AN ONTOGENY OF WING-FLASHING IN THE MOCKING-BIRD WITH REFERENCE TO OTHER BEHAVIORS

Robert H. Horwich

Wing-flashing in Mockingbirds (*Mimus polyglottos*) has been observed in one context in young birds and in two other contexts in adults. The young wing-flash in response to strange situations. Adults perform the behavior in the presence of potential predators (Hicks, 1955; Selander and Hunter, 1960) and in association with foraging (see Hailman, 1960*a*). The latter context is most documented and various attempts have been made to connect wing-flashing during foraging with the presence of insects.

My primary aim is to describe the ontogeny of wing-flashing and associated movements in hand-raised birds. I also identified certain of the stimuli which elicit wing-flashing and have tested their effect throughout the ontogeny. The evidence indicates that wing-flashing is derived from a balancing movement rather than a flight intention movement. Furthermore, wing-flashing appears as a gradation of responses as well as the stereotyped movement which is the "wing-flashing" described by other authors.

Since wing-flashing is not an isolated behavior, it was studied in relation to the ontogeny of closely associated movements. The total ontogeny will be described elsewhere (Horwich, MS.). The function of wing-flashing remains unknown. Lastly, the evolution of wing-flashing and similar patterns of behavior in passerine birds is reviewed.

METHODS

Thirty-five nestlings, three fledglings, and two adults were observed in the laboratory during the period from May 1963 to March 1964. About 20 unmarked adult and young birds were also observed in the field from December 1962 to March 1964.

Containers and cages.—In most cases the nestlings were taken with the whole nest. In the laboratory the original nest or an artificial nest composed of cellulose packing material was used. All except one individual were raised with at least one other nestling in a cage. The nestling cages were 1 foot in width and height by 2 feet in length. At the age of 11 to 20 days the young were transferred to a larger cage 34 inches in width by 36 inches in height by 48 inches in length. Each cage contained two branches placed so the bird could not rub its tail on the wire and at different heights from the floor to allow maximum exercise. These perches had some springiness, were of different widths, and were kept clean to prevent damage to the bird's feet.

Each of these cages usually contained one bird but in a few instances two were kept together until agonistic behavior increased so much that the safety of the birds was involved.

Diet.—The nestlings and hand-raised fledglings were fed roughly 50 per cent wax moth larvae (*Galleria mellonella*), and 50 per cent mealworm larvae (*Tenebrio molitor*), honey bee larvae (*Apis mellifera*), and hard-boiled eggs with supplemental vitamins and minerals. The feeding schedule involved approximately two or three feedings per hour from 7:00 AM to 7:00 PM. Almost all nestlings taken after 7 days of age developed in apparently good health.

A constant supply of food and clean water for drinking and bathing was contained in shallow dishes and placed on several layers of clean newspaper on the floor of the larger cages for the older birds. Food consisted of a mixture of equal parts of Big Red dogfood, turkey starter mash, and a dried fly mix which was moistened with cottonseed oil as suggested by Ficken and Dilger (1961). All birds are in good condition at this time.

Visual isolation.—One bird was visually isolated from other individuals at a time before wing-flashing developed. This was accomplished by covering three sides of the outside of its smaller cage with cardboard. It showed no difference in the development of wing-flashing. Thus I did not isolate any other birds.

Techniques of observation.—Laboratory observations were usually made while 3 to 4 feet from the bird. Notes were recorded by speaking softly into a Minifon Attaché pocket tape recorder. I was in sight of the birds during the whole period of observation. Laboratory observations of nestlings and fledglings were supplemented by field observations of young and old birds and by observations of the juveniles in captivity. An eight-power pair of binoculars was sometimes used in the field observations. These observations were most often summaries recorded after the behavior occurred and not continuous detailed notations as in the laboratory work. The ontogenies of hand-raised birds include life histories of birds up to 10 months after hatching. All notes involving protracted observations were taken with the Minifon recorder.

Presentation of stimuli.—Eight older laboratory birds were presented with various stimuli such as grasshoppers, crickets, and cockroaches of varied sizes, small moths and their larvae, slugs, small beetles, true bugs, and small movable toys about 2 to 3 inches long. At the time of presentation they were 3 to 10 months old. The presentation occurred by manually placing the stimulus object into the center of the cage, withdrawing the hand, closing the door, and stepping back 3 to 4 feet from the cage. The small moths, during later presentations, were presented to the bird through the cage wire about 2 inches above the perch. They were held in a tweezer or between two fingers. In

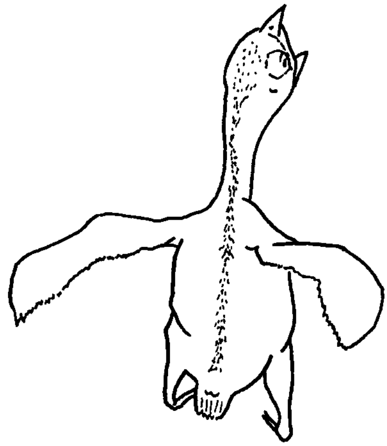

FIG. 1. The balancing movement of a 3-day-old Mockingbird nestling showing wing extension. Drawn from a 16-mm motion picture frame.

addition, observations of the birds during timed periods in a normal situation in which none of the external stimuli were presented, were noted.

