NUMBER OF FEATHERS AND BODY SIZE IN PASSERINE BIRDS

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OTHER things being equal, the amount of heat lost by a warm-blooded animal is directly proportional to the surface area of that animal. The surface area, however, is not directly proportional to the weight, but varies approximately as does weight$^{2/3}$. This means that the surface area per unit of weight is much greater in the small animal than in the large one, and *ipso facto,* that in homoiothermic animals the problem of maintaining body temperature above that of the environment is more difficult for small individuals than for large ones. Kleiber (1932) calculated that if a mouse and a steer had the same heat production per gram of body weight, and if both were required to maintain the same temperature, the mouse would need a specific insulation twenty times that of the steer.

The extensive data of Wetmore (1921), including 1,558 records of body temperature for 327 species of birds, indicate that small birds maintain temperatures just as high as those of larger species. For example, the mean temperature in ten species of Paridae (tits and chickadees) was 107.9° F., exactly the same as for fourteen species of Corvidae (jays, magpies and crows).

Determinations of the metabolic rates of forty-five birds representing thirty-two different species ranging in size from 0.02 to 17.6 kilograms, made by Benedict, Giaja, Terroine and others, as summarized by Brody (1932, pp. 89–97), show that in birds, as in mammals, the metabolism per unit of body weight is highest in the smallest species and decreases with increasing body size. This indicates that maintenance of high temperatures by small birds is accomplished in part by an increase in the metabolic rate. However, the amount of insulation may also be an important factor. If this be so, the greater insulation needed by the smaller birds to maintain temperatures the same as those of large ones, which are from 3° to 12° F. higher than those of mammals, might be obtained by increased length of the feathers, but the resultant disproportion between size of body and length of feathers would probably interfere with flight and hence have little 'survival value.' Since the type of feather changes little within any one order, or group of birds, it is probable that any additional insulation needed by small birds is provided by an increase in the number of feathers per unit of body surface. On theoretical grounds, therefore, there should be many more feathers *per unit of area* in the Chickadee weighing eight to ten grams than in the Blue Jay of about ten times the latter weight. It follows that, since the surface area per unit of weight increases with diminishing body size, there should be a still greater difference between the Chickadee and the Blue Jay, with respect to the number of feathers *per unit of body weight.* On this basis a fairly consistent increase in the number of feathers per gram of body weight is to be expected in progressing from the larger to the smaller species within a group of related birds.

Material

Data have recently been provided by Wetmore (1936) with which the validity of this hypothesis can be tested. Actual counts of contour feathers are given for 152 birds, and for 101 of these there is also given the weight of the bird on the day it was collected. All but four of these 101 belong to the Passeriformes. This one order thus provides for analysis 97 determinations on a group of birds similar in form and homogeneous with respect to many characteristics, but with a range in size from 5.5 grams in a Golden-crowned Kinglet (*Regulus satrapa*) to 117.7 grams in a Purple Grackle (*Quiscalus quiscula*).

Since sex dimorphism in size is not extreme in this order, little error is incurred by disregarding sex in the analysis. Wetmore points out that counts of feathers were in general lower in late spring and early summer than at other seasons, but owing to the comparatively small number of determinations available for analysis and the fact that these were distributed from February to October, it has not been possible in this study to correct for changes with season. This source of error would be most serious if large birds were collected at one season and small species at another. This was not the case. The determinations were well distributed throughout the year, not only in the whole series, but also in the many species having feather counts for several birds.

Analyses

A. Passeriformes

No attempt has been made to relate the number of feathers to surface area by using the von Meeh formula for determining surface from weight. Brody (1932, p. 11) showed that determinations of surface area for one species by different investigators may differ by more than sixty per cent. Since the birds considered here vary greatly in size it is doubtful if any one value for the species constant (k) in the formula would be justifiable. Giaja (1925) determined k as 7.4 for a finch, 8.69 for a shrike, and from 6.54 to 11.5 for chickens of different sizes. For these reasons the numbers of feathers in birds of different sizes have been considered in relation to body weight.

On plotting the data it was found that they conform to the general equation $y = ax^n$, where y = number of feathers, x = body weight in grams and a and n are constants. After fitting the data to this equation by the method of least squares, the values of these constants were found to be a = 910.17 and n = 0.185. The curve for the distribution of feathers in relation to body weight is therefore:

$$y = 910.17\ x^{0.185}.$$

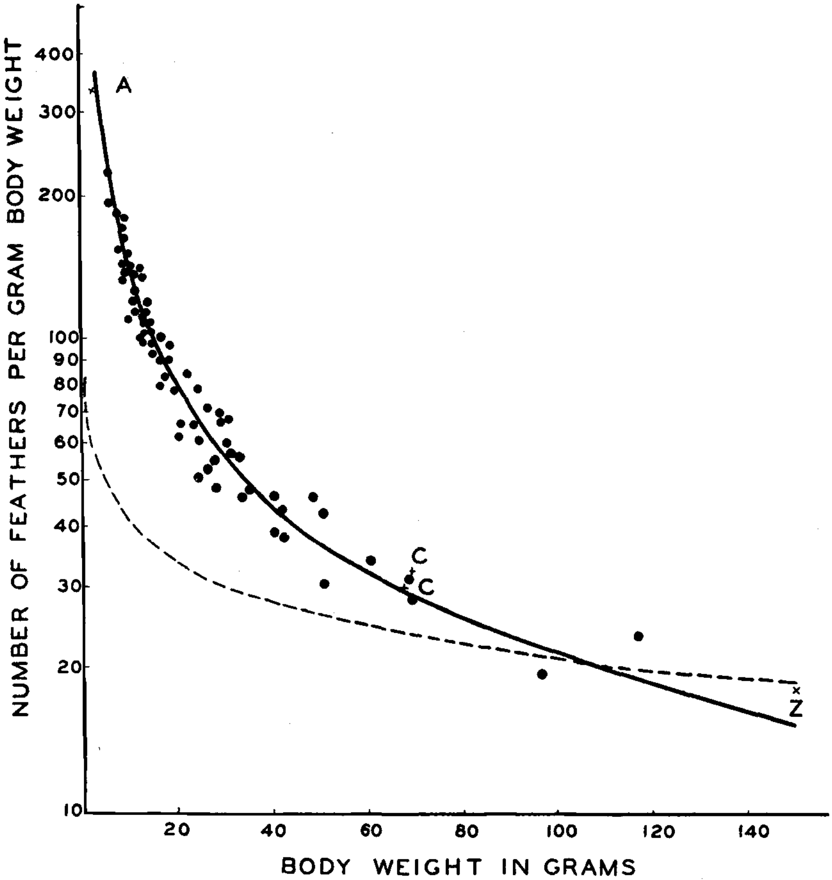
For twenty-nine warblers (Mniotiltidae) representing twenty species, the distribution follows the curve $y = 861.54\ x^{0.2361}$ and for twenty-four sparrows (Fringillidae) of twenty species the corresponding curve is $y = 747.86\ x^{0.236}$. The warblers evidently have denser plumage than the sparrows but the change with size of bird, as indicated by the exponent, is apparently very similar in both families.

If the number of feathers varied directly with the surface, then the exponent in the above equations would be about the same as it is in the equation expressing the surface area to body-weight relation, i.e., approximately 2/3. However, since the exponent for Passeriformes as a whole is only 0.185 it is evident that the number of feathers does not increase directly with body surface.

Actually the ratio $\frac{\text{number of feathers}}{\text{body weight}}$ when plotted against body weight in grams declines as the latter increases (Text-fig. 1). The data fit very closely the curve: $y = 910.17\ x^{-.815}$ where $y = \frac{\text{number of feathers}}{\text{body weight}}$ and x = body weight in grams.

The dotted line in Text-figure 1 shows the approximate increase in surface area to be expected with decreasing body size, assuming that area varies approximately as does weight$^{2/3}$. It is computed from the formula for surface area, $S = 8.19\ W^{.705}$, in which S = surface area and W = body weight. (Of several formulae which have been used by different investigators, this one is chosen because it has been proven by Mitchell (1930) to fit quite well the surface areas actually measured in birds of one species but varying greatly in size.)

If the increase in number of feathers per gram of body weight with decreasing size were attributable solely to the associated and inevitable increase of surface area (with number of feathers per unit of area remaining constant) then Wetmore's feather counts should be grouped along a curve of the shape of the dotted line in Text-figure 1. Actually the number of feathers per gram of body weight increases much more rapidly than surface area. In only five cases out of 97 does the ratio deviate by more than 20 per cent from the theoretical expectation based on the equation for the solid line, given above. It is evident, therefore, that in the Passeriformes the increase in the number of feathers per unit of body weight is much greater than could result solely from the increase in surface area per unit of weight and that there must be a consistent increase in the number of feathers per unit of area with decreasing body size. This probably indicates an adaptation for maintenance of high temperature in the smaller birds.



TEXT-FIG. 1.—Relations between body size and (a) number of feathers (solid line) and (b) surface area (broken line) per unit of body weight in the Passeriformes, both plotted on a semi-logarithmic grid. Each dot represents a count of feathers on one bird except in species smaller than 20 grams where, to avoid crowding, one dot shows the average for one to four individuals. The scale on the ordinate for the broken line must be divided by 10 to show the number of square centimeters per gram of body weight. Non-passerine birds are shown at A (*Archilochus colubris*), C (*Chordeiles minor*) and Z (*Zenaidura macroura*).

