Quantitative Relations in the Physiological Constitutions of Mammals

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THE INVESTIGATION OF VITAL FUNCTIONS customarily ends with the establishment of a relation between process X and process Y. It need not end so; and the object of the present paper is to show how the relations may be multiplied, providing either X or Y is used as a common correlative in further studies.

Most data of physiology concern the rates of processes. The rates represent the events, regardless of the manner in which the processes are performed. By measuring the ordinary events of living in several species, or in several individuals of diverse sizes or activities, the disproportionalities among processes are disclosed. The present description is limited to correlations *among* species and chiefly to data upon mammals. The result illustrates a quantitative method in comparative physiology and in generalized physiology.

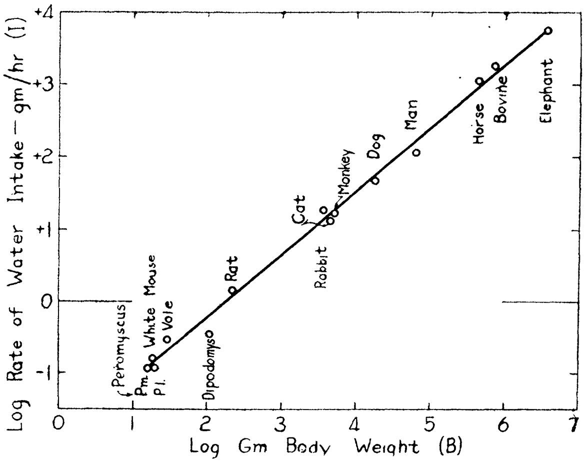

FIG. 1. Rate of water intake (I) in relation to body weight (B) among species of mammals. $I = .010\ B^{.88}$. From Adolph (*1*, p. 270).

In a previous study, rates of water exchanges were correlated with body sizes among mammals (*1*, p. 270). One set of those data is reproduced in Fig. 1. It is evident that logarithms of water intakes (I) are proportional to logarithms of body weights (B). The data fit an equation:

$$I = aB^{k} \quad . \; . \; . \; . \; . \; . \; . \quad (\mathrm{I})$$

which may also be written:

$$\log I = \log a + k \log B \quad . \; . \; . \; . \quad (\mathrm{II})$$

The coefficients a and k can be ascertained from the graph or by computation of least squares. Such power equations have been widely found to express suitably the regressions between organ sizes, and to a more limited extent to relate rates of oxygen consumption with body sizes (*3*).

The empirical relation of Fig. 1 turned out to be

$$I = .010B^{.88} \quad . \; . \; . \; . \; . \; . \quad (\mathrm{III})$$

The exponent means that water turnover (ml/hr) is not proportional to body weight (g); if it were, the exponent would be 1. The larger mammals have, relative to weight, less turnover than the smaller, and many suggestions have been put forward to the effect that rates of diverse processes might be proportional to body surface areas, perhaps to $B^{.67}$, or to other power functions of B. The general form of this equation is referred to as heterogonic; it expresses degrees of disproportionality; it is an equation of similitude. In a group of such equations might be implicit most of the factors by which an elephant differs from a mouse.

From the same source (*1*, p. 271) data are available relating urinary outputs (U) to body weights (B) in mammals. In this case,

$$U = 0.0064\,B^{.82} \quad . \; . \; . \; . \; . \quad (\mathrm{IV})$$

Evidently urine production is slightly more disproportional to body weight than is water intake. The relation implies that small animals (as compared with large animals) lose a slightly smaller fraction of their water turnover by paths other than urinary excretion; the chief other path of loss is evaporation.