Aging.—Age was estimated accurately in some cases since I knew the date of hatching. In other cases the estimation was made by correlating the feather development at the time the nestling was taken with the development in birds of known ages.

Limitations of observation.—An ontogeny of each bird was kept with special emphasis on when behaviors were first seen and when they waned. These individual life histories were then lumped and the earliest and latest appearances of behaviors were used as the limits. Although observations on ontogeny are as accurate as possible, gaps occurred when behaviors were accidentally overlooked or impossible to watch. This ontogeny is therefore open to additions by other observers.

DEVELOPMENT OF WING-FLASHING AND RELATIVE BEHAVIORS

Begging.—Nestling begging consists of a number of components, some of which are replaced by later fledgling begging movements. At one day of age the nestling has little motor control but can extend its neck, gape, and raise its body while resting on its feet and tarsi. The wings are typically extended down at its sides and outward forming an angle of 40 degrees below the horizontal. This I call a balancing movement (Fig. 1) because the wings extended in this manner may be used as balancing props on the nest sides. Motor coordination does not improve much during the second and third day.

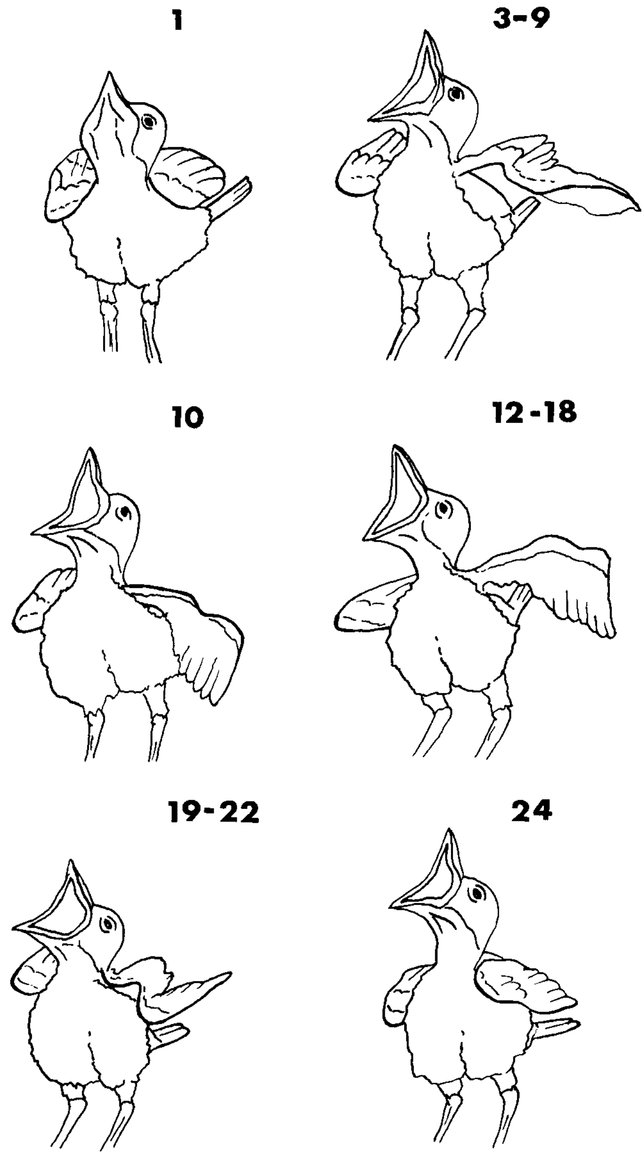

FIG. 2. A begging-balancing sequence of an 11-day-old Mockingbird. Drawn from 16-mm motion picture film taken at 18 frames per second. Frame 1, the wings are close in to the sides and the bill is up. Frames 3–9, and 10, the wings are extended, the tail is raised, and gaping occurs. Frames 12–18, the wings remain extended, the tail is raised, and gaping continues. Frames 19–22, the wings and tail are being lowered. Frame 24, the wings and tail are both lowered and gaping continues.

