compared with Rand's (1941) study of the Curve-billed Thrasher (*Toxostoma curvirostre*).

METHODS

Observations were made of the behavior of 38 captive Mockingbirds (35 obtained as nestlings and three as fledglings) raised in laboratory cages and fed an artificial mixed diet (Horwich, 1965). Some notes on wild nestlings were also kept. A chronological ontogeny was developed on the basis of birds of known ages. Other birds were aged according to their feather development (Horwich, 1966). In the compilation, the day on which a behavior was first or last seen represents the day when at least one individual was seen to have performed or have ceased to perform the action.

RESULTS

Begging—(see Horwich, 1965)—A change in begging behavior takes place from day one to day 12. This transition in the development is from an initial, unsteady, upward stretching of the whole body on the tarsometatarsus (day 1) to a position in which the front of the body is lowered at an angle of 45° to the horizontal, and the flexed legs are planted firmly on the ground (day 12). A few wing movements and a tail component occur within this developmental transition of behaviors. In addition, on the ninth day, a co-ordinated foot component is integrated into the sequence. In this movement the weight of the body shifts, so that the young bird moves first one foot and then the other, usually taking four to eight steps in the same position.

Three vocalizations accompany begging. After day three low intensity "contentment" cries are given after feeding, and muted begging vocalizations are emitted. On day seven, the latter single syllabled call becomes louder, harsher, and more distinct. Gage (1961) noted this change in the voice two to three days before fledging with the possible function of aiding the parents in locating the young.

The stimuli that elicit begging change gradually. On day one a tapping on the nest elicits a stretching of the neck upwards and gaping, which is maintained for only a few seconds. Then there occurs a refractory period during which the response cannot be elicited for some seconds. By the fourth day tapping also elicits a vocalization. This total begging response continues to the sixth or seventh day.

On the sixth to eighth days, sleeping captive birds respond to tapping; however, if their eyes were open they responded to the sight of my hand. In the wild, young of this age may initially respond to the tapping by raising up and gaping without

vocalizations. Then upon further, rougher vibrations and/or the sight of an intruder (human) they will assume the crouching posture described below.

This suppression of begging vocalizations in a strange situation was also shown when three individuals were taken from the nest at nine days. They continually crouched and had to be initially force-fed by inserting food into the closed beak with a forceps, after which they would swallow the food. After a number of feedings in this manner they began to beg by gaping only; the begging vocalizations and the other components were not present until a day later.

By the fourteenth day sight is the most important stimulus to elicit begging by the fledglings and they now orient to the human feeder.

Wing-flashing—(see Horwich, 1965)—Wing-flashing, the jerky extension of both wings dorso-laterally in hitches, first appears usually on day 10 or 11.

Fear crouching and escape—On about the seventh day the young birds no longer beg when the nest is tapped. Instead, they withdraw all parts of their body, pull their head within their shoulders and remain crouched and quiet. On day 12 a tendency to run away in similar fear situations develops and this appears definitely on day 13, fledging day. Occasionally escape was noted on day 12 when I attempted to take nests in the field. These individuals crouched at first but upon further disturbance, some of the birds hopped out of the nest and attempted to escape capture by hopping away.

Defecation—In a three-day old chick, defecation consists of turning the body around and moving it backwards, usually to the edge of the nest. Then it wiggles the tail rapidly from side to side, elevating the cloaca, and ejecting a fecal sac over the nest lip. This pattern wanes by day 16, by which time only tail wiggling and cloacal elevation still occur with defecation. On day 17 some tail wiggling occurs but it was also on this day that the defecating pattern of the juvenile and adult first appears: lowering of the body (usually on a perch), opening of the ventral feather tracts, defecating, closing the feathers, and rising to the normal perching position. In all cases past day eight, when the captive young were precociously out of the nest, the nestling defecation pattern was seen, independent of the nest stimulus.

Stretching—Three types of stretching appear on day nine and persist thereafter. The leg-stretch consists of extending both legs full length almost vertically by pushing them against the perch. This extension pushes the body up and causes it to assume a slanted position with the head lower than the tail. A second stretch which usually precedes the first, is the backward and sideward stretching of the wing and leg on the same side of the body. In performing this movement the primaries and secondaries of the wing are extended and spread. The tail is often twisted slightly in the direction of the spread wing, and it is also spread. Although the former two movements are usually done together, sometimes the order is reversed and sometimes either is done without the other. A third stretch consists of raising both wings up and back to a 90° angle with the horizontal and then lowering them again at about the same rate.

Hopping—On day eight captive birds first hopped to the rim of and often outside of the laboratory nest. Such "premature fledging" appears to be an artifact of laboratory conditions. Since it occurred in the morning, such "fledging" was probably due to the birds not having been fed early enough.

The characteristic walking of the adults probably occurs at about two weeks after fledging, but my records are incomplete. Mockingbirds conform to the ontogenetical pattern of hopping first and later developing the adult walk (Daanje, 1950).

