A comparison between metabolic rates and body composition in rodent populations from different latitudes.

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ABSTRACT

Nine species of voles (genus *Microtus*) and one species of mouse (genus *Mus*) from four different latitudes were used for respirometry to obtain resting metabolic rates (RMR) and average nocturnal metabolic rates (ANMR). After this animals were subjected to carcass analysis. No differences in RMR and ANMR between microtine populations from different latitudes were found, due to seasonal acclimatization in the field and acclimation during captivity. Northern populations have a lower water content than the southern populations.

Metabolic rates and body composition are positively correlated with latitude, due to an increase in body mass and heart+kidney weight.

Keywords: Microtus Metabolic rate Body composition Latitude

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1. INTRODUCTION

At higher latitudes food availibility is reduced, life expectancy decreases, while mortality increases. High reproductive rates have to compensate for these losses. In a reproductive season that is shorter at higher latitude, litter size must increase. Northern animals of the same or closely related species are therefore expected to have a higher work load and hence a higher metabolic rate. Bertin (1990) found that laboratory mice, reared at 22 °C have a higher metabolic rate than mice reared at 28 °C. Elgar & Harvey (1987) showed differences in metabolic rate between several rodent families, which they explained by habitat or diet. Scholander *et al* (1953) found a positive correlation between metabolic rates (at four different temperatures) and latitude in poikilotherms. Data collected by Weathers (1979) and Ellis (1984) compiled literature data and showed that tropical bird families have a slightly reduced BMR for their body size. Hails (1984) found the same for a variety of tropical birds, which he compared with birds from temperate regions of the same weight. Bozinovic & Rosenmann (1988, 1989) found a latitudinal effect on metabolism for cricetid rodents. Bozinovic & Contreras (1990) found the same for two octodontid species.

For small homeotherms the arctic winter air can be 90 °C colder than the body temperature, while it is 24 hours dark. In the arctic summer, air may only be 10 °C colder than the animal, while it is 24 hours light. These seasonal changes in temperature and light-dark cycle (photoperiod, light intensity and duration of twilight) are more moderate with declining latitudes and get extremely small at the equator. This affects the behaviour of animals and has attracted the interest of several investigators: Aschoff (1969); Daan & Aschoff (1975); Lankinen (1986) and Pittendrigh (1989) found a correlation between rhythmicity of behaviour and latitude. Hansson & Hettonen (1985) and Lindén (1988) observed geographical variations in predator-prey cycli. Lord (1960) and Tast (1982) found positive correlations between both litter size and mortality on latitude in American mammals, while Klomp (1970) found the same for clutch size in birds. Curio (1989) found a negative correlation between life expectancy and latitude in birds.

Daan et al (1989; 1990a; 1990b) found that high basal metabolic rate (BMR) and daily energy expenditure (DEE) is due to an association of metabolically active tissue (heart and kidney) in both birds and mammals. Rensch & Rensch (1956) and Graves (1991) found that high latitude species had a relatively higher organ weight than species from lower latitudes.

The aim of this research is to investigate within a closely related group of mammals, the Microtine voles, there is an association between metabolic rate, body composition and latitude.

Several investigators have found that Microtine voles have a relatively high mass-independent metabolic rate compared to other mammals (Packard, 1968; Hayssen & Lacey, 1985; Elgar & Harvey, 1987). They apparentely evolved 2 million years B.P. in the boreal regions of Asia (Hooper,1949; Zakrzewski, 1985). It is possible that their high metabolic rates are adaptive to allow for increased thermogenesis during low temperature stress. (Packard, 1968; Zakrzewski, 1985). Voles are able to persist and even thrive in very cold climates. For example *Microtus miurus* occurs exclusively in northwest Canada and Alaska (Rose & Birney, 1985). Microtines are poorly adapted to conserve water or to thermoregulate (because of thick fur and short ears) at high temperatures, which it avoids by utilization of self-dug burrows and by being predominantly nocturnal (Birney, pers. observ.). Nowadays voles are spread out over Eurasia and North America. The southern borders of their distribution in America and Europe is at about 30 °N: Niethammer, 1982; Hoffmann & Koeppl,1985.

2. MATERIAL & METHODS

Origin and maintenance

Rodents from Spitsbergen (78 °N), Alaska (65 °N), The Netherlands (53 °N) and India (9 °N) were used. Table 1 lists the numbers of individuals, trapping location, period in which they were caught and the conditions during captivity.

Table 1: listing of species, numbers, trapping location, period of catching and coditions under captivity. M symbolises males, F females. T = temperature in °C, Roman figures represent months, LD is light regime.

species	numbers M	numbers F	trapping location	period of catching	captivity T	captivity LD	lights on
Microtus epiroticus	6	10	78° N, 18° E	X 1989	20	18:06	07.00
Microtus oeconomus		1	64°50' N, 147°50' W	IX 1990	16	18:06	07.00
Microtus pennsylvanicus	1	1	64°50' N, 147°50' W	IX 1990	16	18:06	07.00
Microtus miurus	3	2	64°50' N, 147°50' W	IX 1990	12	12:12	08.00
Clethrionomys rutilus	4	4	64°50' N, 147°50' W	IX 1990	12	12:12	08.00
Microtus oeconomus	5	7	51°34' N, 4°12' E	VI 1990	16	18:06	06.00
Microtus arvalis	2	7	53°20' N, 6°18' E	-	20	14:10	08.00
Clethrionomys glareolus	6	6	53°08' N, 6°33' E	IX 1990	22	12:12	08.00
Microtus agrestis	-	11	53°08' N, 6°33' E	IX 1989	-	-	-
Mus booduga	2	2	9°55' N, 78°08' E	II 1991	28	12:12	06.00

M. epiroticus were supplied by Dr R.A. Ims (University of Oslo, Norway), *M. oeconomus*, *M. pennsylvanicus*, *M. miurus* and *C. rutilus* by Dr S. Daan. D. de Klein caught *C. glareolus*, while P. Meerlo caught *M. agrestis*, both at the Frieseveen (village of Eelde). *M. arvalis* was obtained from the breeding colony in the Zoological laboratory (Haren). *M. agrestis* was not kept in captivity because it was measured directly after capture. All animals were fed with 'Hope Farms' rat food pellets. Every second day the animals were given apple, carrot and endive as supplementary food. Time lapse between capture and respirometry varied from 1 till 18 months.

M. oeconomus is the only species originating from two latitudes. In all other cases closely related (resembling) species from different latitudes are compared: *M. arvalis* and *M. epiroticus*, *M. agrestis* and *M. pennsylvanicus*, *C. rutilus* and *C. glareolus*. Because of its extreme tropical habitat *Mus booduga* is used in this research. Although it is no microtine species it might show an intresting trend.

Metabolism

Resting metabolic rates (RMR) and average nocturnal metabolic rates (ANMR) were derived from oxygen consumption in a respirometer: the animals were placed in a respiration chamber (an airclosed perspex box, with a volume of 1 liter, food and water *ad libitum*) for 24 hours. Only *M. agrestis* was placed in a respiration chamber without food. Temperature was 28 °C. This is in the thermoneutral zone for both *Microtus* and *Clethrionomys* (Wiegert, 1961; Packard, 1968; McManus, 1974; Merritt & Merritt, 1978). A constant flow of dry air was sent through the respiration chamber. Every minute the percentage of oxygen was recorded electronically (SA3 Aplied Electrochemistry oxide sensor) and

sent to a printer. Oxygen concentration in incoming and outcoming air could not be measured at the same time. Therefore, the relatively stable incoming air was measured every 2 hours. This reference took 12 minutes and calibrated the sensor for the next period. Every experiment started and finished with a reference. Daan *et al* (1989) describe this system in detail.

The ratio between carbon dioxide formed and oxyen used is known as the respiratory quotient (RQ) and is dependent of nutrition. For carbo hydrates RQ = 1.0, for protein RQ = 0.8 and for fat RQ = 0.7 (Schmidt-Nielsen, 1974). During starvation RQ decreases (Mosin 1982, 1984). For this study RQ was assumed to be 0.8. The respirometry files were compiled in the computer program MEASHAVE.EXE (Steyvers, 1989) to calculate oxygen consumption per minute per gram body weight. These values were plotted in LOTUS. Statistical calculations were done with the computer programs STATISTIX and SPSS. Table 2 states the experimental conditions.

Table 2: Listing of experimental conditions.

species	date	code	file	time in	LD	light on
M.epiroticus	301089	1074	PM301089.107	17.17	DD	-
	301089	1707	PM301089.207	17.17	DD	-
	311089	2000	PM311189.101	18.57	DD	-
	311189	1070	PM311189.201	18.57	DD	-
	011189	1072	PM011189.101	16.50	DD	-
	011189	4000	PM011189.201	16.50	DD	-
	110590	9	BM110590.302	12.37	19:05	07.00
	230590	1072	BM230590.301	12.00	19:05	07.00
	310590	16	BM310590.301	11.31	19:05	07.00
	080690	3	BM080690.301	11.00	19:05	07.00
	110690	6	BM110690.301	11.03	19:05	07.00
	130690	12	BM130690.301	11.35	19:05	07.00
	310790	44	BM310790.102	11.24	19:05	07.00
	270990	20	BM270990.101	16.03	19:05	07:00
	270990	2400	BM270990.301	11.35	19:05	07.00
M.pennsylvan.	140990	1	BM140990.201	15.14	18:06	06.00
	140990	1	BM140990.301	15.14	18:06	06.00
M.oeconomus	210890	20	BM210890.101	10.27	18:06	06.00
	210890	3	BM210890.201	10.27	18:06	06.00
	270890	11	BM270890.101	14.02	18:06	06.00
	270890	14	BM270890.201	14.02	18:06	06.00
	030990	1	BM030990.101	11.49	18:06	06.00
	030990	12	BM030990.201	11.49	18:06	06.00
	040990	-	BM040990.101	13.37	18:06	06.00
	040990	2	BM040990.201	13.37	18:06	06.00
	050990	4	BM050990.101	11.25	18:06	06.00
	050990	10	BM050990.201	11.25	18:06	06.00
	070990	30	BM070990.108	15.34	18:06	06.00
	070990	40	BM070990.208	15.34	18:06	06.00
M.oeconomus	140990	70	BM140990.101	15.14	18:06	06.00
M.miurus	101090	1	SD101090.101	15.42	12:12	08:00
	101090	2	SD101090.201	15.42	12:12	08.00
	101090	3	SD101090.301	15.42	12:12	08.00
	291090	5	SD291090.101	13.09	12:12	08.00
	301090	4	SD301090.201	13.09	12:12	08.00
C.rutilus	050291	1	SD050291.101	17.32	12:12	08.00
	080291	3	LB080291.201	17.30	12:12	08.00
	080291	4	LB080291.101	17.30	12:12	08.00
	090291	6	LB090291.201	20.24	12:12	08.00
	110291	7	SD110291.101	18.13	12:12	08.00
	110291	8	SD110291.201	18.13	12:12	08.00
	130291	9	SD130291.101	17.13	12:12	08.00
	130291	10	SD130291.201	17.13	12:12	08.00

(Table 2, continued)

species	date	code	file	time in	LD	light
M.arvalis	120690	10	BM120690.301	11.13	19:05	07.00
	130690	24	BM130690.101	11.35	19:05	07.00
	140690	15	BM140690.104	15.57	19:05	07.00
	170690	1	BM170690.101	10.40	19:05	07.00
	180690	20	BM180690.101	11.19	19:05	07.00
	190690	19	BM190690.101	10.59	19:05	07.00
	200690	40	BM200690.102	15.08	19:05	07.00
	030890	1	BM030890.101	12.33	19:05	07.00
	070890	30	BM070890.101	10.37	19:05	07.00
Mus booduga	250391	1	BM250391.103	15.07	12:12	06.00
	250391	2	BM250391.202	15.07	12:12	06.00
	010491	4	BM010491.201	09.46	12:12	06.00
	010491	7	BM010491.101	09.46	12:12	06.00
M.agrestis[1)]	200989	15	PM200989.101	10.42	00:24	-
	200989	24	PM200989.201	10.42	00:24	-
	210989	130	PM210989.101	11.00	00:24	-
	210989	172	PM210989.201	11.00	00:24	-
	260989	189	PM260989.101	16.30	00:24	-
	031089	204	PM031089.101	21.36	00:24	-
	031089	207	PM031089.201	21.36	00:24	-
	111089	136	PM111089.101	17.54	00:24	-
	111089	173	PM111089.201	17.54	00:24	-
	121089	197	PM121089.101	16.24	00:24	-
	121089	210	PM121089.201	16.24	00:24	-
C.glareolus[2)]	211290	4	DK211290.201	15.40	12:12	08.00
	221290	12	DK221290.101	15.40	12:12	08.00
	210191	1	DK210191.102	11.00	12:12	08.00
	230191	2	DK230191.201	13.15	12:12	08.00
	260191	3	DK260191.301	11.15	12:12	08.00
	260191	5	DK260191.101	11.15	12:12	08.00
	230191	6	DK230191.101	13.15	12:12	08.00
	210191	7	DK210191.302	11.00	12:12	08.00
	210191	8	DK210191.202	11.00	12:12	08.00
	240191	9	DK240191.301	12.00	12:12	08.00
	240191	10	DK240191.101	12.00	12:12	08.00
	260191	11	DK260191.201	11.15	12:12	08.00

