

## Variability of minor tooth traits and allozymic diversity in brown hare *Lepus europaeus* populations

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Two contrasting hypotheses on the relationship between dental character variability and biochemical-genetic diversity: (1) "influence of developmental homeostasis" and (2) "genetic-phenetic variation correlation" were tested in brown hare *Lepus europaeus* Pallas, 1778 populations. Interindividual variability (IV) and fluctuating asymmetry (FA) of 12 non-metrical characters of third lower premolars ( $P_3$ ) as well as allozymic heterozygosity ( $H$ ) at 13 polymorphic loci was examined in 385 individuals from 19 geographical sampling units (GSU) in Austria. Juveniles and adults were discriminated according to dry eye lens weights. Sex was determined from internal reproductive organs. IV was calculated as the mean standard deviation of the 11 tooth characters in each GSU. GSU-specific FA was calculated as the mean FA of individuals ( $FA_{IN}$ ), where  $FA_{IN}$  was the percentage of characters found asymmetric in individuals of a GSU. While IV did not show any significant relationship with  $H$  at the population level, FA of adults was significantly positively correlated ( $r_s = +0.650$ ,  $p < 0.05$ ) with  $H$ . In juveniles a trend ( $r_s = +0.399$ , ns) for such a correlation was apparent too. This finding corresponds to the "genetic-phenetic variation correlation hypothesis". Variability of both character systems is high in populations with high genomic variability, because both character systems concordantly portray gene pool diversity. Both IV and FA was significantly lower in juveniles than in adults. Since no ontogenic changes in  $P_3$  characters were found, this age-specific difference appears to result from selection against juveniles with low  $P_3$  variability (i.e. low genomic diversity). However,  $H$  was not lower in juveniles as compared to adults.

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### Introduction

In leporids, the third lower premolar ( $P_3$ ) exhibits an extensive non-metrical variability in its occlusal surface pattern, with both inter- and intraspecific respect (Dice 1929, Hibbard 1963, Angermann 1966, Suchentrunk *et al.*, in press). The

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polymorphism mainly concerns number, shape and size of enamel folds or lakes visible on the occlusal surface (e.g. Hibbard 1963, Angermann 1966, Thenius 1989). The P<sub>3</sub> has been used widely in classifying fossil leporids specimens (e.g. Sych 1965, Miller and Carranza-Castaneda 1982, Russel and Harris 1986, Popov 1989) and for reconstruction of phylogenetic relationships. Thus, variants of P<sub>3</sub> were treated as indicators of gene pool differentiation (Hibbard 1963, Angermann 1966, Dawson 1981, Corbet 1983).

In Austrian brown hares *Lepus europaeus* Pallas, 1778 the spatial pattern of population divergence according to non-metrical P<sub>3</sub> variants corresponds fairly well to geographical proximity of populations and to patterns of differentiation as revealed through non-metrical skull traits (foramina etc.) and allozymes of the same individuals (Suchentrunk *et al.*, in press). This suggests microphylogenetic variation of the P<sub>3</sub> characters caused by random historical processes rather than by ecogenetic factors (cf e.g. Sokal 1983, Thorpe *et al.* 1991, for theoretical foundations of geographical variation of phenetic characters and character systems). Hence, there is indication for a largely selective neutrality of the P<sub>3</sub> variants. Nevertheless, despite the good concordance of variation of non-metrical traits and proteins among populations, it remains unclear, as to what extent enzyme diversity within single populations is mirrored through variation in the non-metrical character system of the P<sub>3</sub>.