Preening—The first motion thought to be preening occurs on day one: uncoordinated movement of the bill about the lower breast. By day three actual breast-preening does

occur. The femoral tract is the next area in which preening is noticed; these two regions are the first to develop feathers. On day seven preening on top of the wings occurs. By day 10 direct preening of the underwing (inserting the bill under the wing from the anterior end), and indirect preening (inserting the bill under the wing from the posterior border) appear. Preening of the uropygial region also appears at this time.

Pecking and paper-tearing—Paper-tearing consists of pecking a hole in the newspaper lining the cage floor and pulling a strip of paper from this hole or other frayed paper edges. Often the bird then carries the strip in its bill. Both pecking and paper-tearing occur by day 13, and the pecks are first oriented at small moving objects or small specks on the cage floor. In the case of one male, paper-tearing increased in March at age nine months. This activity is later part of nest-building. The paper strips were used as nest lining materials by both sexes in captivity (Horwich, MS).

Head-scratching—Indirect scratching of the posterior portion of the head is first observed on the ninth day. Because of the balance involved, this action necessitates a well co-ordinated neuro-muscular system. One case of direct head-scratching was noted, but in this case I believe the bird had a vitamin deficiency. It was unable to maintain its balance well even on two feet. In this one instance the wing was lowered even though the bird scratched directly. Hailman (1960a) also observed a fledgling Mockingbird to scratch directly as well as indirectly. In both of these observations the scratching seemed to cause the bird to be off balance. In light of the rarity of these direct scratches I would accept his observation as being an abnormal occurrence rather than any developmental transition.

Bathing—Bathing is often preceded by a partial or full bathing sequence performed before entering the water. Bathing movements superficially resemble the begging of the fledgling. The bird assumes an angle of 45° with the horizontal with its breast and head lower than its posterior end. It then flips its wings out and up, slightly out of phase with each other, in a very agitated manner, a movement that flips water over its body. It continues this motion as it alternately raises and lowers its head and body in and out of the water. When the head and body are out of the water, the bird flips its wings rapidly, and alternately rolls its body and ruffles its contour feathers. The rolling effect seems to be produced by the alternating wing flipping. After bathing the bird goes through a sequence of drying movements. These incorporate many of the same bathing movements without the forward bending of the head and body. In addition, the feathers are ruffled and the whole body is shaken. The wings are usually drooped during this ruffling. Often the bird flutters its wings synchronously at an angle below the horizontal and intermittently preens under them directly. The fluttering consist of spreading the primaries and sometimes the secondaries and extending the manus. The fluttering then takes place while the feathers are half spread. The tail is also spread and it seems to vibrate as the wings are fluttered and as the body rolls. The head may be rubbed on a branch and the breast is preened. The whole body seems to move at once with the wings alternating to give the ruffling and rolling effect. Sometimes after the shaking of the body the bird wags its tail rapidly from side to side on the horizontal.

The whole bathing and drying sequence was first seen on day 11, when the birds were first given a large water dish. In nature this behavior would probably only occur before fledging in the context of rain bathing although I have never seen rain bathing in Mockingbirds. A sequence similar to drying occurs following close contact between two individuals (Horwich, MS).

Song—A subsong which consisted of a low intensity, disorganized, continuous sound

(often sung with the bill closed) was first heard on day 27. On day 48 a song, still considered to be a subsong, was given with the mouth open. These vocalizations became much louder around day 65 and approached the loud "surety" of the true song on day 80. One bird which was caught as a fledgling began singing but stopped between 90 to 100 days of age, possibly due to the loud singing of the other remaining male. He was not heard again until six months later (in February, 1964) when he resumed singing a true song.

Socialization—At about two weeks after fledging the young birds may show a tendency to rush at and chase other Mockingbirds or other species of birds. Two birds at this age showed what might have been the precursor of the "hostile dance" (see Hallman, 1960b). First one hopped toward the second who hopped toward the first and the first retreated from the second. Agonistic behavior gradually increases until day 42 when chasing may become so intense that the birds have to be separated. In one case in which two siblings were left together for 45 days, one was found dead in the cage and was believed killed by the other. A few days after this, the remaining bird began to sing.

DISCUSSION

Nice (1962) has proposed a series of ontogenetic periods which standardize the dimension of time for comparisons among species. As the developmental histories of more species are developed and fit into this basic series of behavioral age classes, a phylogenetic classification can be based on the characters of seven age groups instead of the adult animal alone. This will give additional characters which are not now used in the comparison of species (i.e. relative rates of behavioral development, correlations of structural and behavioral developments, relations of precursors of behaviors, etc.).

The behavioral patterns of the Mockingbird fit quite well into Nice's categories, although the Mockingbird differs in having a slightly slower rate of development than the Song Sparrow (*Melospiza melodia*) which served as the basis for these categories.

