The Size of the Aorta in Warm-Blooded Animals and its Relationship to the Body Weight and to the Surface Area Expressed in a Formula.

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In recent years it has become increasingly evident that many of the most important problems of physiology and of experimental pathology cannot be investigated in a satisfactory manner until accurate data have been made available regarding the quantitative differences which are exhibited by the organs, tissues, and fluids of the body in normal animals of different species and of varying weights. Results obtained with animals of any given weight cannot be applied, even within one and the same species, to yield conclusions regarding animals of a different weight until it has been determined with precision how the various organs and tissues of the body are related to the size of the individual. Moreover, it will not be possible to compare one species with another, or to apply the results deduced from any given species to any other species of animal, until we can establish the existence of some kind of quantitative correlation between the measurements in different species. That this will prove to be possible seems likely from an examination of the results already obtained by us in studying the various factors which influence the circulatory system and determine the size of the heart (1).

In connection with our study of the blood and cardio-vascular system under normal and pathological conditions, it was shown that the blood volume of normal animals of any given species is proportional to their body surface, and follows the formula $B = W^n/k$, where k is a constant for the species and n is approximately 0·70–0·72 (2), (3). Accordingly it became of interest, in view of the theories which have been put forward regarding the volume of the blood and the size of the aorta in chlorotic conditions, to endeavour to determine how the size of the aorta is related to the weight of the individual in any given species of animal.

For this purpose we have made a series of measurements of the aorta in various mammals and birds (4). In the case of the birds some of the measurements which we have made use of were carried out by Mr. H. K. Fry

in connection with other work undertaken in the department in collaboration with one of us (G. D.), but not yet published.

All the animals used were strong and healthy and in good condition. They had been kept in the laboratory under as equable conditions as possible as regards food, etc., and, of course, had not been employed in any previous experiment. Pregnant animals were naturally excluded.

Methods.—The animals were killed, the aorta divided just above the semilunar valves (care being taken that the section should be accurately transverse), and a portion removed from the body by cutting through the aortic arch after careful dissection. The proximal end of this portion of the aorta was then measured in the following manner:—The severed artery is placed in a special holder, closing with parallel limbs by means of which a uniform and gentle pressure is applied to the vessel until its lumen is just obliterated, and the walls meet in a straight line along the middle of the closed vessel. This straight line is then measured with fine-pointed compasses and the measurement pricked off on a piece of hard glazed drawing paper. This length represents half the internal circumference (πr) of the vessel. The external measurement is recorded in a similar manner. The vessel is then released completely and the process repeated again and again until from four to eight independent measurements (both internal and external) have been recorded. Great care is taken to avoid squeezing the vessel unduly. At the same time sufficient pressure must be applied to ensure that the walls lie quite flat against each other. The lengths thus pricked off upon the paper form a permanent record, and are subsequently measured by means of special callipers, fitted with a vernier scale which allows readings to be made to 1/20 mm. From the observed πr the radius and the sectional area of the vessel are determined. The internal measurements are those made use of in the present communication, which deals only with the capacity of the vessel.

It must be observed that while the measurements which we have made give a reliable value for the (internal) circumference of the aorta within each species, they do not necessarily afford an absolute measure of the size of the vessel in these animals at any given phase of the circulation during life.

The method here made use of was selected because it proved to yield the best results in our hands, particularly in the case of small animals. But it is open to considerable experimental error. This source of fallacy, however, is greatly reduced by multiplying the number of individual observations of each artery. It also diminishes greatly with increasing experience.

Own Observations.—In all the tables the body weight recorded is the natural weight (in grammes) of the animal immediately before it was killed,

and consequently includes the weight of the contents of the alimentary canal, *i.e.* it is "Rohgewicht." The aortic radius is calculated in millimetres and the sectional area in square millimetres from the observed πr.

Table I.—Guinea Pigs (individuals).

