

## VARIATION IN AVIAN BRAIN WEIGHTS WITH SPECIAL REFERENCE TO AGE

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Weights and other measurements of the brain are available for a number of Old World species of birds (see Portmann and Sutter, 1940; Portmann, 1942, 1946-1947, 1955, 1959; Sutter, 1943; Stingelin, 1957, 1960). Few data are available for New World species. Hancock (1887, 1888) has given brain weights for a few North American species, and there is a list of weights of organs presented by Crile and Quiring (1940) which includes some data on brains.

In a study of weight characteristics of nocturnal migrants, we noted (Graber and Graber, 1962:86) that immature specimens of passerine birds had heavier brains than adults. The nature of this difference between adult and immature birds deserved investigation, and we determined to pursue the problem whenever additional specimens became available. Thus, a large kill of nocturnal migrants at television towers in central Illinois in September, 1962, was a stimulus for this study. It is the purpose of the study to shed light on two questions particularly. (1) What is the nature of the difference between the adult and immature brain, and (2) does the age variation in the brain have potential utility in ageing populations of birds?

### METHODS

About 500 nocturnal migrants of 31 species were killed at television towers near Champaign and Springfield, Illinois, on the night of September 24-25, 1962. The following morning (September 25), Glen C. Sanderson and R. Graber of the Illinois Natural History Survey gathered birds at the two towers as quickly as possible. Although the specimens had been lying on the ground several hours when retrieved, the night and early morning were cool (about 60°F., or less), and weight loss should not have been excessive. Two specimens, an Ovenbird, *Seiurus aurocapillus* (initial wt.: 24.5 gm.) and a Red-eyed Vireo, *Vireo olivaceus* (19.4 gm.), left exposed to the natural environment on an overcast day when the temperature held almost constant at about 65°F., lost 0.8 per cent of initial gross in the first four hours, and 2.0 per cent after 28 hours. All specimens were processed in the same way; thus, differences in weight between species or between age and sex classes do not reflect differences in treatment. From the towers, the specimens were transported to a laboratory in Champaign where they were weighed, placed in plastic bags, and frozen to await dissection. Even those specimens dissected last (on October 10) showed less than one per cent loss in gross weight from the first weighing. Obviously broken specimens were not used in the study.

To learn more about variation in brain weight in younger birds particularly, we collected 108 specimens, including 25 nestlings, of House Sparrows (*Passer domesticus*) for dissection and weight analysis. Flying juveniles and adults were captured with mist nets. We killed the House Sparrows by collapsing their lungs but processed the specimens just as we had the migrants. The nestlings dissected were of known age, but older specimens were aged on the basis of plumage development and skull ossification patterns (Nero, 1951:85).

Because of its consistency fresh brain tissue is difficult to remove from the cranium. Donald Hyson, who helped us in the early phases of the study, found that it was relatively easy to extricate the brain, intact, from a frozen bird just as it was

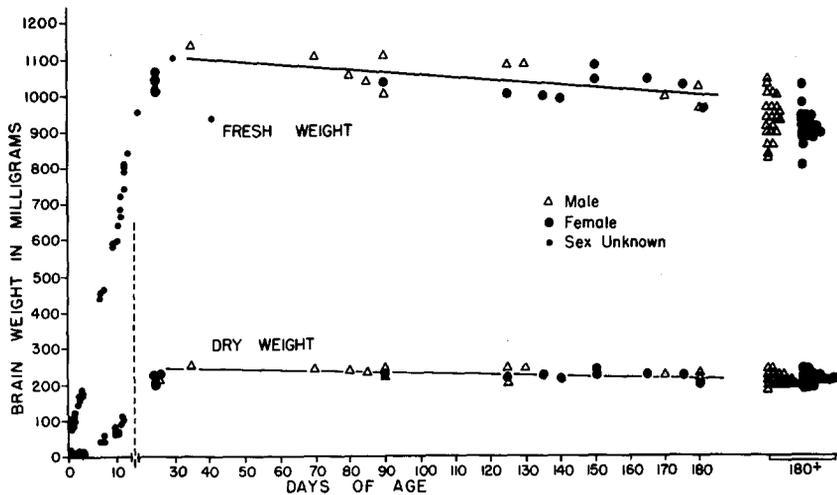


Fig. 1. Variation in weight of the brain of the House Sparrow in relation to growth and maturation. Age determinations beyond 15 days were based on plumage characters and the skull ossification pattern (after Nero, 1951).

beginning to thaw; we followed this procedure in all the dissections reported here. To excise the fresh brain, we first removed the skin from the head, then decapitated the frozen specimen, cutting, with scissors, as close as possible to the occipital condyle. We next removed the eyes and cut away the top and sides of the skull with fine surgical scissors. This left the brain largely exposed, resting on the floor of the cranium. A small, round-tipped forceps was then inserted under the stem and optic lobes, and the brain, still firm and cold, was lifted out, usually intact, sheathed in the dura. Only the stubby bases of the cranial nerves remained attached to the brain. The fresh brain, with meninges, was placed in a small (50 mg.) aluminum weighing dish and weighed immediately on a Roller-Smith Micro Torsion balance (sensitivity: 0.2 mg.). After the fresh weight was recorded, the brain was dried to constant weight in a forced-air oven at 80°C.

To make lipid determinations on the brain tissue, we placed the dried brains (each wrapped in gauze) in an extraction thimble in a soxhlet and extracted the tissue 48 hours with ethanol (99 per cent) and 48 hours with petroleum ether (Skelly F). Following extraction, each specimen was dried and reweighed. Weight loss from extraction represented the lipid content of the brain. In discussing the composition of the brain, we have, unless otherwise stated, related percentage figures to the fresh weight of the whole brain rather than to its dry-matter content. For the species we studied, we have data on the water content of the brain, its lipid content, and the remaining nonfat dry matter. The nonfat dry fraction consists largely, but not entirely, of protein, and when we refer to protein content in our own specimens, we do so in this context.

As a relative index to age of our specimens, we have used primarily the skull ossification (pneumatization) pattern. The studies of Nero (1951) and Harrison (1960-1961) show that, within a species, the skull ossification rate and pattern provide a reasonably dependable index for ageing, although there is considerable variation between species in the time required to reach full pneumatization (Harrison and

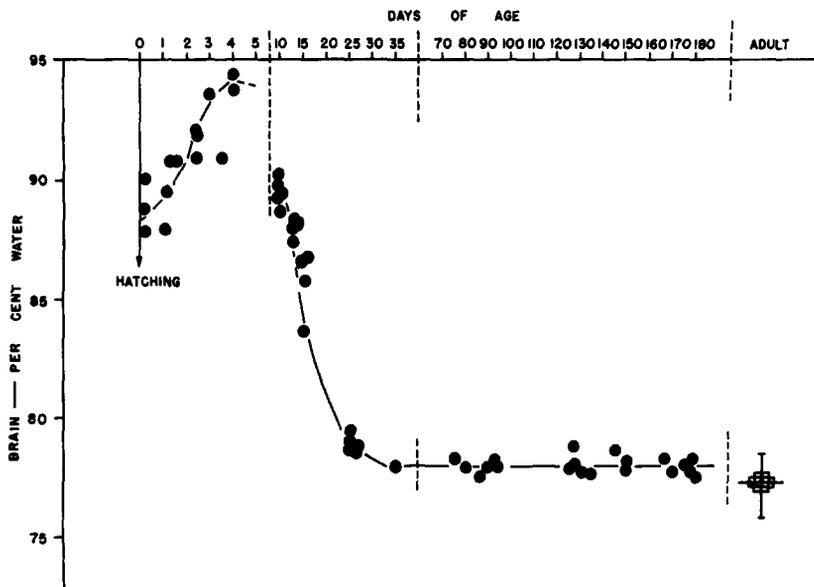


Fig. 2. Variation in the water content of brains of House Sparrows, related to growth and maturation. Age determinations beyond 15 days were based on plumage characters and the skull ossification pattern (after Nero, 1951).