1): Data courtesy of P. Meerlo
2): Data courtesy of D. de Klein

Data of P. Meerlo on *M. agrestis* were used to obtain basal metabolic rates (BMR), measured without food. Lowest oxygen consumption of *M. agrestis* is determined during the first 3 hours of the experiments, when the animals still had some food in their coecum and would reingest nutricious feces (Kenagy & Hoyt, 1980). Their minimum oxygen consumption was defined as RMR instead as BMR. This study was aimed at finding the RMR under thermoneutral conditions. this is not the same as BMR, which requires that animals are not digesting food. For small rodents like *M. miurus* or *Mus booduga* this is not quite possible, therefore we decided to supply all animals with food. Since in Microtines metabolic rates do not differ systematically between day and night, but varies in a strong ultradian alternation (e.g. Kenagy & Vlek, 1982; Gerkema, 1991) we decided to select the lowest nocturnal values.

Carcass analysis

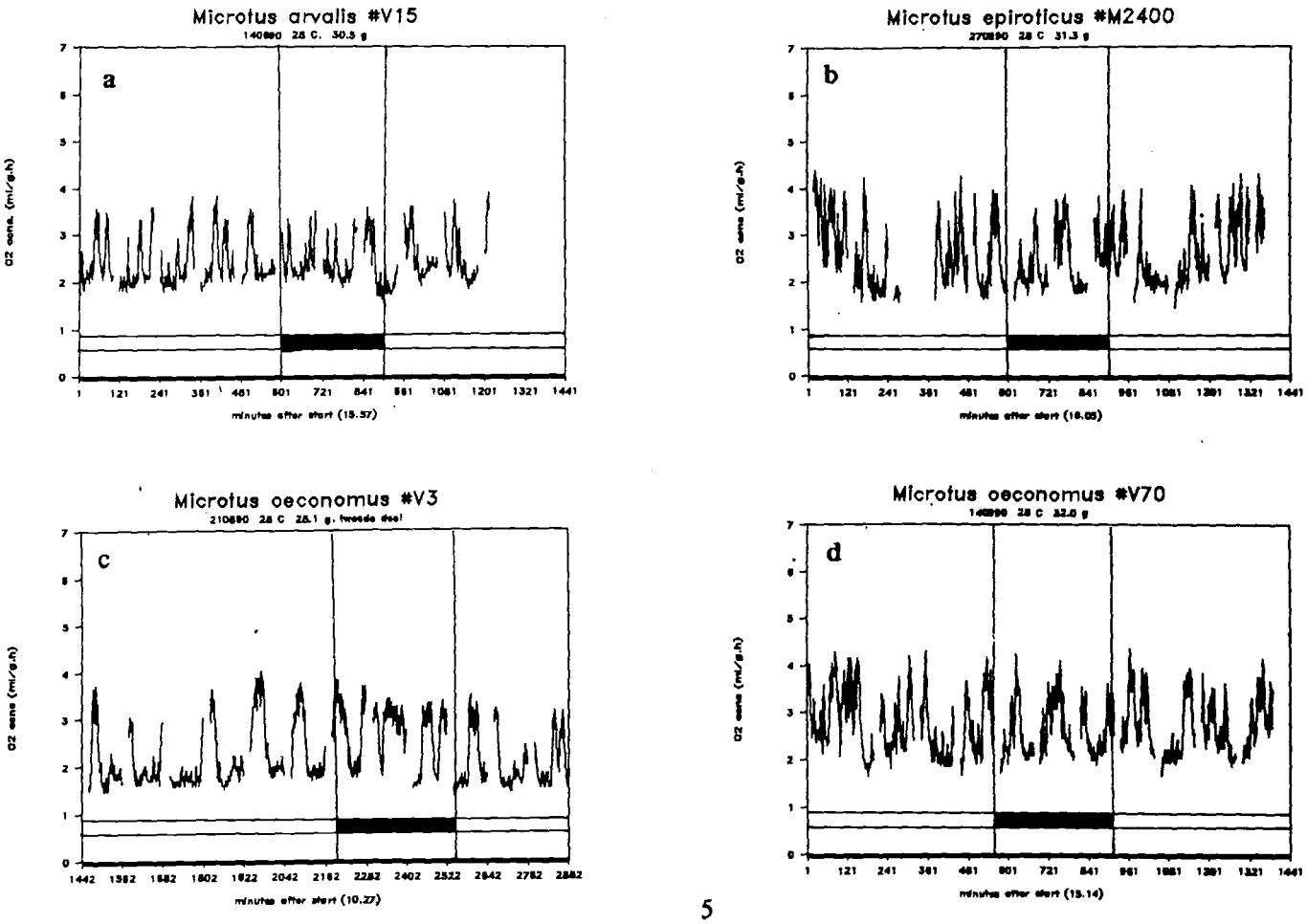
Immediately after respirometry all animals (except *M. arvalis* and *Mus booduga*) were sacrificed for carcass analysis and frozen. The analysis was done (after thawing) by dissecting the body in the following components: skin, leg muscles, gonads, gut and stomach, kidneys, liver, heart, lungs, brain and rest. All parts were immediately weighed to obtain fresh organ weights (accurate at 0.00001 g). After at least 72 hours of drying at 60 °C they are reweighed to obtain dry organ weights. Appendix I lists these data, including body mass, water percentage and RMR.

3. RESULTS

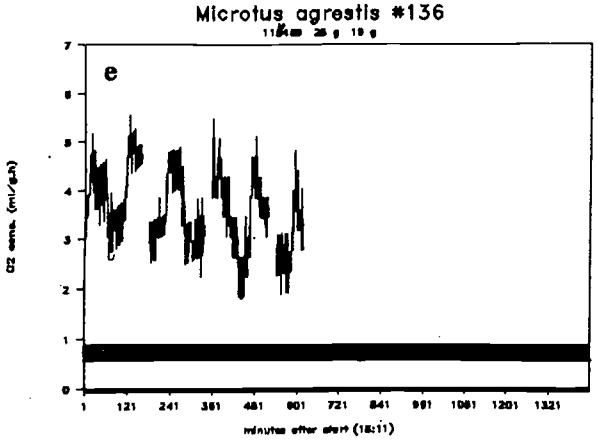
3.1. RESTING METABOLIC RATES (RMR)

RMR was defined as the lowest mean oxygen consumption (ml O_2/g.h) in a time span during the dark period under thermoneutral conditions, and is expressed in Watts. RQ was assumed to be 0.8, resulting in an energetic equivalence of 20 Joule per ml O_2 (Schmidt-Nielsen, 1974). Mean body mass was calculated by averaging body weight before and after the experiment. Figure 1 shows oxygen consumption graphs of the ten species measured.

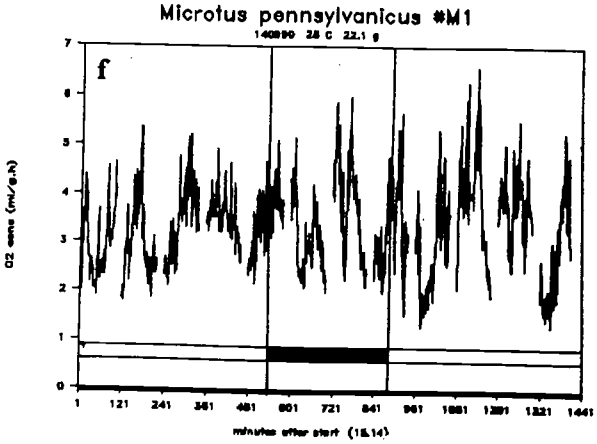
Figure 1a-j. Examples of oxygen consumption registrations.
The horizontal black bar represents dark period.



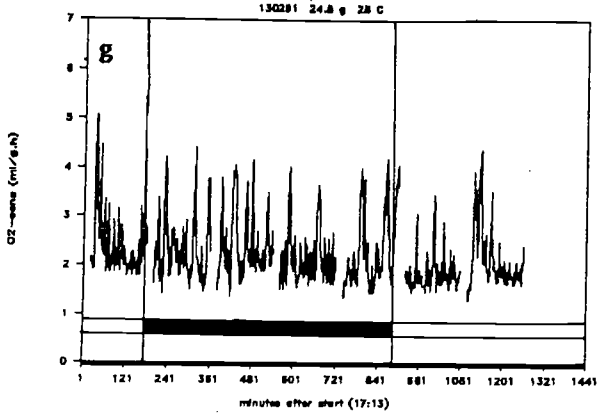
Microtus agrestis #136



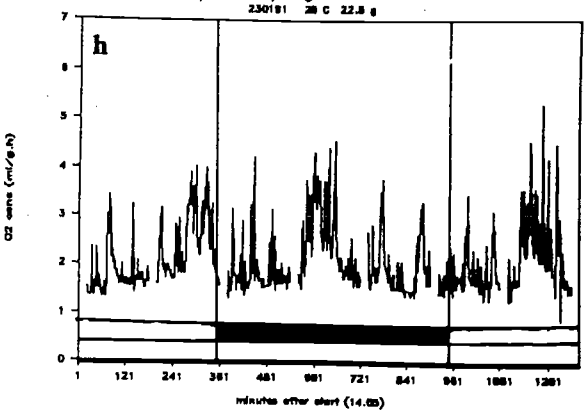
Microtus pennsylvanicus #M1



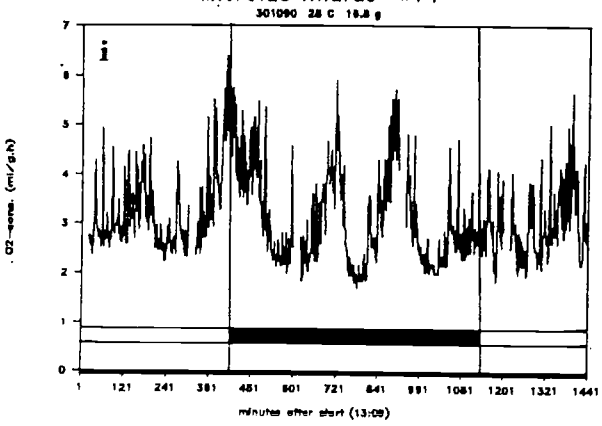
Clethrionomys rutilus #M9



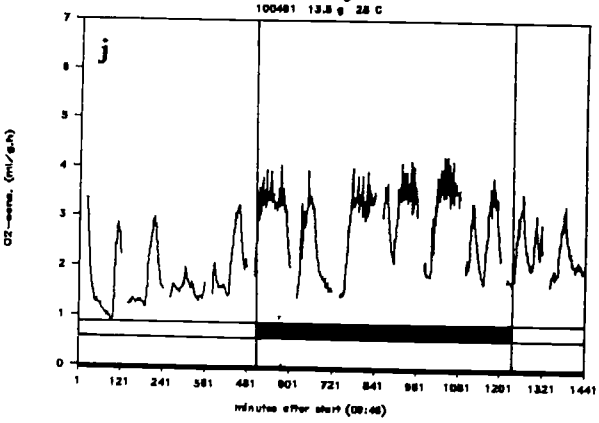
Clethrionomys glareolus #22bm



Microtus miurus #V4



Mus booduga #V7



The question which time span was the best suitable for RMR measurement was solved with the computer program MEAMOVE.EXE (Steyvers, 1991). This program calculates the running means of oxygen consumption for intervals between 1 and 60 minutes. It plots the lowest running mean of oxygen consumption for each interval. At the ordinate, oxygen consumption (in ml O_2/g.h) is plotted. At the absis the interval duration (in minutes) is plotted. The program starts with calculating the running mean (of oxygen consumption) for a one minute interval: minute 1 to 2, minute 2 to 3 ... minute 1440 to 1441 and plots the minimal value of this. Then the same is done for a two minute interval, a three minute interval, a four minute interval .. a 60 minute interval. (figure 2 shows an example of this). A horizontal part in the graph (slope is aproximately 0) indicates a negligible difference in the lowest running means between intervals. The best suitable time span for RMR measurements is within this range of intervals (in figure 2 marked with an arrow) because for these intervals the lowest oxygen consumption is rather independent of interval lenght. After examining all individual MEAMOVE-files we chose for a 10 minute interval as standard time base. The lowest mean oxygen consumption in a 10 minutes interval in the dark period is defined as RMR. table 3 lists the population means of RMR and mass for all species measured.