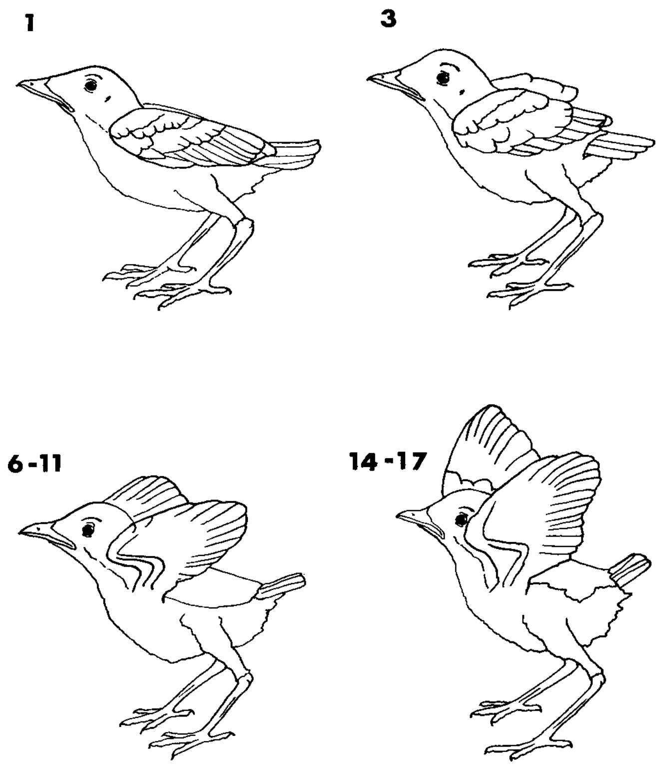

FIG. 3a. A wing-flashing sequence of a 10-day-old Mockingbird. Drawn from 16-mm motion picture film taken at 18 frames per second. Frame 1, the wings are close to the sides and the tail is parallel with the horizontal. Frame 3, the wings are being raised. Frames 6–11, the wings, having been partially raised, are now paused in the first hitch. Frames 14–17, the wings are now held at the second hitch and the tail is raised.

On the fourth day the wings become folded in closer to the sides in begging and are approximately parallel to the body whenever they are extended. The wings are quivered slightly, seemingly because of incomplete development of coordination. The first two well-coordinated wing movements occur on the seventh day or possibly a day or two earlier. They are termed "wing-flapping" and "begging-balancing." In the first, the wings are usually kept in close to the sides of the body. Then they are lifted and spread very slightly so that the leading edge of the outer primary is parallel to the body. While in this position they are raised from the horizontal up to about 30 degrees at the tip by rotation of the proximal elements which remain relatively stationary at a right angle to the body. In begging-balancing (Fig. 2) the wings are

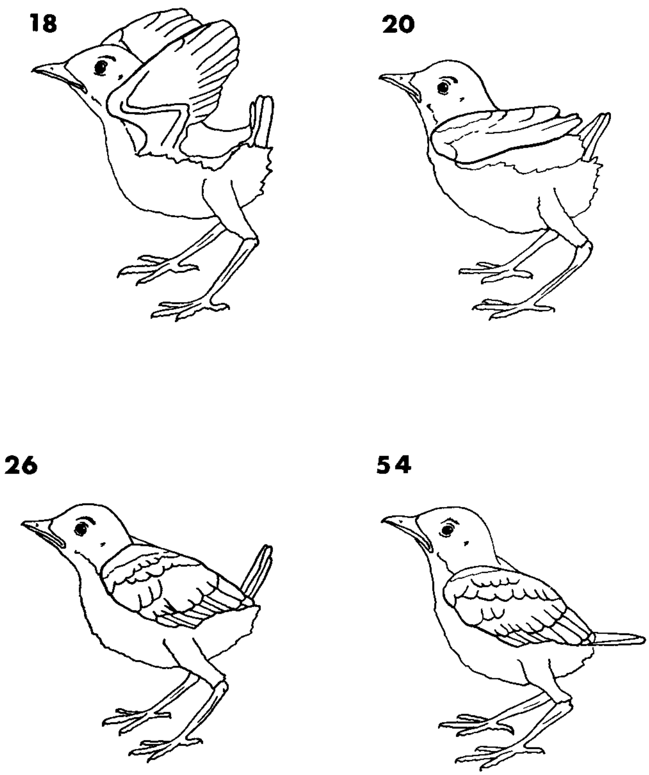

FIG. 3b. Frame 18, at the end of the last hitch the wings are beginning to lower. Frame 20, the lowering of the wings continues but the tail is still raised. Frame 26, the wings are now completely lowered and the tail is still raised. Frame 54, the tail is lowered and the bird is in a similar position as at the start of the sequence in Frame 1.

typically horizontal and extended so that the leading edge is nearly at right angles to the body axis, although extension may be occasionally partial in one or both wings. The wings when extended are either still or shivered slightly. On the ninth day the tail is brought up while begging occurs and is brought down to the normal position after the behavior ceases.

