

AVIAN HEART SIZE AND CARDIOVASCULAR PERFORMANCE

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THE lack of adequate criteria for the interpretation of heart size in birds is apparent in the published attempts to judge "adaptations" of heart size. The pioneer work of Clark (1927) and Brody (1945), and the standardization of technique developed by Norris and Williamson (1955) and its subsequent use by Hartman (1955, 1961) and others, have produced a large number of data on heart and body weight in a wide array of avian forms; however, these data have been incompletely analyzed. It is the purpose of this paper to rework the available information in order to establish a reliable mathematical relationship between heart weight and body weight. This relationship will subsequently be used as a basis for discussion of several aspects of avian circulation.

RESULTS

Heart weight.—Data on heart and body weight from most sources were used directly. Heart weights were calculated from Hartman's (1955) data on heart ratio and body weight for 67 taxonomically diverse species where sample size was five or more individuals.

The curve (Figure 1) that relates heart weight (W_h) to body weight (W_b) in birds that range in weight from 40 to 5,400 g (figured by plotting the data logarithmically and fitting a line by the method of least squares) is described by the equations:

$$W_h = 0.045 (W_b)^{1.084} \quad (1)$$

and

$$\log W_h = -2.653 + 1.084 \log W_b \quad (1a)$$

All weights are in grams. The 90 per cent confidence limits for the slope of the line (1.084) are 0.889 and 1.279.

Although Hartman gives no value, a line which I fitted by eye to his data has a slope of approximately 1, a value to be expected if heart weight is a direct function of body weight. This value and those of Clark (0.90) and Brody (0.921) fall within the 90 per cent limits for the slope given by equation (1a), and therefore are considered as not statistically different. Heart weights computed from either Clark's or Brody's formula fit Hartman's data rather well. Thus it appears to make little difference whether the heart weight of birds is expressed as the 0.9 or 1.0 power of the body weight. Because there is some evidence that the smaller birds, particularly passerines, may deviate from the metabolic patterns of larger birds (King and Farner, 1961; Lasiewski *et al.*, 1964) a separate regression function was determined for 36 species with body weights of less than 100 g (lower

line, Figure 1). The curve which relates heart weight to body weight in smaller birds is given by the equations:

$$W_h = 0.036 (W_b)^{0.639} \quad (2)$$

and

$$\log W_h = -2.556 + 0.639 \log W_b \quad (2a)$$

The slope (0.639) is less steep and is significantly different (at the 5 per cent level) from that in equation (1).

Hartman (1955) considered the slope for smaller birds to be less steep than for larger birds and a line which I fitted by eye for his smaller birds (ranging in size from a 180 g bird [Falconidae] to a 9 g bird [Paridae]) had a slope of 0.5. Because of the small scale in Hartman's published figure, this estimate is not highly reliable but it is not greatly different from that in equation (2).

The existence of two equations which relate W_h and W_b does not imply that the relation is better described by a single curvilinear relationship. When the various groups are broken into taxonomic categories (see Clark, 1927; Bowman, 1961) each is best fitted by a straight line on double logarithmic plots. The suggestion of Brody (1945) that heart weight is better related to body weight by the power equation $Y = a(X)^b$ than by the linear equation $Y = a + b(X)$ is still supported. However, the coefficient of variation (CV) of heart weight is greater among birds weighing less than 100 g (CV = 4.7) than in birds that weigh more than 100 g (CV = 1.03). Since the use of CV corrects for the tendency of variance to increase with absolute size, if we assume this increase in the variability of heart size as body weight decreases is not an observational artifact, then it is unusual and must be explained (see below).

Heart ratio.—The idea that there is a direct correlation between the activity of an organ and its size is implicit in the literature. For example, much has been made of the relative size of the avian heart in relation to its capacity to move blood. Accordingly, the heart ratio (per cent total body weight represented by the heart) has been used as an index of various physiological and ecological adaptations. Indeed, the relation between body weight and heart ratio in birds was plotted by Clark (1927) as heart ratio versus log body weight and was described by the equation:

$$\text{Heart ratio} = 2.0 (W_b)^{-0.1} \quad (3)$$

Although there was considerable scatter present, Clark concluded from this analysis that large birds have smaller heart ratios than small ones, and that heart ratio was inversely related to body weight.

