RELATION BETWEEN BIRTH WEIGHT AND LITTER SIZE IN MULTIPAROUS MAMMALS

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I

It has long been known that there exists a negative correlation between the number of young in a new-born litter of multiparous mammals and the birth weight of the young. This relationship has been shown to hold for rabbits (Kopeć, 1924; Hammond, 1921), for rats (King, 1915; Stotzenberg, 1915), for guinea pigs (Wright, 1922; Ibsen, 1928), and for albino mice (Bluhm, 1929). In man also the relationship seems to hold; Strassmann (1903) reported that triplets are about 5 cm. shorter at birth than single born.

Bluhm (1929), Wishart and Hammond (1933) and other observers have shown that the birth weight is influenced by a variety of factors: weight, age, and state of nutrition of the mother, and so forth. The customary method of estimating the influence of each of the factors upon birth weight has been to calculate the coefficient of correlation between each variable and the birth weight. The coefficient of correlation between the average birth weight of an individual and the size of the litter of which it is a member has been given as:

$$r = -0.37 \pm 0.015 \text{ for the albino mouse, by Bluhm}$$
$$r = -0.66 \qquad \text{for the guinea pig, by Wright}$$
$$r = -0.62 \ (0.60) \quad \text{`` `` `` `` , by Eaton}$$
$$r = -0.866 \pm 0.034 \text{ and}$$
$$r = -0.718 \pm 0.043 \text{ for two races of rabbits, by Kopeć.}$$

Although attempts have not been wanting to arrive at an understanding of the mechanism responsible for this high correlation between birth weight and litter size, no exact formulation of the relationship has been given. In the present experiments an empirical

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equation has been obtained, and its bearing upon the possible mecha-
nism responsible for the correlation is discussed.

II

The material was obtained during an investigation of prolonged
gestation in albino mice (Enzmann, Saphir, and Pincus, 1932). It
consisted of a large series of healthy young females of the Bagg albino
strain. The animals were of the best breeding age, roughly between
the 15th and 30th week of age. The line has been inbred for more

TABLE I

Relation between the litter size and the average weight of the whole litter in
albino mice. Present experiment.

Litter size, N	Litter weight, W
	$gm.$
1	—
2	—
3	4.89
4	5.44 ± 0.122
5	7.70 ± 0.101
6	8.70 ± 0.128
7	10.22 ± 0.186
8	10.96 ± 0.119
9	12.41
10	12.65
11	13.50

than twenty-eight generations. The new-born young of each mother
were weighed as early as it was convenient, which was always within
12 hours after they had been born. New-born mice which had been
fed by the mother were not included. The litter was weighed as a
whole and the results with each group were averaged.

Table I shows the birth weights of litters ranging in size from 3 to
11 young in a litter. The curve resembled that of a power function.
Plotting logarithms of average birth weights (log W) against log-
arithms of litter size (log N), a straight line is obtained (Fig. 1).

The series of animals used here is relatively small (414 individuals).
To test the relationship, data furnished by other authors were ex-

amined. Bluhm (1929) gives figures on the birth weights of over 18,000 albino mice; Marshak (unpublished data) obtained birth weights on a large number of a strain of chocolate mice bred in this
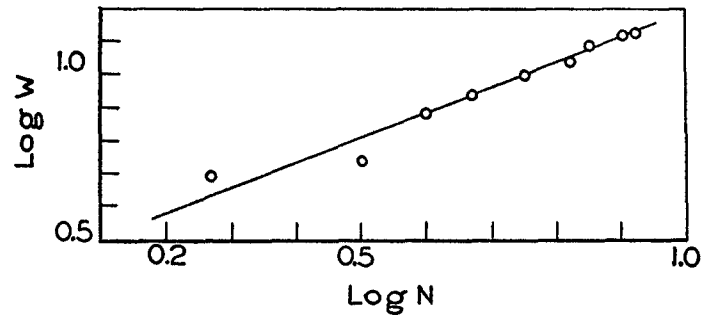

FIG. 1. Relation between the average weight of whole litters and the litter size in multiparous mammals. Data on albino mice. Present experiment.

TABLE II

Relation between the litter size and the average weight of whole litters in different strains of mice. Data by Gates (1925), Bluhm (1929), and Marshak (unpublished).

