METABOLIC RATE = ENERGY METABOLISM (CONSUMPTION)
PER UNIT TIME

Depends on process type and intensity, body T, mass, reproductive state, age, sex, food type, daytime, season ....

MEASURES by (I):

- DIRECT CALORIMETRY : $\frac{\Delta Q}{t}$ (HESS LAW)
    - ACCURATE
    - TECHNICAL DIFFICULTIES
        size of the animal
        altered behavior
        heat by vaporiz. or food contact
        must exclude W_{EXT} and biosynthesis (significant)
- INDIRECT CALORIMETRY : $\frac{\Delta E}{t}$ $\left(= \Delta E\left(\begin{matrix}\text{food} \\ \text{- excrete}\end{matrix}\right)\right)$
    - MUST NOT ALTER THE ORGANISM COMPOSITION (growth, reserve storage/use)
    - ALL RIGHT AT THE STEADY-STATE and AVERAGING on long times
    - not easy to measure
    - not used for M_B, M_{STD} or M_{REST} (better direct methods).

BASAL METABOLISM : CONSTANT METABOLIC RATE (in HOMEOTERMS) measured at REST and without thermal STRESS, after a FASTING period

(BMR)

STANDARD METABOLISM : LIKE BM, AT A GIVEN BODY TEMPERATURE (IN POIKILOTERMS)

(SMR)

AVERAGE (or FIELD) ACTIVITY METABOLISM : AVG. RATE OF ENERGY USE DURING NORMAL ACTIVITY

(FMR)

AEROBIC METABOLIC CAPACITY = $\dfrac{\text{MAX MET. RATE}}{\text{BM (or STD)}}$

VARIES WITH SIZE, but not only.

E.g., $\dfrac{\text{FMR}}{\text{BM}}$
- 100 (flying insects)
- 5 salmon tadpole (5g)
- 16 adult salmon

METABOLIC RATE MEASUREMENT (II)

- RESPIROMETERY : $\frac{\Delta O_2}{t}$

- CO_2 PRODUCED $/t$: less practical

  great CO_2 deposits in the body, thus the measurement can be altered by Δ VENTIL. or acid load (e.g. lactic acid).

  different compounds give different E per l CO_2 produced. One must know what is metabolized.

- LOCAL PHOSPHATE METABOLISM (in TISSUES) with ~ bonds (NMR)

- RADIOACTIVE ISOTOPES (injected, even in free animals)

RESPIROMETERY

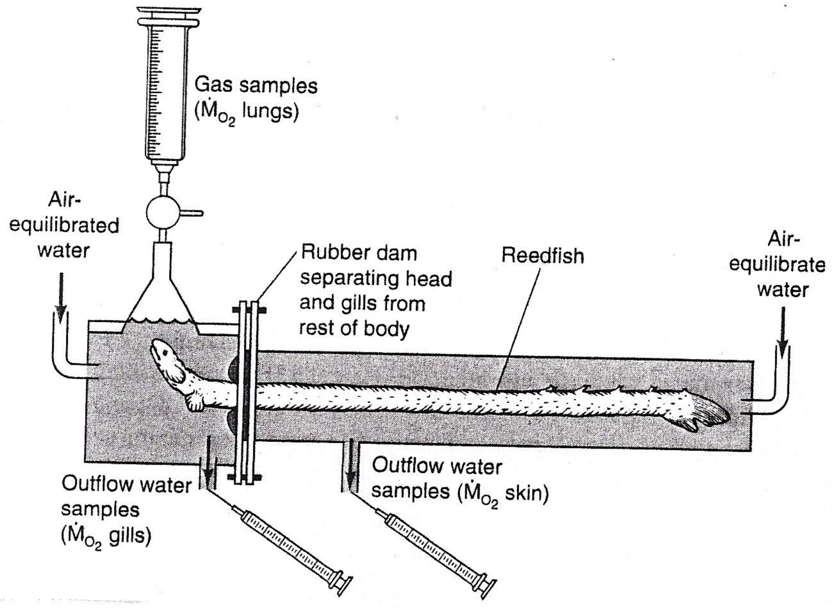


Figure 16-3 Open and closed respirometery can be combined in a single experiment to measure an animal's gas exchange partitioning between various sites. In this experiment on the reedfish *Calamoicthys calabaricus*, two independent open systems are used to determine branchial and cutaneous aquatic oxygen uptake. A third, closed respirometery system includes the air in the funnel above the head, from which the animal breathes air. Gas samples taken after an air breath are used to calculate aerial oxygen consumption. [Adapted from Sacca and Burggren, 1982.]

