

Non-metric traits: remarks on sex dependence, age dependence, and on intercorrelations among characters

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Interdependence among non-metric traits as well as their correlation with sex, age, and body size usually cause methodological problems in phenetic investigations. Based on data on four mammalian species (*Microtus oeconomus*, *M. limnophilus*, *Lepus europaeus*, *Capreolus capreolus*) studied by the author, and on data from the literature these problems were analyzed. Both the number and the coefficients of intercorrelations among traits were found to depend on sample sizes of individuals examined. They were larger in populations with progressive and faster body growth. The number of traits related to sex increased significantly with sex dimorphism across mammalian species. Age dependence of traits did not show a regular pattern within and among species. These results are discussed as to their implications for estimating morphological differentiation within and among populations.

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Introduction

Non-metric traits of the skeleton have been widely used in studies on mammals and humans for analyzing diversity within and among populations and species (eg Wood-Jones 1933–1934, Brothwell 1958, Berry 1963, Berry and Berry 1967, Markowski and Sikorski 1987, Bauchau 1988). Numerous genetical studies on minor variants of the skeleton have been performed by Grüneberg and his co-workers in inbred strains of mice (Grüneberg 1950, 1952, 1955), who showed that these traits are determined by polygenes. The latter produce a continuous variation as to the expression of a non-metric trait, but the ultimate realization of this variation is dependent on whether or not the respective genetic alterations do exceed a particular physiological threshold (Falconer 1960). Generally, results from mouse genetics should not be extrapolated to other mammals or to man without some reservations. However, family and population studies on non-metric variability in humans do support the argument that the variants are inherited in a similar way in mice and men (Berry 1968). The sixties witnessed the formulation

of the main practical and statistical principles for analyzing non-metric variation, and the following advantages of using this technique for assessing variation at the population level were derived: (1) They can be rapidly and easily scored on mammalian skeletons commonly accessible in museum collections. (2) Non-metric variation is not affected by sex and age of the specimens. (3) Non-metric variants are usually not intercorrelated among traits.

The acceptance of the second and especially of the third argument led to the statement that "computation of multivariate statistics is much simpler than it is the case for metrical characters and there are grounds for believing that estimates of divergence between samples based on differences in non-metrical variant incidence more accurately reflect genetical differences than statistics calculated from metrical data" (Berry 1968). Based on this assumption numerous researchers ignored the problem of intercorrelations among traits or considered statistical significance of such observations to be random (eg Truslowe 1961, Berry and Berry 1967, Corruccini *et al.* 1974). Only in the late 1960s and in the 1970s the presence of essential interdependence between non-metric traits as well as sex and age dependence of non-metric variants were pointed out in the course of studies on mammalian and primeval human populations (eg Herzog 1968, Sjøvold 1977). Since that time the value of non-metric traits for population studies has been questioned and, based on data from a limited number of species and populations, problems of intercorrelations, sex dependence and age dependence have been tackled by various authors (eg Finnegan 1972 after Sjøvold 1977, Sjøvold 1977, Cheverud and Buikstra 1982, Dodo and Ishida 1987).

To arrive at more general conclusions about the importance of these phenomena the purpose of the present study is twofold: to examine intercorrelations among non-metric traits in relation to sample sizes of individuals and populations, and to investigate sex and age dependence of non-metric traits within and among populations of various species. Regarding the latter aspect, the relationship between sex dependence of traits and the extent of sexual dimorphism of a species will be emphasized.

Material and methods

A total of 6520 skulls of four mammalian species were studied during the last decade in the course of three different research projects granted to the author (for details see Table 1). For two species of voles [*Microtus oeconomus* (Pallas, 1776), *M. limnophilus* (Büchner, 1889)] and for the roe deer *Capreolus capreolus* (Linnaeus, 1758), data on sex was taken from the records of previous studies (Markowski 1980, 1992, Markowski and Markowska 1988). In the brown hare *Lepus europaeus* (Pallas, 1778), sex determination was performed by inspection of the internal reproductive organs. Age of voles was determined using dry eye lens weight, obliteration of sutures, and development of bone crests following the description by Markowski (1980). Age in roe deer specimens was determined on the basis of the teeth wear (Pielowski 1970). Brown hares were aged exclusively using dry eye lens weight (< 270 mg – juveniles, > 270 mg – adults).