Litter size, N	Birth weight, W (Gates)	Birth weight, W (Bluhm)	Birth weight, W (Marshak)
1	—	1.29	—
2	3.74	2.76	—
3	5.34	3.99	—
4	6.60	5.04	5.64
5	7.10	6.15	7.46
6	8.52	7.14	8.49
7	9.87	8.12	9.41
8	10.64	8.96	10.55
9	11.43	10.08	11.24
10	13.40	10.70	12.36
11	14.63	11.88	14.43
12	15.84	—	—

laboratory; and Gates (1925) has given birth weights of another strain of mice. These data were recalculated and are given in Table II and in Fig. 2. On the whole, these data give a much better fit
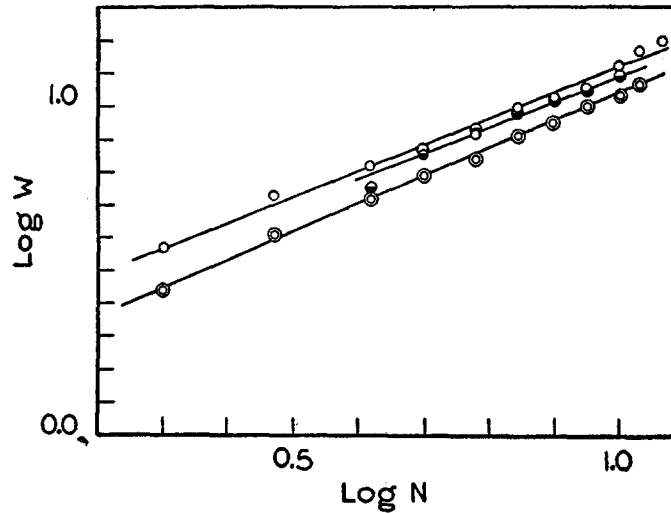
FIG. 2. Relation between the average weight of whole litters and the litter size in multiparous mammals. Data from Bluhm (1929), Gates (1925), and Marshak (unpublished), on various strains of mice.

The double circles represent Bluhm's data, the single circles Gates' data, and the half-filled circles Marshak's chocolate mice.

TABLE III

Relation between the litter size and the average birth weight of whole litters of different species of rodents and of different strains of the same species. Data by Kopeć (1924) on rabbits, by Wishart and Hammond (1933) on rabbits, and by Minot (1891) on guinea pigs.

Litter size, N	Himalayan rabbits (Kopec)	Silver rabbits (Wishart and Hammond)	Rabbits, C strain (Wishart and Hammond)	Rabbits, F strain (Wishart and Hammond)	Guinea pigs (Minot)
	Birth weight, W	W	W	W	W
1	48.7	75.0	90.5	55.4	85.5
2	94.2	—	176.8	100.6	157.0
3	129.6	—	228.3	141.0	204.0
4	154.0	150.8	260.0	172.8	256.4
5	184.5	223.5	327.5	206.5	299.0
6	200.4	240.6	348.6	239.4	373.2
7	227.5	265.3	365.4	275.8	396.7
8	—	291.2	409.6	324.0	417.6
9	—	—	459.9	—	—
10	—	—	482.0	—	—
11	—	—	486.2	—	—
12	—	—	542.4	—	—
13	—	—	487.5	—	—

than do our own data, chiefly due to the fact that they are based on larger series.

Minot (1891) published birth weights of guinea pigs, Kopeć (1924) gave birth weights for several races of rabbits, and Wishart and Hammond (1933) have published birth weights on three races of rabbits. These data have been recalculated and are given in Table III and Fig. 3.
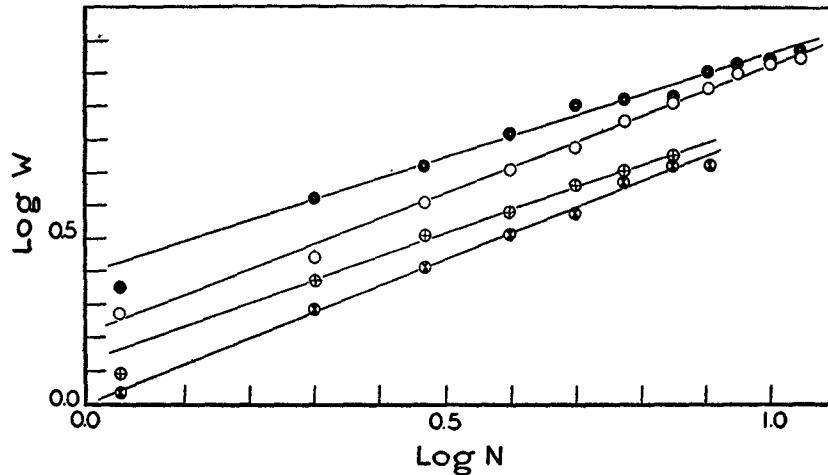

FIG. 3. Relation between the litter size and the average weight of whole litters, for different species of rodents and different strains of the same species. Data by Bluhm (1929) on mice, by Kopeć (1924) on rabbits, by Wishart and Hammond (1933) on rabbits, and by Minot (1891) on guinea pigs.