RESPIROMETERY

CONSUMED O_2 / time

- SIMPLE, WIDELY USED
- not for ANAEROBIC organisms (or better: organisms with significant anaer. metab.)
- ANAEROBIC METAB. must be negligible
- ASSUMPTIONS: negligible O_2 stores
  Q released by 1 l O_2 approximately the same irrespective of the metabolic substrate (max error ~10%)

	$Kcal\ g^{-1}$	$l_{O_2}\ g^{-1}$	$Kcal\ l_{O_2}^{-1}$	QR (R_Q)
CARBOHYDRATES	4.2	0.84	5.0	1
FATS	9.4	2.0	4.7	0.71
PROTEINS (to UREA)	4.3	0.96	4.5	0.81
PROTEINS (to URIC AC.)	4.25	0.97	4.4	0.74
ETHANOL	7.00			

$$1\ cal \simeq 4.2\ J$$

$$QR = \text{RESPIRATORY QUOTIENT}\ (R_Q) = \frac{CO_2 \text{ formed}}{O_2 \text{ consumed}}$$

Using an average value of $4.8\ Kcal/l_{O_2}$ as a measure of metab. rate, the error is negligible (if the diet is varied)

R_Q informs about the metabolized compounds, if one adds a measurement of the excreted N, which measures the consumed proteins.

HUMAN SPECIES:

BM ≃ 2000-2500 Kcal / DAY

≃ 4000-5000 (with heavy work)

≃ 10000-12000 (with aerobic exercise)

≃ 10-15 × BM (more intense exercise)

It also depends on the anaerobic quote

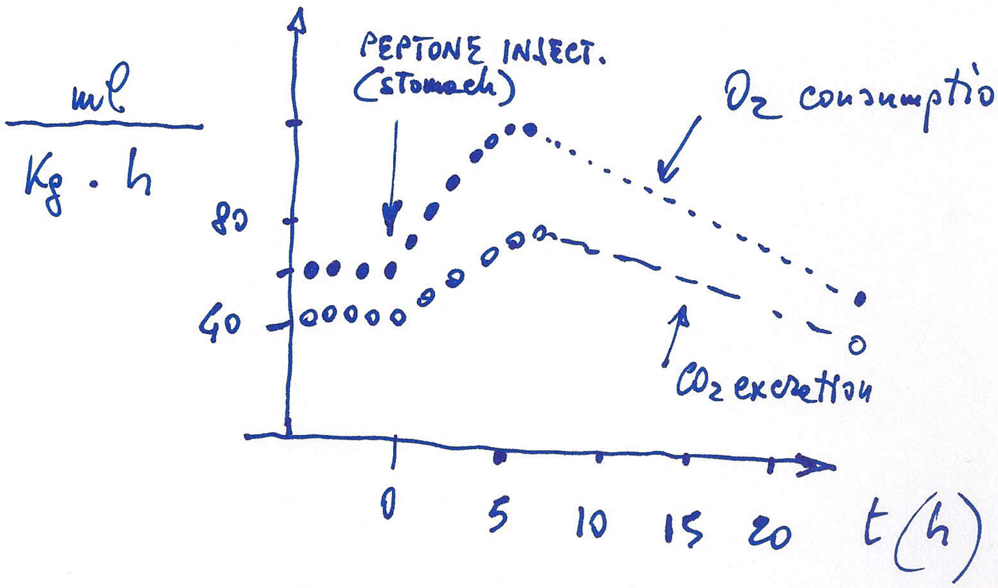
BRAIN WORK ≃ 20% of the total (at rest)

but changes very little with mental activity.

SPECIFIC DYNAMIC ACTION

RUBNER 1885 : ↑ MR DURING INGESTION and ASSIMILATION (in Vertebrates and Invertebrates)

EXAMPLE : *Bufo marinus* (Fig. 16.4 Randall)

