THE DEVELOPMENT OF GRASPING AND BALANCING COORDINATION IN NESTLINGS OF SEVEN SPECIES OF ALTRICIAL BIRDS

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STUDIES of nestling development in the summer of 1963 included the recording of grasping and balancing coordination in several species: the Catbird (*Dumetella carolinensis*), Cedar Waxwing (*Bombycilla cedrorum*), Cardinal (*Richmondena cardinalis*), Field Sparrow (*Spizella pusilla*), Traill's Flycatcher (*Empidonax traillii*), Indigo Bunting (*Passerina cyanea*), and Goldfinch (*Spinus tristis*).

There has been very little description previously of this phase of the development of nestlings. Lea (1942) found that Cedar Waxwing nestlings were able to move their toes but not grasp objects when 2 days old. Further, at 4 days of age the nestlings were unable to right themselves when placed on their backs. By the seventh day, the eyes were reported opening and nestlings could right themselves. On the ninth day they could support themselves on a perch.

King (1955) reported that Traill's Flycatcher nestlings sat erect on their tarsi on day 8 and on day 10 were able to perch on a finger. Laskey (1944) reported young Cardinals perching in the nest shrub when 9 days old. To my knowledge, no one has ever made a study comparing different species of nestlings with regard to the time when they could first balance on a perch. Since ability to grasp and balance on a twig or weed stem at fledging may have an effect on the success of the young bird in becoming an adult, the study of these characters may increase our understanding of age-specific mortality as discussed by Young (1963).

METHODS

These studies were made inside the city limits of Toledo, Ohio from mid-June through mid-September. The nesting areas were predominantly second-growth vegetation, railroad sidings, and dense hedgerows. Most nests were found before incubation had started; thus, the egg weights given in Table 1 represent fresh eggs that had not lost weight appreciably through incubation. Eggs were weighed to the nearest tenth of a gram with the use of a Harvard double-beam balance, on the day following the laying of the final egg.

Once a nest was discovered, it was checked daily for appearance of more eggs and to determine when incubation started, and when the eggs hatched. Individual eggs were not marked.

TABLE 1

AVERAGE EGG WEIGHT AND LENGTH OF INCUBATION PERIOD IN SEVEN SPECIES OF ALTRICIAL BIRDS

Species	Number of eggs weighed	Range of egg weight in grams	Mean egg weight in grams	Incubation period (days)	Source for incubation period
Cardinal	3	4.1–4.6	4.43	12 or 13	Laskey, A. R. (1944)
Catbird	8	2.6–3.5	3.08	12 or 13	Bent, A. C. (1948)
Cedar Waxwing	8	2.6–3.0	2.80	12.2	Putnam, L. A. (1949)
Indigo Bunting	7	1.5–2.3	1.89	12–13	Author
Field Sparrow	18	1.4–2.1	1.69	11 ± 0.5	Crooks, M. P., and G. O. Hendrickson (1953)
Traill's Flycatcher	17	1.4–1.8	1.58	12–14	Stein, R. C. (1958)
Goldfinch	153	0.8–1.6	1.26	12 days 21 hours	Walkinshaw, L. H. (1938)

Nestlings were checked daily for growth rate and gross morphological changes; this included recording of development of grasping and balancing coordination. A small weed or tree stem was used as the grasping and perching foothold. The ability of the young nestlings to grasp the stick was tested daily by placing them feetfirst on the stick and they were always given a second chance if they failed in their first attempt, but were not given more than two chances on a single day. This prevented any artificially induced development of abilities in the nestlings. If they could not grasp the stick they were not allowed to fall more than 2 or 3 inches to the hand of the investigator. The day of hatching was considered as day one.

Notation was made of time delay after hatching when nestlings acquired the ability to (1) grasp a stick for at least 5 seconds without balancing, (2) balance unsteadily, and (3) balance with good coordination.