The black circles represent the birth weights of a strain of rabbits from Wishart and Hammond's paper, the circles enclosing white crosses give the birth weights of a strain of rabbits studied by Kopeć, the circles enclosing slanting crosses represent data on guinea pigs by Minot, and the white circles show the data on Bluhm's mice. In order to save space the scales for different species on the ordinate were telescoped. The scale marked zero at the origin is for the mice; for the guinea pigs the origin of the ordinate should read 1.9 and for the rabbits 1.6.

Our own results as well as those given by other observers show that the relation between the average birth weight of multiparous mammals and the litter size may be expressed by the equation

$$\Delta W/W = K(\Delta N/N)$$

or,

$$W = N^K + C,$$

where W stands for the average weight of a whole new-born litter, N for the litter size, and C and K are constants.

We did not include in our data (Table I and Fig. 1) litters of less than three young. Very small litters are rare and are in many cases due to embryo mortality. One may therefore expect that the figures expressing the average birth weights of very small litters should be too low; this is indeed the case, as most of the data on mice taken from the literature show. In rabbits and guinea pigs the conditions are similar.

<div align="center">III</div>

Several theories have been proposed to account for the correlation between the litter size and birth weight of multiparous mammals; but unfortunately none in its present form is capable of explaining all the facts.

Minot (1891) proposed that the differences in birth weight are due to differences in the time of gestation. This theory explains to a large extent the correlation between birth weight and litter size in guinea pigs, but fails if applied to rabbits and mice. In these forms one may obtain large litters in a pregnancy of short duration and small litters born after a comparatively long pregnancy. For this reason the theory of Keilmann (1891) and others, that internal pressure brings about parturition, meets with similar difficulties. The tension upon the uterine muscles depends upon the size and weight of the embryos enclosed in the uterus. If parturition depended upon reaching a threshold tension of the uterine muscles the length of pregnancy should be roughtly inversely proportional to the litter size. This is certainly not the case, although there is a slight correlation between the length of pregnancy and the litter size (Wishart and Hammond, 1933; et al.).

It might also be assumed that the birth weight is a function of the size of the placenta. There is some evidence for this view. Draper (1920) describes a case where one uterine horn contained one embryo while the other horn held two. The placenta of each of the twins was lighter than the placenta of the single individual. The junior writer observed in some cases of large litters in mice that the crowding led to partial fusion of placentae. One of the objections to this

theory is that it assumes a constancy of the efficiency of the placenta as a nutritive organ. There are indications (Enzmann, unpublished data; Wishart and Hammond (1933)) that this is not the case in either the mouse or the rabbit.

Spiegelberg (1891) advanced the view that the embryos in the uterus release a substance, hormonal in nature, which induces parturition when its concentration reaches a definite limit. The same objections which were brought forward against the uterine tension theory also apply to this explanation. The current view is that the length of pregnancy is conditioned by ovarian hormones (Ancel and Bouin, 1912; Hammond, 1917; Schafer, 1917; Wishart and Hammond, 1933; et al.). The time course of pregnancy may therefore be entirely independent of the number of young carried.

Bluhm (1929) discussed this view and advanced a new one, according to which the weight differences between litters of different sizes are due to the limitations of the mother in assimilating and in providing nourishment for the young. This view is well supported by our observations (to be reported in a subsequent paper) that the growth rate of the suckling young depends upon the litter size in the same manner as does birth weight.

The relationship between litter size and litter weight is not explained by either theory: (1) equipartition of a limited amount of a hormone which induces parturition or (2) equipartition of a limited amount of nutrition provided by the assimilating capacity of the mother. Our experiments on the growth rate of suckling young in the litters of various sizes strongly favor the second idea as a partial explanation.

The present results show that although birth weight depends on a variety of factors the litter size is (within the same strain) the most important. Since

$$\Delta W/W = K(\Delta N/N)$$

we have to suppose that the average increment of litter weight resulting from a unit increase in N is directly proportional to W and inversely proportional to N. This signifies a proportionality between N and the nutritive drain upon the mother, as well as an equipartition among the members of the litter. The remarkable fact that

K is practically identical, within very narrow limits (Figs. 1, 2, 3), for various mammals, shows that the partition coefficient is non-specific. In the case of multiparous mammals, then, we have the possibility of a direct test of the theory of the partition of materials in "heterogonic" growth, of which use has been made by Robb (1929) and Teissier (1934).

IV

SUMMARY

In multiparous mammals there is a definite relation between the litter size N and the total weight of the litter W. Reasons are given showing that this relationship is independent of the mechanism of parturition.

For various forms $W = N^K + const.$ Hence the average increment of W due to unit increase of N is directly proportional to W, inversely to N. This signifies proportionality between N and nutritive drain upon the mother, as well as equipartition among the members of the litter. K is non-specific, and is therefore regarded as a partition index.

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