Clark considered departures from this "standard curve" to be correlated with ecological habits, locomotor capabilities, and other physiological and

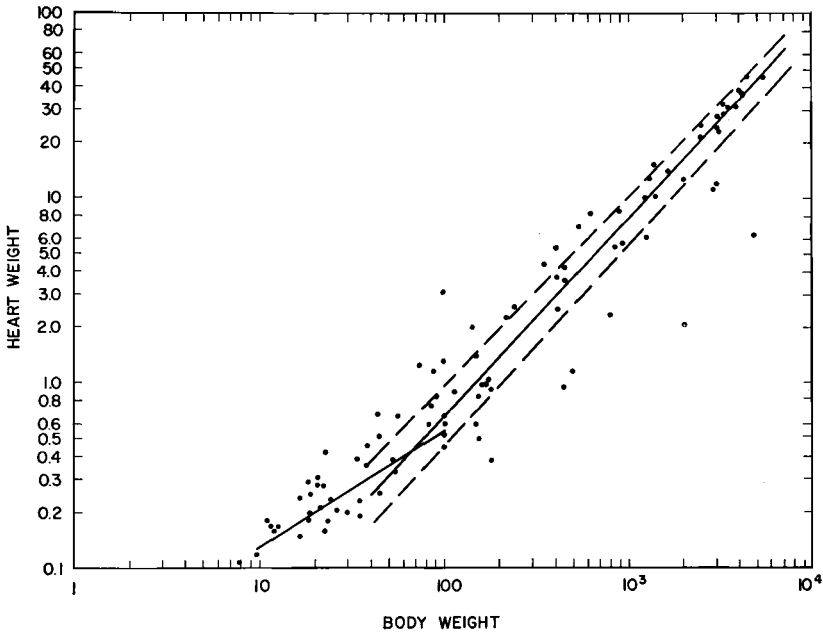


Figure 1. The log of heart weight as a function of the log of body weight in 104 species of birds. Data selected from Hartman (1955), Bowman (1961), Johnston (1963), and Johnston and Williamson (1960). The dashed lines equal two times the standard error of the estimate of $\log W_h$ from $\log W_b$. The lower solid line is a similar regression curve for birds of body weight of less than 100 g.

behavioral patterns. Hartman (1955) concluded that heart ratio may vary with season, general activity, and climate, but not necessarily sex. Johnston's statement (1963: 445) that "arctic species tend to have larger hearts" was based on his comparison of $W_h : W_b$ ratios with Hartman's data for tropical and temperate birds.

Norris and Williamson (1955), Williamson and Norris (1957), and Johnston and Williamson (1960) have investigated trends in heart ratio associated with altitude or geographic distribution in closely related groups of passerine birds. The existence of such gradients may be expected, but due to the small sample sizes involved (e.g., only one individual in 7 of the 16 classes reported by Johnston and Williamson), no statistically satisfactory statement can be made in regard to the slight differences that appeared in the heart ratios in these studies. Further, with accumulation of additional data on heart and body weight, Hartman (1961) showed that altitudinal gradients in various taxa may be non-existent, inverted, or unexplainable (i.e., not at all correlated with general activity patterns, as

in the Cuculidae). Recently, Dunson (1965) has demonstrated with adequate sampling and rigorous statistical analysis that heart weight in subspecies of the Robin, *Turdus migratorius*, shows a positive correlation with increase in altitude.