Basically, two contrasting hypotheses on the relationship between morphological and genotypical variability as indicated by enzyme heterozygosity in the wild living hare populations can be put forward: (1) interindividual variability of P<sub>3</sub> characters should be raised in populations with reduced enzyme heterozygosity due to a low capability of growing individuals of buffering against environmental influences that could affect P<sub>3</sub> character expression (i.e. low degree of developmental homeostasis in individuals with raised allozymic homozygosity, cf e.g. Mitton 1978, Soulé 1979, Handford 1980, Fleischer *et al.* 1983). In this case a high level of intraindividual variation (i.e. fluctuating asymmetry – FA; cf Van Valen 1962) should be observed particularly in populations with low average heterozygosities (Zakharov 1981, Mitton and Grant 1984, Allendorf and Leary 1986, Palmer and Strobeck 1986, Futuyma 1990), and (2) interindividual variability of P<sub>3</sub> characters should be high in populations with an elevated level of enzyme heterozygosity because both character systems concordantly portray the general level of genomic diversity: "genetic-phenetic variation correlation". Examples and a discussion on this concept are given in Schnell and Selander (1981). It implies a relatively high heritability of the traits or/and a high number of genes involved in the development of the traits, hence, a largely additive genetic foundation of character variability. In this case intraindividual variation (FA) may be correlated either positively or inversely with enzyme heterozygosity.

However, varying levels of environmental stress among populations, occurring during the juvenile development as well as varying degrees of heterogeneity of habitat conditions among populations (Howe and Parson 1967, Siegel and Doyle

1975, Doyle and Johnston 1976, Perzigian 1977, Sciulli *et al.* 1979, Pankakoski 1985, Larsson and Forslund 1991, Parson 1992) could obscure these fundamental modes of relationship.

The present paper infers whether there is a clear relationship between the variability of the non-metrical P<sub>3</sub> character system and gene pool diversity as indicated through enzymic heterozygosity in free living brown hare populations in Austria while considering both inter- and intraindividual variability.

## Material and methods

### Data collection

This study is based on the morphological analysis of 770 third lower premolars (P<sub>3</sub>) and on horizontal starch gel electrophoresis of 34 enzyme systems encoding for 54 presumptive structural gene loci using liver, kidney, heart and spleen tissue samples of 385 brown hares. The animals were collected at 19 geographical sampling units (GSUs; Fig.1) in Austria between the beginning of October 1988 and the end of December 1988. Sex determination was based on internal reproductive organs. Dry eye lens weight was used for ageing. Juveniles (JV = young of the year) had eye lens weights lower than 275 mg and adults (AD) had higher weights than JVs (Suchentrunk *et al.* 1991). Third lower premolars placed in cleaned mandibles were studied. For the analysis of the P<sub>3</sub> variation 12 non-metrical characters (CH) of the occlusal surface were scored (Table 1) (cf also Angermann 1966, Suchentrunk *et al.*, in press). Scoring of character states was performed on both body sides (right and

