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Thus it would seem that there is greater metabolic change and winter-fat accumulation in the case of migratory subspecies than in permanently resident ones. In the combined data of *actia* and *ammophila*, there are indications of two peaks throughout the year; one in August after the termination of the nesting season; the other in February.

# SUMMARY

Differences in body weight between the two sexes have been shown. These are probably correlated with sexual differences in size. There are indications that the sexual differences in weight begin to be apparent in the juvenile stage. Juveniles weigh less than adults, but first year birds seem to weigh about the same as adults. Females, it seems, show less seasonal variation in body weights than do males.

In one race, *merrilli*, which shows migratory behavior, the seasonal fluctuations are pronounced in the males which weigh heaviest in February. In contrast, the combined weight data for males of two closely related resident subspecies with adjacent ranges show less pronounced seasonal fluctuation. A difference in physiology affecting weight between resident and non-resident races is thus suggested. In the case of the resident races there are indications of two peaks; namely, in August and February. Horned larks thus appear to show variation in body weight by reason of sex, age, geographic area and season.

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# BIRD WEIGHTS AND EGG WEIGHTS

# BY DEAN AMADON

IN 1922, Heinroth (18) published egg weights and body weights of several hundred species of birds of many orders from all parts of the world. With these data, aided by graphs, he was able to summarize the scattered observations of other ornithologists. Among the more important of Heinroth's conclusions are: (1)-large birds, in general, lay relatively smaller eggs than small birds; (2)-many groups have peculiarities of their own. Thus kiwis lay very large eggs, parasitic cuckoos very small ones, and precocial birds lay larger eggs than altricial ones of the same weight.

Julian Huxley (19) made a further analysis of Heinroth's data.

He realized that egg weight is not a simple linear function of body weight, but thought that it might be a non-linear function. If this were the case, the two might conform to the "Power Formula," which is expressed in general terms as  $Y = bX^a$ . The relationship expressed by this formula, as Huxley (20) has shown in his book, frequently exists between the size of an animal (X) and the size of one of its organs or parts (Y) when the two are changing or growing at different rates. When the formula applies, the ratio of the two rates of change remains constant and is equal to a. In the formula, b is another constant expressing the relative size of Y in terms of X. This formula, when written in logarithmic terms, becomes that for a straight line (log  $Y = \log b + a \log X$ ). Hence if the power law applies in any given case, the logarithms of the various corresponding values of X and Y, when graphed, will fall on a straight line.

Huxley found that egg and body weights in birds do tend to conform to the power formula. This is true both for groups of related birds such as families or orders and for birds in general when grouped into size classes. The logarithmic values of egg weight plotted against body weight for the various groups tend to fall on straight lines. The graphs for the various groups are usually almost parallel lines, whose distance apart is determined by variations in the constant b. However, most of the graphs show a tendency to flatten off somewhat as body weight increases. This would most naturally be attributed to a slight decrease in the value of the constant a, which determines the slope of the line. But the same flattening of the curves might be produced by including in one composite graph several sub-groups with different values of b but the same value of a. The graphs of some groups, for example the Anatidae, strongly suggest this possibility. Heinroth's data are not exact enough to permit an exact mathematical analysis of the problem. Huxley was unable to derive a mathematical expression of the relation between egg weight and body weight for this reason. But he gives an excellent discussion of the significance and possible biological explanation of this relationship, which should be considered in conjunction with the present paper. Huxley stressed the need for further investigations of this problem, based on more exact quantitative data.

The results of such a study form the basis of this paper. The subfamily Emberizinae of the sparrow family, Fringillidae, was selected, since body weights are available for several species. For comparison it was desired to include a distantly related group of non-Passerine birds. The American quail, which comprise the subfamily OdontoVol. 60 1943

phorinae of the Phasianidae or pheasant family, were selected. The data available for this group are less exact and less extensive than those for the Emberizinae. This is reflected in the results given below.

If egg size is a function of body size, obviously an equation expressing this relation can be solved for either value. Hence, we can calculate the weight of a bird from the weight (or measurements) of its egg. This method of estimating bird weights may prove to be of considerable value in studying other problems. Eggs have been so extensively collected that museums contain the eggs of hundreds of species of birds of which no body weights have been recorded.