In the laboratory the birds were often out of the nest by 8 days (rather than the natural 13 days) yet the behavior progression was not altered. Thus the ontogeny is not dependent on the birds being in the nest. It appears that begging movements do not have a regular stimulus–response connection but are rather a function of maturation.

"Fledgling-begging" appears on the 12th day. In this behavior the young

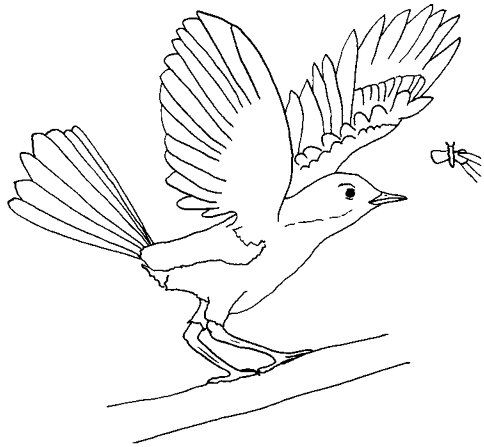

FIG. 4. A high-intensity, extended wing-flash of a subadult bird while being fed a moth. Drawn from a compilation of photographs.

birds not only show wing-flapping or begging-balancing as well as tail-raising, but they also hold the body lowered to a 45-degree angle with the horizontal and increase flexure of the legs. By the 14th day the young birds first approach and follow their human feeder. Fledgling-begging continues from then on to a maximum of the 44th day of age. The young first begin feeding themselves on the 17th day. As they become less and less dependent on hand-feeding the begging sequence becomes incomplete.

Significantly begging-balancing remains only as long as the wing-flapping. Both occurred until about the 37th day while the then incomplete fledgling-begging continued for as long as 8 days after.

Wing-flashing.—Wing-flashing appears between 9 and 13 days of age, most commonly on the 10th or 11th day.

Although wing-flashing is very varied in form, *when it first appears it is at its highest intensity* almost always when the bird is in an "excited state." Often this excitement seems to have been due to my close presence. The bird usually runs from me and tries to get through the wire at the rear of the cage. During this excited running the bird wing-flashes by extending the wings up at an 80- to 85-degree angle to the horizontal and completely extending the remiges. Thus, this movement consists of a prolonged extension *without any hesitations* until eventually the wings are quickly brought down to its sides. Often, just before or just after this movement, the bird chirps and fully extends its wings with a rapid rotation of the humerus causing rapid movements of the edge of the wing from the horizontal to 80 degrees above and back. This is called wing-exercising. Chirping and wing-exercising are first seen on the seventh day and although they both exist in the adult, they seldom occur simultaneously. Chirping occurs when the bird is in an "excited state." Immediately after the birds exhibit the excited running and the extended wing-flash there ensues a series of stereotyped wing-flashes with hitches, which consist of raising the wings by rotation of the humerus in its socket to an angle of 80 to 85 degrees with the horizontal (Fig. 3). There is a pause each time the wings are extended at each hitch. After about two or three hitches the wings are quickly brought down into the normal position (Fig. 3). During the initial extended wing-flash I did not notice whether or not the tail was brought up. However, in all successive wing-flashes the tail is raised during the wing-flash or as the wings are being brought down after the wing-flash has occurred (Fig. 3).

In my observations of juvenile birds I have noticed a gradation of movements which are all similar to and have been designated as wing-flashes. These range from a slow partial extension of the hand and primaries parallel to the horizontal with a quick return to the normal position (resembling very closely a wing-flick in slow motion) to a full extension of both wings up and slightly forward (Fig. 4) observed when enticing the juveniles with a live insect in my hand. In this case the remiges are fully extended and the movement resembles the initial wing-flash done while running excitedly. These wing movements have occurred at an angle of 0 to 80 or 85 degrees with the horizontal. Most often these were observed when the bird's legs were not extremely bent at the intertarsal joint as in flight intention. However, in a situation similar to that in Figure 4, if the bird approached on a slanted branch it sometimes kept its legs in a position bowed at the joint with its body closer to the branch which appeared to be for a balancing purpose. Wing-flashes of one wing were observed infrequently.

Wing-flicking.—This movement is the quick extension and replacement of the hand and primary feathers out to either side of the body. This involves the rotation of the carpometacarpus on the carpels as the hand is extended. It was first noticed on the ninth day and has since been noticed when the birds were agitated or excited. Andrew (1956) suggested that this was a flight intention movement. However, I have rarely observed the wing-flicks when the birds were crouched but they occur, rather, before or after this flight intention movement.