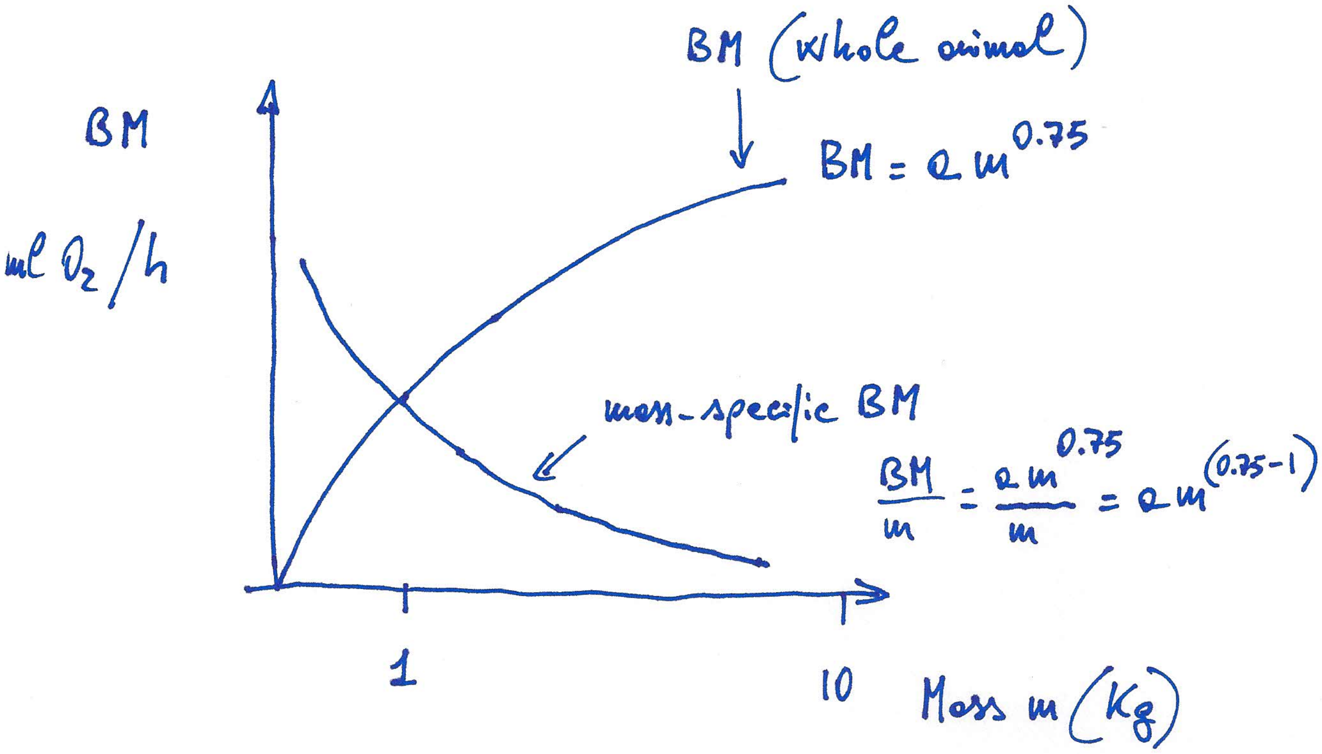


↑ after ~ 1h, max after 3-6 h, slow decay (> 20 h)

In Fishes, Amphybia, Reptiles ↑ even 3 times as BM, with ↑ heart rate and ejected vol - LESS EVIDENT in other animal groups (e.g., humans)

Probably caused by ↑ metabolism of some organs (e.g. liver), digestion work is not enough to account for it.

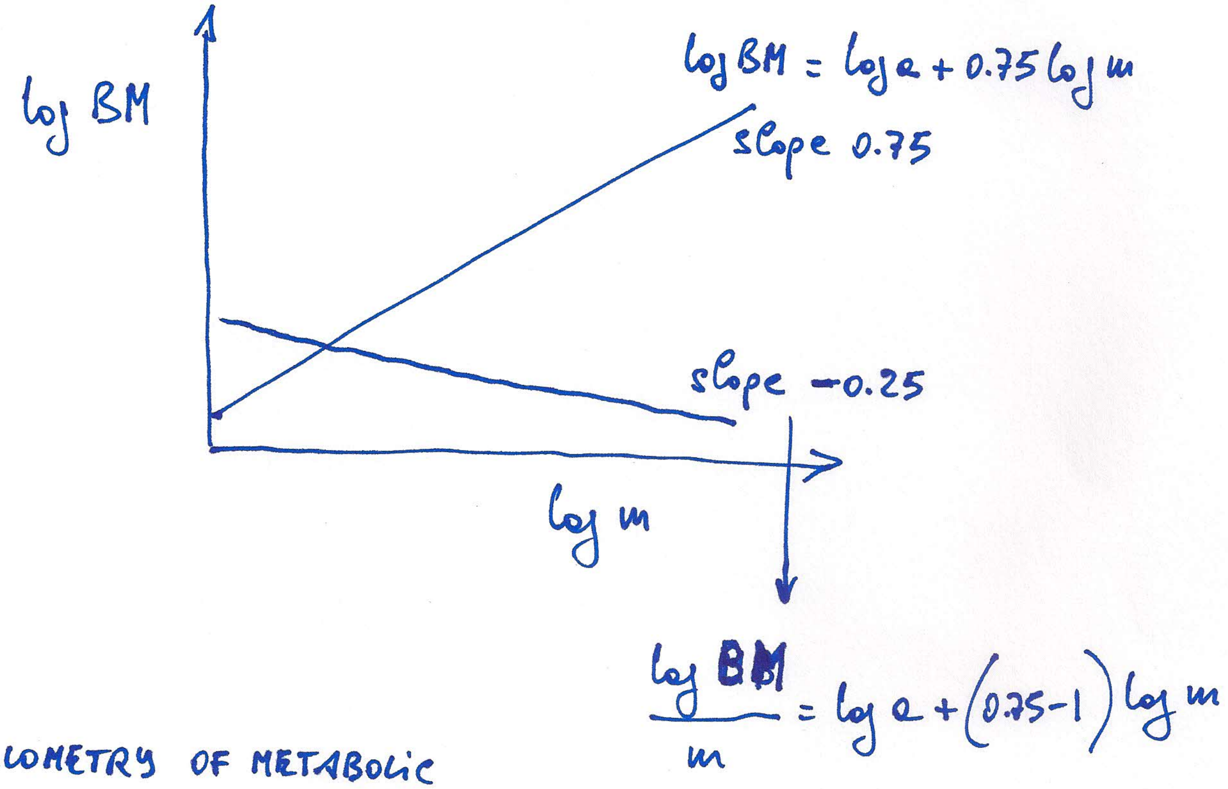
Kinetics important to calculate BM (basal metab.)