The interrelation can be more clearly expressed by the appreciation of the fact that since I and U are each related to B, they are related to each other. Or, more generally,

$$Y = a_1 X^{k_1} \quad . \; . \; . \; . \; . \; . \; . \quad (\mathrm{V})$$

and

$$Z = a_2 X^{k_2} \quad . \; . \; . \; . \; . \; . \; . \quad (\mathrm{VI})$$

or

$$\log X = \frac{\log Y - \log a_1}{k_1} = \frac{\log Z - \log a_2}{k_2} \quad . \quad (\mathrm{VII})$$

then

$$\log Y = \log a_1 + \frac{k_1}{k_2}\,(\log Z - \log a_2) \quad . \quad (\mathrm{VIII})$$

and

$$Y = a_1 \left(\frac{Z}{a_2}\right)^{\frac{k_1}{k_2}} \quad . \; . \; . \; . \; . \quad \text{(IX)}$$

In the specific instance of I and U,

$$\log I = \log .010 + \frac{.88}{.82}(\log U - \log .0064) \quad . \quad \text{(X)}$$

$$= -2.000 + 1.073\,(\log U + 2.194) \quad . \quad \text{(XI)}$$

or

$$I = 2.25\,U^{1.073} \quad . \; . \; . \; . \; . \quad \text{(XII)}$$

The inverse of relation IX has the form

$$Z = a_2 \left(\frac{Y}{a_1}\right)^{\frac{k_2}{k_1}} \quad . \; . \; . \; . \quad \text{(XIII)}$$

from which

$$U = .46\,I^{.93} \quad . \; . \; . \; . \; . \quad \text{(XIV)}$$

and the inverse of relation V has the form

$$X = \left(\frac{Y}{a_1}\right)^{\frac{1}{k_1}} \quad . \; . \; . \; . \; . \quad \text{(XV)}$$

These expressions of quantitative interrelations may be applied to all functions in which log Y is proportional to log Z. Other expressions can be utilized to express interrelations when additional forms of disproportionality may be found.

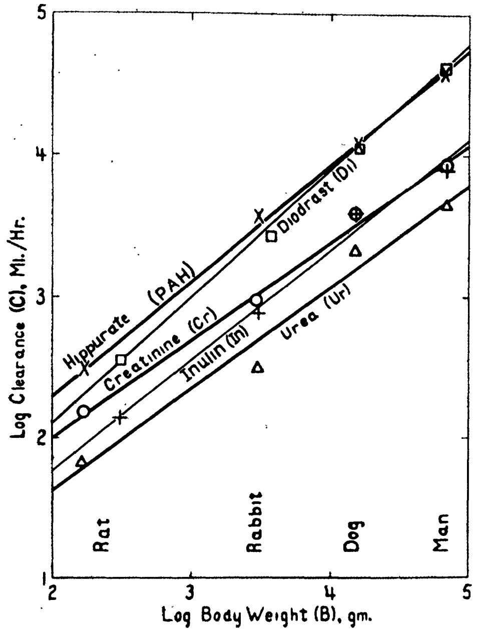

FIG. 2. Renal clearances (C) in relation to body weight (B). Straight lines are fitted on log-log units by least squares from points established for maximal clearances. Rat—Lippman, Dicker, Dicker and Heller (*19, 7, 8*). Rabbit—Kaplan and Smith, Forester and Maes, W. W. Smith (*16, 11, 25*). Dog—Dominguez, Houck, Moustgaard (*9, 15, 22*). Man—Hayman *et al.*, Goldring *et al.*, Chasis *et al.* (*14, 12, 4*).

Since a great many data of anatomy, biochemistry, and physiology can be shown to fit the heterogonic equation, the fruitfulness of this particular form of relation may be illustrated from them.

Renal clearances, which are measurements of excretory functions, have been ascertained for single organic substances in several species; their magnitudes are related with the body weights of those species (Fig. 2). A clearance is a ratio between a rate of disposal of a substance (g/hr) and its concentration in body fluid (g/ml). The data here represented have been selected by the sole criterion of taking, within each species, the arithmetical mean of that series of measurements giving maximal values for clearance of each substance. Evidently the several substances are not cleared in proportion to the body weight; the equations all have exponents less than 1. There is no support for the guess that all the