The following list gives a comparison of the behavioral development of the Mockingbird and the Curve-billed Thrasher (adapted from Rand, 1941) using Nice's system of behavioral age classes. (Numbers in parentheses refer to the age in days when the behavior was first noted; (h) means at hatching; (R) refers to additional observations of Ricklefs (1966); (-) means the behavior possibly occurred earlier.)

I Post-embryonic Period

Mockingbird—(0-4 days)—Nestling begging: neck and body extension, gaping (h), wings extended out and down at the sides (1); soft vocalizations beginning (4); begging response to tapping on the nest (0-5); eyes just begin to open; low intensity contentment calls; nestling defecation (h); preening of the ventral tracts; embryo resting position in the nest (h).

Thrasher—(0-4 days)—Begging by standing on the belly and feet with its wings directed out and down (4) and gaping; start to stand on the tarsi; embryo resting position (h).

II Preliminary Period

Mockingbird—(5-6 days)—Preening of the ventral tracts with initiation of femoral tract preening (3); eyes open; standing on tarsi (5).

Thrasher—(5-6 days)—Eyes open; stand on tarsi (4); head drawn in to rest on nest; wings aid in righting (5); freezing (5).

III Transition Period

Mockingbird—(7-9 days)—Maturation of the begging wing movements; fluttering wings (7); begging in response to a visual stimulus (6-8); change to a harsher begging cry (7); fear crouching (7); stretching (9); wing-flicking; scratching (9); tail component in begging; hopping; alarm chips (7); perching; fanning wings (flight maturation) (7).

Thrasher—(7-13 days)—Eyes wide open; hopping (11); some escape; absence of random movement (7); squealing injury cry (10); stretching (9-R); scratching (22 R); fanning wings (9-R); alarm chip (18 R).

IV Locomotory Period

Mockingbird—(10-17 days)—Landing (15?); perching (8-10); flying (15); sleeping with bill in scapulars (13-14); completes preening; fledgling begging; bowing (12); orient to feeder (14); beg to siblings (14); tail-flicking; wing-flashing (10-11); escape (12); scream (13); flight; pecking (13); paper tearing (13); adult defecation (17); food capture (13); bathing (11-); drinking (11-); intraspecific pecking; landing on others (19?); leaving nest (11-13); bill wiping (13).

Thrasher—(14-20 days)—Escape (12-15); shrinking (17); fits of wildness (18R); flight (19); landing (awkward 14-18) (24-25); walking (14-18); perching (16); exploratory pecking (19); tail flicking; digging (19); pick up food (21); preening; stretching; sleeping with bill in scapulars (18-19); bill wiping (16 R); juvenile defense; leave nest (14-18); orient to feeder (15R); snake display (17-18); kuks.

V Socialization Period

Mockingbird—(18-30* days)—Self-feeding; dependent on adult (13-37); beg to each other (22); subsong (27); indications of aggression (15?); chasing (25); flight perfection; walking (26-27?).

Thrasher—(21-40 days)—Self-feeding; singing (21, 18R); sun bathing (21); flight perfection; dig holes; no actual aggressive behavior for the first 10 weeks.

VI Juvenile Period

Mockingbird—(40-? days)—No data on precocial sexual behavior; true song (80); completely independent of parental care; sunning (late).

Thrasher—(70? days)—Mobbing (89-92).

VII Adult Period

Mockingbird—(270 + days)—Nest building; aggression; sexual activity; etc.

The first two chronological categories are similar in the two mimids but during the Transition Period at about seven days, the thrasher's relative rate of behavioral development becomes slower. The Mockingbird is much more precocial in the development of the preening movements, starting as early as three days to preen its ventral tract. There was no mention of any main-

tenance activities in the thrasher (Rand, 1941) until late in the Locomotory Period at which time preening, stretching, and bill wiping occurred.

The feather development is also slower in the Curve-billed Thrasher. All locomotory activities were concentrated within about three days before and after fledging in the mockingbird but in the thrasher these activities were more dispersed. For example, in the thrasher, hopping on the nest lip was seen at 11 days but flight was not really perfected until day 25, although it did occur by day 18 or 19. As locomotion improved in the thrasher it developed pecking and digging movements. This was much later than in the Mockingbird, but in both it occurred at about the time of fledging or a little after. Digging may show some correlation with the bill development. Independence and self-feeding also occurred later in the thrasher as did the "snake display," a probable homolog of wing-flashing. In addition, the the thrashers showed no actual aggressive behavior for the first 10 weeks whereas Mockingbirds show indications of agonistic behaviors during the Socialization Period.

SUMMARY

The behavioral development of the Mockingbird is established from observations of 38 young birds. Each behavior is described including its modifications with aging, and the initiations and cessations of the behavior are noted. Using the age classification periods and criteria of Nice, an effort was made to compare two related species; the Mockingbird and the Curve-billed Thrasher. This comparison shows a general slower developmental rate in the Curve-billed Thrasher after seven days of age relative to that of the Mockingbird.

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