Table 1. Specimens examined in the present study. $n(I)$ – number of individuals studied, $n(P)$ – number of populations studied.

Species	$n(I)$	$n(P)$	Source
<i>Microtus oeconomus</i>	3950	121	Collections of 18 institutions (Markowski 1992)
<i>Microtus oeconomus</i>	2138	1	Northern Poland (Markowski 1978, 1980, J. Markowski and Z. Pucek, in prep.)
<i>Lepus europaeus</i>	279	7	(J. Markowski, unpubl.)
<i>Capreolus capreolus</i>	432	3	(Markowski and Markowska 1988)

Different sets of non-metric traits were used in the respective species. These were described and illustrated previously by Markowski and Markowska (1988) and Markowski (1992). To minimize inter-observer differences in scoring, all the data were collected by myself.

In cases where otherwise bilateral traits occurred only unilaterally the respective specimen was excluded from the analysis. Frequencies of traits within samples were calculated taking into account sex, age and geographic origin of specimens.

Non-metric variants were examined for intercorrelation among traits, for sex dependence and for age dependence using the Pearson correlation coefficient. Associations between non-metric variants and body size (in terms of body mass) were tested by the point-biserial correlation coefficient of Pearson (Sjøvold 1977). For evaluating the relationship between the extent of sexual dimorphism and the frequency of sex dependent non-metric variants the Spearman rank correlation coefficient was used.

Results

Frequencies of correlations among non-metric traits emerging from the data of the present study along with the results of some previous investigations by other authors are given in Table 2. In a number of species the frequency of significant correlations among traits proved to be higher (ie 0.05) than to be expected by chance. However, the maximum correlation coefficients obtained are, on the whole, rather low (Table 2). A detailed analysis of levels of intertrait correlations in relation to sample sizes was carried out using numerous series of *M. oeconomus* skulls. Separately for males and females, correlation coefficients were calculated for random samples with increasing numbers of specimens ($n = 25-800$). Above a sample size of 200 individuals the frequency of statistically significant intercorrelations was always higher than to be expected by chance and still increased with sample size. By contrast, the maximum correlation coefficient noted in particular samples decreased with sample size in both sexes, especially within the range of 25–100 specimens analyzed (Table 3).

Frequencies of significant correlations of non-metric traits with sex, age, and body mass, along with data presented by other authors are given in Table 4. The

Table 2. Frequency (FR) and maximum value (MV) of significant Pearson correlation coefficients among non-metric traits. (** mean that the frequency is significantly greater than 5% at $p < 0.01$). $n(I)$ – sample size of individuals, $n(T)$ – number of traits studied. F – females, M – males.

Species	Sex	$n(I)$	$n(T)$	FR	MV	Source
<i>Microtus oeconomus</i>	F	998	27	14.8**	0.21	J. Markowski and Z. Pucek, in prep.
	M	1140	27	16.5**	0.19	
	F+M	2138	27	22.8**	0.24	
<i>Microtus oeconomus</i>	F	1930	31	13.1**	0.16	Markowski 1992
	M	1604	31	10.1**	0.12	
	F+M	3679	31	16.1**	0.19	
<i>Microtus limnophilus</i>	F	20	23	3.2	0.48	Markowski 1992
	M	17	23	3.6	0.68	
	F+M	39	23	5.1	0.50	
<i>Mus musculus</i>	F+M	851	36	1.1	0.29	Berry and Jakobson 1975
<i>Apodemus agrarius</i>	F+M	254	26	8.9		Sikorski 1982
<i>Lepus europaeus</i>	F		47	6.9	0.30	J. Markowski, unpubl.
	M		47	7.5	0.32	
	F+M	295	47	9.2**	0.27	
<i>Vulpes vulpes</i>	F	1068	19	5.8**	0.12	Sjøvold 1977
	M	1284	19	5.8**	0.08	
	F+M	2352	19	15.8**	0.11	
<i>Lynx lynx</i>	F+M	100	53	7.8**	0.36	Wiig and Andersen 1988
<i>Capreolus capreolus</i>	F+M	369	78	17.5**	0.25	Markowski and Markowska 1988

