EXPERIMENTS ON THE DIGESTION OF FOOD BY BIRDS*

BY JAMES STEVENSON

INTRODUCTION

Food is a factor of considerable importance in bird life because of the high rate of metabolism maintained in the body and the consequent rapid digestion of food required to maintain such a rate. This high rate of metabolism is indicated by the high body temperature, great rapidity of heart beat and respiration, and ceaseless activity.

Few birds are confined to one particular type of food and many are omnivorous. The quantity of food available, as well as the quality, is of primary importance in bird life. Many data, compiled by the United States Biological Survey under the direction of W. L. McAtee, indicate that birds, within limits, feed on the kind of food most readily available. Much information has been collected in the last fifty years on the kind of food which birds eat, but the amount which is consumed is less often considered. The Biological Survey and other investigators have spent much time in determining the percentage of insects, seeds, and other types of food that are in the stomach at any one time. Most work of this sort is undertaken to determine the economic importance of birds to man. The study, here reported, takes a different point of view in considering the rôle of food in the physiology and activity of the birds themselves. This paper is intended to serve only as an introduction to the general problem. The results are of a preliminary nature but may be suggestive for further research.

TIME OF FEEDING AND HOLDING CAPACITY OF THE STOMACH

At the Baldwin Bird Research Laboratory, Gates Mills, Ohio, where systematic trapping is carried on each year, it has been found that passerine birds spend a large proportion of the day in feeding. Opening the stomachs of over 200 birds, taken at all seasons of the year, has revealed less than ten that were empty. These birds were taken at all hours of the day but not at night, and show that our small birds apparently do not fill their crops and stomachs and then wait until they are empty before refilling them, but eat from time to time. A study was made of the weight of stomach contents in a few species, and Table I gives these data separately for adults and juvenals.

In the English Sparrow (*Passer d. domesticus*) the lower end of the oesophagus was found in a few individuals to be enlarged in the

*Contribution from the Baldwin Bird Research Laboratory (No. 27) and the Biological Laboratory, Western Reserve University, Cleveland, Ohio.

TABLE I. Weight of Stomach Contents in Some Passerine Birds.

Species	Age	Number of Records	Average Weight of Bird	Average Weight of Stomach Contents	Weight of Contents Divided by Body Weight	Maximum Weight of Stomach Contents
			Grams	Grams		Grams
Song Sparrow	Adult	5	20.3	0.261	0.0128	0.390
Song Sparrow	Juvenal	6	18.9	0.335	0.0177	0.730
English Sparrow	Adult	6	27.4	0.269	0.0098	0.387
English Sparrow	Juvenal	24	26.0	0.326	0.0125	0.650
Starling	Adult	4	80.8	1.490	0 0185	1.880
Starling	Juvenal	2	79.9	2.290	0.0287	2.820
Northern White-breasted Nuthatch	Adult	10	20.7	0.311	0.0150	0.550

form of a crop. In adults, the weight of the crop contents averaged 0.228 grams, and in the juvenals, 0.277 grams. The food of English Sparrows and Song Sparrows (*Melospiza melodia*) consisted almost entirely of grain, and that of the Starlings (*Sturnus v. vulgaris*) and Northern White-breasted Nuthatches (*Sitta c. carolinensis*) was composed of insects.

In addition to showing the amount of food contained in the stomach at one time, Table I indicates also that juvenal birds out of the nest may carry more food in their stomachs than do the adults, although the number of records are few. In addition to the data in Table I, the following is of interest in this connection. Five nestling Starlings taken at ages ranging from three to sixteen days had an average full stomach content of 2.85 grams, which is to be compared with 1.49 grams in four adults whose stomachs were full. The three-day nestling had a stomach content weighing 2.86 grams. Nestling birds may require relatively more food than adults, as this is used in their rapid growth.

A few measurements on the size of the stomach (length and width) in adult and nestling birds taken after food had been removed indicate further what may prove to be the greater food-carrying capacity

TABLE II. Size of Stomach in Adult and Nestling Birds.