Harrison, 1949:62). It should be noted, however, that the skull ossification pattern may at times be misleading. Selander (1958:369) found that in some populations a few birds do not complete ossification during the first year.

Reference to significance in this paper indicates statistical significance at the one per cent level of probability (or better) based on the *t* test. We have also noted certain apparent trends that appear in species after species but which need to be tested statistically with larger samples of specimens.

Because we have information on the early postembryonic stages of brain growth in the House Sparrow, but not for other species, we will discuss this sparrow first and the others in phylogenetic sequence.

#### BRAIN WEIGHTS IN VARIOUS SPECIES

*House Sparrow.*—The fresh brains of two neonatal House Sparrows weighed 82 and 88 mg. From this stage, brain weight increased rapidly to 850–950 mg. in juveniles 15 to 20 days of age. The brain reached its maximum weight (1140 mg.) about 35 to 40 days from hatching, and then started a gradual decline (fig. 1). It continued to lose weight at least beyond the completion of skull ossification, that is at 180 to 190 days of age (Nero, 1951:85).

The regression line for decrease in brain weight in the House Sparrow (fig. 1) indicated an average loss of about 0.7 mg. per day between the ages of 35 and 180 days. At this rate of decline, the age represented by the mode of brain weights (910–920 mg.) in our sample of adult specimens would be about 10 months. The lowest brain weight in adults in our sample was about 800 mg., the equivalent of 16 months on the regression line. Our extrapolation assumed a constant rate of decline, and

although the rate appeared to be fairly constant to the age of about 180 days, it is possible that in older birds the loss in brain weight either slows in rate or stops altogether. Data presented by Sutter (1943:40) showed that in the Starling (*Sturnus vulgaris*) the weights of the cerebral hemispheres and cerebellum were still declining in birds 330 days old, whereas the brain stem (especially) and corpora bigemina actually increased slightly in weight in birds over 150 days of age.

The bird brain is largely water, and its presence accounts for most of the difference in brain weight between immatures and adults. The sequence of changes in hydration of the brain in the first 30 to 40 days of a bird's life is especially interesting (fig. 2), because throughout this period, during both the initial saturation and the later reduction in water content, the brain is increasing in weight at a rapid rate (fig. 1). During early nestling life the striking increase in brain weight represents mainly increased hydration. The protein and lipid components of brain tissue develop mainly just before and after the bird fledges. Between the time of fledging (about 15 days) and the attainment of maximum brain weight (about 35 to 40 days), brain growth represents a great increase in the dry-matter content and a consequent relative decline in the water content of the tissue. In early (post-hatching) stages of brain development, then, weight changes reflect, first, a phase of marked hydration with little tissue growth, and, second, a phase of rapid tissue development and relative dehydration. In the later juvenal stages (after 35 to 40 days of age) water content of the organ declines very slowly as the bird matures (fig. 2).

Even juveniles between the ages of 100 and 180 days had heavier brains than adults. For juveniles in this age group, fresh brain weight averaged 1031 mg. (water content, 805 mg. or 78.0 per cent of fresh weight; fat content, 90 mg. or 8.6 per cent). Average brain weight for adults was 922 mg. (water content, 713 mg. or 77.3 per cent; fat, 89 mg. or 9.7 per cent). Except for lipid weights, differences in brain weights between adults and immatures were significant at the one per cent level. Although the difference in lipid content was not significant, it should be noted that nearly every species examined showed the same trend, that is, fat weights were higher in immatures than in adults. The data suggest that fat content of the brain reaches a peak either in the later juvenal stages or in the young adult.

Brain weight in the House Sparrow did not appear to vary seasonally. Eleven adult males collected in June and July had an average gross weight of 28.3 gm. and a mean fresh brain weight of 938 mg. In a November sample of 11 adult males, gross weight was up to 30.4 gm., but brain weight (935 mg.) did not differ significantly from that in the summer sample. Our data also suggest that there is no diurnal variation in brain weight in the House Sparrow; specimens collected at 6:00 a.m. (CST) had the same average brain weight as specimens collected at noon and 8:00 p.m. on the same day.

*Swainson Thrush.*—In our sample of 38 Swainson Thrushes (*Hylocichla ustulata*), only seven were obvious immatures, all with skulls largely unossified. Those immatures in the sample showing the least extensive ossification had the smallest (in weight) brains of the immature group, a fact which suggests that the brain is still growing in some birds even after they have begun active migration.

Fresh brain weights for immature Swainson Thrushes averaged 1003 mg. (water content, 792 mg. or 79.0 per cent; fat, 86 mg. or 8.5 per cent). In adults brain weight averaged 837 mg. (water, 649 mg. or 77.5 per cent; fat, 81 mg. or 9.7 per cent). Differences in brain weights between immatures and adults were significant at the one per cent level, except in the case of lipid content (see comments under

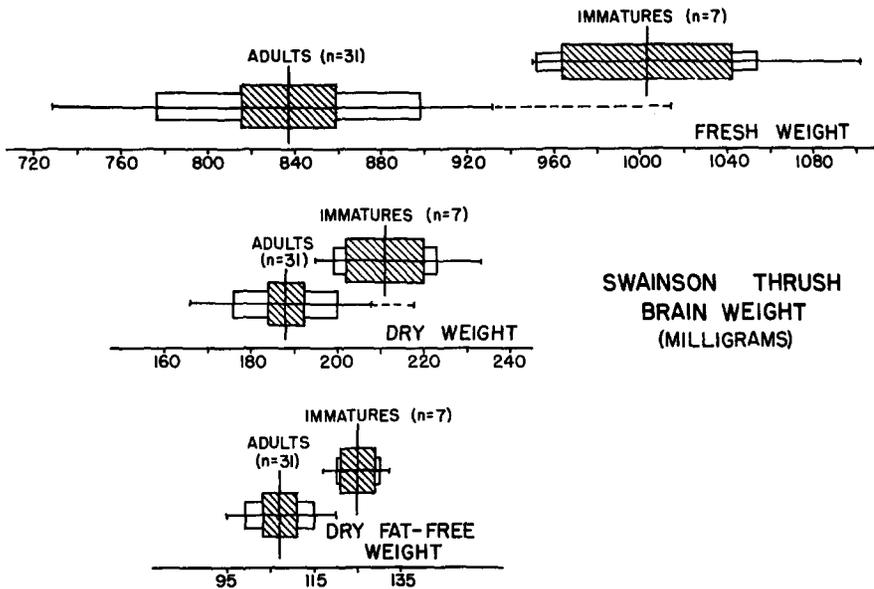


Fig. 3. Brain weights of Swainson Thrushes, showing range (horizontal center line), mean (vertical center line), and 2 standard errors (shaded box) and 1 standard deviation (open box) on each side of the mean, for both age groups. The broken portion of the range line represents only one specimen, probably an immature that has reached the stage of full skull pneumatization.

House Sparrow). Only one bird with a fully ossified skull had a brain weighing more than 935 mg. (fig. 3). In this specimen, both the size of the brain (1014 mg.) and its relatively high water content (78.5 per cent) indicate immaturity, and we would judge that the bird was actually an immature hatched early in the nesting season of 1962. The greater coverts of this specimen were unspotted, but Dwight (1900:311) indicated that precocious immatures may have unspotted coverts. Brain weight may thus provide a helpful index to age ratios and hatching dates, supplementing ossification data and plumage characters.