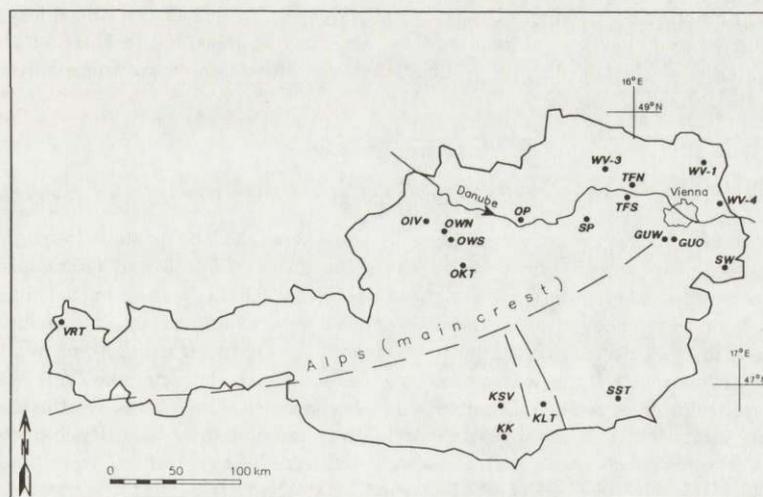


Fig. 1. Location of geographical sampling units (GSUs) of brown hares in Austria. District names are given in parentheses. GB - Gralla (Leibnitz), GUO and GUV - Guntramsdorf (Mödling), KK - Grafenstein and Poggersdorf (Klagenfurt-Umg.), KLT - St. Margarethen/L. (Wolfsberg), KSV - St. Georgen/L. (St.Veit/Gl.), OIV - Wendling (Grieskirchen), OKT - Nußbach (Kirchdorf/Kr.), OP - Naarn (Perg), OVN - Edt, Lambach and Steinerkirchen (Wels-Umg.), OWS - Ried/Trkr. (Kirchdorf/Kr.), SP - Markersdorf and Haindorf (St. Pölten-Umg.), SW - Illmitz (Neusiedl/S.), TFN - Bierbaum and Frauendorf (Tulln), TFS - Rust (Tulln), VRT - Fussach, Höchst and Gaißau (Bregenz), WV-1 - Bullendorf (Mistelbach), WV-3 - Hohenwarth (Tulln), WV-4 - Zwerndorf (Gänserndorf).

Table 1. Non-metrical characters and dichotomized character states (0/1) of the third lower premolar (P<sub>3</sub>) in the brown hare used for analyses of inter- and intraindividual variation.

Current character number	Description of characters and character states
CH1	Mesial reentrant fold (filled with cement): present (1) / absent (0)
CH2	Additional mesial reentrant fold (with cement): present (1) / absent (0)
CH3	Anterior lingual reentrant fold (with cement): present (1) / absent (0)
CH4	Additional anterior lingual reentrant fold (with cement): present (1) / absent (0)
CH5	Posterior external reentrant fold breaking through the lingual enamel wall: yes (1) / no (0)
CH6	Margins of posterior external reentrant fold with an additional fold in its most lingual part; additional fold extends mesiad and/or distad: yes (1) / no (0)
CH7	Both margins of posterior lateral reentrant fold approaching considerably or even touching one another (usually in their central section): yes (1) / no (0)
CH8	Mesial margin of posterior lateral reentrant fold plicate (plication either strong or slight): yes (1) / no (0)
CH9	An enamel lake lingually of posterior lateral reentrant fold: present (1) / absent (0)
CH10	Distal margin of posterior lateral reentrant fold plicate: yes (1) / no (0)
CH11	Distal margin of posterior lateral reentrant fold forming one extra fold in its lateral section: yes (1) / no (0)
CH12	Trigonid with at least one enamel lake: yes (1) / no (0)

left P<sub>3</sub>) in each individual by using a dissecting microscope. The list of iso- and allozymes (electrophoretic characters and character states) used in this study is presented in Hartl *et al.* (1993). For the interpretation of electromorphs and for details on population genetics of these hares see Hartl *et al.* (1993), G. B. Hartl *et al.* (in prep.).

### Statistical analyses

#### Morphology

All analyses of interindividual variability (IV) were conducted using only the right P<sub>3</sub> of each hare. Since a significant association between character states of CH10 and CH11 has been found earlier (Suchentrunk *et al.*, in press), one of these characters (CH11) was omitted from analysis of IV. Occurrence of age-dependence of character states was examined by comparing dry eye lens weights between the two alternative character states for each character using Mann-Whitney *U*-tests. Sex dependence of character states was proved by  $\chi^2$ -tests. In each character the  $IV_{CH}$  was calculated as the standard deviation of the 385 dichotomized (0/1) character state values. On the level of geographical sampling units (GSU) the standard deviation was calculated for each P<sub>3</sub> character using the values of the GSU-specific character states, respectively. In order to obtain an overall index of IV per GSU ( $IV_{GSU}$ ), the standard deviations of all characters but that one of CH11, were averaged in each GSU separately for JV and AD hares. The influence of age class (JV/AD) on  $IV_{GSU}$  was tested using Wilcoxon's signed-rank test. Variation of  $IV_{GSU}$  across the GSUs was tested by Kruskal-Wallis tests based on standard deviations of single CHs separately for JVs and ADs. Dependency of  $IV_{GSU}$  on sample size was examined by Spearman's rank correlation in each of the age classes.