Species	Age	No. of Records	Average Length	Average Width	Range in Length	Range in Width
			Centimeters	Centimeters	Centimeters	Centimeters
Eastern House Wren	Adult	4	1.0	0.9	0.9-1.1	0.8-1.0
Eastern House Wren	Nestling	4	1.2	1.0	1.1-1.3	0.9-1.1
English Sparrow	Adult	2	1.4	1.2	1.3-1.5	1.2-1.3
English Sparrow	Nestling	8	1.7	1.5	1.3-2.1	1.2-1.8
Starling	Adult	3	2.0	1.6	1.9-2.2	1.5-1.6
Starling	Nestling	6	2.2	1.8	2.0-2.4	1 5-2.4

of young birds over adults (Table II). It is desirable that more material on this subject be obtained, as the present data are scanty.

Length of Small Intestine

A study was made of the length of the small intestine in birds collected at the laboratory. Most of these were passerine birds, but a few individuals of other orders were obtained. An attempt was made to distinguish possible differences in the length of intestine in male and female adults and in nestling birds. It was desired to correlate the length of intestine with the length of time for food to pass through the body, with the amount of food consumed, and with the type of food eaten. Of course, the length of intestine is not the actual area of absorption in the intestines. Future studies should take in the width of intestine as well as the length to give more dependable figures on this area. The length of the small intestine was taken to be the distance from stomach to caeca. The large intestine is short and was not included in this study. Gadow and Selenka (1891) have several measurements on the length of the small intestine in their monographic work.

Variation with Sex—The small intestine shows a relationship to sex which will be considered here (Table III). More records were obtained on the Eastern House Wren (*Troglodytes a. aedon*), Starling, and English Sparrow than on any other species. The small intestine of the females of the Eastern House Wren and English Sparrow were found to be 17.9% and 13.0% longer, respectively, in "actual" length than the small intestines of the males. Starling figures favor the males slightly (0.67%). To obtain a better comparison, since the size of the body often varies with sex, the length of the intestine in centimeters was divided by the weight of the body in grams, which gives a measure of the percentage length of the small intestine in terms of the body size (weight). In all three cases, including that of the Starling, the greater proportional length of intestine then favors the female. In the male birds of twenty species studied, the average small intestinal measurement in proportion to body weight averaged 0.762. In females this proportion averaged 0.929, showing that a longer intestine for the female sex is, with a few exceptions, rather generally true in Passeriformes. Riddle and Flemion (1928) found from data on 1,157 ring doves that female doves possessed longer small intestines (from 5% to 10%) than did the males.

Variation with Age—The rate of growth of the small intestine was determined in nestling House Wrens. These data are given in Table IV.

TABLE III. Sex Difference in Length of Small Intestines in Birds.

Species	MALES				FEMALES			
	Number of Birds	Average Length of Intestine	Average Body Weight	Length Divided by Weight	Number of Birds	Average Length of Intestine	Average Body Weight	Length Divided by Weight
		Centimeters	Grams			Centimeters	Grams	
Eastern House Wren	12	10.3	10.7	.962	4	12.15	12.2	.966
Starling	16	29.5	80.4	.367	10	29.3	78.7	.372
English Sparrow	11	17.15	26.3	.652	14	19.5	27.1	.723
Eastern Cowbird	1	13.9	46.7	.297	2	17.5	41.8	.418
Red-eyed Towhee	5	21.34	41.6	.513	3	22.36	39.8	.562
Eastern Purple Finch	7	36.1	25.3	1.425	1	33.0	25.4	1.299
Slate-colored Junco	2	17.8	21.2	.840	1	19.8	21.3	.930
Eastern Field Sparrow	1	14.0	13.7	1.022	1	12.4	12.7	.976
Song Sparrow	8	17.8	20.6	.856	1	17.6	18.0	.980
Eastern Chipping Sparrow	5	12.5	11.5	1.087	3	13.1	11.7	1.199
Red-eyed Vireo	2	14.1	16.0	.881	4	16.2	16.7	.970
Ovenbird	3	15.9	19.2	.828	2	17.8	19.3	.922
Redstart	4	11.3	8.0	1.295	1	9.5	7.2	1.319
Bronzed Grackle	3	31.3	110.4	.283	1	25.0	98.9	.253
Blackburnian Warbler	1	10.0	11.1	.901	1	10.0	9.5	1.053
Eastern Catbird	2	16.8	31.1	.542	1	21.1	38.1	.554
Black-capped Chickadee	7	12.3	12.2	1.008	3	13.2	10.6	1.242
Northern White-breasted Nuthatch	6	15.2	21.0	.724	4	16.4	20.2	.724
Eastern Robin	7	24.2	82.3	.293	2	28.7	77.8	.369
Eastern Hermit Thrush	1	15.5	32.7	.474	1	16.8	31.4	.535
TOTAL, 20 species	104 records			Average .762	60 records			Average .929

TABLE IV. Increase of Intestinal Length in Nestling House Wrens.