TABLE 1

EQUATIONS RELATING QUANTITATIVE PROPERTIES WITH BODY WEIGHTS AMONG MAMMALS*

Intake of water (ml/hr)	I	$=.010\ B^{.88}$ (Fig. 1)
Urine output (ml/hr)	U	$=.0064\ B^{.82}$ (*1*, p. 271)
Urea clearance (ml/hr)	C_{ur}	$=1.59\ B^{.72}$ (Fig. 2)
Inulin clearance (ml/hr)	C_{in}	$=1.74\ B^{.77}$ "
Creatinine clearance (ml/hr)	C_{cr}	$=4.2\ B^{.69}$ "
Diodrast clearance (ml/hr)	C_{di}	$=2.14\ B^{.89}$ "
Hippurate clearance (ml/hr)	C_{PAH}	$=5.4\ B^{.80}$ "
O_2 consum. basal (ml STP/hr)	O	$=3.8\ B^{.734}$ (*3*, p. 370)
Heartbeat duration (hr)	H	$=.000\ 0119\ B^{.27}$ (*5*, p. 89)
Breath duration (hr)	Q	$=.000\ 047\ B^{.28}$ (*13*)
Ventilation rate (ml/hr)	V	$=120\ B^{.74}$ (*13*)
Tidal volume (ml)	T	$=.0062\ B^{1.01}$ (*13*)
Gut beat duration (hr)	G	$=.000\ 093\ B^{.31}$ (*5*, p. 91)
N Total output (g/hr)	N_T	$=.000\ 074\ B^{.735}$ (*3*, p. 377)
N Endogenous output (g/hr)	N_B	$=.000\ 042\ B^{.72}$ (*3*, p. 377)
Creatinine N output (g/hr)	N_{cr}	$=.000\ 001\ 09\ B^{.90}$ (*3*, p. 378)
Sulphur output (g/hr)	S	$=.000\ 001\ 71\ B^{.74}$ (*3*, p. 378)
O_2 consum. liver slices (ml STP/hr)	O_L	$=3.3\ B^{.77}$ (*28*)
Hemoglobin wt (g)	H_b	$=.013\ B^{.99}$ (*10*)
Myoglobin wt (g)	M_y	$=.000\ 039\ B^{1.31}$ (*10*)
Cytochrome wt (g)	P_c	$=.000\ 10\ B^{.84}$ (*10*)
Nephra number	N	$=2600\ B^{.62}$ (Fig. 3)
Diameter renal corp. (cm)	D	$=.0081\ B^{.08}$ (*18*)
Kidneys wt (g)	K	$=.0212\ B^{.85}$ (*3*, p. 625)
Brain wt (g)	E	$=.081\ B^{.70}$ (*3*, p. 592)
Heart wt (g)	J	$=.0066\ B^{.98}$ (*3*, p. 596)
Lungs wt (g)	F	$=.0124\ B^{.99}$ (*3*, p. 627)
Liver wt (g)	L	$=.082\ B^{.87}$ (*3*, p. 626)
Thyroids wt (g)	M	$=.000\ 22\ B^{.80}$ (*3*, p. 621)
Adrenals wt (g)	A	$=.0011\ B^{.92}$ (*3*, p. 585)
Pituitary wt (g)	P	$=.000\ 13\ B^{.76}$ (*3*, p. 596)
Stom. + intes. wt (g)	W	$=.112\ B^{.94}$ (*3*, p. 628)
Blood wt (g)	R	$=.055\ B^{.99}$ (*3*, p. 593)

* Source of equations or data from which equations have been derived are indicated. All values are in ml, g, cm, and hr.

exponents are alike, or, as many physiologists assume, that all are .67. Within one species it may well be that measurement of one clearance foretells all the others; but different proportions evidently prevail within different species. The relations from which such predictions may be formulated are listed in the equations of Table 1; one of them is given as an example in line 2 of Table 2.

TABLE 2

EQUATIONS INTERRELATING SOME QUANTITATIVE PROPERTIES OTHER THAN BODY WEIGHT, DERIVED FROM TABLE 1*

$$\begin{aligned}
U &= .46\ I^{.93} = .0108\ C_{ur}^{1.14} = .000{,}000\ 19\ N^{1.32} \\
C_{ur} &= .35\ C_{PAH}^{.90} = 17{,}700\ N_T^{.98} = 42\ K^{.85} \\
O &= 1300{,}000{,}000{,}000\ H^{2.72} = 11{,}900\ P^{.87} \\
V &= 370{,}000{,}000{,}000{,}000\ H^{2.74} = 4900\ T^{.73} \\
N_T &= .0068\ U^{.90} = 5.4\ N_{cr}^{.82} = .000{,}0162\ C_{cr}^{1.06} \\
O_L &= 30\ L^{.80} = .81\ O^{1.05} = 1290\ M_y^{.59}
\end{aligned}$$

* All values are in ml, g, cm, and hr.