No.	Sex.	Body weight.	Radius of aorta.	Area of aortic cross-section.	$k = W^{0.71}/A$.	Aortic cross-section as percentage of body weight.	Cross-section calculated. $A = W^{0.71}/k$. ($k = 24 \cdot 9$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (0·78) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
1	♂	130	0·643	1·3	24·4	1·0	1·27	2·36	1·01	28·7
2	♀	140	0·679	1·44	23·2	1·03	1·34	7·46	1·09	32·1
3	♀	170	0·586	1·08	35·5	0·64	1·54	29·87	1·33	18·8
4	♀	170	0·599	1·12	34·2	0·66	1·54	27·27	1·33	15·8
5	♀	170	0·860	2·32	16·5	1·36	1·54	50·65	1·33	74·5
6	♀	200	0·774	1·88	22·9	0·94	1·73	8·67	1·56	20·5
7	♂	205	0·829	2·15	20·4	1·05	1·76	22·16	1·6	34·4
8	♀	210	0·796	1·99	22·4	0·95	1·79	11·17	1·64	21·4
9	♂	220	0·745	1·74	26·5	0·79	1·85	5·95	1·72	1·16
10	♀	220	0·752	1·77	26·0	0·8	1·85	4·32	1·72	2·91
11	♂	230	0·749	1·76	27·0	0·77	1·91	7·85	1·79	1·68
12	♀	230	0·739	1·71	27·8	0·74	1·91	10·47	1·79	4·47
13	♂	232	0·952	2·84	16·8	1·22	1·92	47·92	1·81	56·9
14	♂	300	0·78	1·91	30·0	0·64	2·3	16·96	2·34	18·4
15	♂	300	0·854	2·28	25·2	0·76	2·3	0·87	2·34	2·56
16	♂	305	1·03	3·34	17·4	1·09	2·33	43·34	2·38	40·3
17	♂	320	0·939	2·77	21·7	0·87	2·41	14·94	2·5	10·8
18	♂	330	0·745	1·74	35·3	0·53	2·47	29·55	2·57	6·62
19	♀	370	1·01	3·22	20·7	0·87	2·67	20·6	2·89	11·4
20	♀	370	0·933	2·73	24·4	0·74	2·67	2·25	2·89	5·54
21	♂	400	0·971	2·96	23·8	0·74	2·83	4·59	3·12	5·16
22	♂	420	0·905	2·57	28·4	0·61	2·93	12·29	3·28	21·6
23	♂	430	1·03	3·32	22·3	0·77	2·98	11·41	3·35	0·89
24	♂	490	1·02	3·24	25·1	0·66	3·26	0·61	3·82	15·2
25	♀	500	0·955	2·87	28·7	0·57	3·31	13·29	3·9	25·4
26	♀	550	0·939	2·77	31·9	0·5	3·54	21·75	4·29	35·4
27	♀	555	1·15	4·15	21·4	0·75	3·57	16·25	4·33	4·16
28	♂	600	1·29	5·22	18·0	0·87	3·77	38·46	4·68	11·5
29	♀	620	1·13	4·03	23·8	0·65	3·86	4·4	4·84	16·7
30	♂	640	1·3	5·33	18·4	0·83	3·95	34·94	4·99	6·81
31	♀	640	1·03	3·36	29·3	0·53	3·95	14·94	4·99	32·6
32	♀	738	1·12	3·92	27·7	0·53	4·37	10·30	5·76	22·9
33	♂	790	1·29	5·22	21·9	0·66	4·58	13·97	6·16	15·6
34	♀	830	1·21	4·57	25·9	0·55	4·75	3·79	6·47	29·4
35	♂	950	1·23	4·71	27·6	0·5	5·22	9·77	7·41	36·6
				Average	24·9	0·78	—	16·44	—	19·68

A. *Mammals.*—In Table I are given the figures and calculations for 35 guinea-pigs ranging in weight from 130 to 950 grm. (*i.e.* increasing more than sevenfold). From this table it is at once evident that, as would be

expected, the radius of the aorta increases much more slowly than the weight of the animal. The area of the aortic cross-section also increases more slowly than the body weight (though of course much more rapidly than the radius), so that the ratio of the sectional area of the aorta to the body weight decreases steadily as the weight of the animal increases. But it appears on calculation that the body weight (W) to the nth power (where n is approximately 0·70–0·72) divided by the sectional area (A) is a constant (k).

This gives us the formula $W^n/A = k$, which indicates that the sectional area of the aorta is a simple function of the surface of the body since, as was shown in a previous paper, the body surface, which can be calculated from the formula $S = kW^n$ is more accurately determined by taking n to be approximately 0·71 — 0·72 than by taking it equal to 2/3 as was done by Meeh (5). Now it has been proved on former occasions that the blood volume is proportional to the body surface, hence it follows that the sectional area of the aorta is proportional to the blood volume of the individual.

Table I further shows that the average value of k is 24·9, corresponding to an n of 0·71, which is by calculation the best n for these individuals, and that if the aortic cross-section be calculated from our formula $A = W^n/k$ using these values for n and k, the average percentage deviation between calculated and observed values is 16·44. If, on the other hand, the sectional area is expressed as a percentage of the body weight (0·78), the average deviation between the calculated and the observed values is 19·68 per cent.

It may be stated further that if the value 0·72 is taken for n, the average value of k becomes 26·5, and, if the sectional area is calculated from $A = W^{0 \cdot 72}/26 \cdot 5$, the average percentage deviation between the calculated and the observed figures is found to be 16·53.

In order to bring out the various points more clearly, to get rid of irregularities due to individual variations in the animals, and to diminish the influence of experimental error, the animals have been grouped in Table II.

In this table the guinea-pigs are arranged in five groups according to weight, and the weights, the aortic radii, and the aortic cross-sections of the animals in each group averaged. The other figures are calculated from these average values.

It is found that, under these circumstances, the best n is 0·72 (exactly as we found to be the case in calculating the surface from the body weight), and the average value of k is 25·6. Using these values for n and k, the average deviation between the calculated and the observed figures is 2·97 per cent., whereas, if the sectional area be calculated as a percentage (0·78) of the body weight, the average percentage deviation becomes 14·2, that is to say, nearly five times as large. Moreover, it will be observed that, while the k

Table II.—Guinea-pigs (grouped).

Group.	Numbers of individuals from Table I in group.	Average body weight.	Average radius of aorta.	Average area of aortic cross-section.	$k = W^{0.72}/A$.	Aortic cross-section as percentage of body weight.	Cross-section calculated. $A = W^{0.72}/k$. (k = 25·6.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (0·78) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
A	1–5	156	0·679	1·45	26·2	0·93	1·48	2·03	1·22	18·85
B	6–13	218	0·794	1·98	24·4	0·91	1·89	4·76	1·7	16·47
C	14–20	328	0·904	2·57	25·2	0·78	2·55	0·78	2·57	0·0
D	21–27	478	0·998	3·13	27·1	0·65	3·32	5·72	3·73	16·09
E	28–35	726	1·204	4·55	25·2	0·63	4·48	1·56	5·66	19·61
				Average	25·6	0·78	—	2·97	—	14·2

exhibits no periodic variation as the weight of the animal increases, the figure representing the sectional area in percentage of body weight decreases with absolute regularity from 0·93 to 0·63.