RESULTS

Table 1 indicates that the average weight of eggs differs considerably among species, with a low of 1.26 grams in Goldfinches and a high of 4.43 grams in Cardinals. Catbirds and Cedar Waxwings also had larger eggs than did the other four species. The incubation period, however, varies but little among the seven species. Goldfinches had the smallest eggs, but they have an incubation period as long as the Cardinal and Catbird that have the larger eggs. Before reviewing the data, I assumed that perhaps the Goldfinches

TABLE 2

WEIGHT OF FLEDGLINGS AND DAY POSTHATCHING WHEN LEAVING NEST

Species	Day leaving nest	Approximate weight when leaving nest
Cardinal	11	30 g
Catbird	12 or 13	29 g
Cedar Waxwing	16	30 g
Indigo Bunting	10	12 g
Field Sparrow	7–9	10 g
Traill's Flycatcher	13 or 14	12 g
Goldfinch	13 or 14	12 g

might have hatched in a somewhat advanced developmental stage due to the relatively long incubation for such a small egg; due to this advanced development they might be advanced in their ability to grasp a foothold and balance earlier than Catbirds and Cardinals.

The results of the experimentation with nestlings are only given for those nests where the young developed normally; i.e., all of the nestlings received enough food.

Table 2 indicates the day after hatching on which the birds left the nest and also gives the approximate weight of fledglings in grams when they left the nest. It is readily apparent that the Goldfinch, Indigo Bunting, Field Sparrow, and Traill's Flycatcher are about the same size at this time. Cardinal, Cedar Waxwing, and Catbird fledglings all weighed nearly 30 grams when they left the nest. Some young birds left the nest before being able to balance well, thus the final column in Table 3 does not always represent the total number of nests observed.

As observed in Table 3, the Goldfinches were the earliest to develop the ability to *grasp* the stick (fifth day); the Catbirds were the latest in their ability to *balance* well (11th, 12th and 13th day). There was little variation (within species) in time after hatching when the remaining species could grasp well, except in the Traill's Flycatchers the time ranged from the sixth through the ninth days. There was little variation (within species) in the day after hatching when six of the seven species could balance well. The Catbirds appear to lag behind all the others in development of good balance.

When the young birds were first able to grasp the stick, they would always slip underneath and hang bottom-side up. As they attained better ability to grasp and balance they would hang from the side of the stick, attempting to use their wings as a balancing aid. However, in early development the alar tract was not feathered and therefore aided them but little. As good balance

TABLE 3

THE DEVELOPMENT OF GRASPING AND BALANCING COORDINATION OF NESTLINGS GIVEN IN DAYS POSTHATCHING

Species	Number of nests	Grasping	Unsteady balancing	Good balance
		(1)	(1)	(1)
Cardinal	1	7	9	10
		(1)(3)	(1)(2)(1)	(1)(2)(1)
Catbird	4	8, 9	10, 11, 12	11, 12, 13
		(2)	(2)	(2)
Cedar Waxwing	2	7	8	9
		(2)(1)	(1)(1)(1)	(1)
Indigo Bunting	3	6, 7	7, 8, 9	8
		(3)(1)(1)	(1)	
Field Sparrow	5	6, 7, 8	8	—
		(2)(1)(3)(2)	(1)(2)(4)	(2)(1)(4)
Traill's Flycatcher	8	6, 7, 8, 9	7, 8, 10	9, 10, 11
		(14)(11)	(2)(12)(8)(1)	(1)(10)(11)(1)
Goldfinch	25	5, 6	7, 8, 9, 10	8, 9, 10, 11

Numbers in parentheses designate the number of nests of nestlings represented for that day.

was attained the birds sat up well and used their wings but little, if any, as an aid for balance adjustments.

Ability to grasp the stick was present often before full vision was present. However, there was never good ability to balance until the eyes were fully open. Thus, the visual senses may be important for good balance. The early use of the vestibular apparatus, peripheral sensory receptors, gastrocnemius, and peroneus longus muscles, and especially the flexors of the digits aiding in perching may be of great importance. Feathers in the alar tract also may aid in later stabilization of balance, for often the nestlings spread their wings using the weight of the wing and the surface area of the feathers to aid in balancing.

DISCUSSION

Attentiveness in incubation or higher brooding temperature in the species laying larger eggs may account for the relatively small differences found in development of grasping and balancing in six of the seven species studied. In other words, perhaps birds laying larger eggs were more attentive in incubating their eggs or perhaps the birds laying smaller eggs were less attentive.