A very large number of relations between physiological rates taken two at a time becomes available. A limited set of data relating each function to body weight (Table 1) allows its relations with other quantities to be expressed in the manner of Table 2 without need for new measurements. Indeed, the relationships once ascertained on several species of diverse sizes will establish a relation that may then be used to describe the relationships established by the study of entirely different species. Thus, the data of Fig. 1 might have been obtained solely from mouse, cat, horse, and elephant; those of Fig. 2 being derived from four other species. Nevertheless the relation between I and C_{ur} would evidently be derived with almost the same degree of determination as by the use of identical species for both measurements.

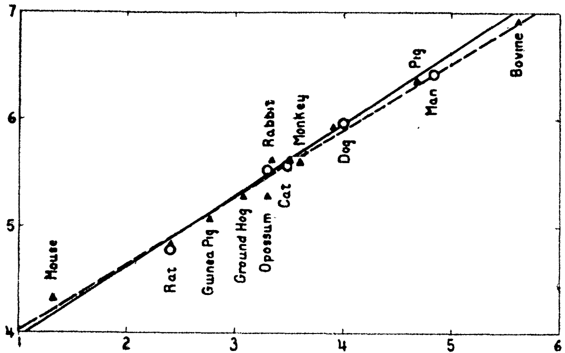

FIG. 3. Number of nephra (N) in two kidneys in relation to body weight (B) among mammals. The solid line ($N = 1900\ B^{.67}$) fits the circles which represent on log-log scales the arithmetical means of counts of glomeruli made by Arataki (*2*) for rat, Nelson (*23*) for rabbit, Vimtrup (*26*) for cat and dog, Moritz and Hayman (*20*) for man. The dotted line ($N = 2600\ B^{.62}$) fits the triangles, which represent arithmetical means of counts made by Kunkel (*18*).

From the reservoir of data upon numerical relationships of structural peculiarities to body sizes, specifically interesting relations with physiological rates may be derived. For instance, the number of nephra in the kidneys of various mammals have been counted; the numbers relate to body sizes (Fig. 3) with heterogony of low power (.62). Then urinary flow, having a higher power in relation to body weight (.82) has an exponent 1.32 in relation to nephra number. This means that when the number of excretory units is 10-fold as great, the rate of urinary excretion is 21-fold as great. In the bovine each nephron puts out 52 times as much urine as in the rat. The diameters of renal capsules increase only slightly with body weight (exponent .08). However, the volumes of renal corpuscles increase with body weight as the exponent .24. Hence the physiological activity of each nephron turns out to have a markedly different magnitude among species; but each unit of volume of renal corpuscles is about proportional to urinary flow, since

$$ND^3 = a\ B^{.86} \quad . \quad . \quad . \quad . \quad . \quad \text{(XVI)}$$

and each unit of surface,

$$ND^2 = a\ B^{.78} \quad . \quad . \quad . \quad . \quad \text{(XVII)}$$

Similarly, the renal clearance of none of the five substances (for which data are presented in Fig. 2) is proportional to nephra number. A nephron in a bovine, approximately identical in structure with that of a mouse, clears more of each excretory substance. Realization of this fact might lead to extensive search for differences among nephra.

A few data upon rates of excretion of solutes have been analyzed in relation to body weights by Brody (Table 1: N_T, N_E, N_{cr}, S). One fact here discovered is that creatinine excretion is not proportional to creatinine clearance among species.

Correlations among physiological processes need not be restricted to processes that utilize in large part any one organ (kidneys) or any one activity (excretion). It is equally useful to find the interrelations among processes that have scarcely been thought of as being interrelated. To the above excretory processes may, therefore, be related basal oxygen consumption (*3*), duration of heartbeat (*5*), duration of one intestinal contraction (*5*), duration of one breath (*13*), respiratory ventilation rate, and tidal volume. All three of the above durations have the property of being correlated with body weight (Table 1) by low exponents. Their reciprocals (frequencies) are negative correlatives of body weight.

