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Intraspecific Allometry: The Kidney

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Abstract

Interspecific and intraspecific allometric relationships between kidney mass and body mass were determined in 4 hamster species, 10 inbred strains of rats and 24 inbred strains of mice. Genetic allometry, as such, was possible on hand from an inherent reduction of genetically based differences by comparing species or strainspecific mean values rather than individual values. Ontogenetic allometry was investigated in growing female individuals of a single inbred rat strain.

The interspecific and intraspecific allometric relationships between kidney and body mass were significant in all cases investigated with the one exception of the intraspecific allometry in the male mouse. This can be explained by an extreme genetic variation between the different inbred strains or species in combination with a narrow range in body weight.

Allometry between the different rat-inbred-strains, however, was statistically significant. The allometric functions within rats (slope males 0.96, females 0.89) and between species (slope 0.85, Prothero 1984) were equivalent. A similar equivalence was, like-wise, found to hold in the ontogenetic allometry (slope 0.82), whereby the intraspecific values for slope and intercept equalled those observed in the interspecific and intraspecific comparisons.

In essence, this study has proven that the investigated mouse-hamster-rat regression displays an allometric function (slope 0.86) statistically equivalent and, therefore, in accordance with the previously established regression for 63 different species of terrestrial mammals (slope 0.85, Prothero 1984). As a result, the general interspecific relationship of kidney mass to body mass which holds true for mammalian species can be transferred onto, and is hence valid in, interspecific and especially intraspecific comparisons of small laboratory rodents.

Introduction

Due to the vital role held by the kidney in water and electrolyte metabolism of the entire organism, there is a close interspecific correlation between kidney mass and total body mass (Calder and Braun 1983). In mammals, Prothero (1984) has numerically expressed the interspecific relationship between kidney mass and body mass in the following allometric equation:

$$\text{kidney mass (g)} = 0.020 \times \text{body mass (g)}^{0.85 \pm 0.01}$$

Similar exponential relationships have been found for glomerular size and number with varying values for the body mass exponent (Rytand 1938). Work by Brody (1945) substantiated these findings.

Among primates (Stahl 1965), an equation nearly identical to Prothero's (1984) comparison of kidney mass to body mass was found. Within adults species of small laboratory animals such as rats (Closkey and Jermanowich 1985) and mice (Hackbarth and Hackbarth 1981), however, either no such relationship could be found, or when present, the body mass exponents differed significantly from those found in interspecies comparisons.

Moreover, within a single inbred strain of mice, the growing kidney did follow the same function for kidney mass as described by interspecific relationship for adults (Hutson et al. 1981).

Considering the lack of a consistent allometry between glomerular parameters and body mass, the question arises as to whether the relationship of kidney mass to body mass within a single species of small rodents follows the same function as among different species. Heusner (1982) recently claimed that there is no a priori reason for such a common allometry within a single species, hence any value for the body mass exponent could be expected.

This study was, therefore, conceptualized to determine a possible intraspecific allometry of kidney mass to body mass in small rodent species. Values for the mass coefficient "a" and the mass exponent "b" of the general allometrical function (Huxley 1932):

$$\text{kidney mass} = a \times \text{body mass}^b$$

are compared to those found between species.

Furthermore, it should be mentioned, that in accordance with Röhrs (1959), a strong separation was made between ontogenetic and intraspecific allometry. While the ontogenetic allometry, on one hand, was determined by comparing growing individuals of one sex of a single inbred strain of rats, intra- and interspecific allometry was derived from comparisons between mean kidney and body weights taken from each sex of 10 different identically aged inbred strains of rats, 24 identically aged inbred strains of mice and 4 adult species of hamsters. These ontogenetic, intraspecific, and interspecific allometries in small laboratory animals were compared to the interspecific allometry reported by Prothero (1984).

Material and methods

Body mass and kidney mass were determined in five adult females and five adult males of each hamster species and each inbred mice and rat strain. Prior to sacrifice physiological kidney functions were determined (Hackbarth and Hackbarth 1981, 1982; Hackbarth et al. 1981, 1982) and histometrical measurements were performed after sacrifice (Hackbarth et al. 1987). The animals were sacrificed with halothane (hamsters), CO_2-inhalation (rats), or cervical dislocation (mice). Body mass was immediately recorded, and the kidneys were removed, bled by drainage, and weighed.