Age	Number of Records	Average Length of Intestine	Average Body Weight	Length of Intestine Divided by Body Weight
Days		Centimeters	Grams	
1	2	4.2	1.5	2.80
2	3	6.5	2.7	2.41
3	3	6.5	3.3	1.97
4	2	7.3	4.1	1.78
5	6	10.4	6.3	1.65
6	7	10.6	6.7	1.58
7	4	11.0	7.1	1.55
8	9	11.6	8.2	1.41
9	3	11.6	8.3	1.40
10	3	12.2	9.3	1.31
11	3	12.5	9.5	1.31
12	2	11.8	9.6	1.23
13	2	11.7	10.3	1.13
14	2	11.6	10.6	1.09
15	3	11.7	10.6	1.10

From Table IV, it is evident that growth in the length of the small intestine is very rapid up to the age of eight days, after which it becomes slower. The maximum length is attained at eleven days, after which there appears to be some actual shrinkage to the length characteristic of the adult (Table IV). The rate of growth of the small intestine in proportion to body weight is shown in the last column. There is a gradual decrease in this proportion with increasing age until the birds become adult. In eight nestling Starlings, the length of the small intestine in proportion to body weight was found to be 0.411, while in twenty-six adults it averaged 0.369; in fourteen nestling English Sparrows this proportion was 0.985, while in twenty-five adults it averaged 0.682. All these data indicate a relatively, if not actually, longer small intestine in nestling birds than in adults.

Variation with Type of Food Consumed—Different species of birds feed on somewhat different types of food. Some correlation is possible between type of food consumed and length of intestine. In Table V this correlation is brought out by comparing the length of the intestine with the total length of the body. The length of body was considered to be the length from shoulder to coccyx and was measured in the manner prescribed by Baldwin, Oberholser, and Worley (1931, p. 62).

The length of the small intestine in the species studied is relatively uniform among insectivorous and omnivorous feeders. In birds feeding upon mammals and birds it appears to be somewhat longer. In one species feeding largely on fish and amphibians, it was found to

TABLE V. Relation between Type of Food Consumed and Length of Intestine in Different Species of Birds.

Species	Predominant Type of Food Consumed	Number of Records	Average Length of Small Intestine	Total Length of Body	Length of Intestine Divided by Body Length
			Centimeters	Centimeters	
Eastern House Wren	Insects	11	10.8	3.6	3.0
Black-capped Chickadee	Insects	6	13.1	3.6	3.6
Northern Downy Woodpecker	Insects	4	20.4	5.7	3.6
Eastern Hairy Woodpecker	Insects	3	24.4	7.3	3.3
Song Sparrow	Omnivorous	6	18.3	4.6	4.0
English Sparrow	Omnivorous	16	18.8	5.3	3.6
Eastern Chipping Sparrow	Omnivorous	5	13.5	3.8	3.6
Red-eyed Towhee	Omnivorous	5	21.2	5.9	3.6
Eastern Robin	Omnivorous	4	24.6	7.6	3.2
Starling	Omnivorous	21	29.4	8.1	3.6
Northern White-breasted Nuthatch	Omnivorous	6	14.7	4.6	3.2
Broad-winged Hawk	Mammals, Birds, etc.	2	89.0	13.8	6.0
Cooper's Hawk	Mammals, Birds, etc.	3	54.7	13.3	4.1
Eastern Least Bittern	Fish, Amphibians, etc.	2	69.6	8.2	8.5

be very much longer. A nine-day-old Bald Eagle (*Haliaeetus l. alascanus*[1]) that had been hatched at Western Reserve University possessed an intestine 147 centimeters long, or twenty-two and one-half times its body length.