$$BM = a\,m^{0.75}$$

$$\frac{BM}{m} = \frac{a\,m^{0.75}}{m} = a\,m^{(0.75-1)}$$

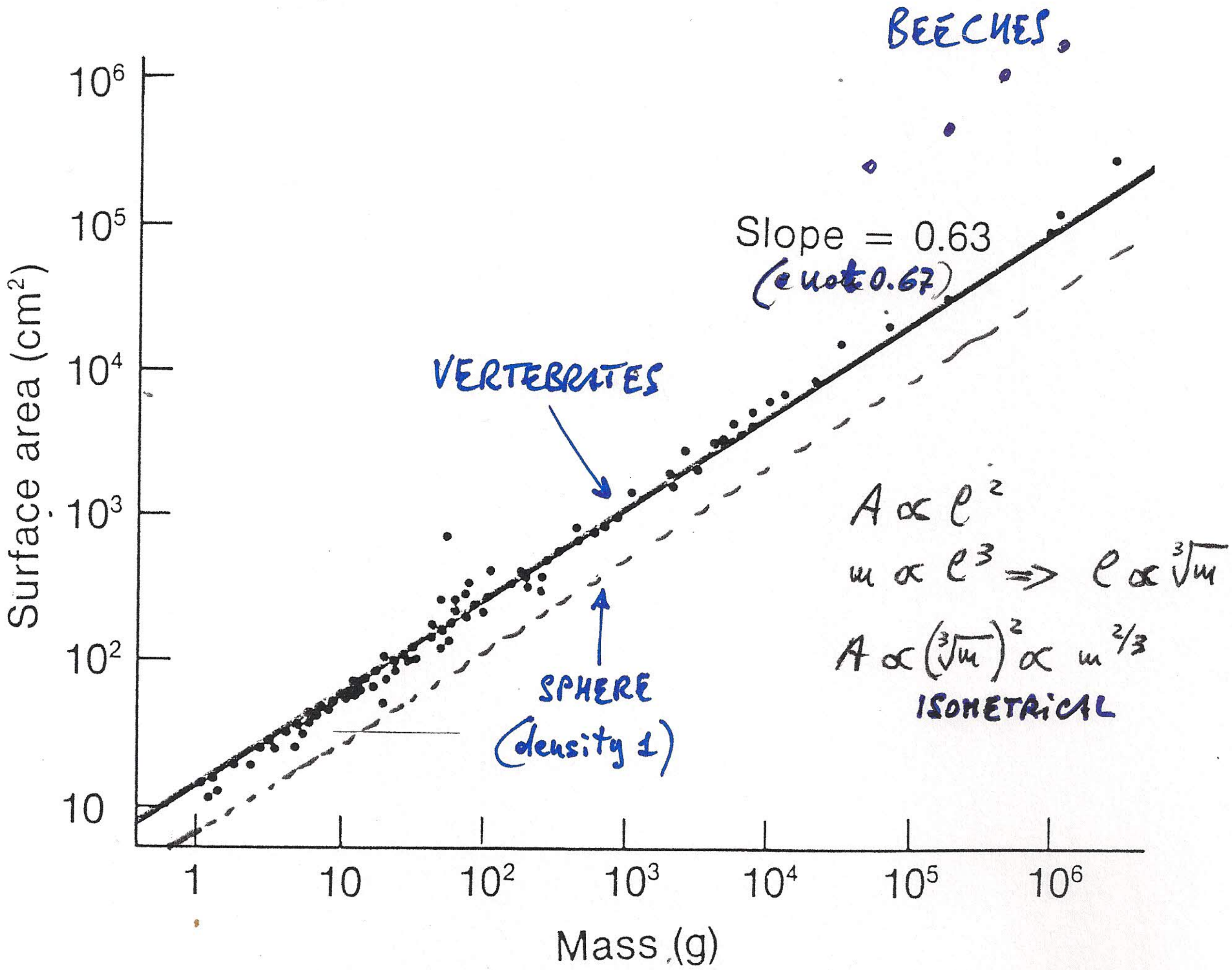
In linear form:



$$\log BM = \log a + 0.75 \log m$$

$$\log \frac{BM}{m} = \log a + (0.75-1) \log m$$

ALLOMETRY OF METABOLIC
CONSUMPTION AS A FUNCTION
OF BODY MASS.