Data are available for intercorrelations with the above quantitative properties, in the rates of oxygen-consumption of tissue slices (O_L) obtained from homologous organs of several species (Table 1). Interest has centered in the fact that these consumptions per unit of tissue *weight* vary as negative powers of body weight (*28*), for that fact indicates that the properties by which large animals consume less oxygen per gram of weight are impressed in their tissues even after isolation. Here these relations are expressed in the form

$$O_L = a\,B^k \quad . \quad . \quad . \quad . \quad \text{(XVIII)}$$

instead of

$$O_L/B = a\,B^{k-1} \quad . \quad . \quad . \quad . \quad \text{(XIX)}$$

Many physiologists are aware that oxygen consumption is proportional (i.e., with exponent 1) to ventilation rate. (Guyton's data [*13*] yield the constant $O = .028\,V$); and some recognize that oxygen consumption is proportional to nitrogen output (Brody's data [*3*] show that $O = 52{,}000\ N_T$). Further, ventilation rate is proportional to nitrogen output ($V = 1850\ N_T$). These three quantities share the exponent 1 in their relations to one another. In a species where one or two of the three are difficult to measure, they may be computed from the third (or from any of the 33 correlatives represented in Table 1).

A number of biochemical correlations may be estimated from extant data. Concentrations of cytochrome C diminish with increased body size (*10*) and suggest thereby a basis for lesser oxygen consumptions per unit tissue mass. To date, most biochemical studies have been limited to one species at a time, and little consideration has been given to the known diversities of composition among species and the implications of those diversities. The interspecific relations here derived may now be regarded in turn as definite functions of all the physiological characters mentioned.

Anatomical characteristics may be added to the total picture. Those that possess known disproportionalities to body weight (Table 1) may have their disproportionalities toward one another computed. The interrelations to function may be illustrated in the weights of kidneys, which are definitely not proportional to many of the clearances and rates of excretion presented above. Altogether, from the 33 equations of Table 1 may be derived 33 × 32 or 1056 equations expressing relations between two properties at a time. Those given in Table 2 are only a few samples. Each of the 1056 has an inverse equation XV.

Alternative sets of data that may confirm any of the above equations are few. For basal oxygen consumptions, the equation $O = 3.8\ B^{.72}$ is computed for rodents of 11 species from data of Morrison (*21*). Weights of seven visceral organs have been analyzed from 20 species of ungulates of diverse sizes by Quiring (*24*), which could replace the corresponding equations of Table 1. Among these seven organs only brain and heart had significantly different (smaller) coefficients than among the corresponding organs analyzed by Brody (*3*). With sufficient measurements it might be, as Morrison's data (*21*) suggest, that diverse orders of mammals will have diverse coefficients of regression in bicorrelations of their properties. It might also turn out that taxonomic orders based upon physiological properties will not segregate species in the same groupings as they are assigned by taxonomists.

There is no reason other than nonavailability for limiting the data mentioned to the physiological properties of mammals. Beginnings have been made in gathering data concerning the oxygen consumptions of diverse crustacea (*29*) and mollusks (*27*) and for water exchanges of aquatic animals generally (*1*, p. 272), as related to body sizes. It must be recognized that no limitation is imposed, by anything but the time and effort of investigation, upon the range of organisms and upon the array of properties that may be considered in interrelations.

A similar analysis may be applied to the changes (growth) in functions during the successive ages of organisms of any one species, or within any one individual.

The fact that all of the properties listed in Table 1 are equally related one to another can be made explicit by means of an alignment chart (Fig. 4). Each vertical scale was constructed by substituting integer values of log Y in each of the equations of Table 1. A horizontal line connects all values that belong together. There is nothing unique about body weight or any other single correlative, except that body weight happens to have been measured in gathering all the original measurements. From this chart, the characteristics of a mammalian organism, such as a cat, can be ascertained with fair precision through a knowledge of any one quantitative characteristic of it. The chart also permits comparisons to be made between any two or more species, as between cat and mouse. One would note, for instance, the great ratio of tidal volumes (T) of the two species, but the small ratio of breath durations (Q). Insofar as mean data can be utilized to describe a species, this chart is valid. For species not yet investigated, predictions are furnished by it. It allows of a probable reconstruction of the characteristics of species now extinct.