An explanation of the differences discovered in intestinal length is not attempted in this paper. A long intestine might work to advantage if it furnishes a greater area for food absorption. Allen (1925, p. 68) says, "The digestion of birds is very rapid, and this is perhaps due in part to the great length of their small intestine." On this basis a longer intestine in adult females and in nestlings may indicate more rapid or efficient absorption than in adult males.

[1]The author's manuscript followed the nomenclature of Peters' "Check-List of the Birds of the World" (Vol. I, p. 258) in designating this subspecies as *washingtoniensis*. The editor has changed it to *alascanus* in conformity with the A. O. U. Check-List, which we accept as authority. If Peters' work were complete so that it might be followed consistently, our practice might be otherwise. —Editor.

Rate of Food Passage through Digestive Tract

A study was made of the rate of food passage through the digestive tract of birds. Birds were placed in cages outside a laboratory window and left without food for at least two hours. Screens made of black cloth containing a small peep hole were placed between the birds and the observer so that the birds might be watched without being disturbed. Finely cracked corn, stained with neutral red, gentian violet, or Janus green, was given the birds in order to note the first appearance of waste particles of this stained food in the excrement. In these cases no difference in time was noted between birds fed unstained food and those given stained grain. A method similar to this was used by Kaupp and Ivey (1923) on chickens. Miller (1931) found that elderberries passed through the digestive tract of shrikes in about three hours.

TABLE VI. Rate of Food Passage through the Digestive Tract of Passerine Birds.

Species	Age	Number of Records	Average Time until First Colored Excrement	Shortest Time Recorded
Birds Starved Two or More Hours, then Fed Stained Cracked Corn				
Song Sparrow	Juvenal	38	1 hour 34 minutes	58 minutes
Song Sparrow	Adult	4	1 hour 42 minutes	1 hour 22 minutes
Eastern Chipping Sparrow	Juvenal	5	1 hour 18 minutes	1 hour
Eastern Chipping Sparrow	Adult	2	1 hour 2 minutes	
Eastern Field Sparrow	Juvenal	2	1 hour 37 minutes	1 hour 14 minutes
Eastern Field Sparrow	Adult	2	1 hour 41 minutes	
English Sparrow	Juvenal	1	1 hour 25 minutes	
Red-eyed Towhee	Juvenal	3	1 hour 32 minutes	1 hour 20 minutes
Five species Fringillidae		57	1 hour 32 minutes	
Birds Starved Two or More Hours, then Fed on Fruit (Raspberries)				
Cedar Waxwing	Juvenal	2	1 hour 40 minutes	
Birds Starved Two or More Hours, then Fed on Insects (Beetle and Moth Larvae—Mealworms)				
Scarlet Tanager	Adult	6	1 hour 25 minutes	
Average Length of Time between Last Stained Food Eaten and Last Colored Excrement Voided				
Song Sparrow		11	2 hours 14 minutes	
Eastern Field Sparrow		3	2 hours 30 minutes	
Birds not Starved Previously (Other Food in Digestive Tract)				
Song Sparrow	Juvenal	5	2 hours 33 minutes	

The average time required for the first stained food to pass through the digestive tract in previously starved birds (Fringillidae) was 1 hour and 32 minutes (Table VI). In instances where birds were not starved previously there was a delay of approximately an hour in the appearance of the first colored excrement. This agrees with the delay of nearly an hour in the interval between last food eaten and last excrement voided. There is evidently a delay, probably in the stomach, in the passage of food after some has already been taken into the alimentary system. It may be noticed that the rate of passage in birds fed insects, fruit, or grain, is practically the same. With such rapid assimilation of food material, birds must keep searching actively for nourishment.

Amount of Food Consumed Daily

The number of meals per day, or times that the stomach is filled daily, has been estimated by various ornithologists. Allen (1914) calculated that adult birds eat eight full meals a day, and Bailey (1905) thought that insectivorous birds filled their stomachs five or six times daily. Rörig (1905) determined amount of food in dry weight consumed daily by certain European birds. This varied in different species from 8-13.4 per cent of the body weight in winter to 11.9-19.5 per cent in summer. Taber (1928) has deduced that a dove will consume from 11 to 20 per cent of its weight daily in grain or weed seeds. Bryant (1914) concluded that meadowlarks could completely digest a meal in four hours and that they took only three meals a day. He believed that grain took longer to digest than insects and that the amount of grain found in a stomach would equal nearly one-half the daily requirement. Miller (1931) working on captive shrikes found that they might eat between fifteen and twenty grams of beefsteak or mice in one day.