$A \propto l^2$

$m \propto l^3 \Rightarrow l \propto \sqrt[3]{m}$

$A \propto (\sqrt[3]{m})^2 \propto m^{2/3}$

ISOMETRICAL

A sphere $4\pi r^2$

Vol " $\frac{4}{3}\pi r^3$

IDEA FROM

BERGMANN'S RULE (1847) : SIZE INCREASES IN COLD ENVIRONMENTS

METABOLIC RATE AS A FUNCTION OF SURFACE AREA (~~and~~ not WEIGHT) IN DOGS (Rubner 1883)
(rounded values)

WEIGHT	SURFACE A	A/WEIGHT	MR/WEIGHT	MR/A
31 Kg	11000 cm^2	344 cm^2/kg	36 $\frac{Kcal}{Kg \cdot day}$	1036 $\frac{Kcal}{m^2 \cdot day}$
24	8800	366	41	1112
20	7500	380	46	1200
18	7660	420	46	1100
10	5300	550	65	1180
7	3700	570	66	1150
3	2400	726	88	1210

HEAT CONSERVATION ? NO, IT IS THE SAME IN FISHES
(von HOESSLIN, 1888)

HEAT DISSIPATION

STEER - MOUSE

MR mouse

SURFACE T

>100°C

MR steer

20 cm fur