The usefulness of bird weights as a standard of comparison for variable appendages such as wing, tail, bill, etc., is not, I believe, sufficiently realized. By their use the general size factor can be eliminated when comparing the measurements of forms of different sizes. When the comparison is of linear measurements, the cube root of the weights can often be used to advantage as a standard of comparison. In work of this general nature, even an approximate, estimated weight will often give useful and valid results.

I am greatly indebted to Drs. Ernst Mayr and George G. Simpson of the American Museum of Natural History for numerous valuable suggestions. Professor F. B. Hutt of Cornell University gave me helpful advice. Miss Margaret Wythe and Dr. A. H. Miller kindly sent me the weights of some quail as recorded on the labels of specimens in the Museum of Vertebrate Zoology, University of California.

METHODS.—The weights of birds used in this paper, with one or two exceptions, have been taken from the literature from sources listed in bibliography "A". For most species only the weights of females were used. In a few, however, it was necessary to use weights taken from non-sexed birds. Since sexual size dimorphism in American sparrows and quail is always slight and often non-existent, it is believed no serious error is involved.

The eggs of but few species of wild birds have been weighed in sufficient numbers to give an average value exact enough for the present study. The loss of weight which occurs during incubation makes it necessary to weigh fresh eggs. This greatly limits the gathering of such data in the field. Fortunately, approximate egg weights can be estimated secondarily from the large collections of eggs, or more correctly egg shells, which exist. A possible method of doing this would be by direct displacement of water. This procedure would be laborious, difficult and rough treatment for the eggs. Heinroth filled egg shells with water and weighed them. This method has all of the difficulties just mentioned, and is very likely to result in injury to the specimens. Bergtold (17) filled eggs with chloroform, which, he said, does not injure the shell. However, filling a small egg with fluid of specific gravity 1.5 must entail danger of breakage.

The third possible method of estimating an egg's volume or weight is from its measurements. Schoenwetter (21) proposed the formula:  $W = \frac{1}{2}$  (LB<sup>2</sup> + w), in which W is weight of egg, L is length of egg, B is breadth of egg, and w is weight of the egg shell. In practice it was found that the egg shell in small Passeres is about 5% of the total egg weight. Hence Schoenwetter's formula may be reduced as follows:  $W = .5 (LB^2 + .05W)$  or  $.5LB^2 + .025W$ . Hence  $.975W = .5LB^2$  and  $W = .5128LB^2$ . Bergtold (17) independently developed another formula: W = 11/21 (LB<sup>2</sup>) S. The symbols are the same; S is the specific gravity of a fresh egg, which Bergtold found to be 1.075 in hens' eggs and 1.043 in fourteen species of native (Colorado) birds. Using the latter value, Bergtold's formula reduces to:  $W = .5463LB^2$ . Worth (23) to get the volume of eggs used yet another method. He found by displacement that hens' eggs have about 15% less volume than an ellipsoid of the same length and breadth. Therefore, he used the formula for an ellipsoid less 15%, or  $V = 1/6\pi LB^2 - 15\%$ , which reduces to  $W = .4749LB^2$ . The formula  $4/3\pi LB^2$ , that of a prolate spheroid, has also been used. These formulas differ only because some have been more carefully corrected to apply to birds' eggs than others.

Two conclusions are immediately apparent from consideration of these formulas: (1)—in eggs of the same shape the volume is equal to  $LB^2$  multiplied by a constant. The egg measurements are the only variables involved. It may well be the size (volume) of an egg that is of biological significance in relation to body size. But if the weight of the egg is considered the important factor, it is obtained by multiplying the volume by another constant, namely, the specific gravity. Probably the latter varies scarcely at all within a family of small Passerine birds, and perhaps not enough in the entire class Aves to affect the result of a study such as the present; (2)—if the size of birds' eggs (as expressed by volume or weight) is a mathematical function of the size of the birds, then  $LB^2$  of the egg measurements is also a function of the size of the bird. For egg volume equals  $LB^2$  times a constant, and the constant will cancel out in comparing different species.