Some physiologists will hesitate to extrapolate from the data upon which the equations of Table 1 and the scales of Fig. 4 are based. A few will also hesitate to interpolate in certain zones.

Fig. 4 condenses an enormous amount of information and inference about mammals, since it represents not only 34 biological characteristics in potentially hundreds of species, but also the interrelations among all of them. The appreciation of the myriads of diverse interrelations cannot be made explicit here.

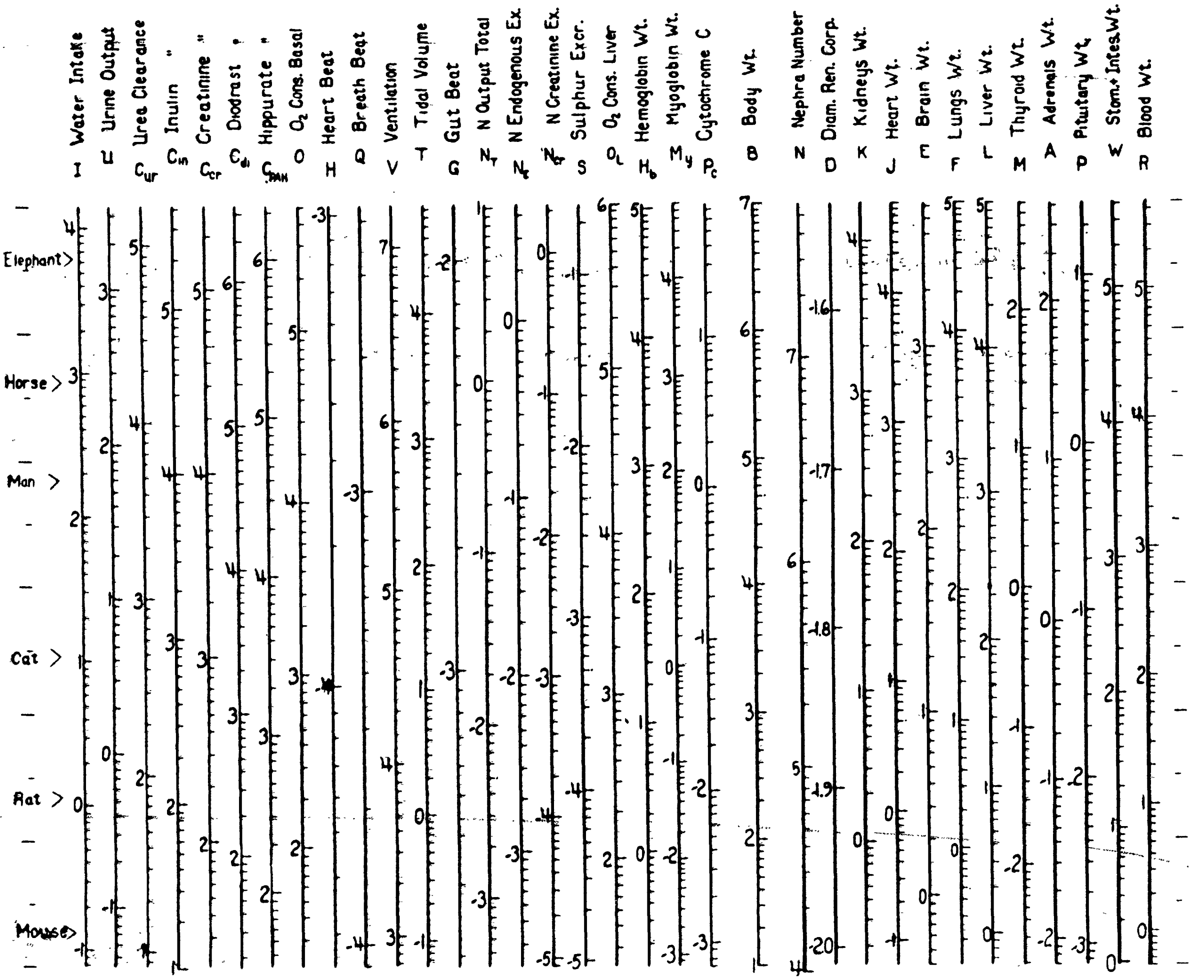

FIG. 4. Alignment chart exhibiting the relations among 34 properties of mammals. The characteristics of one animal are read off along a horizontal thread or ruler that is placed at a known value in any one of the variables. Several species chosen at random are indicated on the left at their appropriate scale positions. Ordinates are numbered as exponents of 10; but the subdivisions between ordinates read arithmetically. Thus, the number 1 means 10^1 and the subdivisions above it mean 20, 30, 40, etc. All values are in ml, g, cm, and hr, as shown in Table 1. The lines and scales represent, and are derived from, the equations of Table 1.

Coefficients of correlation between diverse properties are best computed not from intraspecies means but from single measurements. The correlation coefficients (r) found among some of the functions here named are high; many for instance are 0.95 (see Brody, *3*). The corresponding coefficients of determination (r^2) are therefore 0.90; or in ordinary parlance, process X goes with Y to the extent of 90 percent. The high "determination" is not exclusive, and many other processes are equally highly correlated with both X and Y. The remaining 10 percent allows plenty of latitude for those species peculiarities that are not related heterogonically.

Many physiological properties go hand in hand with one another; their "determination" is reciprocal and not unique. It seems likely that an organism is an integrated system by virtue of the fact that none of its properties is entirely uncorrelated, but that most are demonstrably interlinked; and not just by single chains, but by a great number of crisscrossed linkages.

General comment. The heterogonic or power equation is only one of many conceivable equations which might be empirically found to express the regressions between rates of physiological processes. Among organ sizes and biochemical constituents, however, it is the only one that has been found to apply to a large number of relations. The only interspecies data that have been shown not to fit precisely this equation are a few of the extensive data upon