to keep heat

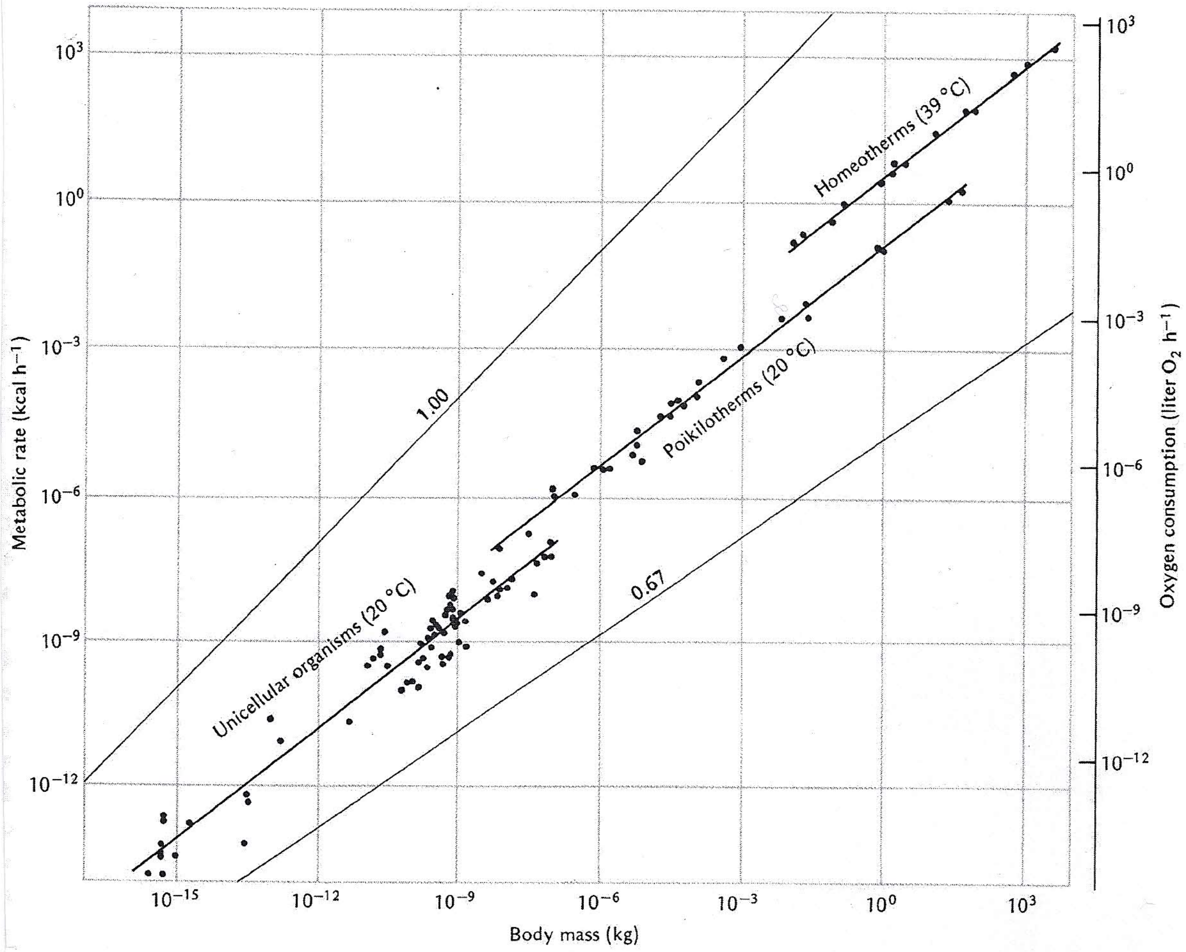


Figure 5.11 The rates of oxygen consumption for a wide variety of organisms when plotted against body mass (log coordinates) tend to fall along regression lines with a slope of 0.75. Note that each division on the coordinates signifies a 1000-fold change. [Hemmingsen 1960]

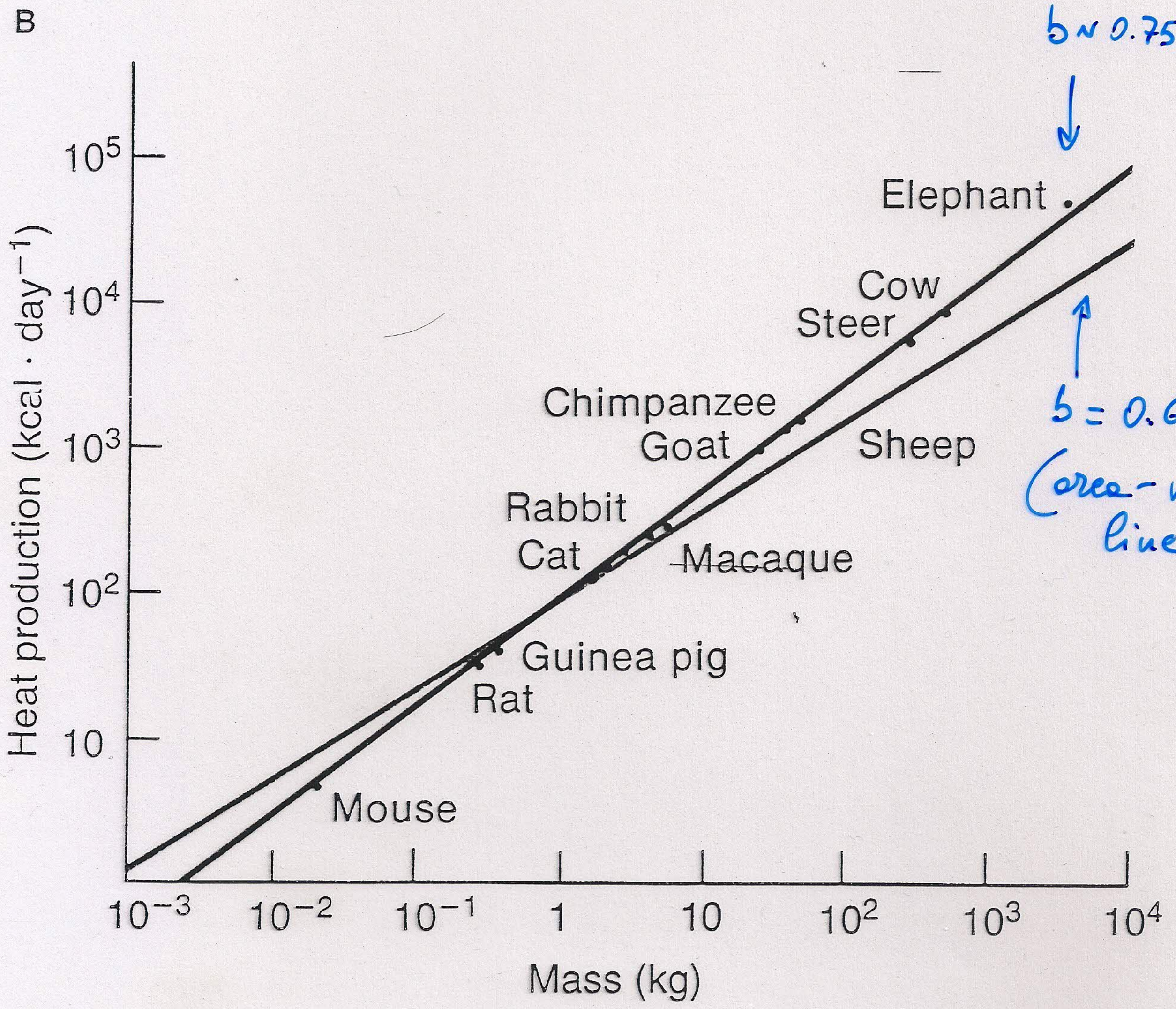
sion lines, although there are some exceptions to this general rule. For example, some insects, pulmonate snails, and a few other groups have oxygen consumption rates that fall on regression lines with a slope closer to 1.0. A slope of 1.0 means that the rate of oxygen consumption is directly proportional to the body mass (i.e., an animal twice as big consumes twice as much oxygen, etc.).