Tail-flicking and related movements.—This motion involves the quick upward vertical movement of the tail followed by a slower resuming of its normal lower position. This was first noticed at 11 days and has continued to date. There is a close resemblance of this to the tail-raising component

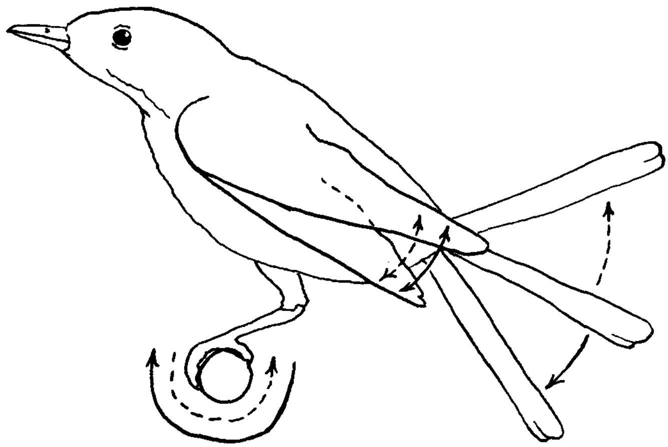

Fig. 5. A diagrammatical sketch exhibiting the compensatory balancing movements of the wings and tail in response to the twisting of the supporting perch. The solid line represents the clockwise twisting of the perch and the consequent wing and tail movements. The dotted line shows the counterclockwise twisting and the bird's compensatory movements.

found in the begging and wing-flashing behaviors (Figs. 2, 3). In addition a slow movement much like that found in wing-flashing can be elicited by causing the tail to act as a balancer when the perch is twisted one way or the other (Fig. 5). In both tail-flicking and tail-raising the tail may be moved along the horizontal (usually when the bird makes a quick movement of its head and body to the side) and it may be spread to varying degrees, exposing the outer white tail feathers (Fig. 4). The main difference between the two movements is the more rapid speed of the tail-flick.

Flight.—Flight consists of movements similar to those mentioned by Andrew (1956). The bird crouches, raises its tail, thrusts its body upwards, raises its wings, beats its wings downwards and pushes off the perch by extending its legs. Flight first occurred at 13 days which is the approximate time of fledging.

Agonistic behavior.—At 10 months of age two birds fly to the adjacent sides of their individual cages, one bird up against the other, giving *kaa* sounds, fluttering their wings against the cage wall, and often extending them in a motion similar to the high intensity wing-flashing that I have elicited from hand-feeding of "wary" juvenile birds (Fig. 4).

RESULTS OF OBSERVATIONS CONCERNING WING-FLASHING

Wing-flashing was observed in all 24 birds raised in captivity past the age of 10 days. Wing-flashing occurs in both sexes and probably the frequency

TABLE 1
AMOUNT OF WING-FLASHES IN RELATION TO AGE AND OTHER BEHAVIORS

Age (days)	Uneasy Situation	Landing	Food water	Balance	Perching	Begging	Pecking paper	Stretching	Chirping	Unknown	Total
10–15	76	9	0	6	0	6	0	3	1	5	106
15–20	49	11	0	1	4	2	0	0	1	5	73
20–25	2	1	1	1	2	0	0	0	0	0	7
25–30	2	5	0	0	0	0	0	0	0	0	7
30–35	41	0	0	0	0	0	0	0	0	0	41
35–40	2	6	0	6	4	0	0	0	0	0	18
40–45	0	0	0	0	0	0	0	0	0	0	0
45–50	0	0	5	0	0	0	0	0	0	0	5
50–55	0	0	14	0	0	0	0	0	0	0	14
55–60	0	0	0	0	0	0	3	0	0	1	4
60–65	59	0	0	0	0	0	0	0	0	0	59
65–70	0	0	0	0	0	0	2	0	0	1	3
Total	231	32	20	14	10	8	5	3	2	12	337
% total	68.6	9.5	5.9	4.2	3.0	2.4	1.5	0.9	0.6	3.6	

of occurrence does not depend on the sex. Most of the observations of wing-flashing occurred from 10 to 20 days after hatching and generally seemed to decrease with the age of the bird. There appears to be a rapid decrease of wing-flashing after 20 days. In one case 59 wing-flashes were elicited from a 60- to 70-day old bird in 2 minutes after a window shade flew up unexpectedly. When all observations of wing-flashes were grouped according to the situations in which they occurred or into categories of behavior most closely associated with the wing-flashes at the time of occurrence, it was found that approximately 69 per cent of all observations were associated with a situation in a state of change in which the birds showed escape tendencies or ambivalent behaviors. These situations included the moving of the bird cages, the placing of a strange object in view of the bird, the sudden winding of a window shade, the initial capturing of the bird, the period after handling the bird, my pursuing of the bird within the cage, and other occasions when the birds appeared to be in a very excited or agitated state for some known or unknown reason. The next highest percentage of wing-flashing occurred in correlation with landing on the ground or on a perch. The third highest correlation was with food, water, and live wax moth larvae. Neither of these last two categories were above 10 per cent of the total observations (Table 1).