For the purposes of the present study the volume or weight of eggs is not of interest *per se*. The value of the expression  $LB^2$ , which is based directly on the egg measurements, has been used without altera-

tion. This is to be preferred to the use of doubtfully accurate estimates of egg volume or weight derived by secondary manipulation of the expression  $LB^2$ . After the value of  $LB^2$  has been computed from measurements taken to the nearest tenth of a millimeter, the result has been divided by 1000 to reduce it to the equivalent of cubic centimeters. It will be noted from the above formulas that such values of  $LB^2$  are roughly twice the volume of the egg in cubic centimeters. Such direct use of  $LB^2$ , it should be emphasized, is valid only for comparisons of eggs of the same shape. This condition is usually met by members of the same family or even higher taxonomic category. Minor discrepancies resulting from variations in the shape of eggs of the same species will be eliminated in averages based on a considerable series of eggs.

The egg measurements used in this paper were taken to the nearest tenth of a millimeter with sliding calipers from specimens in the American Museum of Natural History. Bancroft (16) has described a device for measuring several eggs at one time. This would be of great utility, although not used for the present study. Average measurements of the eggs of many birds have been published. For computing the egg value or volume, unfortunately, such measurements cannot be used without inaccuracy, since the volume increases faster than the linear measurements. Perhaps this error would not be of importance unless a very exact value were needed. Eggs of different sets are likely to show a wider range of variation than those of the same set. Hence if all the available material is not measured, it is much better to measure an egg or two from each set than all the eggs of a few sets.

MATERIALS.—The following list gives the common and scientific names of the birds used in the present study. A note concerning the material from which the body weights and egg measurements were taken is given for each. For the eggs, the average value of the expression  $LB^2$  (called "egg value" in this paper) is given. Unless otherwise mentioned, eggs were collected in the Middle Atlantic and New England states. For the Fringillidae the normal number per clutch, except where mentioned, is four to five eggs. The names marked with an asterisk indicate the species upon which the formulas given below are based. Numbers in parentheses refer to the appended bibliography.

# FAMILY PHASIANIDAE, SUBFAMILY ODONTOPHORINAE

\*NORTHERN BOB-WHITE, Colinus v. virginianus.—107 birds from Ohio and 4 from New England averaged 197.90 grams (1, 13). 76 eggs from eight sets from the northern states average 18.18. The eggs were collected from forty to seventy years

Vol. 60 1943 ago, before the introduction of smaller southern birds into the northeast. Probably the weights of the Ohio birds, at least, are of native northern stock also.

\*TEXAS BOB-WHITE, Colinus virginianus texanus.—32 birds from Texas averaged 170.55 grams (11, p. 74). 64 eggs from 5 sets average 16.88.

\*ARIZONA SCALED QUAIL, Callipepla squamata pallida.—141 birds from New Mexico averaged 197.9 grams (9). 23 eggs from three sets average 20.76.

\*COAST CALIFORNIA QUAIL, Lophortyx californica brunnescens.-652 birds from San Mateo Co., California, averaged 189.5 grams (12, p. 249). 61 eggs from five sets average 20.25.

\*CALIFORNIA QUAIL, Lophortyx c. californica.—29 birds from Los Angeles Co., Calif., averaged 159.3 grams (12, p. 249). However, study of Sumner's table of weights of this species suggests that this figure may be too low. This is also suggested by the results for this species given below. 72 eggs from seven sets from Los Angeles Co. and southern California average 17.93.

\*MOUNTAIN QUAIL, Oreortyx picta.—Specimens in the Museum of Vertebrate Zoology averaged: 30 males, 234.57; 24 females, 230.62 grams. The latter figure is used in this paper. As Dr. A. H. Miller (in litt.) considers the geographical variation in this species not well worked out, these weights have not been divided according to localities. 45 eggs from 6 sets average 22.60.

\*MEARNS'S QUAIL, Cyrtonyx montezumae mearnsi.—One male in the Museum of Vertebrate Zoology weighed 183.1 grams. 22 eggs from two sets average 19.01.

### SUBFAMILY PERDICINAE

EUROPEAN PARTRIDGE, Perdix perdix.—46 birds from Michigan (introduced) averaged 379.88 grams (15, p. 12). 35 eggs from five sets from Washington state, England and Denmark average 26.32.