As regards the question of sex, if the males and females be considered separately in Table I, it will be seen that the average k for the 18 males is smaller than the k for the 17 females. Thus, with n equal to 0·71, the k for the males is 23·9, and that for the females 26, while with n equal to 0·72, k is 25·4 for the males and 27·6 for the females, indicating in each case that the male animals had somewhat larger aortas than had the females of corresponding weights. But this is a point to which we shall return.

In Table III are given the figures and calculations for the aortas of 27 rats, ranging in weight from 30·1 to 303 grm. (*i.e.* increasing more than tenfold). The average aortic constant (k) is 21·37, with an n of 0·71, which is the best n for these observations, and the average aortic percentage (*i.e.* sectional area of aorta expressed as a percentage of body weight) is 1·27. It is seen that, as in the case of the guinea-pigs, the variations of the aortic constant show no periodicity, but the aortic percentage decreases markedly and steadily, although not regularly, as the animals increase in weight. If the area of the aortic cross-section is calculated by our formula, the average deviation between the calculated and the observed figures is 11·09 per cent., while it is 19·72 per cent., or nearly twice as large, when the area is calculated in per cent. of body weight. If the value 0·72 be taken for n, k becomes 22·36, and, if these values be used in calculating the sectional aortic area by our formula, the average percentage deviation of the observed from the calculated figures is 11·37 per cent.

Table III.—Rats (individuals).

No.	Sex.	Body weight.	Radius of aorta.	Area of aortic cross-section.	$k = W^{0.71}/A$.	Aortic cross-section as percentage of body-weight.	Cross-section calculated. $A = W^{0.71}/k$. (k = 21·37.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (1·27) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
1	♀	30·1	0·436	0·597	18·78	1·98	0·525	13·72	0·382	56·28
2	♀	39·1	0·417	0·546	24·74	1·4	0·632	13·61	0·497	9·84
3	♂	40·3	0·468	0·681	20·08	1·7	0·646	6·35	0·512	34·18
4	♂	47·2	0·455	0·657	23·71	1·38	0·722	9·83	0·599	8·68
5	♀	53·0	0·493	0·764	21·94	1·44	0·784	2·56	0·673	13·52
6	♂	56·0	0·510	0·815	21·38	1·46	0·816	0·12	0·711	14·63
7	♀	57·7	0·548	0·941	18·92	1·63	0·833	12·97	0·733	28·37
8	♀	69·7	0·566	1·01	20·16	1·45	0·953	5·98	0·885	14·12
9	♀	75·5	0·599	1·12	19·23	1·48	1·01	1·09	0·959	16·79
10	♀	79·5	0·580	1·06	21·09	1·31	1·05	0·95	1·01	4·95
11	♂	84·5	0·669	1·4	16·67	1·66	1·09	28·44	1·07	30·84
12	♂	96·7	0·484	0·735	34·93	0·76	1·2	38·8	1·23	40·24
13	♂	104·0	0·643	1·3	20·81	1·25	1·27	2·36	1·32	1·52
14	♂	108·0	0·77	1·86	14·94	1·72	1·3	40·38	1·37	35·77
15	♂	140·0	0·669	1·4	23·85	1·0	1·56	10·26	1·78	21·35
16	♂	141·0	0·707	1·57	21·38	1·11	1·57	0·0	1·79	12·29
17	♂	141·0	0·669	1·4	23·97	0·99	1·57	10·83	1·79	21·79
18	♀	141·0	0·678	1·44	23·31	1·02	1·57	8·28	1·79	19·55
19	♂	157·0	0·723	1·64	22·09	1·04	1·69	2·96	1·99	17·59
20	♂	157·6	0·77	1·86	19·54	1·18	1·7	9·41	2·0	7·0
21	♂	160·0	0·819	2·1	17·47	1·31	1·72	22·09	2·03	3·45
22	♂	164·0	0·723	1·64	23·32	1·0	1·75	6·29	2·08	21·15
23	♂	172·0	0·812	2·07	18·67	1·20	1·81	14·36	2·18	5·05
24	♂	175·0	0·732	1·68	23·29	0·96	1·83	8·2	2·22	24·32
25	♂	179·0	0·755	1·79	22·22	1·0	1·86	3·76	2·27	21·15
26	♂	289·0	0·885	2·47	22·62	0·85	2·61	5·36	3·67	32·7
27	♂	303·0	1·01	3·22	17·95	1·06	2·7	17·78	3·85	16·36
			Average		21·37	1·27	—	11·09	—	19·72

In Table IV the rats are arranged in six groups according to weight, and the aortic constant and aortic percentage are calculated from the average figures of these groups. As in the case of the grouped guinea-pigs, the best n is 0·72, giving an average k of 21·9. It will be observed that in these grouped animals the variations in the aortic constants of the groups are very small and are non-periodic, while the aortic percentage falls markedly and very regularly from 1·67 to 0·96. Using the values just stated for n and k, the average deviation between the calculated and the observed figures for the aortic cross-section is only 1·18 per cent., while it is 16·22 per cent. (nearly 14 times as large) if the area be calculated in per cent. of body weight.

Table IV.—Rats (grouped).