Prior to sacrifice, all animals were maintained under identical environmental conditions at a room temperature of 22 ± 2 °C, a relative humidity of 55 ± 5 %, and a 12L : 12D photoperiod. The rats were kept under controlled micro-biological conditions (specific pathogen free, barrier maintained). All animals were fed a standard laboratory diet.

Interspecific allometry

The kidney and body weights of four hamster species were determined: *Cricetus cricetus, Mesocricetus auratus, Cricetulus griseus* and *Phodopus sungorus* (Table 1). On the day of investigation, *Cricetus cricetus* individuals were 204 days, those of the remaining three species 92–100 days old. At these ages, the animals were considered to be adult.

Intraspecific allometry

Genetic allometry

Body and kidney mass of ten different inbred strains of rats *(Rattus norvegicus)* were recorded (Table 1): ACI/Ztm, AS/Ztm, BH/Ztm, BS/Ztm, DA/Ztm, LEW/Ztm, MWF/Ztm, SC/Ztm, SPRD/Ztm, WC/Ztm. All animals were 110–120 days old. The body weights of the females ranged from 137 to 259 g and those of the males from 185 to 401 g.

Body and kidney mass were recorded for 24 inbred strains of mice at the age of 100 days. For strain designation and mean strain values see Table 1, for further details see Hackbarth and Hackbarth (1981).

Ontogenetic allometry

Body and kidney weights were determined in nineteen females of the inbred strain MWF/Ztm ranging in age from 30 to 50 days of age and in body mass from 67 to 180 g. In a pilot study, this growth period alone proved to follow an allometric relation between kidney and body mass predominantly due to an increase in body mass. Prior to 30 days of age, postnatal development seems to have a greater influence on kidney mass than does body mass (Kittelson 1917). After 50 days, the increase of body mass is more and more a function of increasing body fat.

Statistics

Intraspecies allometry was calculated separately for each species, strain and sex. Following logarithmic transformation of the body and kidney weights, linear regression analysis (Sachs 1984) was performed on the mean values for each species, strain, and sex. By statistically excluding environmental influences (e.g. considering mean values rather than individual weights within one strain), the resulting intraspecific allometries reflect the genetically influenced relationship of kidney to body mass within a species (genetic allometry).

Slope and intercept of the regression were calculated. The mass exponent ("b" $\pm$ SD), mass coefficient ("a" $\pm$ SD), and coefficient of correlation "r" were calculated for each relationship. The mass exponents and mass coefficients were first tested for significance and subsequently compared with covariance analysis (Sachs 1984). These values were then compared to those of Prothero's (1984) using a simple t-test (Sachs 1984).

Ontogenetic allometry was determined by taking the body and kidney weights of nineteen females of the inbred rat strain MWF/Ztm. Following logarithmic transformation of the individual data, ontogenetic allometry was calculated as described above. This ontogenetic allometry reflects the non-genetically determined variability within the genetically-identical individuals of an inbred strain.

Results

Intraspecific allometry

Ontogenetic allometry (rat)

Growing females of the MWF/Ztm inbred strain clearly exhibit an allometric relationship between kidney mass and body mass. The weight range covered by these animals between 30 and 50 days of age was 67–180 g. Slope and intercept are equivalent ($p > 0.05$) to those found for adult rats as well as for the interspecific relationship (Prothero 1984) (Fig. 1 and Table 2).

Genetic allometry (rat, mouse)

Rat – There is no difference between sexes in the slope or the intercept of the regression lines ($p > 0.05$). There is a large genetic variation within each sex (Fig. 1 and Table 2). The slopes and intercepts do not differ ($p > 0.05$) from those of other intraspecific regressions determined in this study nor from those found in the general interspecific comparison of Prothero (1984).

Mouse – There is a pronounced sex difference in mice. Males clearly lie above the general regression line (see Fig. 1). Within male mice, strain differences among males were large and the body weight range small. Hence, no significant correlation of kidney to body mass was found (Table 2). Only in females a significant allometry was evident (slope 0.54; Table 1). This is statistically different ($p < 0.05$) from other intraspecific and interspecific allometries described in this study as well as from the general interspecific relationship of Prothero (1984).