brain weights (*6*). Since so many properties have been found to be adequately interrelated by equations of one form, it seems very unlikely that other properties would be related according to a radically different type of equation. For if they were, they would be incompatible with the properties reviewed above. If, however, equations of greater complexity should become necessary to fit new data, the more cumbersome algebra required might impede the study of quantitative interrelations. Whether the heterogonic or some other form of relation between properties prevails does not alter the concept that interrelations may be usefully expressed by equations. The basic assumption in the procedure illustrated is that, among properties common to organisms under comparison, quantities related to a common quantity are related to one another.

Among the heterogonic relationships that prevail among processes, a variety of exponents is found. By tradition, physiologists appear to be conditioned to regard those exponents with certain numerical values more highly than other values. Some persons feel familiar only with exponents of value 1. Others assume that processes in general will reveal exponents in relations to body weights of .67. Empirical considerations have led still others (*17*) to note the prevalence of values about .75. Relations having exponents below 1 will ordinarily be counterbalanced by other relations having exponents above 1. Perhaps most exponents interrelating processes will group themselves in a frequency distribution about the value 1.

Some properties are known to be independent of body sizes (e.g., basal alveolar pressures of carbon dioxide). They are nonetheless connected with properties (such as basal ventilation rates) that are dependent upon body sizes among species.

For every heterogonic exponent below 0, its reciprocal is obviously above 0, and of the same numerical value: that is

$$\frac{1}{Y}=\frac{X^{-k}}{a} \quad . \; . \; . \; . \; . \; . \; (\mathrm{XX})$$

For every negative exponent, then, some related quantity has a positive exponent. Thus, the reciprocal of heartbeat frequency is beat duration. Only by thinking of those two measurements as separable can anyone suppose that the exponent for the frequency is more "important" than the exponent for its reciprocal, the duration.

Use of the heterogonic equations in as general a manner as they are here applied is justifiable from the aspect of their dimensions because the coefficient a takes its dimensions from those of Y and X. Since the equations were derived empirically the relations found are valid and useful no matter what dimensions they contain.