At 88 to 290 days of age eight of the juvenile birds were subjected to various stimuli to detect any behavioral changes. In almost all of the presentations wing-flashes were elicited by the situation. The situation which appeared

TABLE 2
NUMBER OF WING-FLASHES ELICITED BY STIMULI

	1 No external stimuli	2 Insects	3 Models	4 Man with insects
Number of wing-flashes	19	110	101	359
Number of minutes of observation	165	121.5	64.5	85.5
Wing-flashes/minute	0.1152	0.9054	1.566	4.20
% wing-flashes/minute (of total time)	1.70	13.34	23.07	61.89

to elicit the most wing-flashes per minute was the presentation of the moths by hand through the cage wires. The various model toys gave the next highest amount of wing-flashes. All stimuli situations gave more wing-flashes per minute of observation time than observations during a normal period when no external stimuli were present (Table 2).

During many observations a reduced number of wing-flashes was noted towards the end of a test. For example, in one test when a small toy dog was presented, 32 wing-flashes were seen in 5 minutes of observation. Of these, 30 occurred in the first 3 minutes while the bird seemed hesitant about approaching the model. During the last 2 minutes, the bird continually pecked at the model without hesitation and only exhibited a few wing-flashes when the model was set in motion by the pecks of the bird. When this happened the bird would jump back and wing-flash. In other cases the more presentations of a stimuli the less often the wing-flashes would occur.

All observations of wing-flashing in adult birds seen in the field were during foraging, after the bird had stopped between runs. In the three incidents in which I noticed wing-flashing in fledglings, the birds were all being pursued by me. The young appeared excited and made escape attempts.

DISCUSSION

In birds from 9 days to 10 months old, wing-flashing is definitely associated with some type of strange or uneasy situation. Selander and Hunter (1960) and Sutton (1946), who terms it an instinctive behavior which indicates wariness, suspicion, and distrust, cite evidence in favor of this view. The latter also concludes that any association with food is accidental. The report of Eifrig (1948) in which he saw wing-flashing by birds on man-made supports which upon subsequent investigation yielded no insects, also supports this position. On the other hand, Hebard (1949) argued that wing-flashing done on cement or benches might have been due to association of insects seen on previous benches or cement walks. Hailman (1960*a*) concluded that in adults wing-flashing is a foraging motion but in young birds hunger, fear, and curiosity seem to elicit the behavior. My field observations lead me to believe that Hailman's position is correct. However, my captive birds are now 10 months old and there is no indication that the stimuli eliciting wing-flashing will change when they are classified as "adults." Allen (1947) is in disagreement with my conclusions and those of Sutton (1946) for four reasons: 1) He never noticed cause for suspicion on the part of the bird; 2) the wing-flashing seemed deliberate; 3) he noticed the behavior of the parent after the young were hatched; and 4) the necessity for increased insect-gathering activity due to the hatching of the young might have prompted a change in behavior. He mentioned a possible similarity in function of the white wing patches of the Mockingbird to the white breast of the Canyon Wren which Grinnell (1924) interpreted as having the function of lighting crevices during foraging on rocks. Another supposed function is that the behavior may serve to frighten insects (Gander, 1931).

Although there seems to be an association of wing-flashing and foraging, it cannot be assumed that wing-flashing functions in foraging or that it is a causal factor in producing insect movement. In my experiments I found large grasshoppers to be the most successful insects in eliciting the behavior. As the birds became accustomed to the grasshopper, the wing-flashing waned. Thus, the insects must be viewed as the stimuli causing the behavior and the behavior should not be thought of as functioning in foraging.

Hailman (1960*b*) mentions that wing-flashing occurs commonly in the winter in southern states but rarely in the winter in northern states. He postulates that this is due to the unavailability of insects in the north during winter. In Maryland during the spring and summer most of the foraging takes place on the ground and the Mockingbirds are easily seen. During the colder months when it becomes harder to find insects, Mockingbirds appear scarce unless one searches in bushes and shrubs. Mockingbirds have been noticed spending most of their time during the winter eating berries and fruits of such bushes as various species of firethorns (*Pyracantha*), regal privet (*Lingustrum amurensis*), and various species of hawthorns (*Crataegus*).

Beal et al. (1918) present an analysis of Mockingbird stomachs. They have failed to mention the states in which the birds were collected but they have samples from every month of the year. Their results show that most of the animal food is taken in May (85.44 per cent), and the maximum vegetable consumption occurs in December and January (86.55 per cent). The large percentage of beetles and grasshoppers shows that the Mockingbirds gather a considerable amount of food from the ground. Grasshoppers appear to be the insect most consumed. They are eaten every month and average 14.85 per cent per year. The highest consumption occurs in July (43.33 per cent) and in February only a trace of them can be found. In this same month Hailman (1960*b*) found a number of insects in a small area on which a Mockingbird had previously wing-flashed, supporting his association of wing-flashing with the availability of prey.