Within *Mus musculus,* the most obvious difference is the sex difference in kidney mass accompanied by large strain deviations. In general, the weight range is *Mus musculus* in too narrow to allow a reliable statistical analysis. Combining male and female data does not result in a more statistically significant allometry (Hackbarth et al. 1982).

Table 1. Body weight (g) and kidney weight (g) of strains and species

mice strain	males $\bar{x} \pm SD$ body weight	kidney weight	females $\bar{x} \pm SD$ body weight	kidney weight
CE/J	36.90± 3.93	0.383±0.028	22.82± 1.27	0.246±0.011
C3D2F_1/J	35.78± 3.44	0.451±0.030	25.79± 1.49	0.262±0.016
AKR/J	34.03± 1.74	0.442±0.042	31.28± 2.18	0.292±0.039
NZB/BINJ	34.00± 1.31	0.415±0.020	27.17± 1.31	0.281±0.009
CBA/J	33.90± 3.68	0.416±0.041	26.30± 3.52	0.244±0.023
ST/bJ	33.62± 3.16	0.374±0.013	25.59± 2.55	0.250±0.015
C3H/HeJ	32.83± 1.18	0.410±0.028	28.95± 3.09	0.265±0.015
B6D2F_1/J	32.72± 3.07	0.377±0.026	21.01± 0.20	0.197±0.006
BuB/BnJ	32.40± 2.33	0.378±0.042	27.48± 1.60	0.292±0.024
CB6F_1/J	31.73± 1.99	0.390±0.032	24.21± 0.88	0.242±0.011
PL/J	31.16± 2.18	0.354±0.036	11.46± 2.12	0.243±0.027
AKD2F_1/J	31.06± 1.79	0.408±0.032	26.92± 2.31	0.258±0.024
B6AF$_1$/J	30.97± 2.18	0.319±0.019	22.11± 1.89	0.246±0.024
C57Br/cdJ	29.47± 1.91	0.398±0.024	25.22± 0.67	0.284±0.017
Balb/cJ	28.88± 1.84	0.430±0.036	21.58± 1.18	0.231±0.003
CAF$_1$/J	28.83± 1.84	0.366±0.019	21.83± 1.23	0.226±0.012
SJL/J	27.73± 1.60	0.393±0.038	20.25± 1.43	0.268±0.022
C57BL/6J	27.54± 2.29	0.276±0.033	22.03± 2.13	0.266±0.023
A/J	27.28± 1.54	0.373±0.021	21.97± 1.80	0.237±0.018
DBA/2J	27.06± 2.91	0.401±0.040	26.61± 2.73	0.266±0.019
RIIIS/J	26.91± 1.35	0.319±0.021	18.64± 1.03	0.230±0.006
SWR/J	25.47± 1.11	0.318±0.025	20.71± 1.47	0.247±0.012
RF/J	25.29± 2.26	0.418±0.042	24.62± 1.15	0.314±0.026
SM/J	22.41± 1.92	0.425±0.064	16.96± 1.30	0.198±0.020
rats strain	males $\bar{x} \pm SD$ body weight	kidney weight	females $\bar{x} \pm SD$ body weight	kidney weight
ACI/Ztm	213.37± 8.24	1.910±0.178	160.89± 8.30	1.446±0.156
AS/Ztm	290.97± 8.22	2.900±0.142	175.45± 5.53	1.524±0.139
BH/Ztm	318.24± 18.14	2.882±0.274	230.82± 6.00	2.096±0.085
BS/Ztm	314.47± 23.73	2.052±0.091	179.28± 7.22	1.188±0.056
DA/Ztm	184.97± 8.14	1.508±0.083	137.10±21.28	1.226±0.147
LEW/Ztm	335.20± 24.61	2.826±0.188	190.56± 7.33	1.540±0.068
MWF/Ztm	347.60± 20.69	2.684±0.211	188.67±14.47	1.438±0.105
SC/Ztm	401.45± 31.37	3.508±0.265	259.38± 7.83	2.120±0.086
SPRD/Ztm	382.10± 21.50	3.218±0.306	225.30±13.82	1.738±0.104
WC/Ztm	327.69± 33.36	2.558±0.350	211.02± 5.93	1.569±0.060
hamster species	males $\bar{x} \pm SD$ body weight	kidney weight	females $\bar{x} \pm SD$ body weight	kidney weight
Cricetus cricetus	470.21±135.27	1.922±0.570	333.98±89.83	1.410±0.217
Mesocricetus auratus	116.47± 8.36	0.852±0.013	127.80± 8.89	1.036±0.106
Phodopus sungorus	32.91± 4.48	0.336±0.044	33.86± 3.83	0.330±0.012
Cricetulus griseus	35.79± 4.97	0.320±0.047	25.35± 3.25	0.208±0.179