As in the House Sparrow, water accounted for much, but not all, of the weight difference between adult and immature brains in thrushes (fig. 3).

*Gray-cheeked Thrush.*—Our sample of 29 Gray-cheeked Thrushes (*Hylocichla minima*) included nine immatures. As in other species the brains of immatures weighed significantly more than those of adults. Among immatures the youngest birds had the smallest brains, suggesting that brain growth was still in progress in these specimens. These youngest birds were probably at least 30 days old; late egg dates for this species occur in July (Bent, 1949:199). From this age, the increase in brain weight appears to represent water as well as protein and fat (fig. 4). The series of males shows the apparent progression in average weights for different age groups. Thus, the youngest males had brains weighing 920 mg. (water content, 722 mg. or 78.8 per cent; protein, 119 mg. or 12.9 per cent; fat, 79 mg. or 8.3 per cent); the oldest immatures had brains weighing 955 mg. (water, 747 mg. or 78.2 per cent; protein, 125 mg. or 13.1 per cent; fat, 83 mg. or 8.7 per cent); and brains of adult males weighed 854 mg. (water, 660 mg. or 77.3 per cent; protein, 109 mg. or 12.9

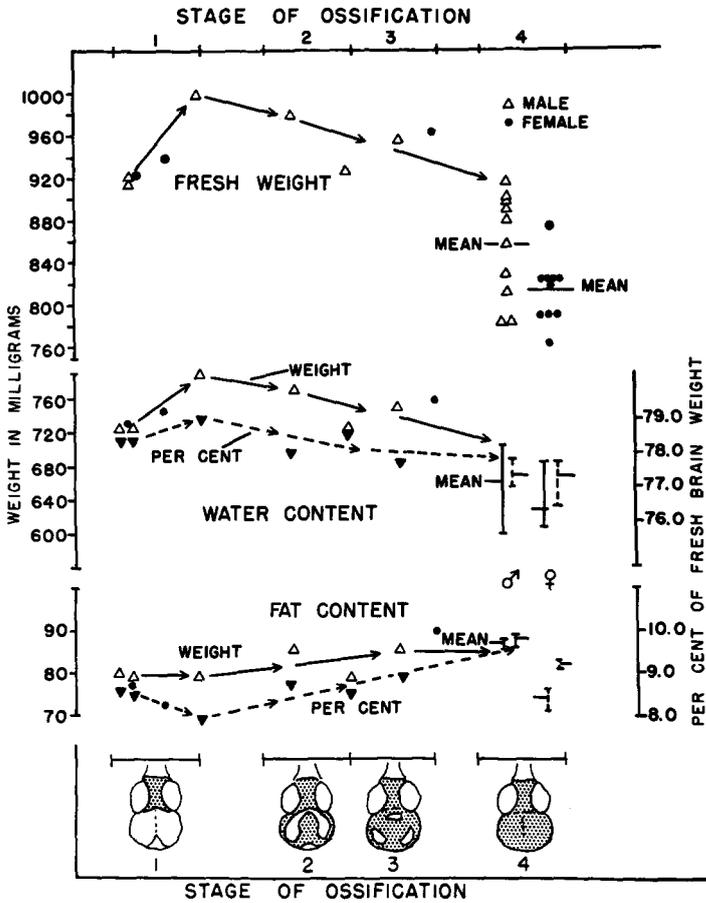


Fig. 4. Variation in fresh weight, water content, and fat content of brains of Gray-cheeked Thrushes. Solid arrows represent actual weight variation in milligrams (left hand scale). Broken lines represent the weight changes expressed as per cent of fresh brain weight (right hand scale). Shading in skull patterns represents the extent of pneumatization (age index).

per cent; fat, 85 mg. or 9.8 per cent). Note that the actual fat content of the brain was almost as high in the oldest immatures as in the adults. Males tended to have brains with more fat than did females, especially in the adults (fig. 4).

*Tennessee Warbler.*—In the Tennessee Warbler (*Vermivora peregrina*), as in other species, adults had relatively drier, smaller brains than immatures. There was, however, less difference in brain weight between adults and immatures in this species than in most other species examined, although differences in brain weight between immatures and adults were significant at the one per cent level, except in lipid content. Fresh brain weight of the six known immatures in our sample of specimens varied from 408 to 458 mg., and averaged 435 mg. (water content, 336 mg. or 77.2 per cent; fat, 41 mg. or 9.5 per cent). In adults brain weight varied from 328 to 429 mg., averaging 389 mg. (water, 298 mg. or 76.6 per cent; fat, 38 mg. or 9.8 per cent). By comparison with other immature birds examined, immatures of this species had

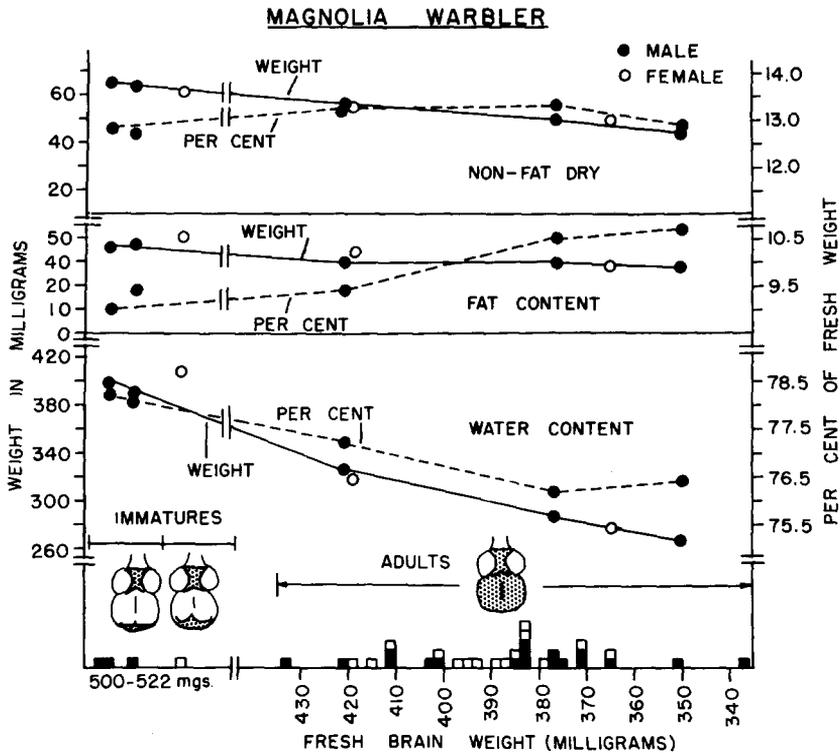


Fig. 5. Variation in the fresh weights, water content, fat content, and protein content of brains of Magnolia Warblers. Shading in skull patterns represents the extent of pneumatization (age index). Data on the chemical composition of the brains are presented in terms of the actual weight of the water, fat, and nonfat dry matter in each brain (left hand scale), and in terms of the percentage these substances comprise of the fresh brain weight (right hand scale). Distribution of fresh brain weights in the sample is shown on the lower scale. Black symbols represent males, open symbols, females.

brains with relatively low water content and a high fat level. Note especially the higher level of hydration in immatures of two species of *Dendroica* (see beyond).

*Magnolia Warbler*.—The distribution of brain weights for 37 Magnolia Warblers (*Dendroica magnolia*) is shown in figure 5. Fresh brains from the four immature specimens averaged 513 mg. (water content, 402 mg. or 78.4 per cent; fat, 48 mg. or 9.4 per cent). For adults the average of fresh brain weights was 389 mg. (water, 297 mg. or 76.3 per cent; fat, 40 mg. or 10.4 per cent). The actual fat content of the brain was higher in immature birds than in adults. The percentage of fat in the brain is consistently higher in adults because of the water loss which accompanies maturation. While the difference in lipid content of the brain between immatures and adults was not statistically significant, nearly all species examined showed the same trend. Other differences in brain weights between immatures and adults were very significant.