### FAMILY CORVIDAE

EASTERN CROW, Corvus b. brachyrhynchos.-45 females wintering in Ohio averaged 491.1 grams, but some of these were (smaller) immatures (4). 10 eggs from as many sets average 37.951.

NORTHERN BLUE JAY, Cyanocitta c. cristata.—44 birds from New England averaged 89.22 grams (13). 10 eggs from 10 sets average 11.956.

#### FAMILY MIMIDAE

CATBIRD, Dumetella carolinensis.--11 birds from New England averaged 38.50 grams (13); 13 from Ohio 35.9 grams (7). 10 eggs from 10 sets average 7.341.

#### FAMILY FRINGILLIDAE, SUBFAMILY RICHMONDENINAE

EASTERN CARDINAL, Richmondena c. cardinalis.-141 birds from Ohio averaged 43.76 grams (1, 7, 10). 46 eggs from 15 sets average 8.617. Only three or four eggs per set.

## SUBFAMILY CARDUELINAE

EASTERN PURPLE FINCH, Carpodacus p. purpureus.—148 females from New England averaged 24.60 grams (14). 29 eggs from 11 sets average 4.197.

EASTERN GOLDFINCH, Spinus t. tristis.—172 birds from Ohio averaged 13.41 grams (10). 18 eggs from 9 sets average 2.718. This species lays five or six eggs.

#### SUBFAMILY EMBERIZINAE

\*RED-EYED TOWHEE, *Pipilo e. erythrophthalmus.*—58 females from Ohio and New England averaged 40.73 grams (1, 13). 76 eggs from 22 sets average 7.552.

\*SAN FRANCISCO TOWHEE, Pipilo maculatus falcifer.—116 male weights averaged 39.03 grams (6). Assuming females to be 1.9% lighter, as they are in the Red-eyed Towhee (1), they would weigh 38.29 grams, which is the figure used. 46 eggs from 12 sets (California) average 7.388. Four, rarely three, eggs are laid per set.

\*SLATE-COLORED JUNCO, Junco h. hyemalis.—171 birds from New England averaged 20.94 grams (13). 20 eggs from 20 sets (partly from southeastern Canada) average 4.469.

\*EASTERN SAVANNAH SPARROW, Passerculus sandwichensis savanna.—82 birds from New England averaged 18.73 grams (13). 19 eggs from 5 sets average 4.019.

\*NEVADA SAVANNAH SPARROW, Passerculus sandwichensis nevadensis.-9 birds averaged 16.25 grams (3). This is the average of the weights for the two sexes as given by Grinnell and is used because only weights of non-sexed birds are available for the Eastern Savannah Sparrow. In any case, the weight of *nevadensis* is very approximate, being based on only 9 birds. 38 eggs from 9 sets from the range of this race average 3.568.

\*EASTERN VESPER SPARROW, *Pooecetes g. gramineus.*—38 birds from Ohio and New England averaged 24.14 grams (1, 13). 20 eggs from 19 sets average 5.018.

\*EASTERN FIELD SPARROW, Spizella p. pusilla.-613 birds from Ohio averaged 12.7 grams (1). 21 eggs from 12 sets average 3.093.

\*EASTERN CHIPPING SPARROW, Spizella p. passerina.—492 females averaged 12.0 grams (1). 51 eggs from 27 sets average 3.009.

TREE SPARROW, Spizella arborea subsp.—472 birds from Ohio averaged 19.53 grams (1). 24 eggs from 8 sets average 4.013. Of these, one set from Churchill, Manitoba, is of the eastern race, one from Alaska the western, and the others are from northern Mackenzie and may be either. The subspecies, however, seem to be based on differences of color and not of size. This species lays five or six eggs.

\*WHITE-THROATED SPARROW, Zonotrichia albicollis.—93 females averaged 25.00 grams (7). 57 eggs from 14 sets (northeastern U. S. and southeastern Canada) average 5.379.

\*EASTERN FOX SPARROW, *Passerella i. iliaca.*—34 birds from Ohio and New England averaged 38.24 grams (1, 13). 39 eggs from 12 sets from Quebec and New Brunswick average 7.102. Both this and the following race of Fox Sparrow lay only three or four eggs.