Group.	Numbers of individuals from Table III in group.	Average body weight.	Average radius of aorta.	Average area of aortic cross-section.	$k = W^{0.72}/A$.	Aortic cross-section as percentage of body weight.	Cross-section calculated. $A = W^{0.72}/k$. ($k = 21·9$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (1·28) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
A	1–3	36·5	0·441	0·61	21·9	1·67	0·609	0·16	0·467	30·62
B	4–7	53·5	0·503	0·793	22·1	1·48	0·802	1·12	0·685	15·77
C	8–12	81·2	0·583	1·07	22·2	1·32	1·08	0·93	1·04	2·88
D	13–18	129·0	0·691	1·5	22·1	1·16	1·51	0·66	1·65	9·09
E	19–25	166·4	0·763	1·83	21·7	1·1	1·82	0·55	2·13	14·08
F	26–27	296·0	0·952	2·85	21·1	0·96	2·75	3·64	3·79	24·8
				Average	21·9	1·28	—	1·18	—	16·22

Table V.—Rabbits (individuals).

No.	Sex.	Body weight.	Radius of aorta.	Area of aortic cross-section.	$k = W^{0.71}/A$.	Aortic cross-section as percentage of body weight.	Cross-section calculated. $A = W^{0.71}/k$. ($k = 22·49$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (0·609) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
1	♀	310	0·996	3·12	18·82	1·006	2·61	19·54	1·89	65·08
2	♀	370	0·926	2·7	24·66	0·73	2·96	8·78	2·25	20·0
3	♀	530	1·14	4·1	20·96	0·774	3·82	7·33	3·23	26·93
*4	—	767	1·43	6·44	17·35	0·84	4·97	33·6	4·67	37·9
5	♂	1330	1·41	6·25	26·43	0·47	7·35	14·96	8·1	22·84
6	♂	1420	1·47	6·77	25·56	0·477	7·7	12·08	8·65	21·73
*7	—	1640	1·85	10·23	18·74	0·624	8·52	20·07	9·99	2·4
8	♂	1885	1·59	7·97	26·55	0·423	9·41	15·3	11·48	30·57
9	♂	2080	1·84	10·64	21·32	0·512	10·09	5·45	12·67	16·02
*10	—	2096	2·07	13·45	16·96	0·642	10·15	32·51	12·76	5·41
11	♂	2100	1·71	9·15	24·97	0·436	10·16	9·94	12·79	28·46
12	♂	2550	1·74	9·52	27·54	0·373	11·66	18·35	15·53	38·7
				Average	22·49	0·609	—	16·49	—	26·34

* The data for the individuals indicated are taken from Keilson (6).

Table V gives the figures for the aortas of 12 rabbits, ranging in weight from 310 grm. to 2250 grm. (*i.e.* increasing more than eightfold). The average aortic constant (k) is 22·49, with an n (best n) of 0·71, and the average

aortic percentage is 0·609. The variations of the aortic constant show no periodicity, but the aortic percentage decreases very greatly (although not regularly) as the animals increase in weight. When the aortic area (*i.e.* area of the cross-section of the aorta) is calculated by our formula, the average deviation of the observed from the calculated figures is 16·49 per cent., while it is 26·34 per cent. if the area be calculated in per cent. of body weight.

If the value 0·72 be taken for n, k becomes 24·15.

Table VI.—Rabbits (grouped).

Group.	Numbers of individuals from Table V in group.	Average body weight.	Average radius of aorta.	Average area of aortic cross-section.	$k = W^{0.71}/A$.	Aortic cross-section as percentage of body weight.	Cross-section calculated. $A = W^{0.71}/k$. (k = 22·1.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (0·628) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
A	1–2	340	0·961	2·91	21·6	0·856	2·84	2·46	2·14	35·98
B	3–4	649	1·29	5·27	18·7	0·812	4·45	18·43	4·08	29·17
C	5–6	1375	1·44	6·51	26·0	0·473	7·65	14·9	8·64	24·65
D	7–8	1763	1·72	9·1	22·2	0·516	9·13	0·33	11·07	17·71
E	9–12	2207	1·84	10·69	22·1	0·484	10·71	0·19	13·86	22·87
				Average	22·1	0·628	—	7·26	—	26·08

In Table VI the rabbits are arranged in five groups according to weight, and the aortic constant and aortic percentage are calculated from the average figures of these groups. In this case the best n is 0·71, giving an average k of 22·1. The variations in the aortic constant are without periodicity, but the aortic percentage falls gradually, though not quite regularly, from 0·856 in the lightest, to 0·484 in the heaviest group. Using the above values for n and k, the average deviation of the observed figures from the calculated is 7·26 per cent., while it is 26·08 per cent. (between three and four times as great) if the area be calculated as a percentage of body weight.

We now return to examine the question of sex as regards its bearing on the size of the aorta in these mammals. Since the number of our observations within any one of the species can hardly be regarded as sufficient to justify a general inference, we have taken all three species of animals together and made the figures comparable, *inter se*, by reducing them in terms of a common standard. When this is done, and the male and female animals are taken separately, it appears that the sectional area of the aorta in the male expressed as a function of the body surface is about 3 per cent. greater than it is in a

female of the same weight. This is of special interest in view of the fact that a difference of the same size and character was observed by two of us in the blood volume of male and female rabbits. It may be noted, further, in this connection that, so far as we have yet ascertained from our data, the heart in the male animal is somewhat larger than in the female of the same body weight and species.

Table VII.—Ducks (individuals).