Intraindividual variation (i.e. bilateral asymmetry) of a character occurred whenever the (dichotomized) character states in the right and left P<sub>3</sub> were different. Each of the 12 characters was examined for occurrence of directional asymmetry (cf Palmer and Strobeck 1986) by applying Wilcoxon's signed-rank tests. Since directional asymmetry was detected in CH3, this character was excluded

from subsequent analysis of asymmetry. Thus, asymmetry in all remaining CHs represented fluctuating asymmetry (FA – Van Valen 1962) that is indicative of the level of developmental homeostasis (Palmer and Strobeck 1986). Sex-dependence of FA was proved in each CH by  $\chi^2$ -tests, respectively. Age-dependence of FA was tested in each CH by comparing dry eye lens weights between individuals with bilateral-symmetric and -asymmetric CHs using Mann-Whitney *U*-tests, respectively. Occurrence of pair-wise associations of FA of CHs was examined by conducting  $\chi^2$ -tests and calculating Yule's *Y* indices of association (cf Sjøvold 1977) for all pairs of CHs that filled each cell of the  $2 \times 2$  contingency table with at least five individuals. For each CH its level of FA was calculated as the percentage of individuals with asymmetric character states. The relationship between  $FA_{CH}$  and  $IV_{CH}$  was examined by a Spearman's rank correlation (two-tailed criterion). Overall FA of an individual ( $FA_{IN}$ ) was calculated as the percentage of characters found asymmetric in an individual (Leary *et al.* 1985). In each of the 19 GSUs the average FA ( $FA_{GSU}$ ) was calculated as the arithmetic mean of all  $FA_{IN}$  values. Since  $FA_{CH}$  was strongly depending on the corresponding  $IV_{CH}$  (see results) and frequencies of character states of CH7 varied across the GSUs (Suchentrunk *et al.*, in press) this character was excluded from the calculations of the  $FA_{GSU}$  values.  $FA_{GSU}$  values of JV and AD individuals were checked for significant differences by using a Mann-Whitney *U*-test. In each GSU,  $FA_{GSU}$  was calculated separately for JV and AD hares.  $FA_{GSU}$  values of JV hares were compared with those of ADs by using Wilcoxon's signed-rank test. Since this comparison yielded a significant difference (see results), all subsequent analyses involving  $FA_{GSU}$  were performed separately for each age class. Variation of  $FA_{GSU}$  across the GSUs was tested by using Kruskal-Wallis tests. Dependency of  $FA_{GSU}$  on sample size was tested by a Spearman's rank correlation.

#### Biochemical-genetic data

All calculations concerning biochemical-genetic diversity (enzyme heterozygosity) of the GSUs were based on the electromorphs found in the following 13 polymorphic isozymes: SDH, LDH-2, MDH-2, IDH-2, PGD, HK-2, ES-1, ES-D, PEP-2, ACY-1, ADA-2, ADA-3, and MPI (for the list of complete names of enzymes including monomorphic ones, the corresponding E.C. numbers and for the alleles detected at the polymorphic loci see Hartl *et al.* 1993). In each GSU the average heterozygosity (*H*) was calculated over the 13 polymorphic loci (Hedrick 1985). Variation of *H* across the GSUs and between the age classes (JV/AD) was tested by a two-way-ANOVA of arc-sine-transformed values of individual heterozygosities.

#### Relationships between morphological and biochemical-genetic variability

On the level of GSUs two-tailed Spearman's rank correlations were carried out separately for the two age classes (JV, AD) between  $FA_{GSU}$  and  $IV_{GSU}$ ,  $FA_{GSU}$  and *H*,  $IV_{GSU}$  and *H*.

## Results

The indices of *IV* (standard deviations of character states) and the levels (percentage frequencies) of FA of the P<sub>3</sub> characters are presented in Table 2. The level of  $FA_{CH}$  increased significantly ( $r_s = +0.955$ ,  $df = 10$ ,  $p < 0.01$ ) with  $IV_{CH}$ . Neither age- nor sex-dependence of character states was found in any of the CHs. The same was true for  $FA_{CH}$ . FA of CH7 was positively associated with FA of CH8 (Yule's *Y* = +0.22,  $p < 0.05$ ). On the level of individuals,  $FA_{IN}$  was significantly ( $p < 0.05$ ) higher in AD (mean = 4.5%) than in JV (mean = 3.4%) hares. In concordance,  $FA_{GSU}$  was significantly ( $p < 0.01$ ) higher in ADs than in JVs (Table 3). In neither age class  $FA_{GSU}$  varied significantly across the GSUs.  $IV_{GSU}$  was significantly higher in ADs than in JVs of the corresponding GSU ( $p < 0.05$ ,