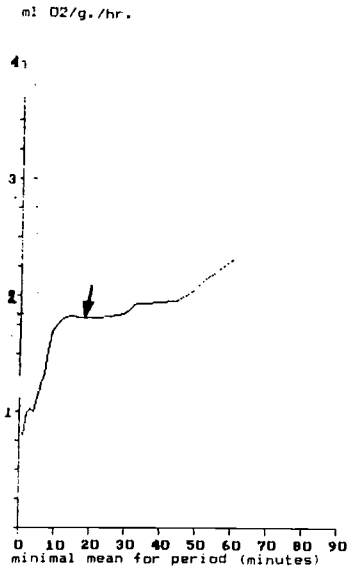


Figure 2. Example of MEAMOVE-graph. See text for more information.

3.1.1. MASS DEPENDENCE

Table 3: Listing of population means of log RMR and log MASS for 10 species. S.D. = Standard Deviation

Species	logRMR	S.D.	logMASS	S.D.
M. epiroticus	-0.433	0.096	1.477	0.063
M. pennsylvanicus	-0.606	0.147	1.412	0.096
M. oeconomus	-0.644	0.121	1.423	0.108
M. oeconomus	-0.442	-	1.505	-
M. miurus	-0.869	0.082	1.269	0.034
C. rutilus	-0.694	0.137	1.333	0.077
M. arvalis	-0.484	0.109	1.427	0.117
Mus booduga	-1.128	0.115	0.955	0.121
M. agrestis	-0.580	0.096	1.277	0.113
C. glareolus	-0.684	0.100	1.373	0.096

comparison between populations of related species

Population means of log RMR and log M (with standard deviations) for the populations compared are plotted in figure 3. No significant differences could be found.

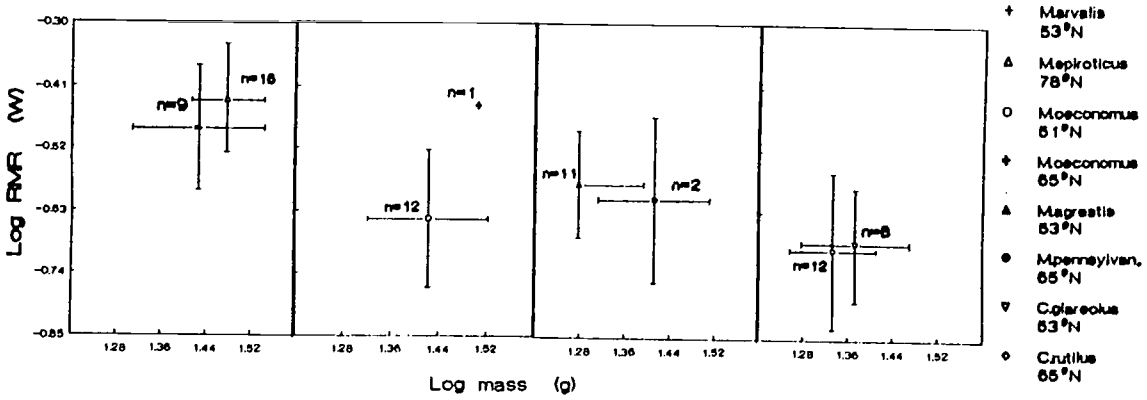


Figure 3. Population means (with standard deviations) of log RMR and log M, separated for the compared species. In all cases no difference in mass dependence is found (see table 4).

To investigate a difference in mass dependence of RMR between related populations, analysis of covariance was used. The compared species are plotted together in table 4.

Table 4: Variation in mass dependence of RMR for related species from different latitudes.

species	regression	n	r^2	p	analysis of covariance
M. epiroticus	log RMR = -1.626 + 0.827 log M	16	0.284	<0.05	r^2 = 0.027
M. arvalis	log RMR = -1.515 + 0.723 log M	9	0.598	<0.05	p » 0.05
M. oeconomus	log RMR = -1.694 + 0.738 log M	12	0.436	<0.05	
M. oeconomus	-	1	-	-	
M. agrestis	log RMR = -1.190 + 0.481 log M	11	0.317	>0.05	r^2 = 0.047
M. pennsylvanicus	log RMR = -1.121 + 0.413 log M	2	0.248	>0.05	p » 0.05
C. glareolus	log RMR = -1.668 + 0.708 log M	12	0.671	0.001	r^2 = 0.065
C. rutilus	log RMR = -2.808 + 1.586 log M	8	0.797	<0.01	p » 0.05
M. miurus	log RMR = 0.104 - 0.767 log M	5	0.102	»0.05	
Mus booduga	log RMR = -2.010 + 0.924 log M	4	0.955	<0.05	

Whether the slopes between species differed was tested by means of analysis of covariance (Manova procedure in SPSS version 3.0). The analysis revealed that the slopes are not significantly different ($F[8,61] = 1.10$, $p = 0.381$). For all species the slope is 0.781. The intercepts did not differ beyond 5 % confidence limits.

Comparison between all northern (>60° N) and all southern (<60° N) microtines

To investigate latitudinal differences of mass dependence, the northern and the southern group were compared. For the northern animals (*M. epiroticus*, *M. miurus*, *M. oeconomus*, *M. pennsylvanicus*, and *C. rutilus*)

$$\log RMR = -2.914 + 1.660 \log M \ (n = 32, r^2 = 0.788, p < 0.001) \quad (1)$$

For the southern animals (without *Mus booduga*)

$$\log RMR = -1.325 + 0.523 \log M \ (n = 44, r^2 = 0.247, p < 0.001) \quad (2)$$

Analysis of covariance (Manova procedure in SPSS) reveals that these slopes are not parallel ($F[1,72] = 26.38$, $p < 0.001$).

Comparison between all individuals

Figure 4a shows the regression of log RMR on log mass (=log M) for all individuals:

$$\log RMR = -2.070 + 1.048 \log M \ (n = 80, r^2 = 0.638, p < 0.001) \quad (3)$$

M. agrestis and *M. arvalis* seem to have a relatively high RMR for their mass . *M. miurus* and the dutch *M. oeconomus* and *C. glareolus* have a relatively low RMR.

For Microtidae only:

$$\log RMR = -1.881 + 0.928 \log M \ (n = 76, r^2 = 0.444, p < 0.001) \quad (4)$$

Because a large number of individuals from a certain population has a larger influence on the regression of log RMR on M than a small number of individuals, population means are calculated:

$$\log RMR = -2.451 + 1.331 \log M \ (n = 10, r^2 = 0.849, p < 0.001) \quad (5)$$

This line is plotted in figure 4b. For Microtidae only

$$\log RMR = -2.447 + 1.328 \log M \ (n = 9, r^2 = 0.612, p < 0.001) \quad (6)$$

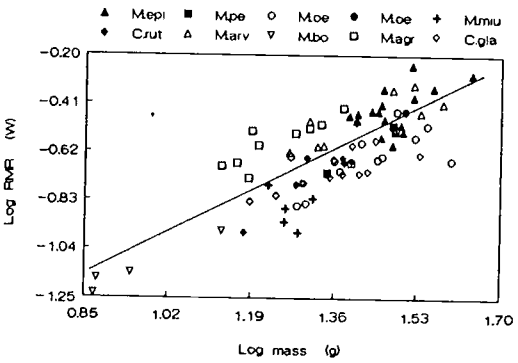


Figure 4a. Mass dependence of log RMR for ten species: log RMR = -2.07 + 1.048 log M (n = 80, $r^2 = 0.638$, $p < 0.001$).

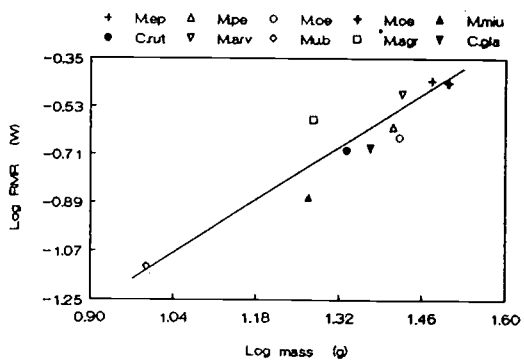


Figure 4b. Mass dependence of log RMR for ten species. Regression is based on population means: log RMR = -2.451 + 1.331 log M (n = 10, $r^2 = 0.849$, $p < 0.001$).

3.1.2. LATITUDE

To investigate a latitudinal dependence of RMR, log RMR was plotted against latitude. Figure 5 shows this for all individuals:

$$\log RMR = -1.081 + 0.008 \text{ latitude } (n = 80, r^2 = 0.383, p < 0.001) \quad (7)$$

M. miurus had a relatively low RMR for its latitude. For Microtidae only:

$$\log RMR = -0.900 + 0.005 \text{ latitude } (n = 76, r^2 = 0.109, p < 0.01) \quad (8)$$

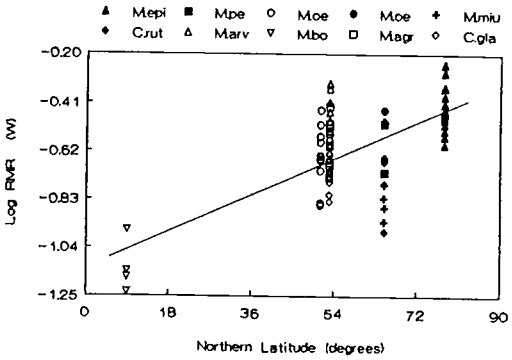


Figure 5. Latitudinal dependence of log RMR for ten species: log RMR = -1.018 + 0.008 Latitude (n = 80, r^2 = 0.383, p < 0.001).

To investigate a latitudinal dependence of body mass, log M is plotted against latitude. Figure 6 shows this dependence for all individuals.

$$\log M = 1.016 + 0.006 \text{ latitude } (n = 80, r^2 = 0.144, p < 0.001) \quad (9)$$

M. miurus and *C. rutilus* seem to have a relatively low mass, *M. oeconomus* a high mass for their latitude. For Microtidae only:

$$\log M = 1.199 + 0.003 \text{ latitude } (n = 76, r^2 = 0.078, p < 0.05) \quad (10)$$

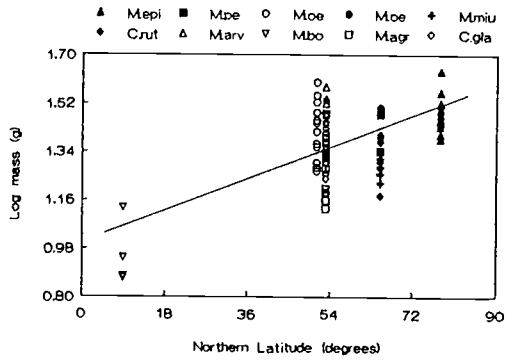


Figure 6. Latitudinal dependence of log M for ten species: log M = 1.016 + 0.006 Latitude (n = 80, r^2 = 0.144, p < 0.001).