No.	Sex.	Body weight.	Radius of aorta.	Area of aortic cross-section.	$k = W^{0.70}/A$.	Aortic cross-section as percentage of body weight.	Cross-section calculated. $A = W^{0.70}/k$. ($k = 10 \cdot 75$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (1·56) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
1	—	70	0·764	1·84	10·66	2·62	1·82	0·82	1·09	68·04
2	—	70	0·758	1·8	10·87	2·57	1·82	1·1	1·09	64·84
3	—	70	0·745	1·74	11·21	2·49	1·82	4·4	1·09	59·34
4	—	520	1·56	7·64	10·42	1·47	7·38	3·52	8·11	5·8
5	—	600	1·66	8·6	10·23	1·43	8·25	4·24	9·36	8·12
6	♀	1180	1·99	12·42	11·39	1·05	13·14	5·48	18·41	32·45
7	♂	1330	2·14	14·3	10·75	1·08	14·3	0·0	20·75	31·09
8	♀	1420	2·16	14·72	10·93	1·04	14·96	1·6	22·15	33·54
9	♀	2070	2·47	19·15	10·91	6·93	19·48	1·69	32·29	40·69
10	♀	2850	2·86	25·8	10·16	0·91	24·37	5·87	44·46	41·97
				Average	10·75	1·56	—	2·87	—	38·59

B. *Birds.*—Table VII gives the figures for the aortas of 10 ducks, ranging in weight from 70 grm. to 2850 grm. (*i.e.* increasing more than fortyfold). The average aortic constant (k) is 10·75 with an n (best n) of 0·70, and the average aortic percentage is 1·56. The variations of the aortic constant are small and show no periodicity, but the aortic percentage decreases very greatly and with absolute regularity as the animals increase in weight. When the aortic area (A) is calculated by our formula, the average deviation of the observed from the calculated figures is only 2·87 per cent., while it is 38·59 per cent. (more than 13 times as great) if the area be calculated in per cent. of body weight.

If the value 0·71 be taken for n, k becomes 11·54 and the average deviation between calculated and observed values is 3·12 per cent.; with n equal to 0·72, k is 12·19. That the value 0·71 for n is very nearly as good as the "best" n (0·70) is shown by the fact that while the average deviations per cent. are 2·87 and 3·12 respectively with $n = 0·70$ and $n = 0·71$, the *mean*

deviations calculated by the method of least squares are 3·67 and 3·63 per cent. respectively with the same values of *n*. That is to say that the value 0·71 gives a very slightly smaller *mean* deviation than the value 0·70.

Table VIII.—Fowls (individuals).

No.	Sex.	Body weight.	Radius of aorta.	Area of aortic cross-section.	$k = W^{0.72}/A$.	Aortic cross-section as percentage of body weight.	Cross-section calculated. $A = W^{0.72}/k$. ($k = 21·21$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (1·14) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
1	—	40·6	0·462	0·669	21·51	1·648	0·679	1·47	0·463	54·13
2	—	42·7	0·462	0·669	22·31	1·567	0·704	4·97	0·487	43·53
3	—	43·9	0·484	0·736	20·54	1·677	0·718	2·51	0·5	47·2
4	♀	919	1·45	6·6	20·61	0·718	6·41	2·96	10·48	37·02
5	♀	1580	1·72	9·3	21·61	0·589	9·48	1·9	18·01	48·31
6	♀	1598	1·77	9·81	20·65	0·614	9·55	2·72	18·22	46·16
				Average	21·21	1·14	—	2·76	—	46·06

In Table VIII are given the figures for the aortas of six fowls, ranging in weight from 40·6 grm. to 1598 grm. (*i.e.* increasing nearly fortyfold). The average aortic constant (k) is 21·21 with an n (best n) of 0·72, and the average aortic percentage is 1·14. The variations of the aortic constant are quite small and show no periodicity, but the aortic percentage decreases very greatly and almost regularly from 1·648 in the lightest animal to 0·614 in the heaviest. When the aortic area (A) is calculated by our formula the average deviation of the observed from the calculated figures is only 2·76 per cent., while it is 46·06 per cent. (nearly 17 times as great) if the area be calculated in percentage of body weight.

With n taken as 0·71, k becomes 20·08 and the average percentage deviation between observed and calculated figures is 3·28.

Table IX contains the figures for 10 ptarmigan purchased from a game-dealer. These were birds which had been shot, and they show the greatest range of weight we were able to obtain, namely, from 470 grm. to 710 grm. The average aortic constant (k) is 11·4 with an n (best n) of 0·71, and the average aortic percentage is 1·4. The variations of the aortic constant show no periodicity, but the aortic percentage decreases from 1·66 in the lightest to 1·23 in the heaviest animal. When the aortic area (A) is calculated by our formula the average deviation of the observed from the calculated figures

is 7·12 per cent., while if the area be calculated as a percentage of body weight it is 7·22. If the value 0·72 be taken for n, k becomes 12·2.

Table IX.—Ptarmigan (individuals).

No.	Sex.	Body weight.	Radius of aorta.	Area of aortic cross-section.	$k = W^{0.71}/A$.	Aortic cross-section as percentage of body weight.	Cross-section calculated. $A = W^{0.71}/k$. ($k = 11·4$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (1·40) of body weight.	Difference between cross-section calculated and observed.
		grms.	mm.	sq. mm.				per cent.		per cent.
1	♀	470	1·58	7·8	10·1	1·66	6·92	12·71	6·58	18·54
2	♀	470	1·4	6·19	12·8	1·32	6·92	10·53	6·58	5·93
3	♀	530	1·48	6·84	12·6	1·29	7·54	9·28	7·42	7·82
4	♀	538	1·59	7·93	10·9	1·47	7·62	4·06	7·53	5·31
5	♀	553	1·51	7·19	12·3	1·3	7·77	7·46	7·74	7·11
6	♀	590	1·63	8·35	11·1	1·42	8·14	2·58	8·26	1·0
7	♀	600	1·68	8·91	10·5	1·49	8·23	8·26	8·4	6·07
8	♀	630	1·65	8·58	11·3	1·36	8·52	0·7	8·82	2·72
9	♀	650	1·75	9·58	10·4	1·47	8·72	9·87	9·1	5·27
10	♀	710	1·67	8·71	12·1	1·23	9·24	5·73	9·94	12·37
				Average	11·4	1·4	—	7·12	—	7·22

Table X.—Ptarmigan (grouped).