This consideration suggests a further point, namely, that the equation $Y = a\,X^k$ may be regarded as the algebraic relation between two simultaneous exponentials such as

$$Y = be^{-\beta t} \text{ and } X = ce^{-\gamma t} \quad . \; . \; . \; . \; (\mathrm{XXI})$$

In these equations the time t is concurrent in both, e is the base of natural logarithms, and b, β, c, and γ are constants. Then

$$k = \beta/\gamma \text{ and } a = b/c^{\beta/\gamma} \quad . \; . \; . \; (\mathrm{XXII})$$

Each equation XXI represents a separable process in time.

Relations expressed by heterogonic equations have often been pictured in terms of special physical inferences from exponents. Substances, dimensions, flows, forces, may perhaps be partitioned in a regular manner. Exponents in the equations express the partitions found, and free the observer from the restriction of confining his descriptions to those partitions that are proportional. Sometimes limiting factors have been conceived for these flows and forces, and specifically in terms of enzyme concentrations or other special controls. For those persons more descriptively minded, it suffices to recognize the orderly relations among quantitative characteristics. There are numerous cases where nothing is known of limiting or other governing factors. Organisms can at least be described as systems of multiple interrelations, of orderly disproportionalities. Could it be that heterogony expresses a major aspect of the ground plan of functional and of structural constitutions?

In summary, interrelations are derived, by use of the heterogonic equation $Y = a\,X^k$, from specific data representing the rates of particular physiological processes. The exponent k expresses the relative rates of X and Y as found by measurements, and for purposes of illustration data available for mammals of diverse species have been analyzed. The interrelations found imply quantitative orderliness among characteristics so diverse as urinary flow, renal clearance, duration of heartbeat, and oxygen consumption. Organisms may be pictured as systems of precise multiple interrelations. These interrelations apply not only to rates of physiological processes, but also to sizes of organs, numbers of reduplicated structures, and biochemical compositions. Some 34 correlatives in mammals are presented nomographically so that from a measurement of any one property, the 33 others can be read.

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Detail and Survey Radioautographs[1]

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QUASI-MICROSCOPIC TECHNIQUES in radioautography have left much to be desired in the study of the cellular distribution of radioactive elements and labeled compounds (*19*). The introduction of nuclear track emulsions in radioautographic techniques (*8*) has brought with it the possibility of studying localization of radioactive substances at oil immersion magnification. Alpha tracks have been studied at high magnification (*1, 8*) in conjunction with soft tissue sections mounted on the emulsion (*8, 9*). The localization of beta emitters has been studied at high magnification in tissue sections and blood smears (*5, 6*). The principles of radioautographic technique have been reviewed recently (*1, 4, 10, 11*) and techniques for special purposes have been described (*3, 5, 13, 14, 17*).

The much used *survey* or *contact* type of radiograph (*2, 12*) illustrated in Fig. 1 is indispensable for a study of the gross distribution of radioactive materials. This figure shows the distribution of plutonium in the tibia of a young rat. The section was cut unsoftened (*15*) at 10 μ. The survey examination, however, gives only the gross picture and does not reveal directly the detailed localization of this heavy metal.

A *detail* radioautograph is equally indispensable. Its application to bone is seen in Fig. 2, which was prepared by mounting a second thin section of the tibia on nuclear track emulsion. The detail radioautograph makes it possible to determine the localization of plutonium with respect to cells.

The interpretation of a detail radioautograph depends upon the determination of the point of origin of the emission. Although this is far more easily accomplished for alpha particle emitters, as in Fig. 2, much information may be obtained by examining at high magnification a beta particle sensitive nuclear track emulsion (*5, 7*). A description of the types of nuclear tracks is given by Powell and Occhialini (*18*).

Nuclear particles leave their points of origin in the tissue and travel in random directions. About half of the particles enter the emulsion and strike silver grains. The series of grains in a single path, when developed, reveal a nuclear track (A, Fig. 2). The mean free path is determined by the type and energy of the emission. Thus, the track can be retraced towards the locus in the tissue from which it origi-

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