To take away mass effects on RMR, the residuals of log RMR: measured RMR - expected RMR based on regression (4), are calculated and plotted (without *Mus booduga*) against latitude:

$$\text{Res RMR} = -0.133 + 0.002 \text{ latitude } (n = 76, r^2 = 0.037, p \gg 0.05) \quad (11)$$

3.2. AVERAGE NOCTURNAL METABOLIC RATE (ANMR)

ANMR was defined as the average oxygen cosumption in the dark period and is expressed in Watts. RQ was assumed to be 0.8, resulting in an energetic equivalence of 20 Joule per ml O_2 (Schmidt-Nielsen, 1974). Mean body mass was calculated by averaging body weight before and after respirometry). These data are obtained during the same experiments as in 3.1, from the same animals. Instead of a running mean of a 10 minutes interval total oxygen consumption is measured and expressed per hour. Table 5 lists population means of ANMR and mass for all species measured.

3.2.1. MASS DEPENDENCE

Table 5: Listing of population means of log ANMR and log MASS for ten species. S.D. = Standard Deviation.

Species	logANMR	S.D.	logMASS	S.D.
M. epiroticus	-0.272	0.099	1.477	0.063
M. pennsylvanicus	-0.365	0.038	1.412	0.096
M. oeconomus	-0.462	0.121	1.423	0.108
M. oeconomus	-0.318	-	1.505	-
M. miurus	-0.662	0.075	1.269	0.034
C. rutilus	-0.497	0.105	1.333	0.077
M. arvalis	-0.379	0.112	1.427	0.117
Mus booduga	-0.862	0.139	0.955	0.121
M. agrestis	-0.419	0.086	1.277	0.113
C. glareolus	-0.486	0.079	1.373	0.096

Comparison between populations of related species

Population means of log ANMR and log M (with standard deviations) for the compared species are plotted in figure 7. No significant differences could be found.

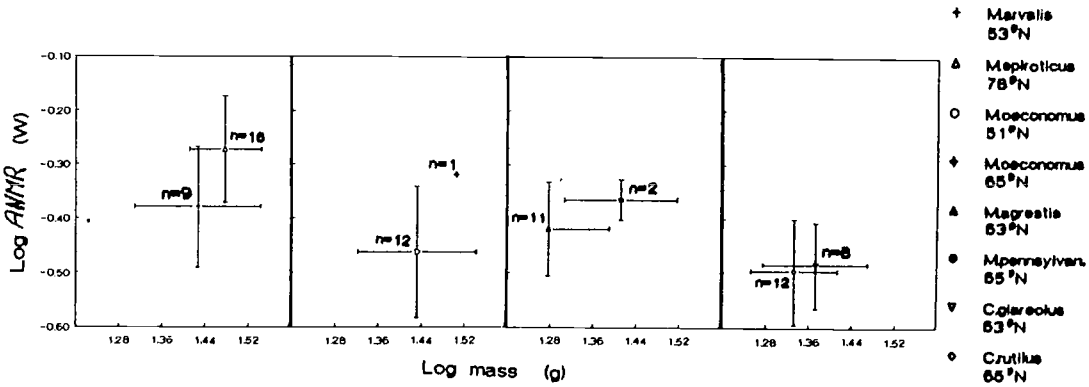


Figure 7. Population means (with standard deviations) of log ANMR and log M, separated for compared species. In all cases no difference in mass dependence is found (see table 6).

To investigate a difference in mass dependence of ANMR between related populations, analysis of covariance was used. The compared species are plotted together in table 6.

Table 6: Variation in mass dependence of ANMR for related species from different latitudes.

species	regression	n	r^2	p	analysis of covariance
M. epiroticus	log ANMR = -1.150 + 0.594 log M	16	0.146	>0.05	r^2 = 0.031
M. arvalis	log ANMR = -1.523 + 0.807 log M	9	0.714	<0.01	p » 0.05
M. oeconomus	log ANMR = -1.793 + 0.900 log M	12	0.644	<0.05	
M. oeconomus	-	1	-	-	
M. agrestis	log ANMR = -1.119 + 0.548 log M	11	0.497	<0.01	r^2 = 0.055
M.pennsylvanicus	log ANMR = -1.078 + 0.514 log M	2	0.213	>0.05	p » 0.05
C. glareolus	log ANMR = -1.361 + 0.652 log M	9	0.558	<0.05	r^2 = 0.046
C. rutilus	log ANMR = -1.855 + 1.019 log M	8	0.561	<0.05	p » 0.05
M. miurus	log ANMR = 0.648 - 1.033 log M	5	0.219	»0.05	
Mus booduga	log ANMR = -1.899 + 1.086 log M	4	0.914	<0.05	

Whether slopes between species differed was tested by means of analysis of covariance (Manova procedure in SPSS). The analysis reveals that the slopes are not significantly different ($F[8,61] = 1.11$, $p \gg 0.05$). For all species the slope is 0.774. The intercepts did not differ beyond 5 % confidence limits.

Comparison between all northern (>60° N) and all southern (<60° N) microtines

To investigate latitudinal differences of mass dependence, the northern and the southern group were compared. For the northern animals

$$\log ANMR = -2.309 + 1.361 \log M \ (n = 32,\ r^2 = 0.681,\ p < 0.001) \qquad (12)$$

For the southern animals (without *Mus booduga*)

$$\log ANMR = -1.178 + 0.541 \log M \ (n = 44,\ r^2 = 0.386,\ p < 0.001) \qquad (13)$$

Analysis of covariance (Manova procedure in SPSS) reveals that these slopes are significantly different ($F[1,72] = 26.63$, $p < 0.001$).

Comparison between all individuals

Figure 8a shows a significant correlation between log (ANMR) and log M for all individuals:

$$\log ANMR = -1.684 + 0.909 \log M \ (n = 80,\ r^2 = 0.648,\ p < 0.001) \quad (14)$$

M. miurus, the dutch *M. oeconomus* and *C. glareolus* seem to have a low mass dependent ANMR, *M. agrestis* and *M. epiroticus* high mass dependent ANMR.

For Microtidae only:

$$\log ANMR = -1.558 + 0.821 \log M \ (n = 76,\ r^2 = 0.466,\ p < 0.001) \quad (15)$$

For population means the regression is:

$$\log ANMR = -1.958 + 1.102 \log M \ (n = 10,\ r^2 = 0.857,\ p < 0.001) \quad (16)$$

This line is plotted in figure 8b. For Microtidae only

$$\log ANMR = -1.968 + 1.109 \log M \ (n = 9,\ r^2 = 0.628,\ p < 0.05) \quad (17)$$

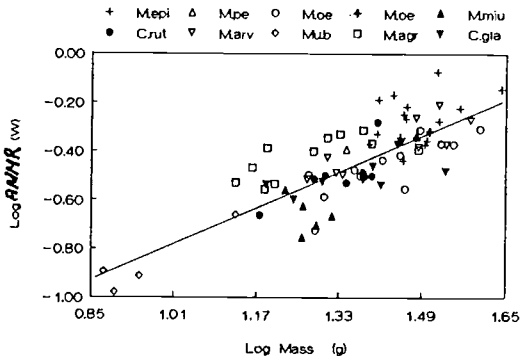


Figure 8a. Mass dependence of log ANMR for ten species: log ANMR = -1.684 + 0.909 log M (n = 80, r^2 = 0.648, p < 0.001).

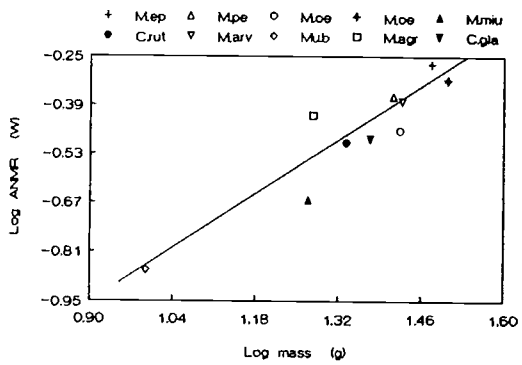


Figure 8b. Mass dependence of log ANMR for ten species. Regression is based on population means: log ANMR = -1.958 + 1.102 log M (n = 10, r^2 = 0.857, p < 0.001).

3.2.2. LATITUDE

To investigate a latitudinal dependence of ANMR, log ANMR was plotted against latitude. Figure 9 shows this for all individuals:

$$\log \text{ANMR} = -0.852 + 0.007 \text{ latitude } (n = 77,\ r^2 = 0.405,\ p < 0.001) \quad (18)$$

M. miurus has a relatively low ANMR for their latitude. For Microtidae only:

$$\log \text{ANMR} = -0.731 + 0.005 \text{ latitude } (n = 73,\ r^2 = 0.251,\ p = 0.001) \quad (19)$$

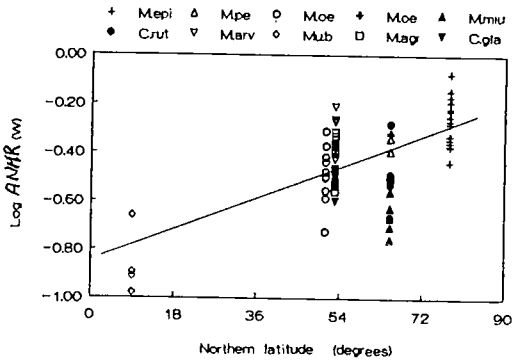


Figure 9. Latitudinal dependence of log ANMR for ten species: log ANMR = -0.852 + 0.007 Latitude ($n = 77$, $r^2 = 0.405$, $p < 0.001$).

To take away the mass effects on ANMR, the residuals of ANMR: measured ANMR - expected ANMR, based on regression (15) are calculated and plotted (without *Mus booduga*) against latitude:

$$\text{Res log ANMR} = -0.155 + 0.003 \text{ latitude } (n = 73,\ r^2 = 0.068,\ p < 0.05) \quad (20)$$

3.3. BODYCOMPOSITION

Appendix I lists the fresh and dry organ weights of the animals. Northern animals seem to have a lower water percentage (an indication they might have more fat) than southern animals (Two sample T test, $p < 0.01$). Table 7 and 8 list the correlations between metabolic rate and fresh and dry organ weights respectively.

Table 7: Correlations between RMR and fresh organ weight for all individuals (without Mus booduga). Log (HLK) is log (heart + liver + kidney), log (HK) is log (heart + kidney), HM = hind leg muscle, FM = fore leg muscle. N = 56.

Body components	r^2	p
log RMR = -0.645 + 0.044 log skin	0.068	<0.05
log RMR = -0.587 + 0.166 log intensine	0.079	<0.05
log RMR = -0.528 + 0.211 log liver	0.068	<0.05
log RMR = 0.127 + 0.672 log kidney	0.235	<0.001
log RMR = 0.126 + 0.581 log heart	0.213	<0.001
log RMR = -0.304 + 0.173 log spleen	0.121	<0.01
log RMR = -0.595 + 0.053 log HM	0.016	>0.05
log RMR = -0.393 + 0.252 log FM	0.171	<0.01
log RMR = -0.642 - 0.001 log gonads	0.005	»0.05
log RMR = -0.209 + 0.391 log brains	0.133	<0.01
log RMR = -0.388 + 0.229 log lungs	0.085	<0.05
log RMR = -0.711 + 0.158 log rest	0.086	<0.05
log RMR = -0.514 + 0.341 log (HLK)	0.118	<0.01
log RMR = 0.011 + 0.712 log (HK)	0.259	<0.001

Table 8: Correlations between RMR and dry organ weight for all individuals (without Mus booduga). Log (HLK) is log (heart + liver + kidney), log (HK) is log (heart + kidney), HM = hind leg muscle, FM = fore leg muscle. N = 56.

Body components	r^2	p
log RMR = -0.723 + 0.175 log skin	0.051	<0.05
log RMR = -0.703 + 0.189 log intensine	0.061	>0.05
log RMR = -0.665 + 0.503 log liver	0.277	<0.001
log RMR = -0.131 + 0.884 log kidney	0.483	<0.001
log RMR = -0.603 + 0.794 log heart	0.373	<0.001
log RMR = -0.424 + 0.164 log spleen	0.141	<0.01
log RMR = -0.629 + 0.021 log HM	0.023	>0.05
log RMR = -0.805 + 0.519 log FM	0.329	<0.001
log RMR = -0.622 - 0.002 log gonads	0.002	»0.05
log RMR = -0.442 + 0.418 log brains	0.142	<0.05
log RMR = -0.419 + 0.449 log lungs	0.171	<0.01
log RMR = -1.004 + 0.397 log rest	0.185	<0.001
log RMR = -0.767 + 0.625 log (HLK)	0.336	<0.001
log RMR = -0.309 + 0.979 log (HK)	0.496	<0.001

3.3.1. HEART+KIDNEY DEPENDENCE

The logarhithm of the sum of dry heart+kidney weight (log HK) gives the highest correlation with RMR (Table 8) and will be used for further calculations. Table 9 lists population means of log HK, mass and fraction HK (HK/mass = %HK) for all species measured.