*Bay-breasted Warbler*.—The distribution of brain weights for 42 Bay-breasted Warblers (*Dendroica castanea*) is shown in figure 6. Fresh brains of immatures averaged 540 mg. (water content, 422 mg. or 78.1 per cent; fat, 50 mg. or 9.3 per

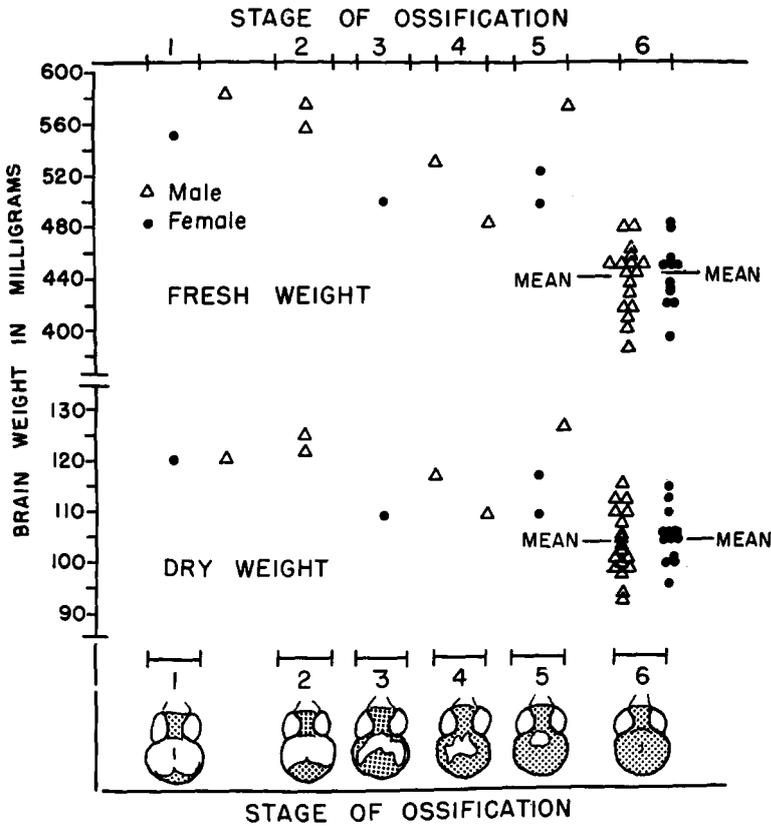


Fig. 6. Brain weights of Bay-breasted Warblers. Shading in skull patterns represents the extent of pneumatization, an age index.

cent). Average weight for adult brains was 443 mg. (water, 338 mg. or 76.4 per cent; fat, 49 mg. or 11.0 per cent). See comments on statistical significance under Magnolia Warbler.

*Ovenbird*.—Distribution of weights of fresh brains from 46 Ovenbirds (*Seiurus aurocapillus*) is shown in figure 7. The average weight for brains of 14 known immatures was 756 mg. (water content, 591 mg. or 78.1 per cent; fat, 67 mg. or 8.8 per cent). For adults the average of brain weights was 647 mg. (water, 499 mg. or 77.1 per cent; fat, 65 mg. or 10.0 per cent). At least three specimens with fully ossified skulls were probably actually immatures; all had heavy brains (over 680 mg.) with water content over 78 per cent. For comments on statistical significance of differences see under Magnolia Warbler.

*American Redstart*.—Our sample of specimens of the American Redstart (*Setophaga ruticilla*) showed a lower ratio of immatures to adults (3 : 52) than any other species examined. Only one of the immatures (a female) was dissected; its brain weighed 398 mg. (water content, 313 mg. or 78.7 per cent; fat, 39 mg. or 9.8 per cent). For adult redstarts, average brain weight was 312 mg. (water, 237 mg. or 76.1 per cent; fat, 34 mg. or 11.0 per cent).

*Bobolink*.—Our sample of Bobolinks (*Dolichonyx oryzivorus*) consisted of four

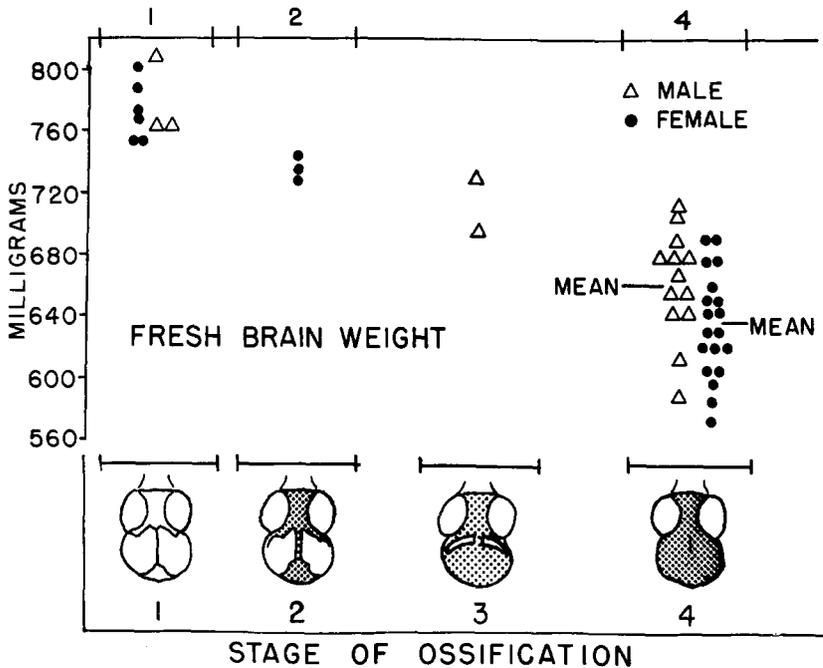


Fig. 7. Brain weights of Ovenbirds. Shading in skull patterns represent the extent of pneumatization, an age index.

immatures and nine adults. The fresh brain of the only immature male in the group weighed 1232 mg. (water content, 974 mg. or 79.1 per cent; fat, 111 mg. or 9.0 per cent), while the heaviest brain among immature females (fig. 8) weighed only 1052 mg. (water, 827 mg. or 78.6 per cent; fat, 95 mg. or 9.0 per cent). Notable sexual dimorphism in brain weight was apparent in adult specimens also. The average weight for brains of adult males was 1011 mg. (water, 783 mg. or 77.4 per cent; fat, 103 mg. or 10.2 per cent) and for adult females, 907 mg. (water, 700 mg. or 77.2 per cent; fat, 91 mg. or 10.0 per cent). Differences in brain weights between sexes and between immatures and adults were significant at the one per cent level, except in lipid content.

Migrant Bobolinks are noted for their extremely high fat loads. Judging from fat-free weights presented by Connell, Odum, and Kale (1960:7), fat accounted for about 65 to 75 per cent of the gross weight of Bobolinks in our sample. These percentages are from two to three times higher than the fat levels in the fattest of the other species considered here, yet fat content of the brains of Bobolinks was not higher than in several other species (table 1). We calculated that gross fat accumulations of individual adult Bobolinks in our sample varied from 11 to 22 gm., and brain fat varied from 83 to 112 mg., but there was no significant correlation in this series, between fat content of body and fat content of brain; in fact, there tended to be negative correlation ( $r = -0.70$ ).