Group.	Numbers of individuals, from Table IX in group.	Average body weight.	Average radius of aorta.	Average area of aortic cross-section.	$k = W^{0.72}/A$.	Aortic cross-section as percentage of body-weight.	Cross-section calculated. $A = W^{0.72}/k$. ($k = 12·1$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (1·41) of body weight.	Difference between cross-section calculated and observed.
		grm.	mm.	sq. mm.				per cent.		per cent.
A	1–2	470	1·49	6·69	12·0	1·49	6·94	0·72	6·63	5·43
B	3–4	534	1·53	7·39	12·5	1·38	7·6	2·76	7·53	1·86
C	5–7	581	1·61	8·15	12·0	1·4	8·08	0·87	8·19	0·49
D	10–12	663	1·69	8·96	12·0	1·35	8·89	0·78	9·35	4·17
				Average	12·1	1·41	—	1·28	—	2·99

In Table X the ptarmigan are arranged in four groups according to weight, and the aortic constant and aortic percentage are calculated from the average figures of these groups. In this case the best n is 0·72, giving an average value for k of 12·1. The variations in the aortic constant are small and non-

periodic, but the aortic percentage falls gradually though not quite regularly from 1·49 to 1·35. Using the above values for n and k, the average deviation of the observed figures from the calculated is 1·28 per cent., while it is 2·99 per cent. (more than twice as great) if the area be calculated as a percentage of the body weight.

Table XI.—Sparrows (individuals).

No.	Body weight.	Radius of aorta.	Area of aortic cross-section.	$k = W^{0.71}/A$.	Aortic cross-section as percentage of body weight.	Cross-section calculated: $A = W^{0.71}/k$. ($k = 22.6$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (1·771) of body weight.	Difference between cross-section calculated and observed.
	grm.	mm.	sq. mm.				per cent.		per cent.
1	22·05	0·35	0·385	23·1	1·743	0·398	3·26	0·391	1·53
2	22·55	0·366	0·42	21·8	1·782	0·405	3·7	0·399	5·26
3	23·1	0·398	0·487	19·1	2·105	0·412	15·77	0·409	19·03
4	24·6	0·414	0·537	18·1	2·098	0·429	25·18	0·436	23·2
5	26·55	0·35	0·385	26·6	1·45	0·453	15·01	0·47	18·09
6	26·6	0·35	0·385	26·7	1·448	0·454	15·2	0·471	18·3
			Average	22·6	1·771	—	13·02	—	14·24

Table XI gives the figures for the aortas of six sparrows ranging in weight from 22·05 grm. to 26·6 grm., a very small range indeed, but the best which we were able to obtain at the time. The average aortic constant (k) is 22·6 with an n (best n) of 0·71, and the average aortic percentage is 1·771. The variations of the aortic constant show no periodicity. When the aortic area (A) is calculated by our formula the average percentage deviation between the calculated and the observed figures is 13·02, and it is 14·24 if the area be calculated as a percentage of body weight.

If n be taken as 0·70 the value of k is 21·9, and with an n of 0·72 k is 23·4.

C. *Thoma's Observations on Man.*—Table XII contains the figures for the aortas of 33 human individuals calculated from the grouped observations published by R. Thoma (7). The individuals in question ranged in *age* from two months to 29 years and the range in weight of the groups is from 8941 grm. to 49,000 grm. The best n is 0·70, which gives an average value for k of 5·03. The variations in the aortic constant are without periodicity, but the aortic percentage falls gradually though not quite regularly from 1·309 in the lightest group to 0·804 in the heaviest. Using these values for n and k, the average percentage deviation of the observed from the

Table XII.—Man (grouped). Thoma's Observations.*

Group.	Number of individuals in group.	Average body weight.	Average radius of aorta.	Average area of aortic cross-section.	$k = W^{0.70}/A$.	Aortic cross-section as percentage of body weight.	Cross-section calculated. $A = W^{0.70}/k$. ($k = 5·03$.)	Difference between cross-section calculated and observed.	Cross-section calculated as percentage (1·052) of body weight.	Difference between cross-section calculated and observed.
		grms.	mm.	sq. mm.				per cent.		per cent.
A	7	8941	6·1	117·0	**4·99**	**1·309**	**116·0**	**0·86**	**94·1**	**24·34**
B	9	11950	6·7	141·0	**5·07**	**1·18**	**142·1**	**0·77**	**125·7**	**12·17**
C	5	13630	7·25	165·0	**4·75**	**1·211**	**155·8**	**5·91**	**143·4**	**15·06**
D	3	17510	7·65	184·0	**5·08**	**1·051**	**185·7**	**0·92**	**184·2**	**0·11**
E	4	43250	10·2	326·0	**5·4**	**0·754**	**349·6**	**6·75**	**455·0**	**28·35**
F	5	49000	11·2	394·0	**4·87**	**0·804**	**381·5**	**3·28**	**515·5**	**23·57**
				Average	**5·03**	**1·052**	—	**3·08**	—	**17·27**

* Thoma's data are printed in light type. The figures calculated by us are printed in heavy type.

calculated figures is 3·08, while it is 17·27 (more than five and a-half times as great) if the area be calculated as a percentage of the body weight.