The slope of the line that describes the relation between avian heart weights and body weights over a wide range of heart and body weights indicates that proportional differences in the heart weight relative to body weight should be very small. This applies to any system which varies as $(\text{body weight})^b$, where b approaches unity, and thus shows no proportional change. It is apparent, however, that even among bird species of similar body weight the heart weight differs. In view of this and because of the lack of rigorous statistical treatment of heart ratio data, and the broad generalities that have been drawn from them, it is of interest to consider the heart ratio further.

Figure 2 is a scatter diagram of the data on heart ratio and body weight available from the literature. Data from some workers (e.g., Rensch, 1930, 1948, and 1960; see critique by Moreau, 1944) were not included because body weight was reported as "net body weight," that is, fat free weight, which resulted in abnormally high heart ratios.

Theoretically, if a plot of heart ratio versus body weight on log-log coordinates gives a line with a slope of zero, then heart ratio is constant and independent of body weight. A slope of one would indicate a complete correlation of these variables. Hence, if

$$\text{Heart ratio (Hr)} = \frac{W_h}{W_b} \times 100$$

and

$$W_h = 0.045 (W_b)^{1.084} \quad (1)$$

then, by substitution,

$$\text{Hr} = \frac{0.045 (W_b)^{1.084} \times 100}{W_b} \quad (4)$$

or

$$\text{Hr} = 4.5 (W_b)^{0.084}$$

and

$$\log \text{Hr} = 0.653 + 0.084 \log W_b \quad (4a)$$

The slope of this function (0.084) is only slightly different, but opposite in sign to a similar value (-0.1) derived by Clark (1927), who plotted a power function on a semilogarithmic grid and therefore obtained a curve rather than a straight line. A regression line fitted to the data of Figure 2 by the method of least squares has a slope of 0.108 (with 95 per cent confidence limits of 0.063 and 0.153).

It is apparent that neither the original slope of Clark (-0.1), nor that derived theoretically (0.084), nor that fitted statistically (0.108) indicates

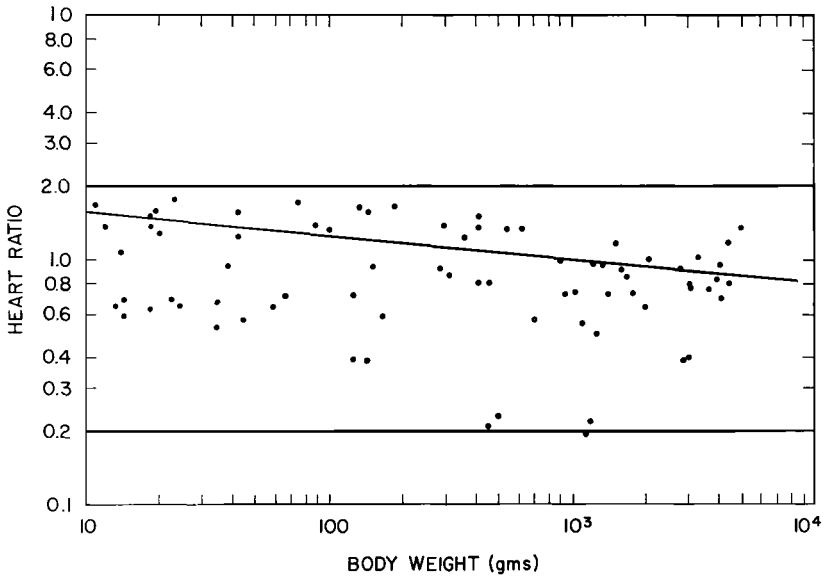


Figure 2. The log of heart ratio as a function of the log of body weight in 77 species of birds. The curve is derived from the equation of Clark (1927). Horizontal lines represent the observed limits of heart ratios. Data from Hartman (1955, 1961), Johnston and Williamson (1960), Bowman (1961), Norris and Williamson (1955), and Johnston (1963).

a strong correlation between heart ratio and body weight (a fact apparent from the curve that relates heart weight to body weight). Contrary to Clark (1927) the sign of the slope in the latter two cases indicates that heart ratio varies directly with body weight, but the magnitude of the exponent makes this correlation extremely weak. It is also apparent that relative heart weight provides little insight into phylogeny (Stahl, 1965).