Interspecific allometry

Hamster – The wide range of body mass covered by these species, facilitates to detect significant correlations, when kidney mass is plotted versus body mass in a double logarithmic system (Fig. 1 and Table 2). There is no significant difference ($p > 0.05$) between the regression lines for males and females. This is evident in figure 1, but not striking. The slope and the intercept of the hamster regression are not significantly different from those for intraspecific regressions of small laboratory animals investigated here or from those found in the general interspecific comparison for mammals of Prothero (1984).

Intraspecific versus interspecific allometry

Table 2 summarizes the parameters of the allometric equations, resulting from interspecific and intraspecific comparisons. These values are, furthermore, compared with those published by Prothero (1984) for 63 species of mammals. No significant ($p > 0.05$)

Table 2. Intra- and interspecific allometric parameters

species	sex	No. of points	b ± SD	ln a ± SD	r	p <
rat	males	10	0.956±0.155	-4.542±0.889	0.909	0.01
	females	10	0.887±0.188	-4.222±0.989	0.858	0.01
rat growing	females	19	0.823±0.035	-3.588±0.172	0.984	0.01
mice	males	24	0.251±0.198	-1.817±0.674	0.261	n.s.
	females	24	0.540±0.119	-3.086±0.376	0.696	0.01
hamster	males	4	0.682±0.044	-3.500±0.203	0.996	0.01
	females	4	0.741±0.117	-3.802±0.524	0.976	0.05
all		95	0.862±0.202	-3.992±0.086	0.976	0.01
Prothero (1984)		117	0.85 ±0.01	-3.912±0.023	0.993	0.01

difference appears between the slopes or the intercepts of the overall intraspecific equation versus that of Prothero (1984). With respect to the amount of data contributing to the present analysis, it is surprising that such a limited amount suffices to establish and confirm the close approximation of the regression found in laboratory rodents to that found in the more extensive interspecific comparison.

Discussion

Intraspecific allometry often faces the problem of a limited weight range within a single species. This problem can be solved by reducing variation across the regression to be calculated. The most efficient way to achieve this reduction in variance is by defining intraspecific allometry as was done by Röhrs (1959). He subdivided intraspecific allometry into:

1. ontogenetic allometry
   a. allometry of an identical growing individual
   b. allometry of growing individuals in one population at various stages of growth
2. intraspecific allometry
   a. allometry of different sized adult individuals of the same population of a single species
   b. allometry of different sized adult individuals of different subspecies.

In the present study, intraspecific allometry of kidney mass to body mass was obtained by comparing different genotypes (inbred strains) of two species (*Mus musculus* and *Rattus norvegicus*). An allometric relationship resulting from this approach is exclusively due to genetic differences between the different inbred strains compared. This genetic allometry within mice and rats contrasts with that of different sized adult individuals of different species; i.e. interspecific allometry (Röhrs 1959).

Ontogenetic allometry (i.e. correlations among growing individuals) was also investigated by comparing individuals of a single rat inbred strain. All animals were of the same genotype, hence the resulting allometry is comparable to that which results from a single growing individual. Despite the small body weight range within each species, the applied experimental design led to significant correlations for the best fit (ln "kidney mass" to ln "body mass") in all species investigated.

Only within male mice genetic variation among inbred strains was so extreme and the weight range so narrow that a significant correlation could not be detected. The high degree of variation within males ruled out any statistical significance. Within females, the body mass coefficient as well as the body mass exponent of the allometric function had large standard deviations (Table 1). An obvious sex difference is, thus, evident in mice. Males have larger kidneys than females at the same relation to body mass. This sex difference in kidney mass has been previously shown to be testosterone dependent (Crabtree 1941). The mass exponent within female mice ($b = 0.54$) is much lower than that of the interspecific allometry (Table 2). Due to the large genetic variation and narrow weight range, however, the difference is only slightly significant ($p < 0.05$), and its value must be carefully interpreted. Nevertheless, most values for inbred strains of mice lie close to the overall line of regression calculated for all small laboratory animals (Fig. 1).