If the value 0·71 be taken for n the value of k becomes 5·55, and with an n of 0·72 k is 6·13. Taking n as 0·71 the average percentage deviation of the observed values from those calculated by our formula is 3·16 as compared with the deviation of 3·08 per cent. with n equal to 0·70. Or if the appropriate allowance be made for the number of individuals in each of the groups, the figures for the average percentage deviation of the observed values from the theoretical values given by our formula are 2·69 with an n of 0·70 and 2·73 with n of 0·71, indicating the fact that the value 0·71 for n is only very slightly less good in these observations than the value 0·70.

Thoma himself, who, in his great monograph (7) on the size and weight of the various parts of the human body under normal and diseased conditions, endeavoured to establish a definite quantitative relation between the body weight and the aortic radius, defined the correlation which he found to exist in the statement that the body weight divided by the cube of the aortic radius was approximately constant over a wide range of weight.

This he expressed in the formula $W/r^3 = K$. The formula was purely empirical, and possessed no special biological significance, though it represented the experimental data in an extremely satisfactory manner. It will be seen, however, that it is readily transformable into the formula $W^{\frac{2}{3}}/\pi r^2 = k$, which is the formula deduced by us from our observations

upon animals ($W^n/A = k$) if one gives n the value $\frac{2}{3}$ or 0·67 instead of 0·70–0·72, as we have found it to be. This latter formula is a rational formula, since it indicates, as has already been pointed out, that the aortic area (like the blood volume) is a function of the body surface.

Table XIII.—Man (grouped). Thoma's Observations.*

Group.	Number of individuals in group.	Average body weight.	Average radius of aorta.	$K_1 = W/r^{n_1}$ ($n_1 = 3$).	$K_2 = W/r^{n_2}$ ($n_2 = 2·82$).	Aortic radius calculated. $r_1 = \sqrt[n_1]{(W/K_1)}$. ($n_1 = 3$, $K_1 = 38·3$.)	Difference between aortic radius calculated and observed.	Aortic radius calculated. $r_2 = \sqrt[n_2]{(W/K_2)}$. ($n_2 = 2·82$, $K_2 = 55·8$.)	Difference between aortic radius calculated and observed.
		grm.	mm.				per cent.		per cent.
A	7	8,941	6·1	**39·4**	**54·6**	**6·16**	**0·97**	**6·05**	**0·83**
B	9	11,950	6·7	**39·7**	**56·0**	**6·78**	**1·18**	**6·71**	**0·15**
C	5	13,630	7·25	**35·8**	**51·8**	**7·09**	**2·26**	**7·03**	**3·13**
D	3	17,510	7·65	**39·1**	**56·4**	**7·70**	**0·65**	**7·68**	**0·39**
E	4	43,250	10·2	**40·8**	**61·9**	**10·41**	**2·02**	**10·58**	**3·59**
F	5	49,000	11·2	**34·9**	**53·9**	**10·86**	**3·13**	**11·06**	**1·27**
		Average		**38·3**	**55·8**	—	**1·70**	—	**1·56**

* Thoma's data are printed in light type. The figures calculated by us are printed in heavy type.

In Table XIII we have calculated K for Thoma's figures from the formula $W/r^n = K$, first giving n the value 3 as in Thoma's formula, and then giving it the value 2·82, which corresponds to $n = 0·71$ in our formula, and is the best n for Thoma's observations. It then appears that if the aortic radius be calculated by means of these values of K the average percentage deviation between r calculated and r observed is 1·70 when n has the value 3, while it is only 1·56 when n has the value 2·82. Moreover, if the appropriate allowance be made for the number of individuals in each group the figures become 1·65 with n taken as 3, and 1·35 with n taken as 2·82. It will, of course, readily be apprehended that differences of this amount in the radius assume a considerable importance when calculations are made by area (*i.e.* πr^2), as is necessary in referring the aortic area to the body surface.

In Table XIV are tabulated our main results arranged in such a manner as to show at a glance the range of weight, the best n, the value of k, the percentage deviation, and so forth for each species of animal. It will be seen from the averages brought out at the foot of the table that taking all

Table XIV.—Constants, Average Deviations, etc.

Animal.	Range of weight.	Weight of heaviest in terms of lightest.	Best n.	Aortic constant (k). $k = W^n/A$.			Average percentage deviation.				Deviation by weight divided by deviation by best n.
				$n = 0·70$.	$n = 0·71$.	$n = 0·72$.	$n = 0·70$.	$n = 0·71$.	$n = 0·72$.	As percentage of body weight.	
	grm.										
Guinea-pig: individual ...	130–950	7·31	0·71	—	24·9	26·5	—	16·44	16·53	19·68	1·2
" grouped	156–726	4·65	0·72	—	24·2	25·6	—	3·33	2·97	14·20	4·78
Rat: individual	30·1–303	10·1	0·71	—	21·4	22·4	—	11·09	11·37	19·72	1·78
" grouped	36·5–296	8·11	0·72	—	20·9	21·9	—	—	1·18	16·22	13·8
Rabbit (tame): individual	310–2550	8·22	0·71	—	22·5	24·2	—	16·49	—	26·34	1·6
" grouped...	340–2207	6·5	0·71	—	22·1	23·7	—	7·26	—	26·08	3·59
Duck: individual	70–2850	40·7	0·70	10·8	11·5	12·2	2·87	3·12	—	38·59	13·5
Fowl: individual...........	40·6–1598	39·4	0·72	—	20·1	21·2	—	3·28	2·76	46·06	16·7
Ptarmigan: individual ...	470–710	1·51	0·71	—	11·4	12·2	—	7·12	—	7·22	1·01
" grouped	470–663	1·41	0·72	—	—	12·1	—	—	1·28	2·99	2·34
Sparrow: individual	22·05–26·6	1·21	0·71	21·9	22·6	23·4	—	13·02	—	14·24	1·09
Man: grouped..............	8941–49000	5·48	0·70	5·03	5·55	6·13	3·08	3·16	—	17·27	5·61
Average percentage deviation taking best n { individual								9·97		24·55	
Average percentage deviation taking best n { grouped								3·15		15·35	