Table 3. Frequency (FR) and maximum value (MV) of significant Pearson correlation coefficients among non-metric traits in relation to sample size [$n(I)$] in randomly chosen samples of *M. oeconomus*. *, ** mean that the frequency is significantly greater than 5% at $p < 0.05$ and $p < 0.01$, respectively.

$n(I)$	Females		Males	
	FR	MV	FR	MV
25	3.16	0.72	2.37	0.66
50	3.55	0.69	2.63	0.55
100	3.16	0.39	3.55	0.41
200	5.53	0.18	3.95	0.24
400	6.32**	0.20	5.94*	0.15
800	7.90**	0.14	7.11**	0.18

percentage of traits related to sex in the present study was very low and varied between 0 and 4%. In the voles and the brown hare this result was largely the

Table 4. Frequency (FR) of significant Pearson correlation coefficients between non-metric traits and sex (S), age (A), and body mass (B) in various mammalian species. $n(T)$ – number of traits examined. F – females, M – males.

Species	$n(T)$	FR(S)	FR(A)	FR(B)	Source
<i>Microtus oeconomus</i>	27	0	11.0	11.0	J. Markowski and Z. Pucek, in prep.
<i>Microtus oeconomus</i>	31	3.2	F 0 M 0 F, M 0	F 9.7 M 3.2 F, M 6.4	Markowski 1992
<i>Microtus limnophilus</i>	23	0	F, M 0	F, M 0	Markowski 1992
<i>Mus musculus</i>	36	2.8	–	–	Berry and Jakobsen 1975
<i>Apodemus agrarius</i>	26	7.7– 11.5	F, M 19.2	–	Sikorski 1982
<i>Lepus europaeus</i>	47	4.3	F 6.4 M 4.3	F 2.1 M 0	J. Markowski, unpubl.
<i>Vulpes vulpes</i>	19	0–28.6	F 0–10.5 M 5.2–21.0	F 36.8 M 42.1	Sjøvold 1977
<i>Lynx lynx</i>	53	7.5	F, M 15.1	–	Wiig and Andersen 1988
<i>Cystophora cristata</i>	18	27.8	–	–	Wiig and Lie 1984
<i>Capreolus capreolus</i>	78	3.6	F 3.6 M 5.0	F 6.4 M 11.7	Markowski and Markowska 1988

same in both sexes, but in the roe deer the males showed a considerably higher number of sex-correlated traits than the females (Table 4). Condylbasal length for the species studied (Markowski 1980, Wiig and Lie 1984, Wiig and Andersen 1986, and own unpublished data on *Capreolus capreolus* and *Lepus europaeus*) was used for calculating the index of sexual dimorphism according to Storer (1966). This index is the quotient obtained by dividing the mean difference between condylbasal lengths of mature males and females by the sum of the mean values of both sexes. Storer's index was significantly positively correlated with the frequency of traits related to sex ($r_S = 0.79$, $n = 8$, $p < 0.02$). Non-metric traits displayed the highest frequency of correlations with age (0–0.11) and with body mass (0–0.13, Table 4).

Discussion

Only in the first studies on non-metric traits the number of significant associations between traits has been low enough to be due to chance (Truslowe 1961, Berry and Berry 1967, Corruccini 1974, Berry and Jakobsen 1975, Kellock and Parsons 1970). Later a much higher number of significant associations among traits has been reported in several mammalian species (Sjøvold 1977, Sikorski

Table 5. Frequency (FR) of significant Pearson correlation coefficients among non-metric traits in relation to geographical latitude for *M. oeconomicus* samples of similar size [n(I)].