The oxygen consumption rates of microorganisms also fall on lines with a similar slope, and even some trees show the same relationship between oxygen consumption and size (Hemmingsen 1960). The fact that oxygen consumption bears the same relationship to size in so many different organisms suggests that the phenomenon represents a general biological rule.

Several physiologists who have worked with these problems have attempted to reach a rational explanation for the regular relationship between oxygen consumption, or metabolic rate, and body size.

More than 100 years ago the German physiologist

FROM: SCHMIDT-NIELSEN, ANIMAL PHYSIOLOGY, 1997.



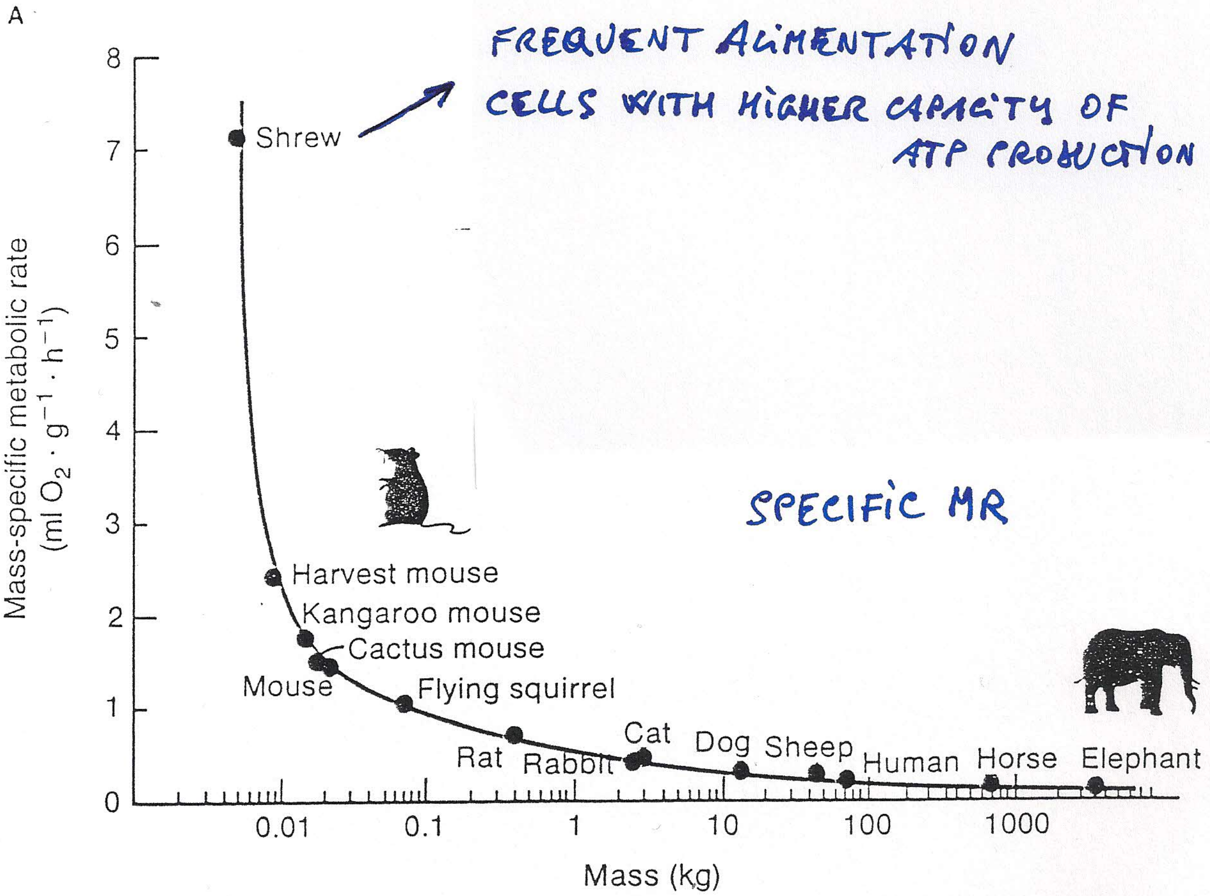
$b \sim 0.75$

$b = 0.63$ (area-mass line)