Within the genus of hamster, four species were available. The advantage of choosing four genetically different species was the inherent large weight range covered by these species. Disadvantageous was the non-simultaneous maturity of the various species. Unlike the three other hamster species, *Cricetus cricetus,* was according to its growing curve not considered adult at 100 days of age. As a result, kidney and body mass of this species were determined when males and females had reached adulthood at 204 days. Whether this peculiarity of *Cricetus cricetus* is responsible for mean values far below the overall regression line remains unclear (Fig. 1). The values of the three hamster species reaching adulthood at 100 days plot well along the general regression for all species investigated. No significant difference is apparent between the allometric function of males and females. Variation among females was, however, larger. This resulted in larger standard deviations of the mass coefficient and exponent and in a reduced correlation coefficient "r" (Table 2). The mass exponents are lower than those found in the interspecific relationship. This difference in slope remains insignificant due to the small number of hamster species investigated. It should be noted, however, that additional species of larger laboratory hamsters are not available.

Within the different strains of rats, genetic as well as ontogenetic allometry was determined. Although genetic variation in body mass between strains was large, highly significant correlations were found. Within females as well as males, the mass coefficient and the mass exponent did not differ significantly from those found in the interspecific relationship (Prothero 1984). Furthermore, no significant sex difference exists between the allometric functions computed for males and females.

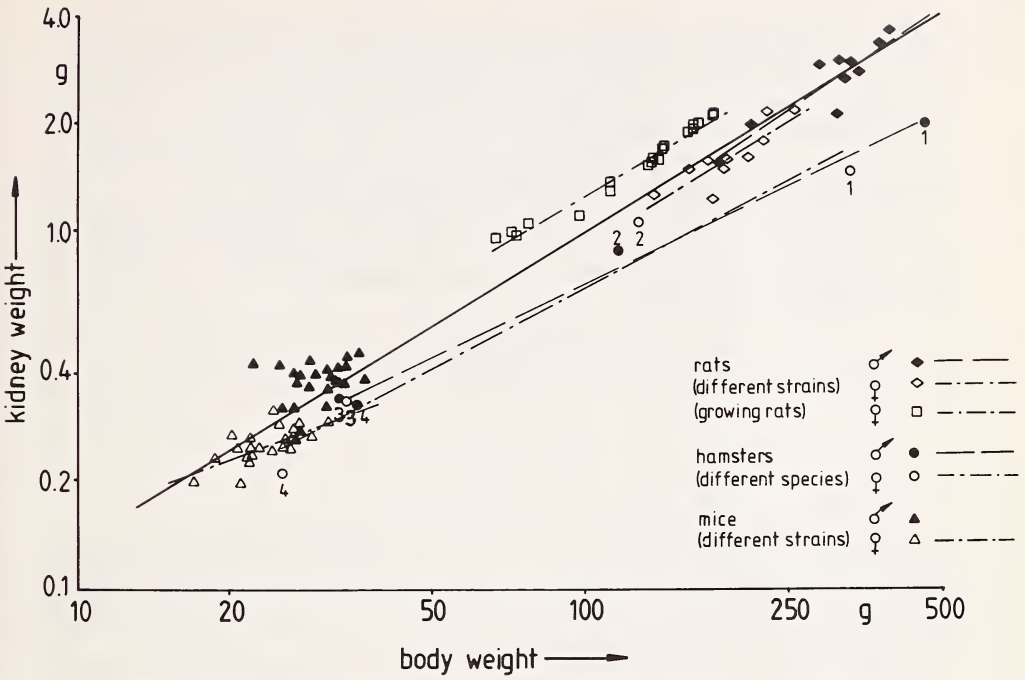

Fig. 1. Intra- and interspecific allometry of kidney mass to body mass. Intraspecific (rats and mice): open triangles = female mice; solid triangles = male mice; open diamonds = female rats; solid diamonds = male rats. – Ontogenetic (rats): open squares = growing female rats. – Interspecific (hamster): open circles = female hamster; solid circle = male hamster. 1: *Cricetus cricetus;* 2: *Mesocricetus auratus;* 3: *Phodopus sungorus;* 4: *Cricetulus griseus*. Dashed lines = males

Growing rats of the inbred strain investigated cover a wide range of body weight (67–180 g). Within this inbred strain less variation is apparent when growing individuals were compared as between different strains. This small variance across the ontogenetic function is evident in the small standard deviation of the mass coefficient and exponent. The mass exponent is equivalent to that of the interspecific comparison. The line of the regression, however, appears shifted, even though there is no statistical difference between the mass coefficient of the ontogenetic and the intra- and interspecific allometries.