Table 9: Listing of population means of mass, log HK and %HK for ten species. S.D. = Standard deviation. Data *M. arvalis* courtesy M. Kalk.

Species	logMASS	S.D.	logHK	S.D.	%HK	S.D.
M. epiroticus	1.477	0.063	-0.825	0.084	0.439	0.037
M. pennsylvanicus	1.412	0.096	-0.766	0.071	0.465	0.033
M. oeconomus	1.423	0.108	-0.883	0.108	0.416	0.045
M. oeconomus	1.505	-	-0.720	-	0.487	-
M. miurus	1.269	0.034	-1.034	0.046	0.355	0.016
C. rutilus	1.333	0.077	-0.861	0.115	0.425	0.049
M. arvalis	1.499	0.175	-0.879	0.181	0.421	0.069
Mus booduga	0.955	0.121	-	-	-	-
M. agrestis	1.277	0.113	-0.987	0.076	0.373	0.028
C. glareolus	1.373	0.096	-0.915	0.083	0.402	0.033

Comparison between populations of related species

Population means of log RMR on log HK (with standard deviations) for the compared species are plotted in figure 10. No significant differences could be found.

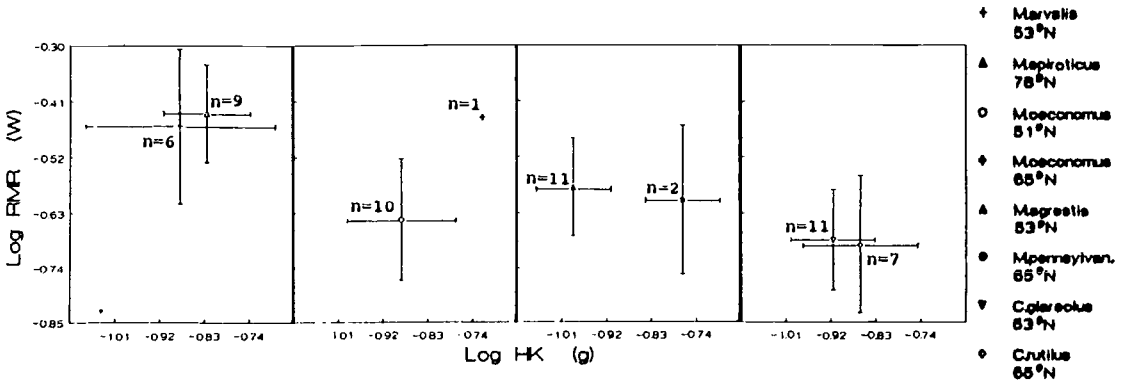


Figure 10. Population means (with standard deviations) of log RMR and log HK, separated for the compared species. In all cases no difference in HK dependence is found (see table 10).

To investigate a difference in heart+kidney dependence of RMR between related populations, analysis of covariance was used. The compared species are plotted together in table 10.

Table 10: Variation in RMR dependence of heart+kidney weight for related species from different latitudes.
For M. arvalis and Mus booduga no data are available.

species	regression	n	r^2	p	analysis of covariance
M. epiroticus	log RMR = -0.142 + 0.369 log HK	9	0.092	»0.05	
M. oeconomus	log RMR = -0.069 + 0.661 log HK	10	0.302	>0.05	
M. oeconomus	-	1	-	-	
M. agrestis	log RMR = -0.219 + 0.366 log HK	11	0.082	»0.05	r^1 = 0.029
M. pennsylvanicus	log RMR = -0.442 + 0.149 log HK	2	0.029	»0.05	p » 0.05
C. rutilus	log RMR = 0.249 + 1.104 log HK	7	0.748	<0.05	r^1 = 0.041
C. glareolus	log RMR = -0.428 + 0.288 log HK	11	0.056	»0.05	p » 0.05
M. miurus	log RMR = -1.229 - 0.348 log HK	5	0.038	»0.05	

Whether the slopes between species differed was tested by means of analysis of covariance (Manova procedure in SPSS). The analysis revealed that the slopes are not significantly different ($F[6,42] = 0.84$, $p \gg 0.05$). For all species the slope is 0.603. The intercepts did not differ beyond 5 % confidence limits.

Comparison between all northern (>60° N) and all southern (<60° N) microtines

To investigate latitudinal differences of mass dependendce, the northern and the southern groups were compared. For the northern animals

$$\log RMR = 0.421 + 1.199 \log HK \ (n = 24,\ r^2 = 0.539,\ p < 0.001) \qquad (21)$$

while for southern animals (without *Mus booduga*)

$$\log RMR = -0.457 + 0.198 \log HK \ (n = 32,\ r^2 = 0.027,\ p \gg 0.05) \qquad (22)$$

Analysis of covariance (Manova procedure in SPSS) reveals that these slopes are significantly different ($F[1,72] = 29.58$, $p < 0.001$).

Comparison between all individuals

Figure 11a shows the regression of log RMR on log HK for all individuals:

$$\log RMR = 0.011 + 0.712 \log HK \ (n = 56, r^2 = 0.259, p < 0.001) \quad (23)$$

M. pennsylvanicus, *M. miurus*, *C. rutilus* and *C. glareolus* seem to have a relatively low heart+kidney weight for their RMR, *M. agrestis* and *M. epiroticus* a relatively high heart+kidney weight. For population means the regression is:

$$\log RMR = 0.227 + 0.968 \log HK \ (n = 8, r^2 = 0.52, p < 0.05) \quad (24)$$

This line is plotted in figure 11b.

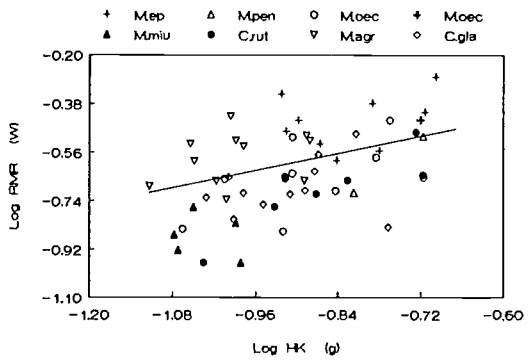


Figure 11a. HK dependence of log RMR for eight species: log RMR = 0.011 + 0.713 log HK (n = 56, r^2 = 0.259, p < 0.001).

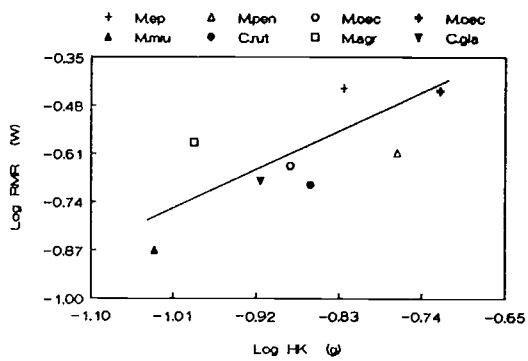


Figure 11b. HK dependence of log RMR for eight species. Regression is based on population means: log RMR = 0.227 + 0.968 log HK (n = 8, r^2 = 0.520, p < 0.001).

3.3.2. MASS DEPENDENCE

Comparison between populations of related species

Population means of log HK and log M (with standard deviations) for the compared species are plotted in figure 12. No significant differences could be found.

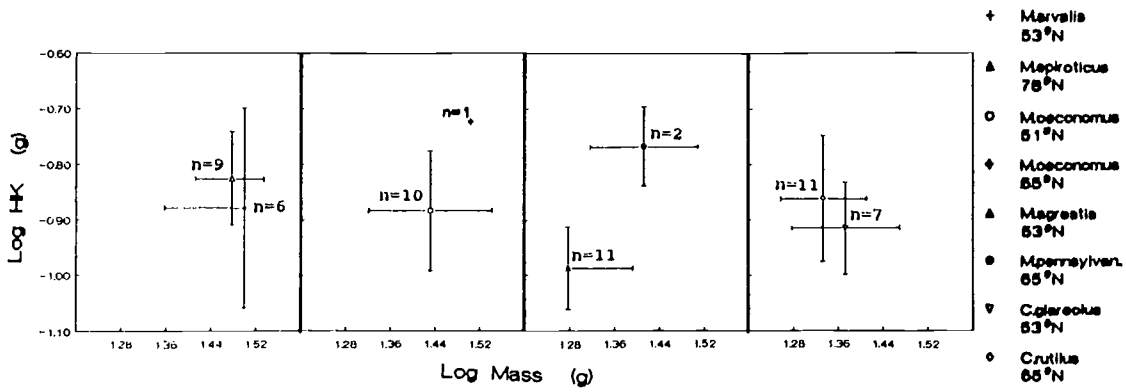


Figure 12. Population means (with standard deviations) of log HK and log M, separated for compared species. In all cases no difference in mass dependence is found (see table 11).

To investigate a difference in mass dependence of heart+kidney weight between related populations, analysis of covariance was used. The compared species are plotted together in table 11.

Table 11: Listing of intraspecific variation in mass dependence of heart+kidney weight for 4 groups. Data M. arvalis: courtesy M. Kalk.

species	regression	n	r^2	p	analysis of covariance
M. epiroticus	log HK = -2.199 + 0.913 log M	8	0.681	<0.05	r^2 = 0.101
M. arvalis	log HK = -2.119 + 0.827 log M	6	0.643	<0.05	p » 0.05
M. oeconomus	log HK = -1.863 + 0.687 log M	10	0.424	<0.05	
M. oeconomus	-	1	-	-	
M. agrestis	log HK = -1.709 + 0.566 log M	11	0.717	<0.01	r^2 = 0.016
M. pennsylvanicus	log HK = -1.955 + 0.773 log M	2	0.694	<0.01	p » 0.05
C. rutilus	log HK = -2.349 + 1.114 log M	7	0.638	<0.05	r^2 = 0.019
C. glareolus	log HK = -1.724 + 0.517 log M	10	0.468	<0.05	p » 0.05
M. miurus	log HK = -2.271 + 0.971 log M	5	0.532	>0.05	

Whether the slopes between species differed was tested by means of analysis of covariance (Manova procedure in SPSS). The analysis revealed that the slopes are not significantly different ($F[6,42] = 1.30$, $p \gg 0.05$). For all species the slope is 0.545. The intercepts did not differ beyond 5 % confidence limits.

Comparison between all northern (>60° N) and all southern (<60° N) microtines

To investigate interspecific latitudinal differences of mass dependence, the northern and southern group were compared. For the northern group

$$\log HK = -2.071 + 0.864 \log M \ (n = 24,\ r^2 = 0.601,\ p < 0.001) \quad (25)$$

while for the southern group

$$\log HK = -1.778 + 0.619 \log M \ (n = 31,\ r^2 = 0.605,\ p < 0.001) \quad (26)$$

Analysis of covariance (Manova procedure in SPSS) revealed that these slopes are not significantly different ($F[1,53] = 2.99$, $p = 0.091$). For both groups the slope is 0.639. The intercepts did not differ beyond 5% confidence limits.