The occurrence of more wing-flashing in the summer might also be attributed to the large precentage of naive juvenile birds who would have the tendency to wing-flash more often.

The study of the ontogeny has led me to the conclusion that wing-flashing has its basis in a balancing movement. I am not sure whether or not the first balancing movement at 1 to 3 days is a precursor. However, the begging-balancing movement which occurs later has very distinct similarities to wing-flashing. Figures 2 and 3 show the similarities of components. In both instances the legs are not bent much and the body is held high. The bent legs and lowered body would connote flight intention. In both, the tail-raising and subsequent lowering is involved. The tail comes up during wing-flashing and begging. In both series of photographs there is a lifting of the wings and a large extension of the hand. On occasion I have noticed balancing movements and wing-flashes done with one wing as well as with two.

At this point, another movement should be mentioned. It is possible to elicit a lifting of the wings with an extension of them, without the typical slight shivering seen in the begging-balancing movement. When perched on a stick which is moved downward, the bird will produce this movement. In addition one may sometimes elicit wing-flashes and wing-flicks by twisting the perch. This also elicits a tail-raising or lowering, depending in which direction the perch is twisted (Fig. 5). In this case there is no lowering of the body as in flight intention.

Since I have seen such a gradation of movements all of which are variations of wing-flashing and since I have seen low intensity wing-flashes which resembled wing-flicks in slow motion, I would like to suggest that both the wing-flicks and wing-flashes have a common basis in balance. Often definite balancing movements in adult birds can be seen. They consist of extending the hand and primaries out and then quickly drawing them in. The movement resembles an extended wing-flick. Daanje (1950) and Andrew (1956) believe wing-flicking to be a flight intention movement. Andrew (1956) believes both tail-flicking and wing-flicking to be ritualized intention movements which are given when a tendency to fly is accompanied by a tendency to give some incompatible response. These occur before flight and after landing. I would disagree with this because I have rarely see a wing-flick in

Mockingbirds occur when a bird was crouched. Andrew (1956) suggests that wing-flicking has lost its association with the other components of flight intention and has become emancipated from most of the other flight intention movements. Balancing would especially appear as a better explanation of the occurrence of wing-flicking upon landing when it would be of utmost importance. I have seen on many occasions a Mockingbird land with its wings extended in a wing-flash. In addition, following the assumption of Marler (1956) that the "functional acts" are more primitive than displays, balancing offers as good an explanation as flight intention because it too is functional. Since many birds have a balancing movement it is conceivable that they could have ritualized them into wing-flicks. The Mockingbird perhaps, in addition, has slowed these movements down and caused a ritualization of the wing-flash which could possibly serve as a social signal.

Hailman (1960*a*) suggested that since the wing-flashes he had seen during foraging did not resemble begging nor any other wing movements, and so must represent the acquisition of an entirely new behavior. However, I would agree with Cade (1962) who regards this as an assumption which goes against the rule of parsimony. He thinks a more likely idea would be that wing-flashing is a highly transformed or ritualized behavior derived from previously existing components which can no longer be identified with certainty.

Wing-flashing has occurred predominantly in the Mimidae. Occurrences have been reported in the Calandria Mockingbird (*Mimus saturninus*) (Halle, 1948), the Graceful Mockingbird (*Mimus gilvus*) (Haverschmidt, 1953), the Galápagos Mockingbird (*Nesomimus trifasciatus*) (Hundley, 1963), the Catbird (*Dumetella carolinensis*) (Batts, 1962), and young Brown Thrashers (*Toxostoma rufum*) (Whitaker, 1957), none of which have white wing patches. In addition, a probable homologous movement was observed in the California Thrasher (*Toxostoma redivivum*) (Sargent, 1940) and in the Curve-billed Thrasher (*Toxostoma curvirostre*) (Rand, 1941). Some of my conclusions as to the ontogeny and general conditions responsible for wing-flashing are similar to those of Rand. Other birds have been said to perform a movement called wing-flashing but the descriptions were usually too vague to judge any similarities. Vaurie (1957) mentions a similar movement in the courtship of the Western Red-legged Thrush (*Mimocichla plumbea*). Sutton (1946) speaks of a similar motion in captive Roadrunners (*Geococcyx californicus*) which caused insects to reveal themselves by moving but seems to have no other similarity to wing-flashing. Hailman (1959) reported a "wing-twitching" in the Starling (*Sturnus vulgaris*) which also functions in food getting. Monroe (1964) mentioned the exact behavior performed by the Red-backed Scrub-robin (*Erythropygia zambesiana*). This turdid species has a considerable amount of white in the wing. The foraging behavior was exactly like that of *Mimus polyglottos*. In feeding it would run, halt, elevate the tail, and wing-flash. The wing-flash consisted of a raising of the wings at an angle of 45 degrees to 60 degrees with the horizontal, in two movements with a pause in the middle. Dilger (1956) vaguely described a wing-flashing in the genera *Catharus* and *Hylocichla* which he did not compare to Mockingbird wing-flashing. The display was described as probably having been evolved and ritualized from an intention movement such as balancing or flying.