Table 2. Interindividual ( $IV_{CH}$ ) and intraindividual variation (i.e. level of fluctuating asymmetry,  $FA_{CH}$ ) of 12 characters of the third lower premolar ( $P_3$ ) of 385 brown hares. The calculation of  $IV_{CH}$  is based on right teeth only. For description of characters and character states see Table 1 (cf also Angermann 1966, Suchentrunk *et al.*, in press). The IV of CH11 and the FA of CH3 have not been considered (cf material and methods).

Character	$IV_{CH}$	$FA_{CH}$	Character	$IV_{CH}$	$FA_{CH}$
CH1	0.124	3.9	CH7	0.430	10.1
CH2	0.113	1.8	CH8	0.382	10.7
CH3	0.471	–	CH9	0.113	1.0
CH4	0.072	1.6	CH10	0.211	4.2
CH5	0.222	4.7	CH11	–	4.2
CH6	0.309	5.7	CH12	0.206	3.6

Table 3. Overall interindividual variability ( $IV_{GSU}$ ) and average fluctuating asymmetry ( $FA_{GSU}$ ) of the third lower premolar ( $P_3$ ) and average observed heterozygosity ( $H$ ) in geographical sampling units (GSU) of Austrian brown hares.  $n$  – sample number, JV – juveniles, AD – adults (according to dry eye lens weights). For locations of GSUs see Fig. 1.

GSU	$n$		$IV_{GSU}$		$FA_{GSU}$		$H$	
	JV	AD	JV	AD	JV	AD	JV	AD
WV-1	11	8	0.047	0.143	2.0	1.25	0.139	0.154
WV-3	13	5	0.138	0.264	0.0	2.0	0.148	0.154
WV-4	8	4	0.127	0.189	3.75	3.33	0.25	0.058
TFN	16	12	0.166	0.249	2.67	7.0	0.149	0.167
TFS	17	0	0.208	–	5.63	–	0.158	–
GUW	12	4	0.109	0.196	2.5	2.5	0.154	0.205
GUO	11	1	0.164	–	4.17	–	0.185	–
SW	2	11	0.129	0.209	0.0	0.8	0.192	0.185
SP	10	14	0.106	0.186	3.0	4.3	0.182	0.182
OP	9	2	0.211	0.065	5.0	0.0	0.146	0.188
OIV	5	11	0.182	0.115	2.0	7.27	0.159	0.215
OWN	18	9	0.141	0.199	3.89	8.89	0.215	0.228
OWS	8	0	0.137	–	5.0	–	0.196	–
OKT	2	3	0.065	0.210	1.0	0.0	0.269	0.277
VRT	3	4	0.0	0.100	0.0	2.5	0.239	0.205
KLT	15	10	0.282	0.283	5.0	7.0	0.19	0.154
KK	5	7	0.182	0.216	2.0	2.86	0.169	0.154
KSV	4	6	0.196	0.306	2.5	3.33	0.215	0.176
GB	7	5	0.251	0.223	4.29	6.0	0.189	0.257

two-tailed criterion). In both age classes  $IV_{GSU}$  did not vary significantly across the GSUs. While no significant correlation between sample size and  $IV_{GSU}$  was found,  $FA_{GSU}$  was positively correlated (two-tailed criterion) with sample size, both in JVs ( $r_s = +0.519$ ,  $p < 0.05$ ) and ADs ( $r_s = +0.584$ ,  $p < 0.05$ ). In order to

Table 4. Spearman's rank correlation coefficients (two-tailed criterion) for relationships between overall interindividual variability ( $IV_{GSU}$ ), average fluctuating asymmetry ( $FA_{GSU}$ ) of the P<sub>3</sub>, and average observed heterozygosity ( $H$ ) of geographical sampling units (GSU). \* – significance at  $p < 0.05$ , ns – not significant. Correlation coefficients are given separately for juvenile (JV) and adult (AD) hares. Calculations are based on GSUs with a minimum sample size of five individuals (see Table 3).