\*MARIPOSA FOX SPARROW, Passerella iliaca mariposae.-150 birds averaged 31.44 grams (5, p. 314). 19 eggs from 6 sets from the range of this race average 6.415.

\*EASTERN SONG SPARROW, Melospiza m. melodia.—267 females averaged 21.3 grams (8, p. 20). 98 eggs from 22 sets average 4.537.

SWAMP SPARROW, Melospiza georgiana.—30 birds in immature plumage from New England averaged 17.61 grams (13). 9 eggs from 9 sets average 4.408.

\*EASTERN LINCOLN'S SPARROW, Melospiza l. lincolni.-29 birds from Ohio averaged 19.24 grams (1, 7). 21 eggs from 5 sets from New Brunswick, Canada, average 4.134.

EASTERN SNOW BUNTING, Plectrophenax n. nivalis.—2 birds from Ohio average 33.75 grams (10); 6 from Long Island, New York, weighed to the nearest gram only, averaged 32 grams (personal data). 9 eggs from 9 sets from Greenland average 6.299. This species lays five, six, or even seven eggs.

Note.-It was originally planned to include the entire family Fringillidae in this

study. After some data had been collected, it became apparent that the Goldfinch and Purple Finch, which belong to the subfamily Carduelinae, lay relatively smaller eggs than the Emberizinae. Hence the study was further restricted to the subfamily Emberizinae, which includes most of our common sparrows. Text-figure 1 shows a logarithmic plotting of egg value against body size for thirteen forms of this subfamily. Eleven species and eight genera are represented.



TEXT-FIGURE 1—Numbered points on the graph represent the following species: 1, Eastern Chipping Sparrow; 2, Eastern Field Sparrow; 3, Nevada Savannah Sparrow; 4, Eastern Savannah Sparrow 5, Eastern Lincoln Sparrow; 6, Slate-colored Junco; 7, Eastern Song Sparrow; 8, Eastern Vesper Sparrow; 9, White-throated Sparrow; 10, Mariposa Fox Sparrow; 11, Eastern Fox Sparrow; 12, San Francisco Towhee; 13, Red-eyed Towhee.

All the points on the graph lie close to the 'line of best fit' plotted from the formula derived below. The deviations are so slight as to suggest that they may be due to the inevitable errors in the data. Of especial interest is the fact that although more than a threefold increase in weight is represented (from 12 to 40.73 grams), there is no suggestion of a relatively smaller egg size in the larger birds. Both b and a are constant in this group of species.

Having shown that the logarithmic graph of egg value against body weight is approximately a straight line in the species studied, it seems probable that the formula  $Y = bX^a$  applies. It remains to calculate the values of the constants b and a from the data. This can be done by the method of least squares. The use of this method in zoölogical problems is illustrated by Simpson and Roe (22, p. 365). The data supplied by the thirteen forms of Emberizinae gives the formula: Body Weight =  $3.114 (LB^2)^{1.265}$ . To simplify the calculation of bird weights from egg measurements, the dependent variable (X) is here represented by  $LB^2$ , although the causal relationship would be better shown by letting it be Y. However, despite similarities to the 'which came first' conundrum, probably all will admit that in the final analysis the size of the egg does not determine the size of the bird.

To learn how well this formula works, theoretical body weights can be computed for each species, using the egg values given above. The results are summarized in the following table:

Species	Weight of Bird	Theoretical Weight Calcu- lated from Egg Measurements	Error in Theoretical Weight
Red-eyed Towhee	40.73 grams	40.19 grams	-1.3%
San Francisco Towhee	38.29	39.09	2.1%
Slate-colored Junco	20.94	20.70	-1.1%
Eastern Savannah Sparrow	18.73	18.52	-1.1%
Nevada Savannah Sparrow	16.25	15.57	-4.2%
Eastern Vesper Sparrow	24.14	23.96	-0.8%
Eastern Field Sparrow	12.7	12.70	0.0%
Eastern Chipping Sparrow	12.0	12.53	4.4%
White-throated Sparrow	25.0	26.16	4.6%
Eastern Fox Sparrow	38.24	37.19	-2.8%
Mariposa Fox Sparrow	31.44	32.69	4.0%
Eastern Song Sparrow	21.3	21.10	-0.9%
Eastern Lincoln's Sparrow	19.24	18.76	-2.5%

The calculated, theoretical weights given in the table are, without exception, remarkably close to the actual recorded weights. As would be expected, this is true of both species and subspecies. The eggs of the two races of Fox Sparrow, for example, are as different in size as they would be if the two were distinct species.