If the time required to empty completely the stomach and intestines in a Song Sparrow is 2 hours 14 minutes, and the average daily duration of total possible sunlight during June, July, and August is 14 hours 35 minutes at Cleveland, Ohio, then this species must consume the equivalent of six and one-half meals per day. Since birds may be active before sunrise and after sunset (Shaver and Walker, 1931), another meal may be consumed, which is not fully digested until after dark, to make a total of seven and one-half meals per day. If the average weight of a normal stomach full of food in the song sparrow is 0.261 grams, the total food consumed during the day will equal 1.957 grams, or 9.6 per cent of the body weight of the adult. Experiments on a Scarlet Tanager fed meal worms, the larvae of moths and beetles, showed that the bird would eat an amount equivalent to 32.1 per cent to 40.8 per cent of its body weight daily.

Percentage of Food Digested

Most of the food given sparrows used in these experiments consisted of "chick feed" or finely cracked corn. In order to determine the percentage digested (Table VII) a specific amount of food was given in each case and the amount eaten was calculated by subtracting what was left at the end of the experiment. The "sac" in which the excrement was voided, was separated from the undigested food, and later the air dried feces were weighed on a chainomatic balance. A total of nineteen records showed that 90.4 per cent of the food eaten was digested and absorbed.

Table VII. Percentage of Food Digested and Absorbed by Birds Fed Finely Cracked Corn.

Species	Records	Average Amount of Air-dried Food Eaten	Average Amount of Air-dried Excrement	Percentage Digested and Absorbed
		Grams	Grams	
Song Sparrow	11	0.254	0.0296	91.1
Eastern Chipping Sparrow	3	0 334	0.060	85.3
Eastern Field Sparrow	3	0 207	0 015	92.9
English Sparrow	1	0.124	0 010	91.9
Slate-colored Junco	1	0.384	0.038	90.0
Average of 5 species	(19)	0.259	0.0315	90.4

Effect of Environment on Rate of Feeding

Certain environmental factors influence the extent of feeding and may curtail activity along this line for periods of time. Wind or rain storms will send birds hurrying to cover just as periods of intense heat will decrease movements and tend to keep birds rather quiet and in the shade. In this latter case the amount of movement is reduced but some feeding does take place.

In order to study the effect of air temperature upon amount of feeding by birds, a study was made of banding records. For the past several years, intensive bird trapping for banding purposes has been accomplished at the laboratory during the warmer months. Traps were baited with various foods and were visited regularly throughout the day. The birds captured were taken to the laboratory, weighed, and immediately released. The traps were not operated during severe rain storms, although light rain, not lasting over a few hours, does not seem detrimental, as far as occupancy of the traps is concerned.

A survey taken of the number of new, return, and repeat birds in the traps daily was made for the months of June (latter portion only), July, and August of the years 1925, 1926, 1928, and 1930. Birds taken were resident species and included both adults and juvenals. Table VIII tabulates trapping of Song, Eastern Field, and Eastern Chipping Sparrows during these months. Some individuals exhibited little fear, visiting the traps four or five times daily for food, and handling does not appear to frighten birds. The trapping days were assorted into groups having the same mean temperature within 5° F., and an average was made of the number of birds taken in the traps on those days. The lower ranges of air temperature are not included since they occur early in the summer when juvenal birds are not available and so are not comparable with records obtained later. A rapid decline is shown in the number of birds trapped daily when the mean daily temperature rises above 71° F.

TABLE VIII. Effect of Daily Mean Temperature on the Feeding and Trapping of Song, Eastern Field, and Eastern Chipping Sparrows.