Comparison between all individuals

Because log HK gives the best correlation with log RMR, mass dependence of log HK is calculated. Figure 13a shows the regression of log HK on log M for all individuals:

$$\log HK = -1.828 + 0.674 \log M \ (n = 61,\ r^2 = 0.492,\ p < 0.001) \quad (27)$$

M. miurus, *M. oeconomus*, *M. epiroticus* and *C. glareolus* have a relatively low heart+kidney weight for their mass, *M. pennsylvanicus* and *C. rutilus* a high. Because a large number of individuals has a bigger influence on the regression population means are calculated and plotted in figure 13b:

$$\log HK = -2.339 + 1.059 \log M \ (n = 8,\ r^2 = 0.762,\ p < 0.001) \quad (28)$$

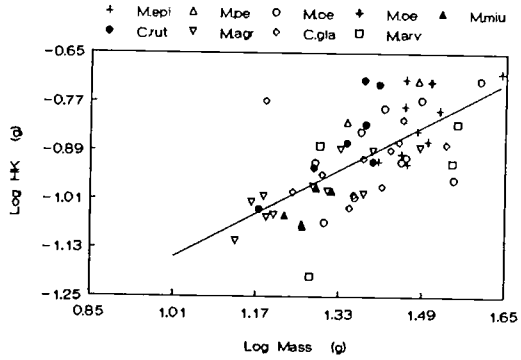


Figure 13a. Mass dependence of log HK for nine species: log HK = -1:828 + 0.674 log M (n = 61, r^2 = 0.492, p < 0.001).

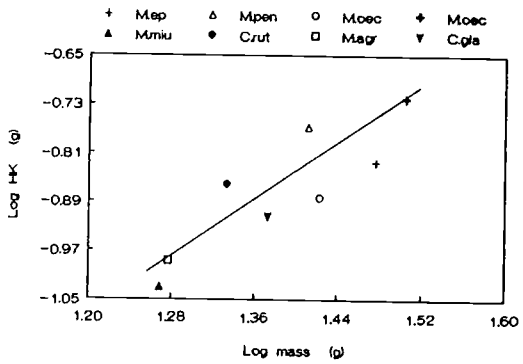


Figure 13b. Mass depenency of log HK for nine species. Regression is based on population means: log HK = -2.339 + 1.059 log M (n = 9, r^2 = 0.762, p < 0.001).

3.3.3. LATITUDE

To investigate a latitudinal dependence of heart+kidney weight, log HK is plotted against latitude. Figure 14 shows this for all individuals:

$$\log HK = -1.081 + 0.003 \text{ latitude } (n = 57, r^2 = 0.120, p < 0.05) \quad (29)$$

M. miurus has a relatively low heart+kidney weight. *M. pennsylvanicus* has a relatively high heart+kidney weight.

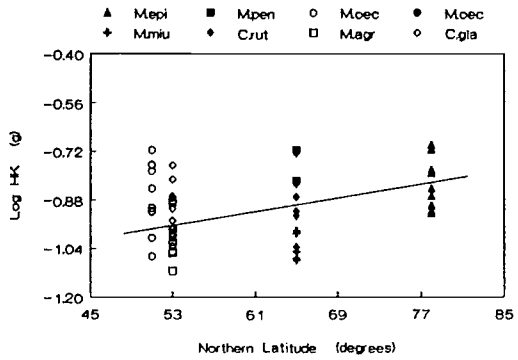


Figure 14. Latitudinal dependence of log HK for eight species: log HK = -1.081 + 0.003 Latitude (n = 57, r^2 = 0.120, p = 0.000).

To take away the mass effect of log HK, the residuals of log HK (measured log HK - expected log HK, based on the regression (28) are calculated and plotted against latitude.

$$\text{Res } (\log HK) = -0.075 + 0.002 \text{ latitude } (n = 56, r^2 = 0.027, p \gg 0.05) \quad (30)$$

4. DISCUSSION

Only in *M. arvalis* & *M. epiroticus* and *C. glareolus* & *C. rutilus* sample sizes are sufficient to draw conclusions upon. No differences in RMR, ANMR and heart+kidney weight are found between compared populations from different latitudes. An explanation is that RMR is plotted against fresh mass instead of lean mass: northern animals seem to have much more fat than the southern animals (an indication for the percentage of fat = 100 - percentage of water, listed in Appendix I). If one compares two species of voles from different latitudes with the same fresh mass and RMR, the data points will overlap. The northern animals have more fat, so their metabolically active mass is overestimated. If lean mass was used rather than fresh mass, body mass would shift to the left (the metabolically inert fat is gone). Northern animals possibly will shift more to the left (more fat) and might reveal a difference in metabolic rate between them (Lavigne *et al*, 1986).

An other explanation is seasonal accimatization: the Alaskan animals are caught during summer, when their metabolism is only 60 to 70 percent of their winter-metabolism (Wunder et al, 1977; Feist & Morrison, 1981; Holleman et al, 1982; Heldmaier, 1989; Heldmaier et al, 1989).

A third explanation is that the animals are acclimated to the moderate temperatures in captivity (Schmidt-Nielsen, 1974; Bartholomew, 1977; Wunder, 1979; Bertin et al, 1990; Haim & Levi, 1990). In birds this acclimation occurs already after one week (Steen, 1958).

Even when these explanations are not valid, ANMR is not a good measure to reveal differences in metabolic rate between northern and southern populations. Hayes (1989) found that the maximum oxygen consumption of *Peromyscus* populations from high altitudes did not differ from low altitude populations. High altitude populations are just operating closer to the maximal sustainable oxygen consumption. A gradient in altitude may be comparable with a latitudinal gradient. In both cases a climatical gradient exists which positively correlates with bodysize (Visher, 1924; Moreau, 1957). ANMR of high latitude and low latitude animals is the same, but the high latitude animals might operate closer to their maximum metabolic rate.

A latitudinal dependence of metabolic rates and body composition can be shown, but the mass-independent residuals are not significantly correlated with latitude. Only for the residuals of ANMR the correlation is significant ($p < 0.05$). However, less than 7 % of the variation in mass-independent ANMR (r^2) can be explained by latitude. This is far too little to have any biological significance.

The ecogeographical rule of Bergmann (1847) and more recently James (1968) and Brown & Lee (1969): the tendency that bodysize is positively correlated with latitude, is confirmed. The increase in metabolic rate at higher latitudes found in this study, is due to an increase in body mass or heart+kidney weight. It was not possible to distinguish between them. One can speculate which is the most reasonable: there are some indications that the latter might be more probable than the former. However fat (=big) animals have a better insulation, they are more vulnerable to diseases (e.g. Connelly & Taberner, 1989; Dolphin *et al*, 1990; King & Rohrbach, 1990), while animals with a "leveled up engine" can cope better with physical effort and extreme temperatures. Possibly Bergmann's rule affects primary heart+kidney weight which on its turn affects body mass and metabolic rate.

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Appendix I. Data listing of body composition, body mass and RMR. Body components (fresh and dry weight) are expressed in gram, body mass in gram and log(gram) and RMR in log(Watt). Individuals are coded both for place of origin and individual number: MeS = *M. epiroticus* from Spitsbergen, Mp.A = *M. pennsylvanicus* from Alaska, Mo.N = *M. oeconomus* from The Netherlands, Mo.A = *M. oeconomus* from Alaska, Mm.A = *M. miurus* from Alaska, Cr.A = *C. rutilus* from Alaska, Ma = *M. arvalis* from The Netherlands, Mb = *Mus booduga* from India. Mag = *M. agrestis* from The Netherlands (data P. Meerlo), Cg = *C. glareolus* from The Netherlands (data D. de Klein). Codes with '/' are indicate *M. arvalis* from The Netherlands (data M. Kalk). Missing values are marked with 'm'. Female animals are marked with 'V', male animals with 'M'.

DRY WEIGHTS

individu	Me.S44	Me.S1072	Me.S9	Me.S6	Me.S12	Me.S3	Me.S16	Me.S20	Me.S11	Me.S2400	Me.S4000	Me.S1072P	Me.S1070
V	V	M	V	V	V	M	V	M	V	M	V	M	V
Log mass	1.454844	1.640481	1.456366	1.404833	1.448706	1.522444	1.4594	1.4786	1.4997	1.4955	1.4362	1.5623	1.4623
massa	28.5	43.7	28.6	25.4	28.1	33.3	28.8	30.1	31.6	31.3	27.3	36.5	29
log(RMR)	-0.5549	-0.2808	-0.4121	-0.4821	-0.4414	-0.3801	-0.3439	-0.5901	-0.5297	-0.5013	-0.4394	-0.34	-0.4765
huid	1.84077	3.48706	8.03068	2.10135	2.72719	4.39356	2.04705	2.46515	5.7256	2.22468	m	m	m
maagd	0.88007	0.93437	0.79521	0.74412	0.8446	0.81991	2.05466	1.03444	0.83238	0.86725	m	m	m
nieren	0.10174	0.12362	0.10679	0.07019	0.06724	0.09944	0.06598	0.08899	0.0841	0.09079	m	m	m
lever	0.48916	0.75805	0.69099	0.35674	0.32127	0.36229	0.09669	0.45099	0.3787	0.3781	m	m	m
gonaden	0.03366	0.47654	0.02573	0.02392	0.07228	0.15323	0.09609	0.28807	0.07533	0.32418	m	m	m
hart	0.06434	0.07677	0.08665	0.05119	0.05939	0.06295	0.05361	0.05504	0.0521	0.04968	m	m	m
long	0.10596	0.10517	0.8847	0.07081	0.10086	0.09826	0.11538	0.07672	0.0998	0.08912	m	m	m
hersenen	0.09347	0.11054	0.11755	0.06033	0.05321	0.05823	0.08941	0.06823	0.0703	0.10364	m	m	m
RA-	0.1833	0.20432	0.13687	0.15471	0.17598	0.14941	0.09072	0.137	0.13995	0.16872	m	m	m
RV-	0.23618	0.14096	0.13497	0.18975	0.13564	0.19046	0.08927	0.17199	0.21133	0.11114	m	m	m
LA	0.37986	0.44968	0.48435	0.38564	0.32142	0.47073	0.06636	0.41346	0.40833	0.40126	m	m	m
LV	0.33302	0.25862	0.34818	0.29324	0.25772	0.32581	0.0685	0.25691	0.37124	0.205	m	m	m
rest	5.17716	6.45764	9.2093	3.97847	4.04015	5.03856	2.08309	4.63739	5.71293	4.81834	m	m	m
milt	0.01363	0.01403	0.01521	0.01075	0.00705	0.01655	0.0536	0.02091	0.01149	0.03663	m	m	m
	23.736	35.173	66.613	34.528	36.146	40.164	m	34.282	46.778	32.079	m	m	m
% water	76.264	64.827	33.387	65.472	63.854	59.836	m	65.718	53.222	67.921	m	m	m

individu	Me.S2000	Me.S1707	Me.S1074	Mp.A1	Mp.A1	Mo.N20	Mo.N3	Mo.N11	MoN14	Mo.N1	MoN12	Mo.N-	Mo.N2
V	V	V	M	V	M	M	V	M	V	M	V	V	M
Log mass	1.3891	1.4065	1.519	1.480006	1.344392	1.599883	1.448706	1.414973	1.283301	1.487138	1.457881	1.526339	1.301029
massa	24.5	25.5	33	30.2	22.1	39.8	28.1	26	19.2	30.7	28.7	33.6	20
log(RMR)	-0.4616	-0.4525.	-0.243	-0.502	-0.7103	-0.6545	-0.6525	-0.58	-0.8548	-0.4244	-0.6396	-0.5556	-0.845
huid	m	m	m	1.70745	2.43144	6.23196	3.1286	1.40653	2.0509	6.46231	2.57107	m	2.85907
maagd	m	m	m	1.13181	0.84146	2.59769	0.76711	1.18332	0.73592	0.98551	0.59777	m	0.53244
nieren	m	m	m	0.12022	0.07937	0.12352	0.07347	0.09756	0.07565	0.09603	0.06748	m	0.0469
lever	m	m	m	0.45188	0.34803	0.69792	0.12428	0.4997	0.34605	0.59153	0.33228	m	0.31862
gonaden	m	m	m	0.02256	0.03403	0.62653	0.65363	0.15763	0.03275	0.89966	0.04694	m	0.30636
hart	m	m	m	0.07191	0.07308	0.06879	0.04758	0.06661	0.0446	0.07593	0.05663	m	0.03902
long	m	m	m	0.27181	0.06559	0.14925	0.08266	0.0858	0.08961	0.11447	0.08322	m	0.07447
hersenen	m	m	m	0.08409	0.09351	0.08476	0.09202	0.09169	0.05947	0.05973	0.08982	m	0.04483
RA-	m	m	m	0.07752	0.10413	0.3132	0.184	0.19689	0.16584	0.24768	0.15749	m	0.15346
RV-	m	m	m	0.12132	0.08608	0.22537	0.12799	0.084	0.09988	0.14771	0.09956	m	0.09651
LA	m	m	m	0.31928	0.76891	0.68788	0.36776	0.36418	0.32296	0.68889	0.30183	m	0.34003
LV	m	m	m	0.28454	0.21508	0.37522	0.2056	0.22551	0.07313	0.40036	0.18793	m	0.18415
rest	m	m	m	4.18823	m	9.05133	5.90708	3.69699	4.04876	7.97562	4.20797	m	3.93456
milt	m	m	m	0.03502	0.01163	0.03351	0.0215	0.08674	0.04699	0.03275	m	m	0.01125
	m	m	m	33.069	25.387	m	39.613	30.425	m	42.352	29.881	m	41.313
% water	m	m	m	66.931	74.613	m	60.387	69.575	m	57.648	70.119	m	58.687