*Rose-breasted Grosbeak.*—Our sample of Rose-breasted Grosbeaks (*Phœnicurus ludovicianus*) included two immatures and 27 adults. The fresh brain of an immature male with skull largely unossified weighed 1483 mg. (water content, 1162 mg. or

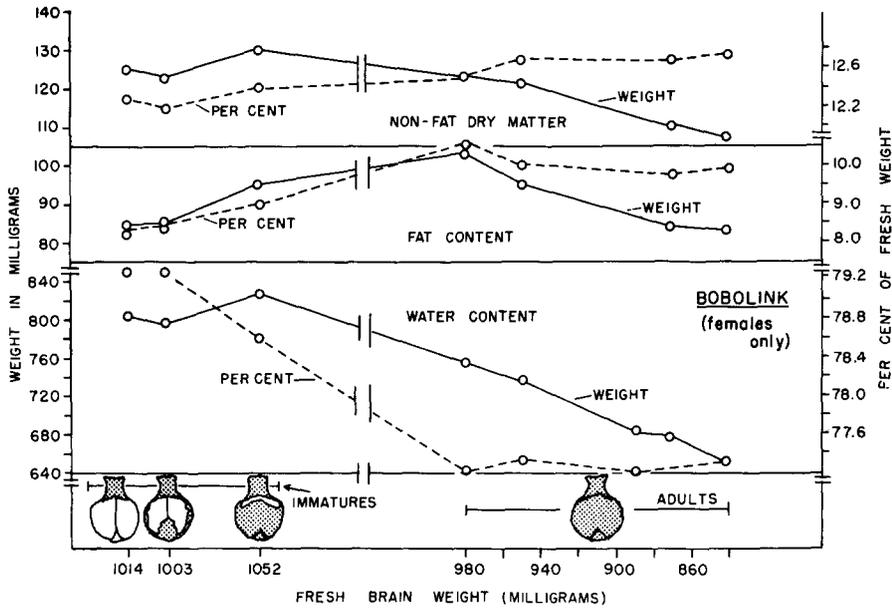


Fig. 8. Variation in the water, fat, and protein content of the brain in specimens of female Bobolinks. Shading in skull patterns represents the extent of pneumatization (age index). Data on the chemical composition of the brains are presented in terms of the actual weight of the water, fat, and nonfat dry matter in each brain (left hand scale) and in terms of the percentage these substances comprise of the fresh brain's weight (right hand scale).

78.3 per cent; fat, 144 mg. or 9.7 per cent). Fresh brain weights of adults averaged 1266 mg. (water, 979 mg. or 77.4 per cent; fat, 131 mg. or 10.3 per cent).

DISCUSSION

Although there is a paucity of data on the growth and development of the brain in New World species of birds, studies by Latimer (1925), Portmann (1938, 1955, 1959), Portmann and Sutter (1940), Sutter (1943, 1944, 1950), Kocher (1948), and Haefelfinger (1958) provide extensive data on various aspects of the subject for species of *Gallus*, *Phasianus*, *Coturnix*, *Melopsittacus*, *Columba*, *Tyto*, *Micropus*, *Apus*, *Jynx*, *Corvus*, *Turdus*, and *Sturnus*. Portmann (1938, 1946-1947, 1959) and Sutter (1943, 1951), particularly, pointed out basic differences in brain development between altricial and precocial species. The brains of precocial species, advanced at hatching, have generally low cerebral indices, while altricial species, poorly developed at hatching, attain high cerebral development (see also Portmann and Stingelin, 1961:7). The time of completion of the mitotic phase of brain development is apparently unknown for any altricial species, but in the precocial chicken, the cell pattern of the brain is essentially that of the adult pattern by the 12th day of incubation, although the cells are small and growth from this stage involves expansion of cell size (Romanoff, 1960:280).

The pattern of postnatal development of the brain is apparently very similar in a number of passerine species. The sequence of events in this development parallel, to some extent, the development of the skull and the growing need by the bird for an

TABLE 1  
FRESH WEIGHTS, WATER CONTENT AND FAT CONTENT OF BRAINS FROM ADULT BIRDS OF  
VARIOUS SPECIES

Species	No.	Sex	Mean gross wt. (gm.)	Mean brain wt. (gm.)	Standard error	Per cent water	Per cent fat
Swainson Thrush	16	M	32.2	0.824	0.012	77.4	9.7
	15	F	30.6	0.839	0.015	77.5	9.7
Gray-cheeked Thrush	10	M	33.8	0.854	0.016	77.3	9.8
	10	F	30.6	0.811	0.010	77.3	9.2
Tennessee Warbler	9	M	10.0	0.379	0.008	76.4	9.8
	7	F	9.8	0.402	0.006	76.8	9.9
Magnolia Warbler	18	M	8.6	0.386	0.006	76.2	10.2
	15	F	8.1	0.392	0.004	76.4	10.6
Bay-breasted Warbler	18	M	12.4	0.441	0.006	76.4	10.8
	13	F	12.6	0.446	0.007	76.4	11.4
Ovenbird	13	M	20.2	0.662	0.010	77.2	10.1
	20	F	19.0	0.637	0.009	77.0	9.9
American Redstart	19	M	8.5	0.317	0.005	76.2	10.9
	17	F	8.1	0.307	0.005	76.0	11.5
House Sparrow	23	M	29.4	0.936	0.013	77.3	9.7
	22	F	29.9	0.912	0.009	77.4	9.6
Bobolink	4	M	41.3	1.011	—	77.4	10.2
	5	F	40.2	0.907	—	77.2	10.0
Rose-breasted Grosbeak	13	M	47.3	1.269	0.014	77.4	10.2
	12	F	47.6	1.263	0.014	77.5	10.3

increasingly complex central nervous system. The cerebral requirements of the altricial neonate are modest, and the precipitous weight increase of the brain during early nestling life represents marked hydration rather than rapid protein or lipid formation. In this period, water comprises well over 90 per cent of the brain's weight (fig. 2, and Sutter, 1943:67). The lipid and protein content is thus necessarily low at this stage. The significance of the marked hydrocephaly in the nestling is unknown. This abruptly increased water load in the cranium must represent something of a physical burden to the neonate, which often seems to be straining to hold its head aloft to feed, and typically rests with head deeply bowed ("egg" or "embryo" posture). Banks (1959:100) noted that this posture was characteristic of nestling White-crowned Sparrows (*Zonotrichia leucophrys*) until the fifth day. Water, although heavy, would appear to be an excellent protective matrix in which to grow delicate nerve tissue. Young tissues in general seem to be characterized by high water content.

Just as the early postnatal weight increase of the brain is characterized by hydration, the immediate pre- and post-fledging period is characterized by the marked increase in lipid and protein components. Migrants, such as immature thrushes of the genus *Hylocichla* and northern warblers, were apparently still adding to the lipid and protein content of their brains during migration hundreds of miles south of their nesting grounds; thus, this phase of the development may continue for months. Behavioral changes appear to be correlated with these chemical changes. Kuhlmann (1909:56) referred to the altricial neonate as being inert, but the nestling's survival would appear to depend very little on the bird's cerebral attributes. Nesting success among passerines is probably influenced more by the location of the nest site (see Nice, 1957:311) and possibly camouflage of the plumage (see Ingram, 1960:341).