B. Other Orders

Some indications that this principle might apply equally well to some non-passerine species is provided by the four such birds for which Wetmore gives both feather count and body weight, and also to a lesser degree by

Ammann's (1937) swan (Table 1). For these birds the expected ratios of feathers/weight have been calculated by determining for the given body weight the corresponding value of y in the equation used for the Passeriformes, $y = 910.17\ x^{-.815}$. The actual determinations, with the exception of that for the swan, are shown in Text-figure 1 at A, C, and Z. It is quite evident that, with the exception of the swan, these birds conform closely to the curve established for the Passeriformes. This is all the more remarkable because one would not expect single determinations, like those for the hummingbird and Mourning Dove, to conform to the rule as closely as would the average of several determinations for a species.

TABLE 1

Application of the equation for the feathers/weight ratio in Passeriformes to birds of other orders

Order and Species	Feathers No.	Body weight grams	Ratio: $\frac{\text{No. of feathers}}{\text{Body weight}}$ Observed	Expected
MICROPODIFORMES				
Ruby-throated Hummingbird, *Archilochus colubris*	940	2.8	335.71	393.23
CAPRIMULGIFORMES				
Eastern Night-hawk, *Chordeiles minor*	2265	69.3	32.68	28.76
Eastern Night-hawk, *Chordeiles minor*	2034	67.9	29.96	29.24
COLUMBIFORMES				
Mourning Dove, *Zenaidura macroura*	2635	152.7	17.26	15.03
ANSERIFORMES				
Whistling Swan, *Cygnus columbianus*	25216	6123.0	4.12	0.75

The excess of feathers above the theoretically expected number in the swan is not surprising because of the elongation of the neck, a densely feathered region in this species. Ammann's data show that 80 per cent of the swan's feathers are on the head and neck. Presumably the values of k and n in this equation should be somewhat different in Anseriformes from those applicable in Passeriformes and other birds like them.

DISCUSSION

Wetmore (1936) points out that the hummingbird had the smallest number of feathers of all the species counted and that such a condition was to be expected, since it was the smallest of all birds examined. It seems equally noteworthy that in this diminutive species the number of feathers per gram of body weight (and presumably, therefore, the insulation) is greater than in any other of the sixty-six species for which data are available. It would be of interest to know if the northward-ranging Ruby-throated Hummingbird carries more feathers per unit of weight than those members of its family which remain in the tropics. On theoretical grounds one would expect fewer feathers in the latter.

In the curve expressing for Passeriformes the change in the ratio feathers/weight, the exponent is $-.815$. This curve is satisfactory for representation of three other Orders. In the corresponding curves for warblers and for sparrows the exponent is $-.764$. It seems justifiable to formulate the following general rule:

The number of contour feathers per unit of body weight (y) increases with decreasing body weight (x) according to the relation $y = ax^{-n}$, in which the values of n thus far determined are of the order of 0.8.

The finding that the number of feathers per unit of body weight increases with decreasing body weight is in accordance with the original hypothesis that small birds need more insulation than large ones if both groups are to maintain the same body temperature. It would appear to indicate a special adaptation for conservation of heat in the smaller species. However, since the general tendency is for the smaller birds to have higher rates of metabolism, it is probable that both adaptations contribute to the maintenance of high temperatures.

It is beyond the scope of this paper to determine the relative importance of these two influences, but the importance of the plumage and retention of the heat produced are indicated by recent studies of the physiology of birds lacking normal plumage. It was shown by Hutt (1930) that fowls homozygous for the frizzling mutation have defective plumage and may become practically bare when defective feathers break off. According to Benedict, Landauer and Fox (1932) such birds have abnormally high rates of metabolism, and, associated with it, a lack of fat deposits, enlarged thyroids, increased heart rate, hypertrophy of the heart, decrease of hemoglobin and frequent sterility. These conditions are decidedly not conducive to the survival of a species so affected, either in domestication or in Nature. It seems probable, therefore, that while the temperature of the smaller birds is maintained in part by an increase in the rate of metabolism, any adaptation for more efficient retention of the heat produced is equally important, if not more so. The inverse relationship between the number of feathers and body size provides exactly such an adaptation.

It would be of interest to know how closely this rule applies to variations in size within a species such as the Domestic Fowl, where mature males may weigh, according to the senior author's determinations, from 550 to 4970 grams in different breeds. Equally interesting would be tests of its validity in aquatic species and in the Ratites which, because of lack of barbules, have a somewhat unusual type of plumage.

SUMMARY

Analysis of Wetmore's counts of contour feathers in ninety-seven birds of the order Passeriformes shows that the number of such feathers per unit of

body weight (v) increases with decreasing body weight (x), according to the relation $y = ax^{-n}$, where $a = 910$ and n approximately 0.8. In spite of seasonal variation, in only five cases out of ninety-seven did the number of feathers per gram of body weight deviate by more than 20 per cent from the numbers calculated from body weight with this equation. In warblers (Mniotiltidae) the plumage was slightly denser than in sparrows (Fringillidae). Feather counts for representatives of three other orders fitted closely to the numbers computed from the equation for Passeriformes. It is concluded that while the increased metabolism of smaller birds is instrumental in their maintenance of high temperatures, the rapid increase in the number of feathers per unit of body weight with decreasing size of bird is an adaptation for retention of the heat produced.

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