individu	MoN4	Mo.N10	Mo.N40	Mo.N30	Mo.A70	Mm.A1	Mm.A2	Mm.A3	Mm.A4	Mm.A5	Cr.A1	Cr.A4	Cr.A3
V	M	V	V	V	V	M	M	M	V	V	M	V	M
Log mass	1.550228	1.371067	1.359835	1.269512	1.505149	1.315970	1.257678	1.260071	1.225309	1.285557	1.380211	1.404833	1.376576
massa	35.5	23.5	22.9	18.6	32	20.7	18.1	18.2	16.8	19.3	24	25.4	23.8
log(RMR)	-0.5045	-0.704	-0.6411	-0.6592	-0.4415	-0.8228	-0.9255	-0.8661	-0.764	-0.971	-0.6655	-0.4877	-0.6465
huid	3.86276	2.59625	■	2.00389	2.5656	2.81019	3.72309	2.08153	1.73442	3.99827	4.44675	3.38744	0.25943
maagd	1.08354	1.24775	■	0.7514	0.62307	0.71015	0.66944	0.59637	0.74112	0.59408	0.68173	1.04737	0.21668
nieren	0.07503	0.08881	■	0.06016	0.10533	0.07201	0.05319	0.055	0.05591	0.05863	0.082	0.107	0.11799
lever	0.49797	0.59993	■	0.2649	0.44605	0.3197	0.31418	0.17806	0.19049	0.30939	0.32339	0.87919	0.17909
gonaden	0.7965	0.22985	■	0.07449	0.04641	0.23637	0.3797	0.14166	■	0.34327	0.63383	0.16427	0.10214
hart	0.04912	0.05453	■	0.03876	0.08521	0.03058	0.0315	0.02868	0.03323	0.04573	0.06737	0.08061	0.07401
long	0.1067	0.09267	■	0.08095	0.131	0.07787	0.08532	0.06143	0.07455	0.07124	0.11438	0.16427	0.10701
hersenen	0.09924	0.10883	■	0.06921	0.13059	0.040014	0.04513	0.06874	0.04522	0.06893	0.06551	0.08269	0.1004
RA-	0.20478	0.12884	■	0.14219	0.15719	0.14156	0.12692	0.15407	0.08964	0.14735	0.14619	0.15643	0.14166
RV-	0.12383	0.18004	■	0.09004	0.14636	0.08278	0.13741	0.12766	0.14549	0.10882	0.12197	0.13266	0.08895
LA	0.51481	0.38177	■	0.2822	0.45798	0.33216	0.37028	0.294	0.26743	0.32195	0.38673	0.41657	0.14306
LV	0.30027	0.25829	■	0.2143	0.38288	0.14356	0.18465	0.19046	0.16081	0.1803	0.28262	0.23893	0.11633
rest	6.77221	4.65546	■	3.42009	5.56874	2.89883	3.59448	2.81578	2.61133	3.42738	4.35315	4.50269	0.31157
milt	0.0165	0.01842	■	0.02431	0.02686	0.00686	0.00313	0.01068	0.00951	0.00272	0.01575	0.01439	0.13814
	■	37.471	■	39.066	36.789	44.387	50.291	39.574	38.417	53.872	50.918	47.077	39.458
% water	■	62.529	■	60.934	63.211	55.613	49.709	60.426	61.583	46.128	49.082	52.923	60.542

individu	Cr.A6	Cr.A7	Cr.A8	Cr.A9	Cr.A10	Ma20	Ma19	Ma40	Ma1	Ma10	Ma24	Ma15	Ma1
V	V	M	V	M	V	V	V	V	M	V	V	V	V
Log mass	1.281033	1.176091	1.303196	1.394451	1.344392	1.3243	1.5366	1.3075	1.5821	1.4786	1.3365	1.4843	1.2672
massa	19.1	15	20.1	24.8	22.1	21.1	34.4	20.3	38.2	30.1	21.7	30.5	18.5
log(RMR)	-0.7622	-0.9706	-0.6472	-0.6589	-0.7147	-0.5964	-0.4489	-0.4859	-0.4069	-0.3479	-0.5926	-0.5267	-0.6232
huid	3.78175	1.65123	■	4.25724	4.78767	■	■	■	■	■	■	■	■
maagd	0.69133	0.42824	■	0.78836	0.58133	■	■	■	■	■	■	■	■
nieren	0.05697	0.04407	■	0.06251	0.07686	■	■	■	■	■	■	■	■
lever	0.27987	0.23396	■	0.4793	0.45143	■	■	■	■	■	■	■	■
gonaden	0.05532	0.1058	■	0.53973	0.11173	■	■	■	■	■	■	■	■
hart	0.05987	0.04822	■	0.05866	0.05765	■	■	■	■	■	■	■	■
long	0.09023	0.09635	■	0.09683	0.1002	■	■	■	■	■	■	■	■
hersenen	0.07184	0.08596	■	0.08106	0.0247	■	■	■	■	■	■	■	■
RA-	0.1142	0.11235	■	0.17159	0.12872	■	■	■	■	■	■	■	■
RV-	0.08016	0.0985	■	0.10792	0.07345	■	■	■	■	■	■	■	■
LA	0.26642	0.25098	■	0.39321	0.3058	■	■	■	■	■	■	■	■
LV	0.17651	0.15005	■	0.22415	0.19769	■	■	■	■	■	■	■	■
rest	4.07209	2.90825	■	4.47584	3.7138	■	■	■	■	■	■	■	■
milt	0.0074	0.01015	■	0.01142	0.01131	■	■	■	■	■	■	■	■
	53.757	41.22	■	49.212	51.302	■	■	■	■	■	■	■	■
% water	46.243	58.78	■	50.788	48.698	■	■	■	■	■	■	■	■

individu	Ma30	Mb1	Mb2	Mb4	Mb7	Mag15	Mag24	Mag130	Mag172	Mag189	Mag204	Mag207	Mag136
V	M	V	M	M	V	V	V	V	V	V	V	V	V
Log mass	1.5224	0.8751	0.9445	0.8692	1.13	1.377	1.484	1.394	1.19	1.185	1.1614	1.307	1.279
massa	33.3	7.5	8.8	7.4	13.5	23.8	30.5	24.8	15.5	15.3	14.5	20.3	19
log(RMR)	-0.3273	-1.1696	-1.1429	-1.2334	-0.9646	-0.4272	-0.5179	-0.6669	-0.5302	-0.7354	-0.6674	-0.5171	-0.5397
huid	m	m	m	m	m	0.92282	1.30448	0.97526	1.07239	0.89391	0.88083	1.11143	0.96834
maagd	m	m	m	m	m	0.36435	0.51495	0.37765	0.27342	0.28943	0.24868	0.33504	0.37971
nieren	m	m	m	m	m	0.06047	0.08293	0.0808	0.05425	0.05226	0.05434	0.05908	0.06351
lever	m	m	m	m	m	0.25426	0.33357	0.23333	0.21424	0.21398	0.15943	0.21731	0.20362
gonaden	m	m	m	m	m	0.16448	0.12243	0.01491	0.00275	0.0036	0.0042	0.00792	0.00849
hart	m	m	m	m	m	0.04026	0.04862	0.04827	0.03391	0.04719	0.04182	0.0435	0.04165
long	m	m	m	m	m	0.0573	0.09729	0.06791	0.04718	0.04568	0.04992	0.05575	0.0526
hersenen	m	m	m	m	m	0.12008	0.1186	0.1118	0.10888	0.11482	0.11603	0.12342	0.1148
RA-	m	m	m	m	m	0.08982	0.10951	0.10594	0.05641	0.06407	0.06661	0.09862	0.08563
RV-	m	m	m	m	m	0.07661	0.09529	0.09061	0.05305	0.06201	0.05793	0.08468	0.07241
LA	m	m	m	m	m	0.2212	0.24741	0.19301	0.16574	0.13059	0.11768	0.17082	0.17829
LV	m	m	m	m	m	0.20499	0.229	0.18322	0.1542	0.12267	0.10773	0.19197	0.15819
rest	m	m	m	m	m	2.61462	3.09367	2.53181	1.84609	1.7318	1.40952	2.30906	1.95443
milt	m	m	m	m	m	0.01046	0.01434	0.00803	0.0123	0.0098	0.01594	0.00786	0.00681
	m	m	m	m	m	28.332	28.138	30.353	37.464	31.957	30.082	32.495	32.797
% water	m	m	m	m	m	71.668	71.862	69.647	62.536	68.043	69.918	67.505	67.203

individu	Mag173	Mag197	Mag210	Cg1	Cg2	Cg3	Cg4	Cg5	Cg6	Cg7	Cg8	Cg9	Cg10
V	V	V	V	M	M	M	M	M	M	V	V	V	V
Log mass	1.332	1.13	1.204	1.3766	1.358	1.444	1.396	1.535	1.412	1.188	1.241	1.297	1.35
massa	21.5	13.5	16	23.8	22.8	27.8	24.9	34.3	25.8	15.4	17.4	19.8	22.4
log(RMR)	-0.4995	-0.6857	-0.5928	-0.7167	-0.6536	-0.5686	-0.5918	-0.6308	-0.7122	-0.8386	-0.8097	-0.7545	-0.7282
huid	1.22527	0.81377	0.90752	2.39771	2.25768	2.85703	m	2.80000	2.23419	0.89319	1.59246	2.39168	2.42867
maagd	0.32916	0.25093	0.3489	0.22134	0.19587	0.28015	m	0.30209	0.23599	0.43441	0.21273	0.19377	0.27062
nieren	0.08396	0.04372	0.05517	0.07659	0.06305	0.09105	m	0.09299	0.07238	0.09978	0.06403	0.06850	0.06147
lever	0.25856	0.20011	0.25948	0.29830	0.28634	0.38601	m	0.29622	0.39820	0.32927	0.15206	0.43982	0.32994
gonaden	0.0139	0.00097	0.00819	0.95217	0.73655	1.25987	m	1.26221	1.42830	0.01873	0.15356	0.19309	0.38379
hart	0.04607	0.03329	0.03425	0.04664	0.03713	0.04436	m	0.04067	0.03290	0.07119	0.03782	0.04400	0.03169
long	0.06325	0.03932	0.04896	0.09105	0.11991	0.09344	m	0.09929	0.06529	0.09723	0.06565	0.08516	0.09470
hersenen	0.12286	0.11055	0.11152	0.09033	0.07314	0.12942	m	0.10338	0.07067	0.07339	0.10613	0.08163	0.09788
RA-	0.09357	0.06156	0.06601	0.10107	0.10860	0.10366	m	0.14677	0.10596	0.08345	0.13195	0.09406	0.08877
RV-	0.08382	0.05464	0.14012	0.07440	0.07881	0.09508	m	0.09872	0.07055	0.06951	0.07223	0.08116	0.08608
LA	0.1913	0.12139	0.0443	0.29971	0.30202	0.39122	m	0.44202	0.33482	0.19240	0.35789	0.27185	0.32734
LV	0.17076	0.11926	0.14665	0.29597	0.23511	0.33702	m	0.37209	0.26739	0.16102	0.20385	0.25239	0.28963
rest	2.18835	1.5238	1.71197	3.86263	3.81964	4.39236	m	4.65289	3.55455	2.16593	2.68224	3.32699	3.72391
milt	0.01516	0.01675	0.01787	0.00823	0.00545	0.00600	m	0.01421	0.01325	m	0.00522	0.01047	0.01271
	31.469	32.772	32.756	m	m	m	m	m	m	m	m	m	m
% water	68.531	67.228	67.244	m	m	m	m	m	m	m	m	m	m