Thorpe (1951:20), citing the work of Tinbergen, suggested that improvement in skill, independent of practice, was largely related to growth of the nervous system itself, and Scott (1962:957) pointed out that the acquisition of motor and intellectual skills depends on the relative rate of maturation of various organs. Because lipids and proteins develop slowly in the brain, development of motor coordination is necessarily slow. Even among relatively "quick-fledging" fringillids, coordination is poor until late in the nestling period. Thus, White-crowned Sparrows attain a crouching posture for the first time on their fifth day (Banks, 1959:100), Vesper Sparrows (*Pooecetes gramineus*) can first stand (awkwardly) on their sixth day (Dawson and Evans, 1960:339), and Song Sparrows (*Melospiza melodia*) rapidly acquire motor coordination at seven to nine days of age (Nice, 1943:14). The fact that coordination develops rapidly late in the nestling period is particularly interesting, because this is also the time of rapid development of solids (lipids and proteins) in the brains of altricial birds (fig. 1; and data presented by Sutter, 1943; Kocher, 1948). Fledging greatly increases the demand for awareness, and motor capability in the bird, and Nice (1962:156) noted that development of coordination is accelerated in species which characteristically fledge early. Portmann (1959) has hypothesized that certain features of growth and differentiation of the brain cannot be contracted to much less than 11 to 14 days, because both altricial and precocial types appear to require this amount of time to reach that particular growth stage. Although Portmann and Sutter (1940:202) theorized that fledging in passerines was related to the completion of growth of the cerebral hemispheres, later studies (including this) indicate that brain growth may not be completed in any species of bird at the time of fledging.

Protracted brain growth in passerine birds is particularly interesting in view of the relatively sophisticated behavior (nest building, parental behavior, and so on; see Nice, 1943, 1962) evinced by some juveniles during the postfledging period. Pertinent here is the relationship between brain growth and orientation ability of birds. The native species considered in this paper are all primarily nocturnal, long-distance migrants of acknowledged orientation ability. We might logically expect that this ability has some dependence on the brain, yet most of the immatures were still in the process of developing the makeup and organization of the mature brain. Sauer (1958) showed that navigation ability is exhibited by immature birds, but the question of when the ability arises, relative to the course of brain development, remains to be answered.

#### BRAIN WEIGHTS, MATURATION, AND AGEING

Following the sharp increase in brain weight from the time of hatching through a hydration stage in early nestling life, and (later) a rapid tissue-growth stage, the brain in passerines reaches its maximum weight sometime before skull ossification is completed. The time required to attain maximum brain weight varies between species. For example, the House Sparrow and the Starling achieve maximum brain size at about 30 to 40 days of age (fig. 1; Sutter, 1943:37), whereas the brain of the Alpine Swift (*Apus melba*) is still increasing at 55 days (Kocher, 1948:63) and the pigeon (*Columba livia*) attains maximum brain weight at about 100 days of age (Koch and Riddle, 1919:90). There is even greater variation in the time required for dry matter in the brain to reach maximum weight (30 to 40 days for the House Sparrow, fig. 1; 250 or more days for the Starling, Sutter, 1943:37). This dry matter consists largely of proteins and lipids. Koch and Riddle (*op. cit.*:102) showed that in pigeons of various ages, proteins accounted for 47 to 51 per cent of the brain's dry matter, lipids

36 to 39 per cent, and the two combined, 85 to 87 per cent. Mitchell (1948:720) stated that the glycogen content of the brain amounts to less than 0.1 per cent and that nerve cells apparently contain no significant amount of carbohydrate reserve.

The principal gross constituents of the brain (water, protein, and lipids) all vary in quantity with age. In the postfledging period, when brain weight in passerines reaches its peak, the water content of the brain is at its maximum weight, although not its maximum percentage (fig. 2). Beyond this stage, the water content of the brain (both weight and percentage) declines, while its fat content (percentage, but not necessarily weight) is increasing. These changes have definite parallels in other animals. In the human brain, water decreases with maturation of the individual, while cholesterol and other lipids increase (Macarthur and Doisy, 1919:467-468). In the rat, water content of the brain declines at least to 530 days of age (Donaldson and Hatai, 1931:289). This change is particularly striking in the brain stem of the rat, but in birds (see Koch and Riddle, 1919:96; Sutter, 1943:40) the cerebrum shows the most marked dehydration. Because water so dominates the pattern of weight changes in the brain, it may be misleading to emphasize the relative (percentage) changes in the brain's fat and protein content. In the absolute terms of weight, even the protein and fat content of the brain appears to decline in passerines after reaching a peak during maturation. In nearly every species examined, the weight of fat in the brain was higher in immatures than in adults. Fat content of the brain apparently reaches a peak in the young adult or in the immature at about the time the skull becomes fully ossified.

In passerine birds, decline in brain weight during maturation continues at least beyond the time of complete skull pneumatization (figs. 1, 4, 6, 8). Sutter's (1943:40) graphs for the Starling indicate that the cerebrum and cerebellum are still losing weight 330 days after hatching. In man, brain-weight decline begins sometime before the age of 20 years and continues throughout life (see Pearl, 1905:53-56). Despite the apparent similarity between altricial mammals and altricial birds in these maturation characteristics, precocial birds do not appear to show brain-weight decline. Various parts of the chicken's brain reach maximum weight between 130 and 170 days of age (Latimer, 1925:296), but the brain shows no subsequent decline in weight by the 300th day. Figures on the Ring-necked Pheasant (*Phasianus colchicus*) and the Japanese Quail (*Coturnix coturnix*), presented by Sutter (1943:29), indicate that brain weight in these species is still increasing at 240 days of age. Obviously, striking differences between altricial and precocial development (Sutter, 1943, 1951; Nice, 1962) continue past the juvenal stage.

Gerontology, even relating to human studies, is in its early stages, but it is known that the central nervous system in particular shows the effects of age (Shock, 1962:100-102). The weight loss of the brain, with age, may to some extent represent the disintegration of nerve tissue. Ellis (1920:24) observed that the number of Purkinje cells in the human cerebellum declines steadily from birth to old age and (p.32) this decline appears to be correlated with the impairment of motor strength and skill in old age. Similarly, in examining chicken cerebellums, we have often seen Purkinje cells in various stages of disintegration. Although cut nerve fibers have been known to regenerate (Young, 1948:57), degenerating neurons are rarely replaced, at least in mammals (Maximow and Bloom, 1952:196).

Apparently, little is known about ageing and old age in birds. In view of the marked and consistent changes which accompany ageing in a variety of species of animals (Strehler, *et al.*, 1960), there are probably useful morphological or physiologi-

cal age characters to be discovered for many species of birds. Our data show that the brain in passerine birds continues to lose weight beyond the time when other commonly used marks of age disappear. This poses the question of whether the brain continues to lose weight throughout the life of the individual, as in the case of man (see preceding discussions). If so, brain weight could have utility in ageing populations of birds in much the same way that the eye lens has been used in ageing mammals (Lord, 1959). In species, such as the northern thrushes and warblers, which have a well synchronized, relatively short reproductive period in their annual cycle, we might logically expect that the weights of brains from a sample of adult birds would show a "clumped" (polymodal) distribution. The clumps (modes) would represent different age (year) classes, and the spaces between modes would represent the months of the annual cycle in which no production of young occurred. This hypothesis could be tested statistically with a very large sample of birds, such as that reported by Kemper (1964). Such age-variable characteristics as the numbers of certain types of cells (for example, the Purkinje cells already mentioned) and the accumulation of certain pigments or other cell inclusions in nerve cells (Ariëns Kappers, Huber, and Crosby, 1936:17-19; Sosa, 1953:395) offer other paths of investigation of age characteristics. Despite the inherent difficulties of working with brain tissue, almost any age character is better than none for students of population biology.