The most striking resemblance was described by Cade (1962) and was also reported by Zimmerman (1955) in Northern Shrikes (*Lanius excubitor*). Cade's description of a wing-flashing in these shrikes indicates similarity with two movements in Mockingbirds. From his description the low-intensity wing-flashing seems similar to the begging-balancing in Mockingbird fledglings. In this movement the wings are extended from the sides and are fluttered up and down rapidly during which the wing patches flash. He notes a similarity of this to the food-begging in young shrikes. During this wing-flashing the tail is spread and closes rapidly. At a higher intensity the movement seems similar to the highest intensity of Mockingbird wing-flashing (Fig. 4). In this case in shrikes the wings are greatly extended from the body but are drooped so that the primary tips are below the body axis and are swept forward with a conspicuous extension of the hands and a maximum exposure of the wing patches. The tail is also spread. Anatomically there may be some similarity but more importantly both behaviors occur under almost identical experimental conditions. In the case of the shrikes the movement occurred when a large rat was inserted in the cage, alive at first and then later when dead. In the latter case the bird still seemed reluctant to touch the rat and seemed to be testing to see if it would move. During this time wing-flashing occurred. It waned when the shrike seemed to lose interest in the rat. This situation of ambivalent behavior was noticed in Mockingbirds. Cade concludes that there is an association of this wing movement in hunting and hostile situations. With Mockingbirds if a large grasshopper is inserted in the cage the bird will approach it and the closer it gets to this new stimulus the more it appears to wing-flash. After pecking at the insect, the wing-flashing subsides. Wing-flashing appears to be due to a conflict of two motivational factors, slight fear or uneasiness and the incentive of food. This unsteady state may have led to the ritualization of the balancing movement so often employed during this conflict.

In discussing the evolution of wing-flashing it must be noted that five of the six species of Mimidae that do wing-flash do not have prominent wing patches. Thus if we regard the abundance of one character throughout the family as being an indication of its being more primitive, wing-flashing can be considered more primitive than white wing patches. Mimids have most probably originated in South or Central America as seen by the abundance of its members there. *Mimus polyglottos* probably originated south of its present range and is even now extending itself north. This would also point to the wing patches as an innovation. Therefore, in attributing a function to wing-flashing perhaps the place to look would be in those species without the wing coloration. The patches, if they have a function as a social signal such as in species identification or population density regulation, would signal during flight landing as well because in this motion Mockingbirds often behave similarly to shorebirds by spreading the wings way out to break the flight. The wing patches then become prominent. I did not notice this behavior in three observations of landings in Graceful Mockingbirds in Panama.

In conclusion, the majority of theories on the subject of wing-flashing hypothesize its derivation from some connection with food. Food-getting is a functional act and most important to the survival of the species. However, balance as well as food-getting and flight is a functional act and must not be overlooked in a hypothesis of the evolution of wing-flashing.

SUMMARY

The ontogeny of wing-flashing in 38 hand-raised young Mockingbirds was observed. All components of the wing-flash were investigated. Wing-flashing developed in both sexes in 9 to 13 days with the average on day 10 or 11. It also occurred in one bird visually isolated from all other birds. In addition the study revealed that the ontogenetical progression of behavior was not dependent upon the stimulus of being in the nest. Although the captive nestlings were out of the nest earlier than normal, they did not attain their fledgling behavior until the usual chronological age.

The form of wing-flashing varies to a great degree, and a whole gradation of responses was noticed, from an intense, fully extended wing motion without hitches to a slow, partial extension similar to wing-flicking. Wing-flashing first occurs at its highest intensity without previous practice or imitative learning. However, a begging-balancing motion is believed to be the precursor of wing-flashing due to many similarities between the two movements.

Wing-flashing was associated with an "uneasy situation" in birds up to 10 months old. This situation in which the birds are "wary" but not completely frightened is caused by: a) strange objects; b) unexpected movements, noises, or other stimuli; c) in semi-tame birds, coming too close to man and in young birds, being handled by man. Thus wing-flashing is related to food only as it pertains to such a situation involving large, live, moving insects. The amount of wing-flashing was also influenced by age, individualities of the birds, and tameness.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF MARYLAND, COLLEGE PARK, MARYLAND, 8 SEPTEMBER 1964