individu	Cg11	Cg12	50/1	50/2	35/1	35/2	20/1	20/3
V	V	V	M	M	M	M	M	M
Log mass	1.428	1.452	1.660865	1.665580	1.546542	1.556302	1.292256	1.274157
massa	26.8	28.3	45.8	46.3	35.2	36	19.6	18.8
log(RMR)	-0.7033	-0.4935	m	m	m	m	m	m
huid	2.83766	2.48441	3.72173	2.45917	1.7215	1.90105	1.08299	1.15564
maagd	0.28729	0.38201	0.24943	0.26309	0.2037	0.17707	0.16719	0.10729
nieren	0.08323	0.09845	0.11123	0.09199	0.07167	0.08953	0.07306	0.02588
lever	0.39355	0.54792	0.71418	0.62585	0.32587	0.42531	0.28609	0.2284
gonaden	0.38850	0.37819	0.10357	0.15801	0.11565	0.14338	0.0905	0.0556
hart	0.04630	0.05527	0.0875	0.08873	0.04855	0.06063	0.0592	0.03617
long	0.07090	0.08014	0.09652	0.09579	0.07081	0.12251	0.052	0.05409
hersenen	0.07897	0.09591	0.04936	0.06078	0.05633	0.06024	0.05384	0.05146
RA-	0.10424	0.11902	0.14333	0.14502	0.11443	0.14629	0.0928	0.09077
RV-	0.08423	0.08244	0.14108	0.12473	0.10859	0.11442	0.0839	0.06901
LA	0.37976	0.39949	0.43609	0.35702	0.31	0.39004	0.2538	0.20172
LV	0.35563	0.40970	0.36268	0.26941	0.24215	0.24502	0.17662	0.15791
rest	4.46510	5.22472	4.90019	4.68949	4.12657	4.32228	2.46378	2.25794
milt	0.00743	0.00704	0.02651	0.01031	0.01149	0.00998	0.01306	0.00942
	m	m	m	m	m	m	m	m
% water	m	m	m	m	m	m	m	m

FRESH WEIGHTS

	moec70	mpen1	mpen2	mep9	mep3	mep11	mep44	mep6	mep13	mep16	mep2400	mep1072	mep20
huid	4.4249	3.12904	4.16879	11.51406	7.35377	8.16286	4.40757	3.94626	4.87847	4.70021	4.90813	6.886	4.92932
maagd	2.999	4.9112	3.86732	4.17542	3.87286	3.60046	3.93953	4.00823	3.76311	2.49069	3.68324	4.97125	4.08306
nieren	0.40542	0.47965	0.29115	0.37361	0.34227	0.29192	0.42549	0.31598	0.27477	0.2638	0.3578	0.50541	0.32557
lever	1.64704	1.70334	1.28083	2.54114	1.41659	1.37732	1.86309	1.32842	1.25383	0.79172	1.42826	2.59966	1.61054
gonaden	0.08062	0.06326	0.04673	0.06978	0.21676	0.1158	0.07883	0.09102	0.1052	0.01611	0.79349	1.04738	0.68212
hart	0.30691	0.26747	0.25329	0.30457	0.24104	0.19781	0.27062	0.22346	0.23884	0.17371	0.21557	0.28867	0.23412
long	0.56144	1.0973	0.2902	0.39182	0.42416	0.39634	0.49256	0.34982	0.41948	0.40716	0.43845	0.51457	0.3341
hersen	0.57793	0.37286	0.41937	0.50575	0.26488	0.31552	0.4168	0.27064	0.23903	0.59455	0.46757	0.48467	0.32234
R.A.-	0.24138	0.14014	0.19642	0.23459	0.29128	0.29219	0.39995	0.35203	0.4027	0.18182	0.40891	0.45929	0.41653
R.V.-	0.32575	0.33079	0.18728	0.27888	0.53351	0.52414	0.41112	0.54361	0.35937	0.16962	0.29194	0.34573	0.34733
L.A.	1.18223	0.91974	0.56831	1.11603	1.18298	1.02595	1.99056	0.96032	0.84164	0.59255	1.25664	1.2813	1.25302
L.V.	1.06587	0.85101	0.5992	0.86333	0.94462	0.95605	1.0615	0.88852	0.74327	0.92556	0.64972	0.74103	0.79807
rest	15.63189	12.46946	m	9.2093	13.31399	12.98739	16.01896	11.26344	10.97534	9.52143	15.70645	18.47057	14.22112
milt	0.10515	0.14036	0.04074	0.04831	0.07514	0.05544	0.06845	0.05069	0.9133	0.0687	0.15676	0.06257	0.09462

	moec20	moec10	moec1	moec11	moec3	moec20	moec30	moec4	moec12	moec2	crut4	crut9	crut7
huid	3.60067	4.62303	9.79428	3.29134	4.88372	9.58837	3.0642	4.12763	9.58837	4.10736	4.77308	5.58686	2.55241
maagd	2.44582	5.27213	4.01502	5.57551	3.41111	10.6827	3.12513	3.32454	10.6827	2.30806	3.22962	2.45877	1.57252
nieren	0.24929	0.32464	0.34031	0.38963	0.28818	0.48018	0.23625	0.28886	0.48018	0.1718	0.37739	0.24618	0.16075
lever	1.13303	2.04742	2.01819	1.81048	1.59048	2.43913	0.94974	1.22042	2.43913	1.11619	2.48773	1.60387	0.82166
gonaden	0.06538	0.46848	1.59984	0.45845	1.33737	1.85469	0.10396	0.06511	1.85469	0.57744	0.19603	0.66109	0.16574
hart	0.20136	0.21119	0.27188	0.27449	0.18656	0.2365	0.14628	0.17243	0.2365	0.14702	0.30068	0.21703	0.18168
long	0.35133	0.39433	0.57628	0.42781	0.38154	0.57531	0.35966	0.39131	0.57531	0.29134	0.59076	0.38221	0.37957
hersen	0.4066	0.48741	0.25656	0.43006	0.43257	0.37983	0.31182	0.27292	0.37983	0.20059	0.3591	0.36567	0.38024
R.A.-	0.31451	0.29927	0.5285	0.44766	0.38185	0.69741	0.2918	0.34549	0.69741	0.29351	0.32425	0.35866	0.22305
R.V.-	0.21633	0.34393	0.35572	0.18158	0.29975	0.38049	0.20471	0.23339	0.38049	0.21154	0.31763	0.24074	0.24085
L.A.	0.81669	0.98254	1.89127	1.08858	1.00827	1.91149	0.75964	0.94377	1.91149	0.93403	0.94108	0.89871	0.64259
L.V.	0.49354	0.67051	1.04723	0.68065	0.54135	0.97716	0.54028	0.41527	0.97716	0.50208	0.57007	0.54603	0.43454
rest	10.27879	12.19301	21.4225	11.65559	14.9013	23.23585	9.04319	11.49634	23.23585	10.28635	9.6536	10.26364	7.30261
milt	0.07012	0.08152	0.2207	0.38117	0.102	0.12914	0.10501	0.19357	0.12914	0.4963	0.04037	0.04231	0.04147

	crut3	crut6	crut10	crut1	mmiu3	mmiu2	mmiu5	mmiu1	mmiu4	magr210	magr172	magr189	magr136
huid	5.03612	4.68073	5.82617	5.66949	3.01849	4.70294	4.79949	3.63075	2.53612	1.99402	1.58802	2.03104	2.14492
maagd	2.00114	2.1121	2.39137	2.10952	3.29061	2.81475	2.22117	3.09154	3.28502	1.58562	1.25165	1.35882	1.71607
nieren	0.21741	0.20147	0.28284	0.25413	0.22433	0.20989	0.19521	0.22397	0.20945	0.22206	0.2099	0.21146	0.25905
lever	0.97669	0.94036	1.5922	1.06951	0.6548	0.93243	0.92109	0.9924	0.68426	1.01225	0.77953	0.80926	0.75907
gonaden	0.5181	0.06465	0.14464	1.35338	0.18606	0.45206	0.38276	0.45728	m	0.03796	0.01136	0.01515	0.0371
hart	0.26388	0.21915	0.20865	0.24237	0.11594	0.11584	0.14775	0.10628	0.12391	0.13836	0.13056	0.19903	0.17455
long	0.41878	0.33861	0.39071	0.36596	0.24846	0.30193	0.26352	0.29818	0.28216	0.22165	0.211	0.21194	0.22319
hersen	0.37269	0.31586	0.35568	0.29446	0.32206	0.20204	0.29405	0.16816	0.18389	0.5176	0.48995	0.52828	0.52002
R.A.-	0.29702	0.2161	0.23746	0.28397	0.33424	0.28746	0.27991	0.29502	0.32343	0.11874	0.09561	0.12506	0.15839
R.V.-	0.17749	0.18392	0.14827	0.84029	0.32538	0.32852	0.23768	0.18066	0.20551	0.41984	0.11644	0.15279	0.1559
L.A.	1.03799	0.59193	0.63383	0.8147	0.72519	0.79716	0.69848	0.76861	0.68447	0.09506	0.44862	0.41088	0.53145
L.V.	0.65367	0.3978	0.47629	0.67553	0.51402	0.45928	0.43197	0.36541	0.40509	0.47428	0.45476	0.40982	0.51103
rest	10.16519	7.9524	7.97881	9.00263	7.19324	7.70332	7.08247	7.19492	7.07077	4.99824	5.09044	5.32687	5.85858
milt	0.03344	0.02254	0.03849	0.04403	0.04068	0.01665	0.00952	0.03091	0.03849	0.07334	0.05225	0.0434	0.02648

	magr15	magr24	magr130	magr204	magr207	magr173	magr197	marv35/1	marv35/2	marv50/1	marv50/2	marv20/1	marv20/3
huid	2.19827	3.42533	2.55241	2.20844	2.28634	2.81078	1.71195	7.19128	5.96057	10.99305	13.67961	2.49032	3.54666
maagd	1.75576	2.6259	1.80412	1.23487	1.65434	1.58616	1.11642	1.12146	0.7903	1.28645	1.73413	0.84038	0.5872
nieren	0.26766	0.37412	0.3482	0.22891	0.25267	0.31763	0.18104	0.37868	0.39928	0.51949	0.48253	0.34681	0.24382
lever	1.04117	1.3836	0.92547	0.66048	0.93487	1.02919	0.78583	1.36021	1.7434	2.76998	2.42475	1.21895	0.99924
gonaden	1.49073	0.84688	0.07147	0.01971	0.03334	0.06899	0.00347	1.16023	1.70732	0.64572	1.67754	0.72036	0.51494
hart	0.16896	0.21327	0.19431	0.18823	0.1942	0.19313	0.14322	0.19991	0.25116	0.377	0.35478	0.26597	0.16478
long	0.29638	0.52962	0.34138	0.25981	0.26827	0.30366	0.18993	0.30822	0.53116	0.4415	0.442	0.23744	0.25072
hersen	0.55405	0.55261	0.51875	0.54533	0.54251	0.55198	0.52228	0.37833	0.4184	0.33332	0.40188	0.34615	0.34282
R.A.-	0.16709	0.21228	0.20267	0.14074	0.18316	0.1742	0.13118	0.17828	0.27347	0.229	0.25495	0.16588	0.1582
R.V.-	0.17125	0.21732	0.2081	0.15695	0.18178	0.20155	0.13546	1.02546	1.32786	1.49111	1.18955	0.84717	0.68457
L.A.	0.70557	0.82335	0.56576	0.36287	0.4999	0.59004	0.36004	0.20468	0.26946	0.27212	0.27225	0.17882	0.10634
L.V.	0.73227	0.83525	0.6073	0.37617	0.6451	0.58029	0.38931	0.85524	0.93151	1.21431	0.93516	0.64123	0.53067
rest	8.76173	10.68055	8.17117	4.61937	7.11199	7.05417	4.6033	16.27974	16.43162	19.90166	17.28147	8.71141	8.01321
milt	0.04877	0.06813	0.03558	0.06995	0.03356	0.06445	0.0709	0.05805	0.05146	0.12016	0.05713	0.05949	0.04819