	$IV_{GSU}$	$FA_{GSU}$
$H_{JV}$	+ 0.098 ns	+0.399 ns
$H_{AD}$	- 0.319 ns	+ 0.650*

account for these dependencies all Spearman's rank correlations with  $H$  were based on GSUs with a minimum sample number of five individuals. This is a compromise between saving a reasonable number of GSUs for correlation analyses with  $H$  values and obtaining reliable indicators of morphological variability. Thereby, no significant correlation between morphological variability and sample size was found. When using this criterion for minimum individual numbers per GSU, no significant correlation between  $IV_{GSU}$  and  $FA_{GSU}$  was detected. However, as already found for the complete data set,  $FA_{GSU}$  ( $n = 9$ GSUs) again was significantly higher in ADs than in JVs.

Polymorphism was detected in 14 electrophoretical loci. However, variability in  $\beta$ -GAL was not considered presently because of the presumptive occurrence of a 0-allele (Hartl *et al.* 1993). Average observed heterozygosities ( $H$ ) varied significantly ( $p < 0.05$ ) across GSUs (see also Table 3) but did not differ between the two age classes. In addition, regarding variation of  $H$  there was no significant two-way interaction factor of age class and GSU.  $IV_{GSU}$ - and  $FA_{GSU}$ -values are listed in Table 3 for each of the 19 GSUs together with the corresponding  $H$  values. Spearman's rank correlation coefficients between  $IV_{GSU}$ ,  $FA_{GSU}$  and  $H$  are presented in Table 4, separately for JV and AD hares based on calculations involving only GSUs with a minimum sample size of five individuals.

### Discussion

In the brown hare populations, which apparently have not been subjected to recent genetical bottlenecks (G. B. Hartl *et al.*, in prep.), interindividual variability (IV) of the specific morphological system of non-metrical P<sub>3</sub> traits does not covary significantly with genomic diversity as indicated by electrophoretically detectable protein variants. This is in accordance with findings concerning the relationship between IV in non-metrical skull traits and enzyme heterozygosity of the same hare populations (Hartl *et al.* 1993) and some other studies in poikilothermic or homeothermic vertebrates using either metric or meristic characters (e.g. Handford 1980, McAndrew *et al.* 1982, Kieser and Groeneveld 1991). However, in

various vertebrate species a negative association between IV in morphological characters and enzyme heterozygosity was detected (e.g. Mitton 1978, Fleischer *et al.* 1983, Yezerinac *et al.* 1992). The latter findings have been interpreted mostly as evidence for the negative influence of reduced levels of enzyme heterozygosity on developmental stability leading towards an enhanced probability of departures of morphological characters from the genetically determined "normal" expression through the impact of internal or environmental stressors (e.g. Mitton and Grant 1984). In this context an inverse relationship is expected to become particularly apparent if intraindividual variability (fluctuating asymmetry) is studied (e.g. Zakharov 1981, Allendorf and Leary 1986, Palmer and Strobeck 1986, G. B. Hartl *et al.*, in prep.).

Though fluctuating asymmetry (FA) does occur in the P<sub>3</sub> character system of brown hares it is generally of very low extent (Table 2) as compared to the level of FA in non-metrical skull traits of the same individuals (G. B. Hartl *et al.*, prep.). This could indicate a relatively high level of developmental stability in the P<sub>3</sub> character system. Among others, Leary *et al.* (1983, 1985) argued that an inverse relationship between FA and enzyme heterozygosity should become apparent particularly in traits with little functional constraints. Nevertheless, although the P<sub>3</sub> variants have a low level of FA, they are considered as largely selectively neutral (Suchentrunk *et al.*, in press, see also introduction). Contrary to the positive correlation between FA and enzymic heterozygosity found presently, FA in non-metrical skull traits of the same individuals did covary inversely with allozymic heterozygosity at the population level (G. B. Hartl *et al.*, in prep.). Hence, reduced developmental homeostasis appears to exert a negative effect on bilateral symmetry of the brown hare skull in the course of ontogenic development. But it does not increase non-metrical FA in the investigated cheek teeth. This demonstrates that increased FA due to low allozymic heterozygosity is not necessarily a phenomenon that affects all morphological systems in the brown hare.