The poor correlation between heart ratio and body weight is partly explicable by the large range of body and heart weights that may produce any given heart ratio. This low correlation greatly reduces the predictive value of the regression equation of heart ratio on body weight. However, the variation of heart ratio in any body weight class is of importance and may provide, with sufficient complementary information, an index to mechanisms involved in cardiac adjustments. Thus Brush (1965, and unpublished observations) demonstrated that birds of similar body weight but different heart size employed different combinations of capacity (stroke volume) and intensity (heart rate) to adjust to increased cardiovascular loads. These differences were not predictable from either heart size or heart rate alone. Further, birds with relatively larger hearts possess

a temperature independent zone of heart rate not seen in species with lower heart ratios. That is, in species with relatively small hearts the curve which relates minimal heart rate to ambient temperature shows no zone of thermal neutrality similar to that demonstrated for the metabolic rate. In species of approximately the same body weight, but with relatively larger hearts and lower heart rates, a zone of thermal neutrality may be demonstrated. Thus, in the first case (as exemplified by the California Quail, *Lophortyx californicus*), there is a constant adjustment of heart rate with changes in ambient temperature even though there is no detectable change in mean metabolic rate. In the second case (as shown by the Mourning Dove, *Zenaidura macroura*, and the quail, *Coturnix coturnix*), both heart and metabolic rates show a zone of thermal neutrality. This implies that heart size to some extent determines the type of cardiac adjustment made to various physiological demands.

The lack of any obvious relation between heart ratio and body weight has further physiological implications. The overall heart size, which may be considered an indication of the stroke volume, is an important determinant of the resting cardiac output (cardiac output = stroke volume \times heart rate). Nevertheless, the stroke volume appears to be of only minor importance in most adjustments to increased metabolic loads. The major circulatory adjustments to increased load are executed through increased heart rate (tachycardia) and increased oxygen extraction (for discussion see Ruch and Fulton, 1960: chapter 32). Thus heart ratio *per se* is not indicative of the nature of the adjustments made to increased load. Stroke volume is indicative only of cardiac reserve and therefore reflects only potential cardiac performance in birds (Hudson and Brush, 1964). Stroke volume is only one of two variables involved in any adjustment and therefore, by itself, is not sufficient to explain completely changes in cardiac output. The variability in heart weight of small birds is therefore considered to be the result of the presence of various pathways of adjustments to the metabolic inefficiency, and the resultant load, of hearts with low reserve. No single factor is responsible completely for the particular physiological abilities of a species, and large variations in heart size can be compensated for by various heart rate adjustments. The stability (i.e., high reserve) in cardiac performance that accrues with increased heart size is indicated by the low variability in heart size in larger birds. This low variability is presumably the product of selection for a high capacity, low frequency circulatory system. Hartman's data (1961) demonstrate that the one ultimate end (i.e., flight ability) can be accomplished variously through a balance of several systems which include heart size, flight muscle mass, and the size and shape of the flight surfaces. The present analysis indicates that heart rate is at least as important in adjustments to increased

metabolic demands, as is heart size, that the mechanism of adjustment cannot be predicted from heart size alone, and that birds of similar size may employ different combinations of capacity and intensity in making these adjustments.

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SUMMARY

The log of heart weight is a linear function of the log body weight in birds of body weights greater than 100 g (slope of regression curve = 1.0). In birds of body weight less than 100 g the slope of the regression equation (0.6) is significantly less steep.

There is no correlation between heart ratio and body weight for a wide array of birds of different ecological and taxonomic relationships. Hence, heart ratio is not necessarily sufficient to indicate the cardiovascular adjustments made by birds. The significant information lies in the variability of heart size in birds. In small birds heart size as well as heart rates are probably of equal importance in determining cardiovascular adaptation. Both aspects must be considered in any interpretation of the mechanism of adjustment to any set of particular circumstances.

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