Location	n(I)	FR
Kisbalaton (46°40'N, 17°20'E)	100	2.77
Augustowska Forest (53°22'N, 23°22'E)	100	4.33
Hardangervidda (60°32'N, 7°30'E)	100	5.02
St. Lawrence (63°10'N, 170°30'W)	116	5.53
Ogoturuk Creek (68°04'N, 165°58'W)	97	7.11
Pitmegea (68°55'N, 164°36'W)	86	5.13
Kilpisjärvi (69°03'N, 20°49'W)	101	5.13

1982, Wiig and Andersen 1988, Markowski and Markowska 1988) as well as in human populations (Herzog 1968, Benfer 1970, Corruccini 1974). What are the causes of the increased number of correlations among traits? Sjøvold (1977), who has paid much attention to the problem of interdependence among traits in the red fox *Vulpes vulpes*, stated that significant correlations among traits may be due to genetic or environmental influences, yet the increase of such correlations in pooled samples should be mostly a statistical effect. Sjøvold's hypothesis is corroborated by the data presented in Table 3. Since non-metric traits have a pleiotropic genetic basis (Berry and Berry 1967) intercorrelations among traits may be due to a variety of genetic and environmental influences. *Microtus oeconomicus* with its circumpolar distribution may be a good model to verify the role of environmental influences on the number of intercorrelations among traits. To avoid sample size effects on the number of intercorrelations observed, only populations with more than 80 specimens sampled were considered. In each of three populations with sample sizes higher than 150, a total of 100 individuals were randomly chosen. The results revealed a higher percentage of traits to be correlated in the northernmost population (Table 5). Altogether, the geographic location (in terms of latitude) proved to be strongly positively correlated with the percentage of correlated traits observed ($r_S = 0.82$, $n = 7$, $p < 0.01$), which may be explained by a progressive and more rapid growth of the skull during postnatal development (see below).

A number of other authors have stressed the occurrence of significant correlations among traits belonging to the same topographic and topological group on the skull (Rössing 1982, Molto 1985, Česnys 1988). For example, in analyzing pairwise intercorrelations in 44 cranial non-metric traits on human skulls, Česnys (1988) generally detected both a relatively low frequency of correlations (7.5%), and low correlation coefficients (0.08–0.14). However, traits belonging to the same anatomical type (eg sutures, foramina, fenestrae) displayed correlation coefficients up to 0.30. In contrast, Coopriider *et al.* (1980) attributed at least half of the significant correlations among traits to physiological processes related to ossi-

fication in general. Also cranial deformation is known to have an influence on correlations among metric variables in humans, but its effects on the expression of non-metric traits has not been worked out in detail so far (see Konigsberg *et al.* 1993). In experiments on rats, Pucciarelli (1974) was able to demonstrate that deformation of the skull can increase the frequency of wormian bones. However, since in *M. oeconomus* also the frequency of wormian bones increased gradually from southern to northern populations (Markowski 1992), their occurrence may be due to adaptation as well. Similar results were obtained in *Lynx rufus* (Manville 1959) and in *Dyromys nitedula* (Pucek 1962).

The information available in the literature on relationships between non-metric traits and sex, age, and body size is controversial. The investigation of a considerable number of skeletons of *Mus musculus*, both from wild populations and laboratory strains revealed a correlation with sex in some non-metric traits (Berry and Jakobson 1975). The same was found by Sjøvold (1977), Sikorski (1982), Wiig and Lie (1984), Wiig and Andersen (1988) in some further mammalian species (Table 4). By contrast, Wiig and Lie (1979) did not find any correlation of non-metric traits with sex in the American mink *Mustela vison*, a species introduced to Norway at the beginning of the 1970s. Similar results were obtained by J. Markowski and Z. Pucek (in prep.) for a population of the root vole from Augustowska Forest (north-eastern Poland).