The two races of Fox Sparrow and the San Francisco Towhee lay only three or four eggs. It is of interest that their relative egg size is no larger than that of the other species, which all lay four or five eggs. In other groups of birds, variations in clutch size may be much greater, even among closely related forms. Undoubtedly such variations do have an effect on relative egg size, which it will be of interest to measure when the necessary data become available. Possibly a correction factor might be worked out to permit the same formula to be used for all members of a group, regardless of clutch size.

There is no reason to doubt that the above formula will give good results for other species of Emberizinae. Three for which inadequate data are available are as follows:

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Species	Weight	Theoretical Weight	
Tree Sparrow (two races)	19.53	18.06	
Swamp Sparrow	17.61 (all immature)	20.34	
Snow Bunting	32.44	31.95	

As already noted, other subfamilies of Fringillidae seem to lay eggs of different relative size than do the Emberizinae. The results for three such species follow:

	Species	Weight	Theoretical Weight
Cardinal	(Richmondeninae)	43.76	47.50
Purple Finch	(Carduelinae)	24.60	19.11
Goldfinch	(Carduelinae)	13.41	11.03

Perhaps if a correction were made for clutch size in the Cardinal, which lays only three or four eggs, the theoretical weight would be closer to the recorded weights. The two finches lay relatively smaller eggs than the Emberizinae. Assuming that a is the same (1.265) for them as for the Emberizinae, the value of b can be computed for the Purple Finch; it is 4.008. If this value is inserted in the general formula, and the weight of the Goldfinch is estimated, the result is 14.20 (5.9% error). This is quite accurate, especially since the Goldfinch lays five or six eggs and may have a relatively small egg. Data for other species of Carduelinae are needed to improve this formula, and to determine if smaller relative egg size is a characteristic of this entire subfamily.

OTHER PASSERIFORMES.—Although the formula developed for the Emberizinae is unsatisfactory for some other subfamilies of Fringillidae, it gives a surprisingly good estimate for the Catbird, a member of a different family. The average weight of eleven Catbirds from New England was 38.50 grams; the theoretical weight based on eggs from the same region is 38.80 grams. Perhaps this is, so to speak, too good to be true. Nevertheless, it suggests that in some instances the same formula may apply to birds of different families. This can only be determined by trying it for several species of the groups in question.

For the Blue Jay and Crow, on the other hand, the Emberizinae formula predicts a weight far below (19% and 34%, respectively) the actual figure. If the value of b is calculated for the jay, again assuming a to be constant, and the weight of the Crow is predicted with the new value, the result is still much too low. Data for other

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Corvidae will show whether this is caused by differences in the values of b or a, or both, for the two species.

PHASIANIDAE.—Calculating in the same manner from the data given above, a formula for the seven forms of Odontophorinae, or American quail, the result is: Body weight ==  $10.386 (LB^2)^{.982}$ . This formula is based on poorer data than those available for the Fringillidae. Nevertheless, the errors in the theoretical weights calculated from this formula exceed ten per cent only once. This occurs in the California Quail, for which the weight used, as mentioned above, is probably too low. The weights are:

Species	Weight	Theoretical Weight
Northern Bob-white	197.90	179.4
Texas Bob-white	170.55	166.5
California Quail	159.3	176.6
Coast California Quail	189.5	199.0
Scaled Quail	197.9	204.1
Mountain Quail	230.62	221.9
Mearns's Quail	183.1	187.2

This formula is unsatisfactory for a member of one of the Old World subfamilies of the Phasianidae, namely, the European Partridge, *Perdix perdix*. This species weighs about 380 grams, the calculated weight is only 257.6 grams.