Although we have emphasized intraspecific variation in the brain, interspecific variation in brain size and structure among birds has long intrigued ornithologists (Turner, 1891; Portmann, 1942; Sutter, 1951; Stingelin, 1960; and others). Within rough limits, organ weight (size) is genetically tied to the size of the animal. To compare the size of the brain between different species, therefore, gross size of body should be taken into consideration. Amadon (1943:176) pointed out that weight measurements reflect differences in general size more sensitively than do linear measurements, and we have used weight as an index to the size of the brain and body. Our impression of the size of the body based on weight of a given bird may be vastly distorted, however, because of large accumulations of stored fat on the bird's body. Such accumulations are particularly characteristic of long-distance migrants (Odum, 1960:575) like those considered in the present study. Even among these migrants, the amount of body fat varied greatly from species to species. Based on published fat-free weights, the fat load in our migrant specimens varied from about 17 per cent (of lean weight) in female Swainson Thrushes to 75 per cent in female Bobolinks. The amount of fat in the brains of these specimens also varied from species to species (table 1), but Bobolinks, which carried by far the greatest fat load, did not have the fattest brains. Furthermore, within a species, fat individuals had no more fat in their brains than lean individuals. Because body fat has no apparent bearing on brain weights and distorts our impression of body size, it seems logical to base interspecific comparisons of brain size on fat-free gross weights (fig. 9) rather than on standard gross weight.

On this basis, it is clear that brain weight, relative to body size, varies considerably from species to species. In general, brain size (relative to body size) decreases as body size increases (fig. 9). Thus, a Bobolink has a relatively smaller brain than a Tennessee Warbler. Brody (1945:626) stated that brain weight in mature mammals of different species varied with approximately the 0.70 power of body weight, and noted that the exponent was considerably less for birds. The regression which best fits our brain-weight data to gross-weight (see table 1) indicates that brain weight among the various species of migrants studied, varies with approximately the 0.57

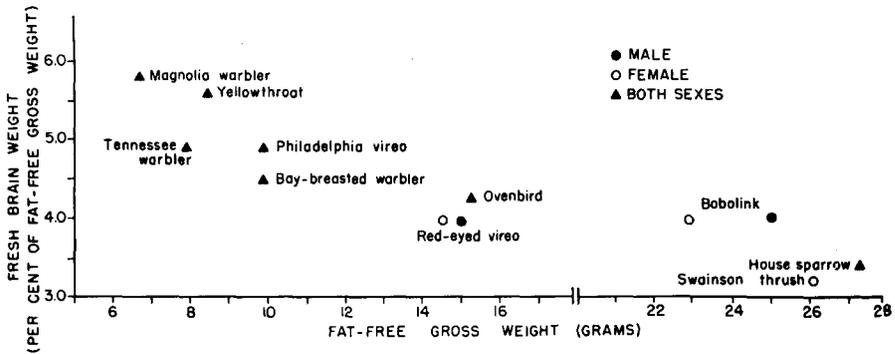


Fig. 9. Interspecific variation in brain weight related to fat-free gross weight. Figures for brain weight are the means for specimens in our samples (data for the Yellowthroat and vireos from Graber and Graber, 1962). Figures for fat-free gross weights are based on data from Connell, Odum, and Kale (1960) and Odum and Connell (1956).

power of gross weight. Such generalizations tend to conceal important differences between species, however. Even between species roughly similar in body size, there may be marked difference in brain size. Thus, the Bobolink is large-brained by comparison with the Swainson Thrush, and the Magnolia Warbler and Yellowthroat (*Geothlypis trichas*) are large-brained by comparison with the American Redstart (see p. 307) and Tennessee Warbler (fig. 9). Data presented by Portmann and Stingelin (1961:33) show that the cerebral index varies notably between passerine species, even between species of the same genus. The significance of this interspecific variation is largely unknown. According to Driesch's law of constant cell volume (see Robertis, Nowinski, and Saez, 1948:61), the difference in total mass of organs of different size is due to the number and not to the volume of cells. Differences in brain weight between species, therefore, reflect differences in cell number, at least to some extent. Water accounts for most of the weight of the brain, however, and the blood supply to the brain is all out of proportion to the weight of the organ (Brody, 1945:622). This large volume of blood is related to metabolic regulation in the organism (Brody, 1945:622, 628), and variation in the amount of blood in the brain might represent both individual and interspecific variation. Other factors may affect brain weight and structure. Cobb (1959:58) has shown that even a species' feeding adaptations may grossly affect the shape of the brain in birds. Clearly, we must understand the effect of age on the brain before we can truly evaluate other factors. Because brain weight varies with age, what we have termed interspecific variation (fig. 9) may actually be age variation. Thus, are the Magnolia Warbler and the Yellowthroat actually large-brained species (fig. 9), or have we obtained that impression because our sample of specimens was comprised of relatively young birds? Detailed studies on the morphological and chemical characteristics of brains of birds of known age should be encouraged for their potential usefulness to students of avian populations.

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#### SUMMARY

Postnatal growth of the brain in the House Sparrow involved an initial stage of marked hydration early in the nestling period, followed by pronounced increment of the protein and lipid constituents of the brain in the pre- and post-fledging period. Although in the House Sparrow, brain weight reached a peak in about 40 days, there appears to be marked variation between bird species in the time required to reach maximum brain weight. Immature migrants of several species, killed in migration at an Illinois television tower in late September, were still apparently adding to the water, protein, and lipid makeup of their brains, although they were hundreds of miles south of their breeding grounds.

In all passerines for which data are available, brain weight reaches a peak before skull ossification is completed, then declines as the bird matures. In this pattern of growth and decline, there appears to be greater similarity between altricial birds and mammals than between altricial birds and precocial birds. The decline in brain weight associated with maturation involves mainly a loss of water from the brain. In nearly all species examined, the actual weight of lipids in the brain was higher in full grown immatures than in adults. Lipid content of the brain probably reaches a peak either late in juvenal life or in young adult life, and then it declines. That the percentage of fat in the brain is higher in adults than in juveniles merely reflects the great weight loss, through dehydration, which accompanies maturation. The brain continues to lose weight beyond the time when other commonly used marks of age disappear. If the brain continues to lose weight throughout the life of the individual, then brain weight data may have utility in ageing specimens for population studies.

It is hypothesized that apparent interspecific variation in brain size may actually be age variation. The hypothesis needs to be tested by studies on known-aged birds. The brains of species having large amounts of body fat did not necessarily have high fat content, and, within a species, fat birds did not have more brain lipid than lean birds.

#### LITERATURE CITED

- Amadon, D.  
1943. Bird weights as an aid in taxonomy. *Wilson Bull.*, 55:164-177.
- Ariëns Kappers, C. U., Huber, G. C., and Crosby, E. C.  
1936. *The comparative anatomy of the nervous system of vertebrates, including man*. Vol. 1 (The Macmillan Co., New York).
- Banks, R. C.  
1959. Development of nestling white-crowned sparrows in central coastal California. *Condor*, 61:96-109.
- Bent, A. C.  
1949. Life histories of North American thrushes, kinglets, and their allies. *U.S. Nat. Mus. Bull.* 196.
- Brody, S.  
1945. *Bioenergetics and growth* (Reinhold Publ. Corp., New York).
- Cobb, S.  
1959. On the angle of the cerebral axis in the American woodcock. *Auk*, 76:55-59.
- Connell, C. E., Odum, E. P., and Kale, H.  
1960. Fat-free weights of birds. *Auk*, 77:1-9.