The percentage of traits related to sex in the mammalian species investigated varied within a broad range (0–29%). The same was true for adjacent populations of the same species, (eg in *Apodemus agrarius* – Sikorski 1982, and in *V. vulpes* – Sjøvold 1977) and for races of man. Corruccini (1974) found 31% and 15% of the traits correlated with sex in whites and blacks, respectively. Similarly high values were recorded for populations in Lithuania (Česnys 1982) and Hungary (Finnegan and Marčsik 1979), while estimates were lower for North Americans (4%, Ossenbergs 1976), Australians (8%, Milne *et al.* 1983), and Japanese (9.7%, Mouri 1976). These results made anthropologists believe that non-metric traits are generally related to sex (Perizonius 1979, Milne *et al.* 1983). In further investigations certain traits have been in fact considered typical for males and females, respectively (see Dodo 1974, Mouri 1976).

To avoid mistakes in estimating morphological distances among human populations, Finnegan (1972) after Sjøvold (1977) suggested to use similar numbers of males and females, while Gaherty (1974) recommended a separate treatment of traits related and not related to sex. Cheverud and Buikstra (1982) were rigorous in excluding sex-related traits totally from population analyses, but Ossenbergs (1976), and Dodo and Ishida (1987) stated that such traits do not lead to seriously biased MMDs, and measurements of both sexes may be combined. Irrespective of the concept adopted for calculating MMDs, the presence of sex-related traits remains to be explained. Ossenbergs (1970) emphasized the ethiological subdivision of traits into hypo- and hyperostotic. According to her, hypoostotic traits occur more frequently in females and hyperostotic traits more frequently in males.

However, further investigations on human populations revealed the presence of male and female traits, which were not always congruent with the classification of Ossenberg (Dodo 1974, Mouri 1976). Altogether, due to a comparatively low number of traits correlated with sex and the difficulty of their unequivocal assignment to one of the two ethiological groups Ossenberg's hypothesis could not be verified. Another explanation was presented by Sjøvold (1977). In his opinion the presence of traits related to sex is associated with sexual dimorphism in terms of body size. This hypothesis is strongly supported by the results of the present study and those of other investigations (Sjøvold 1977, Wiig and Andersen 1988).

The percentage of traits related to age and body size in the mammalian species studied so far ranges from 3% in *M. oeconomus* to 42% in *V. vulpes* (see Table 4). Regarding age dependence of traits, studies on human populations yielded a similar result (4% – Corruccini 1974, 2.3% – Česnys and Konduktorova 1982, 50% – Česnys 1988, 62% – Piontek 1985). Age dependence of traits can be explained by changes in the skeletal structure during postnatal development, which are strongly influenced by both pleiotropic genetic effects and environmental factors (see eg Berry 1968, Pucciarelli 1974).

Many foramina (for nerves and blood vessels) appear together with a progressive development of the faciocranium, especially in nasal, maxillary or dental bones. This is supported by the results of Wiig and Andersen (1988), who found altogether 13% of the traits analyzed in *Lynx lynx* correlated with age, but this value decreased to 5.6% when only individuals older than 18 months were considered. Similar results were obtained in our study on populations of *Capreolus capreolus* (Markowski and Markowska 1988) where 3.6% of the traits were age dependent in the total material, but none of these correlations were found in animals older than two years. Based on material from human populations Ossenberg (1970) and Rössing (1982) suggested progressive development to be characteristic for hyperostotic traits and regressive development for hypoostotic ones. But in studies on mammals contradictory results were obtained. In *C. capreolus* and *M. oeconomus* age dependent traits all belonged to the hyperostotic group, while in *L. lynx* foramina of the frontal and orbital region (included to the hyperostotic group) proved to be either positively or negatively correlated with age (Wiig and Andersen 1988).

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