our animals together the average percentage deviation for the individual animals between the calculated and the observed figures for the aortic area is 9·97 when the calculation is made in terms of the body surface, while it is 24·55 (two and a-half times as great) when the area is expressed in percentage of body weight. The corresponding figures for the grouped animals are 3·15 and 15·35 per cent. respectively, a deviation nearly five times as large.

Attention may further be drawn to the fact that although the technique of these aortic measurements is in the nature of the case much less exact than that employed by two of us in measuring the blood volume, and therefore gives much larger figures for the percentage deviation, yet this deviation is found to be reduced to precisely the same extent in both cases by grouping the animals. Thus in the present instance the ratio between individual and grouped percentage deviations (of course reckoning by the body surface) is 9·97/3·15, *i.e.* 3·2, while in the case of the blood volume experiments it was 4·43/1·39, or 3·2 again. From the table it is also clearly seen that the greater the range of weight of the animal observed the more misleading and erroneous is the result obtained by calculating the aortic area in percentage of the body weight. Thus, while in the case of the ptarmigan and sparrow, where we have only a small range of weight, the difference is comparatively small, in the case of ducks, fowls, and rats, which show the widest range, the difference may properly be spoken of as enormous, being from 13·5 to 16·7 times as large. This shows that if one were to attempt to calculate the sectional area of the aorta of a small animal, for example, from the ascertained aortic area of a large one of the same species, expressed as a percentage of body weight, the result would inevitably be grossly misleading, while if it were calculated by our formula a true estimate would be obtained, correct within the limits of the experimental errors.

In Table XV are given the mean deviations as calculated by the method of least squares for the eight species concerned in these observations, both individually and grouped. From the averages of these it can be seen that if one were to make only a single observation and this differed by **30** per cent. from the theoretical value given by our formula it would be probable that the aortic area in question was abnormal in size, while if it were expressed as a percentage of body weight it would have to differ from the theoretical area by at least **60** per cent. before one could say with the same degree of certainty that it was abnormal.

If, however, a series of observations were made and averaged, it follows from our figures for the mean deviation for grouped animals that if the difference between this average and the theoretical value given by our

Table XV.—Mean Deviations.

Species.	Best n.	Mean deviation using best n in the formula $A = W^n/k$.	Mean deviation when aortic area is calculated in percentage of body weight.
Guinea-pig: individual	0·71	21·51	25·76
„ grouped	0·72	3·91	17·81
Rat: individual	0·71	15·75	23·54
„ grouped	0·72	1·8	20·45
Rabbit (tame): individual	0·71	19·47	32·08
„ grouped	0·71	11·92	29·96
Duck: individual	0·70	3·67	45·93
Fowl: individual	0·72	3·25	50·7
Ptarmigan: individual	0·71	8·41	9·1
„ grouped	0·72	1·78	4·11
Sparrow: individual	0·71	16·51	17·84
Man: grouped	0·70	4·32	21·57
Average mean deviation taking best n.	individuals	14·21	29·27
	grouped	4·75	18·78

formula was as much as 10 per cent., the aortic area would probably be abnormal, and if it amounted to 15 per cent. it would be almost certain that the aortic area was abnormally large or small. But if the measurements were expressed in percentage of body weight it would only be possible to say with the same degree of certainty that the aortic area of an animal was abnormal when it differed from the calculated value by 60 per cent.

Conclusion.

Within a wide range of weight in any given species of warm-blooded animal the sectional area of the lumen of the aorta is proportional to the body surface, and can be calculated from the body weight by means of the formula $A = W^n/k$, where n has the value 0·70–0·72 and k is a constant to be ascertained for each particular species.

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The Size of the Trachea in Warm-Blooded Animals, and its Relationship to the Weight, the Surface Area, the Blood Volume, and the Size of the Aorta.

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The analysis of data collected in connection with the investigation of a number of problems in immunity has led to a series of results, in part already published, bearing upon the blood and circulation. The conclusion was reached that in certain cases a precise and definite relationship to the body surface exists in warm-blooded animals in accordance with the formula $W^n/a = k$, where W is the body weight of the animal, a represents the mass of the body fluid, tissue, or organ under investigation, k is a constant, and the value of n is approximately 0·70–0·72.

In view of the fact that the carriage of oxygen is one of the chief functions of the circulation, and that the volume of the blood (1), (2), and the aortic area (3), (4), (area of cross-section of aorta), have been shown by us to be proportional to the body surface in warm-blooded animals, while, as we have also found, the total oxygen capacity is the main factor in determining the size of the heart (5), it appeared to be of interest to examine the size of the channel by which the oxygen gains access to the lungs.

Accordingly, the trachea was measured in two species of mammal and one bird, namely, guinea-pig, rabbit, and ptarmigan. The animals used were healthy individuals in good condition, not previously experimented upon,