- Crile, G., and Quiring, D. P.  
1940. A record of the body weight and certain organ and gland weights of 3,690 animals. *Ohio Jour. Sci.*, 40:219-259.
- Dawson, W. R., and Evans, F. C.  
1960. Relation of growth and development to temperature regulation in nestling vesper sparrows. *Condor*, 62:329-340.
- Donaldson, H. H., and Hatai, S.  
1931. On the weight of the parts of the brain and on the percentage of water in them according to brain weight and to age, in albino and in wild Norway rats. *Jour. Comp. Neurology*, 53:263-307.
- Dwight, J., Jr.  
1900. The sequence of plumages and moults of the passerine birds of New York. *Ann. N.Y. Acad. Sci.*, 13:73-360.
- Ellis, R. S.  
1920. Norms for some structural changes in the human cerebellum from birth to old age. *Jour. Comp. Neurology*, 32:1-33.
- Graber, R. R., and Graber, J. W.  
1962. Weight characteristics of birds killed in nocturnal migration. *Wilson Bull.*, 74:74-88.
- Haefelfinger, H. R.  
1958. Beiträge zur vergleichenden Ontogenese des Vorderhirns bei Vögeln (Helbing und Lichtenhahn, Basel).
- Hancock, J. L.  
1887. The relative weight of the brain of *Regulus satrapa* and *Spizella domestica* compared to that of man. *Amer. Nat.*, 21:389.  
1888. The relative weight of the brain to the body in birds. *Amer. Nat.*, 22:537-539.
- Harrison, J. G.  
1960-1961. A comparative study of the method of skull pneumatization in certain birds. *Bull. Brit. Ornith. Cl.*, 80:167-172; 81:12-17.
- Harrison, J. G., and Harrison, D. L.  
1949. Some developmental peculiarities of the skulls of birds and bats. *Bull. Brit. Ornith. Cl.*, 69:61-70.
- Ingram, C.  
1960. Camouflage in nestling birds. *Proc. 12th Int. Ornith. Congr. (Helsinki)*, 1958, 1:332-342.
- Kemper, C. A.  
1964. A tower for TV: 30,000 dead birds. *Audubon Mag.*, 66:86-90.
- Koch, M. L., and Riddle, O.  
1919. Further studies on the chemical composition of the brain of normal and ataxic pigeons. *Jour. Comp. Neurology*, 31:83-110.
- Kocher, C.  
1948. Das Wachstum des Gehirns beim Alpensegler (*Micropus m. melba* L.). *Rev. Suisse Zool.*, 55:57-116.
- Kuhlmann, F.  
1909. Some preliminary observations on the development of instincts and habits in young birds. *Psychol. Rev. (Mon. Suppl.)*, 11:49-85.
- Latimer, H. B.  
1925. The postnatal growth of the central nervous system of the chicken. *Jour. Comp. Neurology*, 38:251-297.
- Lord, R. D., Jr.  
1959. The lens as an indicator of age in cottontail rabbits. *Jour. Wildl. Manag.*, 23:358-360.
- Macarthur, C. G., and Doisy, E. A.  
1919. Quantitative chemical changes in the human brain during growth. *Jour. Comp. Neurology*, 30:445-470.

Maximow, A. A., and Bloom, W.

1952. A textbook of histology (W. B. Saunders Co., Philadelphia, Pa.).

Mitchell, P. H.

1948. A textbook of general physiology. 4th ed. (McGraw-Hill, Inc., New York).

Nero, R. W.

1951. Pattern and rate of cranial 'ossification' in the house sparrow. *Wilson Bull.*, 63:84-88.

Nice, M. M.

1943. Studies in the life history of the song sparrow II. The behavior of the song sparrow and other passerines. *Trans. Linn. Soc. New York*, 6:viii + 1-328.

1957. Nesting success in altricial birds. *Auk*, 74:305-321.

1962. Development of behavior in precocial birds. *Trans. Linn. Soc. New York*, 8:xii + 1-212.

Odum, E. P.

1960. Lipid deposition in nocturnal migrant birds. *Proc. 12th Int. Ornith. Congr. (Helsinki)*, 1958, 2:563-576.

Odum, E. P., and Connell, C. E.

1956. Lipid levels in migrating birds. *Science*, 123:892-894.

Pearl, R.

1905. Biometrical studies on man. I. Variation and correlation in brain-weight. *Biometrika*, 4:13-104.

Portmann, A.

1938. Beiträge zur Kenntnis der postembryonalen Entwicklung der Vögel. I. Vergleichende Untersuchungen über die Ontogenese der Hühner und Sperlingsvögel. *Rev. Suisse Zool.*, 45:273-348.

1942. Die Ontogenese und das Problem der morphologischen Wertigkeit. *Rev. Suisse Zool.*, 49: 169-185.

1946-1947. Études sur la cérébralisation chez les oiseaux. I. *Alauda*, 14:2-20; II, *Alauda*, 15: 1-15; III, *Alauda*, 15:161-171.

1955. Die postembryonale Entwicklung der Vögel als Evolutionsproblem. *Acta XI Congr. Int. Ornith. (Basel)*, 1954:138-151.

1959. Die Entwicklungsperiode vom 11. bis 14. Bruttag und die Verkürzung der Brutzeit bei Vögeln. *Vjschr. Naturf. Ges. Zurich*, 104:200-207. Original reference not seen. See review in *Ibis*, 102, 1960:482.

Portmann, A., and Stingelin, W.

1961. The central nervous system. *In Biology and Comparative Physiology of Birds*, edited by A. J. Marshall. Vol. 2 (Academic Press, New York), pp. 1-36.

Portmann, A., and Sutter, E.

1940. Über die postembryonale Entwicklung des Gehirns bei Vögeln. *Rev. Suisse Zool.*, 47: 195-202.

Robertis, E. D., Nowinski, W. W., and Saez, F. A.

1948. General cytology (W. B. Saunders Co., Philadelphia, Pa.).

Romanoff, A. L.

1960. The avian embryo. Structural and functional development (The Macmillan Co., New York).

Sauer, F.

1958. Celestial navigation by birds. *Sci. Amer.*, 199:42-47.

Scott, J. P.

1962. Critical periods in behavioral development. *Science*, 138:949-958.

Selander, R. K.

1958. Age determination and molt in the boat-tailed grackle. *Condor*, 60:355-376.

Shock, N. W.

1962. The physiology of aging. *Sci. Amer.*, 206:100-110.

## Sosa, J. M.

1953. (Discussion of paper—'Observations on lipochrome pigment.')
- Jour. Histochem. and Cytochem., 1:395.

## Stingelin, W.

1957. Vergleichend morphologische Untersuchungen am Vorderhirn der Vögel auf cytologischer und cytoarchitektonischer Grundlage (Helbing and Lichtenhahn, Basel, Switzerland). Original reference not seen. See review in Auk, 78, 1961:284-286.
1960. Vorderhirn und Anpassungstypus. Proc. XIIth Int. Ornith. Congr. (Helsinki), 1958, 2:681-693.

## Strehler, B. L.

1960. The biology of aging. Amer. Inst. Biol. Sci., Publ. No. 6 (Washington, D.C.), 364 pp.

## Sutter, E.

1943. Über das embryonale und postembryonale Hirnwachstum bei Hühnern und Sperlingsvögeln. Denkschr. Schweiz. Naturforsch. Ges., 75:1-110.
1944. Wachstumsbeobachtungen an Speckten. Arch. Suisses d'Orn., 2:124-130. Original reference not seen. See review in Bird-Banding, 17, 1946:172.
1951. Growth and differentiation of the brain in nidifugous and nidicolous birds. Proc. Xth Int. Ornith. Congr. (Uppsala) 1950:636-644. Original reference not seen. See review in Bird-Banding, 23, 1952:187.

## Thorpe, W. H.

1951. The learning abilities of birds. Ibis, 93:1-52; 252-296.

## Turner, C. H.

1891. Morphology of the avian brain. Jour. Comp. Neurology, 1:39-92, 107-133, 265-286.

## Young, J. Z.

1948. Growth and differentiation of nerve fibres. Symposia Soc. Exper. Biol., No. 2:57-74.

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