Daily Mean Temperature	Number of Days	Average Number Trapped Daily
71-75° F.	71	7.6
76-80° F.	44	4.7
81-85° F.	9	3.7

SURVIVAL TIME OF BIRDS WITHOUT FOOD

The amount of reserve food in the body which the bird can call on in times of stress is of considerable importance in affecting its abundance and migration. Experiments by S. C. Kendeigh and the author (unpublished) on resistance of birds to various degrees of air temperature show that certain species, such as the English Sparrow, have the longest survival time without food at a relatively high air temperature. Sixteen English Sparrows, confined one or two at a time in an incubator at a constant temperature of 92.2° F. and a relative humidity of 56 per cent, lived on the average, for 47.9 hours. Apparently death was here due to complete starvation and exhaustion of food reserves. At higher or lower air temperatures, the regulation of body temperature is affected and death comes more quickly, apparently before complete exhaustion of reserve food can take place. The average loss in weight at death of these birds at 92.2° F. was 34.5 per cent of their original weight at the beginning of the experiments. This represents a loss of 0.7 per cent of the original weight during each hour of survival. Excrement was voided more or less regularly throughout the survival period, in spite of the fact that no food was passing through the alimentary tract. It probably consisted largely of urinary wastes. This experiment indicates that even at the most favorable air temperature, the survival time of birds without food is relatively short, although considerable emaciation of the body occurs before death results.

Discussion

Among many theories as to the cause of bird migration and the determination of the time at which migration occurs, the importance of food has received much support. Change in temperature is another factor of importance and a combination of the food and temperature factors may well be made. Migration in its early stages, according to Taverner (1904), was a dispersal to seek food. This search for a shifting food supply may have become habitual, and the direction and time of this movement may be influenced by temperature. Obtaining an adequate amount of food is necessary to maintain a resistance against low air temperature, particularly at night. The hours of daylight in which this food may be obtained are shorter in winter, and hence those species, which are not physiologically adjusted, migrate out of the region in autumn.

English (1923) has brought out the point that birds that breed in northern latitudes have larger broods than those species that nest further south. There may be some relation here between size of broods and the longer period of daylight available for securing food. This would indicate an advantage in a northward spring migration away from the tropics.

Movements of birds are not all regular migrations but may consist of sporadic invasions or dispersals instigated on most occasions as a search for food. Snowy Owls (*Nyctea nyctea*) travel south at the sign of a scarcity of rabbits, and crossbills and waxwings will move if their winter supply of pine seeds and berries is lacking. Even normal winter residents will effect a slight seasonal movement if the food supply fails. The regular resident species in northeastern United States are those that make use of food not easily obscured by snow.

Food is often an important direct factor controlling the number of species wintering in northern Ohio, wherein climate may act only as an indirect factor. Severe storms with snow obscuring the ground and ice covering tree trunks are fatal to many birds (Rice, 1924; Wetmore, 1926; Errington, 1931). There are some birds capable of withstanding low winter temperatures providing they are able to find food. In mild winters food is less difficult to find and representatives of species that normally move southward may remain in the vicinity. The winter of 1930-31 was a mild one in northern Ohio with little snow. It was accompanied by the occurrence of eighty-three species of birds, some of which are not normally resident at this season, and testified to a sufficient food supply for this population.

Food is also a factor in regulating the abundance of birds. In this instance, food plays a part in determining the relative size of the territory set up by adult birds during the nesting season. In winter great mortality and diminution in abundance of a species may result when food becomes unavailable.

Summary

1. Passerine birds feed more or less continuously during the daylight hours.

2. Female birds of several passerine species possess relatively longer small intestines than do males, and immature birds of some species possess relatively longer intestines than do the adults. The relative length of the small intestine is uniform among many insectivorous and omnivorous species, but there is an indication that it is longer in some birds living on small mammals, birds, amphibians, and fish.

3. In some species of passerine birds, the first voided excrement from a stomach full of food appears in about one and one-half hours, the last in about two and one-half hours.

4. Some species of birds when feeding on grain daily consume an amount equivalent to 9.6 per cent of their body weight. About 90.4 per cent of the food ingested is utilized by the bird, the rest is excreted.

5. Passerine birds tend to decrease the amount of their feeding on hot days.

6. The survival time of small passerine birds without food is relatively short, even at the most favorable temperature.

7. Food in sufficient quantity is a factor of considerable importance in controlling the migration and regulating the abundance of birds.

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