Consideration of all measured data (95 individual values taken from both sexes of six different species) in the "interspecific" (mouse-rat-hamster) allometric analysis, without selection or exclusion of data, results in an allometric function (Table 2) that is surprisingly close to the regression previously found by comparing 1105 animals from 63 species (Prothero 1984). This indicates that animals lying in the relativ narrow weight range from 20 to 500 g follow the same allometric function as described for much larger species. It does not, however, coincide with published data concerning oxygen consumption, whereby animals less than 260 grams follow a different regression than those greater than 260 grams (Bartels 1982).

Moreover, the present analysis is an example of the caution needed in interpretation of intraspecific allometries. Even though intraspecific variance can be statistically reduced to genetic or ontogenetic variation through exclusion of environmental influences, resulting allometries in these smaller species are often unreliable.

Nevertheless, the Figure 1 indicates a clear similarity between the intraspecific regression of laboratory species investigated and the common interspecific regression. Intra-

specific deviations from the general allometric function appear to be more a function of excessive variation than a systematic trend inherent in intraspecific allometry. The mass coefficients of the different species are not significantly different from those in the interspecific allometric function. Thus, no obivous generalized discrepancy is apparent between intraspecific and interspecific kidney to body mass allometry. In contrast to kidney mass, energy metabolism (Heusner 1982) and brain mass (Röhrs 1961) follow different slopes of regression in intra- and interspecific allometries.

In conclusion, the allometric relationship of kidney mass to body mass seems genetically determined as a quantitative, multivariate trait. This genetic trait is responsible for genetic variation within a single species, during the period of growth, as well as for the differentiation between species.

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Zusammenfassung

Intraspezifische Allometrie: Die Niere

Inter- und intraspezifische Allometrien von Nieren- zu Körpergewicht wurden an Hand von 4 Hamsterspezies, 10 Ratteninzuchtstämmen und 24 Mäuseinzuchtstämmen bestimmt. Die Bestimmung genetischer Allometrien war möglich durch eine Reduktion auf ausschließlich genetische Varianz durch die Verwendung von Merkmalsmittelwerten der einzelnen Spezies bzw. Inzuchtstämme an Stelle der Einzelwerte. Ontogenetische Allometrie wurde ermittelt an Hand von wachsenden weiblichen Individuen eines einzelnen Inzuchtstammes.

Sämtliche Inter- und Intra-Spezies-Allometrien von Nieren- zu Körpergewicht sind signifikant mit der einen Ausnahme der Intra-Spezies-Allometrie der männlichen Mäuse. Diese Ausnahme kann durch eine extreme genetische Variation zwischen den Mäuseinzuchtstämmen in Verbindung mit dem nur schmalen Körpergewichtsbereich erklärt werden.

Innerhalb der Spezies Ratte ergeben sich statistisch signifikante Allometrien. Die genetischen Allometriefunktionen (Allometrieexponent bei den Männchen 0,96, bei den Weibchen 0,98) sind equivalent der Inter-Spezies-Allometrie (Prothero 1984). Ähnlich vergleichbar ist auch die ontogenetische Allometrie (Allometrieexponent 0,82), so daß die Intra-Spezies-Werte für Allometrieexponenten und -koeffizienten sich nicht von denen der Intra- und Inter-Spezies-Allometrien unterscheiden.

Weiterhin zeigen die vorliegenden Untersuchungen, daß die erstellte Maus-Hamster-Ratte-Allometrie mit einem Allometrieexponenten von 0,86 der an Hand von 63 verschiedenen Spezies von Landsäugetieren (Allometrieexponent 0,85, Prothero 1984) gleicht. Daraus folgt, daß die allgemeine Intra-Spezies-Allometrie von Nieren- zu Körpergewicht für Säugetierspezies verläßlich und auch für den Inter- und Intra-Spezies-Vergleich kleiner Versuchstiernager tauglich ist.

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