Skutch (1962) reported that increased constancy of incubation may possibly decrease the incubation period for some species. However, Prescott (1964) did not expect that increased constancy shortens the incubation period of the Scarlet Tanager. Stoddard (1946) reported that the Bobwhite

is more attentive to the nest in cool weather than on warm days, thus indicating that the constancy of incubation is effected by the environmental temperature. Wetherbee (1961) reported that artificially incubated eggs of the Catbird required a maximum of 317 ± 3 hours for incubation. Berger (1951) and Burns (1915) reported periods of incubation for the Catbird lasting up to 15 days which would be about 360 hours. Wetherbee also reported a maximum of 298 ± 9 hours of artificial incubation for the Cardinal, whereas Laskey (1944) found the incubation to be 12 or 13 days, a possible 312 hours. The evidence above indicates that constant incubation does shorten the length of time required for hatching.

Skutch used a formula for calculating the constancy of incubation which can be applied to some data from other sources. The formula is:

$$T = \frac{100\ S}{S + R}$$

where T is the constancy, S is the average length for the sessions of incubation, and R the average length of the recesses.

Putnam (1949) and Kendeigh (1952) found a constancy of 89 and 85 per cent, respectively, for the Cedar Waxwing. Applying the above formula to their data the same percentages are derived.

Laskey (1944), in reporting on the Cardinal, included limited data on the time the female was on and off the nest. A constancy of 90 per cent was found when the formula was applied. Application of the formula to Kendeigh's data on the Goldfinch gave a 94 per cent constancy for this species.

Zimmerman (1963) found an incubation constancy of but 64 per cent for the Catbird, and Kendeigh (1952) and Skutch (1962) reported a constancy of 75.9 and 78 per cent, respectively, for the Catbird. I could find no data indicating the constancy of incubation in the Indigo Bunting, Field Sparrow, or Traill's Flycatcher.

Skutch (1962) reported that instances of the acceleration of embryonic development by constant sitting are difficult to find. However, while there may be very little interspecific difference in the length of incubation as given in Table 1, the complete ontogeny of the nestlings may be somewhat slower in species whose incubation is less constant. The details of growth patterns and the development of coordination may reveal indirectly the effect of the constancy of incubation. Of the four species about which information is available, the Cedar Waxwing, Cardinal, and Goldfinch all have an incubation constancy above 85. The highest incubation constancy reported for the Catbird is about 78, ranging to a low of 64. The Catbird nestlings were the slowest in their ability to grasp or balance. This retardation of ability to coordinate body movements or develop muscle tonus, etc., may be due to retarded development at hatching due to effects of incubation while in the

egg. On the other hand, the exceptionally rapid development of ability to grasp and balance in the Goldfinch may be due to the relatively faster development of the embryo as a result of more constant incubation.

The development of abilities to grasp and balance may be faster in nestlings of some species because of genetically controlled characters that have adaptive significance. Sutton (1959) described the nestling Goldfinches as follows: "Nestling Goldfinches are wholly unlike the young of other fringillids which breed on the Reserve in that, during the latter days of their fledging period, they use their toes in clinging to the nest. There is a possible correlation between this propensity and the position of the nests far out on branches that toss in the wind, as well as between it and the clinging, climbing habits of the adult while feeding. Young Goldfinches which I have banded have clung so tenaciously to their nests that I have lifted the lining out with them." This may in part explain why the Goldfinch nestlings in the present study were the earliest in their ability to grasp and balance.

Wetherbee (1961) suggested that the whole life history of a bird and its biogenetic burden are involved in any real understanding of the developmental condition of the young at hatching. Perhaps when the embryos begin to develop, there may be faster development of anatomical structures which are prominent as adaptive characteristics of the species.

SUMMARY

Seven species of altricial birds were studied with regard to development of coordination in grasping and balancing.

There was little variation in incubation time among these species.

There was considerable variation in egg weights among species. Most nestlings could grasp a perching stick for at least five seconds by the seventh day after hatching.

Most nestlings could balance upright well by the 10th day.

Catbirds appeared slowest in development of this character among species studied.

Vision and equilibrium changes, development of peripheral sensory elements, muscular strength, and alar plumage may effect the development of grasping and balancing.

Greater nest attentiveness and/or *higher brooding temperature* may speed the development of the embryos of species laying the larger eggs, but incubating for nearly the same time interval as species laying smaller eggs. This may account for small differences noted in the day after hatching when grasping and balancing is well developed in nestlings of these different species.

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