The positive correlation between FA and allozymic heterozygosity in AD hares (and the same trend in juveniles) could indicate that increased allelic variation at loci of the polygenic system that is responsible for the expression of the P<sub>3</sub> characters enhances variation in liabilities of the right and left P<sub>3</sub> traits (for further details on the concept of liability and thresholds of polygenic all-or-none traits cf e.g. Nicholas 1987). This allelic hypothesis receives support from a separate data set (F. Suchentrunk, unpubl.) consisting of 257 brown hare skulls from seven Polish populations, which produced a significant positive correlation ( $r_s = +0.793$ ,  $n = 7$ ,  $p < 0.05$ , one-tailed criterion) between IV in the same P<sub>3</sub> traits and allozymic heterozygosity as calculated from variation at 39 loci (cf Hartl *et al.* 1992). Likewise, variability in root patterns of upper molars in an inbred strain of rats *Rattus norvegicus* was reduced in successive generations whereas outbred rats maintained a comparatively high variability (Matthies and Richter 1980). Similar results were reported for the metrical variability in mandibles in inbred and outbred strains of mice *Mus musculus* by Festing (1976). However, while

giving an allelic interpretation of the positive relationship between FA and heterozygosity, one should also expect this correlation between IV and heterozygosity. The lack of such a correlation in the present study could be due to relatively higher errors of estimation of *IVGSU* at relatively low variation of *IVGSU* across populations (CV for JVs = 36.5, *n* = 15 GSUs, CV for ADs = 26.3, *n* = 11 GSUs) as compared to errors of estimation of *FAGSU* which, in turn, show relatively higher variation across populations (CV for JVs = 45.5, *n* = 15 GSUs, and CV for ADs = 59.9, *n* = 11 GSUs). This could conceal an existing relationship. Furthermore, *IVGSU* of P<sub>3</sub> traits could be more susceptible to environmental stressors (cf e.g. Larsson and Forslund 1991) than *FAGSU*, which could also obscure a positive relationship.

Unequivocally, variability in the P<sub>3</sub> character system turned out to be higher in AD hares than in JVs. This age-difference concerns both IV and FA. Regarding FA it is apparent both at the individual and the population level. Since no significant changes in the course of the ontogenic development were detected in character states (cf also Angermann 1966) the raised level of P<sub>3</sub> variability can be interpreted as resulting from selection against low P<sub>3</sub> variability in JV hares. Taking into account the allelic interpretation of the positive relationship between the P<sub>3</sub> variants and heterozygosity given above, the age-difference could indicate a better survival of individuals with a somewhat increased genomic diversity (as mirrored through high FA in P<sub>3</sub> characters). Contrary to this, higher levels of FA in adults could result from a longer lasting impact of environmental stressors on this continuously growing cheek tooth. This interpretation could be given provided there was some indication for a general positive (though not significant) relationship between FA and age class in single P<sub>3</sub> characters. Since this was not the case the selection hypothesis is favoured.

Partly in contradiction to the allelic interpretation of the positive correlation between FA and enzyme heterozygosity, the strong association of right and left P<sub>3</sub> traits in individuals (Suchentrunk *et al.*, in press), which is also indicated through the generally low levels of FA of single characters (Table 2), suggests some common genomic factor for a coupled expression of the same variants on both body sides. Similarly, the exact bilateral symmetric manifestation of a particular P<sub>3</sub> anomaly which affects the whole tooth in some Polish brown hares (Suchentrunk and Markowski 1992) could be caused by a major gene that is responsible for correct bilateral expression. Furthermore, the inverse relationship between IV in non-metrical skull traits and coefficients of inbreeding in the presently investigated hare populations (Hartl *et al.* 1993) represents another contrasting argument to the allelic interpretation given above. Thus, further studies on the heritability of the P<sub>3</sub> traits and on the relationship between FA, IV and coefficients of inbreeding in hares are necessary to clarify these ambiguous results.

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