Kleiber 1932

Brody et al. 1934

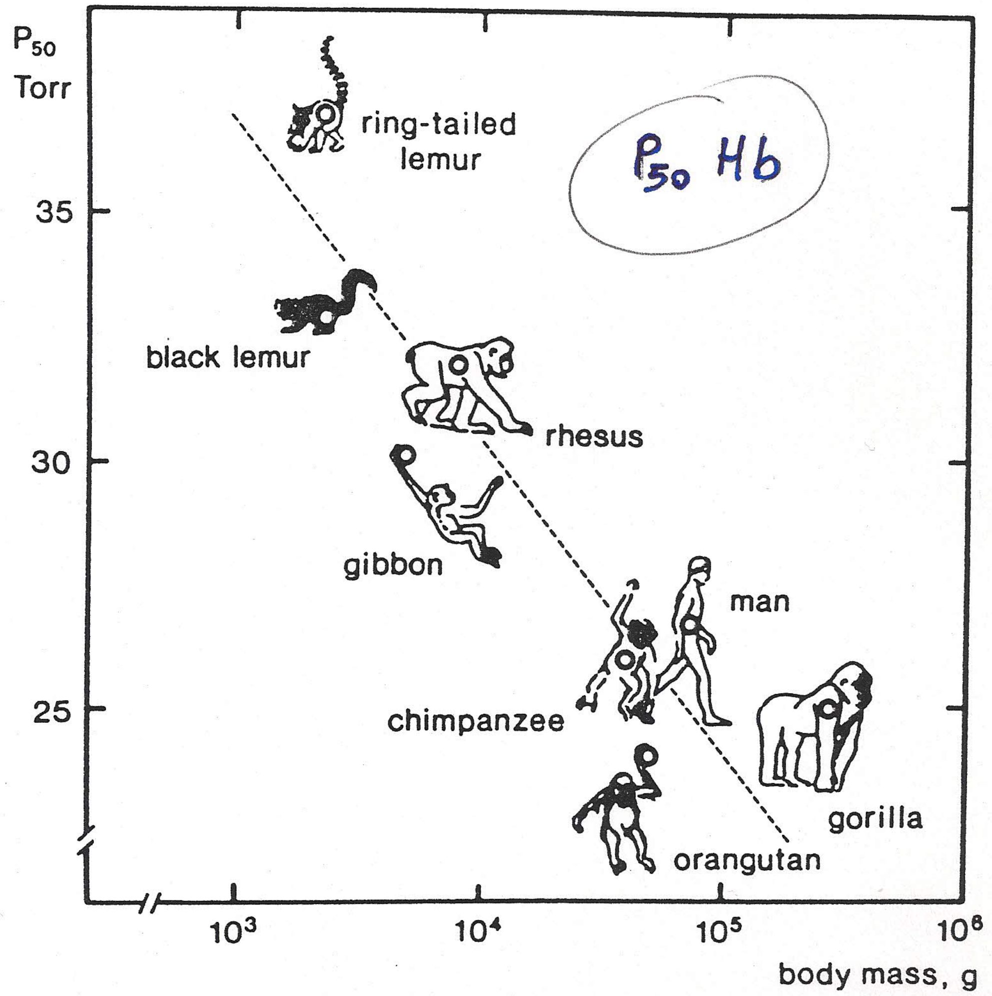
Benedict 1938



FREQUENT ALIMENTATION
CELLS WITH HIGHER CAPACITY OF ATP PRODUCTION

SPECIFIC MR

O_2 and nutrients must be supplied at a rate even 100 times as high as in larger animals.



P_{50} Hb

- ALVEOLAR AREA $\propto$ O_2 CONSUMPTION
- DIFFERENT CELLULAR FEATURES, e.g. MITOCHONDRIAL DENSITY
- CAPILLARY DENSITY (higher in small animals up to rats)
- HIGHER BOHR EFFECT IN SMALL ANIMALS (but not e.g. in chihuahua – other dogs)
- ↑ CARBONIC ANHYDRASE IN SMALL ANIMALS.

	BODY MASS (Kg)	RESTING HEART FREQ.	CARDIAC MASS PER UNIT BODY MASS
Elephant (Afr.)	4100	40 min'	5.5 g/Kg
HORSE	420	47	7.5
HUMANS	70	70	5.2
DOG	20	105	9.2
CAT	3	180	4.1
RAT	0.34	340	2.9
MOUSE	0.03	580	4.0

IT ALSO HOLDS FOR RESPIRATION.

E.g. :

HUMAN	12	events/minute
MOUSE	100	" "

FROM Hill et al.