VARIATION IN a.—To facilitate discussion of variation in the values of a and b, these constants were recalculated, letting body weight be X, and egg value Y. The resulting formulas are:

Emberizinae:	Egg value $= .413$ (Weight).786
Odontophorinae:	Egg value $\pm .577$ (Weight). <sup>669</sup>

Although the value of a for the quail is based on rather inadequate data, it seems quite certain that its value in this group is less than in the Fringillidae. Until exact determinations of this constant have been made for other groups, it is unprofitable to discuss the possible significance of variation in a, except to refer to Huxley's remarks (19) on this point.

VARIATION IN b.—If egg weight were proportional to body weight, a would be unity, and the formula expressing this relationship would be: Egg weight = b (Body Weight)<sup>1</sup>. Here b is the simple ratio of egg weight divided by body weight. But in the present problem a is not unity, and the value of b is now equal to egg weight divided by the body weight raised to a power. Hence the ratio of egg weight to body weight is not an index of true relative egg weight.

If the value of a were the same for the quail and sparrows, the respective values of b would be directly proportional to the relative egg sizes of the two groups. Since a is not the same, it is difficult to make a valid comparison of the relative egg sizes. By extrapolating from the formulas, however, the theoretical egg weights of birds assumed to be of the same weight can be calculated and compared. Such comparisons are of limited significance, because it is unlikely that the same formulas would apply over such a wide range in weight.

The average egg value of the thirteen sparrows listed in the above table is 5.053. The egg value of a quail assumed to be of the same weight as the average sparrow would be, from the formula, 4.909. The largest sparrow included in this study weighs about 40 grams, and the smallest quail about 160 grams. It is of interest to determine what egg values would be expected in birds assumed to be of intermediate size; *e. g.*, 100 grams. The respective theoretical egg values are: for the sparrow 15.42, for the quail 12.57. Finally, the egg value of a sparrow assumed to be of the same weight as the average quail can be compared with that of the average quail. The two values are: for the sparrow 25.51, for the quail 19.37.

In comparing these three pairs of values it is surprising to find that the eggs of the altricial sparrows are always larger than those of the precocial quail. Two possible reasons for this may be suggested: (1) clutch size in the quail is more than three times as large as in the sparrows, which would tend to increase the relative egg size of the latter; (2) the rate of decrease of egg size with increase of body size may be different (greater) in birds of quail size than it is in those of sparrow size. It will be interesting to compare the relative egg size of the sparrows with that of large birds which lay about the same number of eggs, such as herons, Cracidae, or shorebirds.

The difference in egg shape also tends to invalidate this comparison of relative egg size in sparrows and quail. An attempt was made to correct this error by the use of actual egg weights available for the Song Sparrow and Bob-white. The results seemed to indicate that error due to this factor is negligible, but this conclusion is based on such scanty data as to be of doubtful validity.

CONCLUSIONS.—(1) Egg size is a non-linear function of body size in birds. The relation between the two is expressed by the general formula  $Y = bX^a$ . (2) The constant *a*, which expresses the ratio of the rate at which egg size increases to that at which body size increases Vol. 60 1943

from species to species, is shown to be constant (within the limitations of the data) for a subfamily of small birds having a weight range of from twelve to forty grams. There is considerable evidence that a has a somewhat smaller value in birds of large size, but more exact determinations are needed to calculate the extent of variation. (3) In the formula, b is a constant of proportion, which in this case reflects variations in relative egg size. Relative egg size is subject to great variation. Among the numerous factors affecting it are: body size, clutch number, condition of young at hatching, natural selection (parasitic cuckoos), or even artificial selection (Leghorn hen). Hence b is highly variable. However, in groups of closely related species, or groups in which the factors affecting relative egg size are similar, the value of b tends to be constant. (4) Since egg size is a function of body size, it is possible to calculate the size (weight) of a bird from the weight (or measurements) of its eggs. The variations in a and bmake it impossible to use one formula for all birds, but a single formula will often serve for a group containing many species. In the only group studied with adequate data, weights calculated from egg measurements were accurate within 95%. This method of estimating the weights of birds is believed to be of considerable potential importance as an aid in other studies. (5) The relation between egg weight and body weight in other groups of birds should be investigated as rapidly as the necessary weights and egg measurements become available.

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