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GENETIC VARIABILITY AND DIFFERENTIATION IN WILD BOARS SUS-SCROFA-FERUS L.
COMPARISON OF ISOLATED POPULATIONS

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GENETIC VARIABILITY AND DIFFERENTIATION IN WILD BOARS (*SUS SCROFA FERUS* L.): COMPARISON OF ISOLATED POPULATIONS

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ABSTRACT.—Wild boars (*Sus scrofa ferus* L.) from four populations in Austria and their domestic descendant (*Sus scrofa domestica*) were examined for isoenzyme variability at 42 to 52 enzyme loci by means of horizontal starch gel electrophoresis. The wild boar samples were polymorphic at 22% of their loci and had an average heterozygosity of 0.031, which is among the highest values observed in large mammals. The domestic pigs were polymorphic at 14.6% of their loci and had an average heterozygosity of 0.062. The comparatively high values of average genetic distance found between the isolated wild boar populations ($\bar{D} = 0.0045$) may be the result of founder effects and genetic drift caused by wildlife management.

The last two decades have witnessed a tremendous increase in data on genetic variability of a great variety of species. Most of this research has focused on rather small animals, such as insects or rodents (Nevo, 1975; Selander, 1976; Selander and Kaufman, 1973). Studies on large mammals have been restricted to rather few species (see Baccus et al., 1953, and Hartl, 1983, for review). Increasing artificial alteration of landscape and intensive wildlife management may serve as potential forces for genetic change within populations of these species.

In wild boars (*Sus scrofa ferus* L.) human influences on population structures and sizes are especially high. Many populations were established artificially with a small number of founder individuals, sometimes from very different geographic origins. Furthermore during their development these populations were kept completely isolated in game parks or lattices, where population size is drastically reduced by hunting every year. Thus, genetic founder effects and a loss of genetic variability by random genetic drift are to be expected. To get a first insight into the genetic structure of isolated wild boar populations we investigated four populations from eastern Austria with different histories and individual numbers.

MATERIALS AND METHODS

Samples of liver, kidney, spleen, and muscle of 145 wild boars were collected by local hunters during the hunting season of 1983-1984. Specimens originated from four different populations in Lower Austria and the Burgenland (game park of Lainz, SW border of Vienna; Gaaden, 15 km S Lainz; Fischamend, 20 km E Vienna; Eisenstadt, 50 km SE Vienna).

The population at Lainz was founded nearly 200 years ago by fencing a small number of individuals resident in the locality. As far as it is known by the estate management the population has developed without any further immigration. At present the population consists of approximately 600 individuals, but population size, as in all other populations studied, is reduced to nearly one-half every year by hunting ($n = 26$, 15 males and 15 females). The population at the game park of Eisenstadt was founded several decades ago again by fencing a small number of autochthonous individuals. After World War II, however, the wild boars were damaged for about 10 years. Estate management reported that wild-living wild boars immigrated into the game park during that time; present population size is about 300 individuals ($n = 53$, 29 males and 24 females). The population at Gaaden was founded only ten years ago. The number of founder individuals did not exceed 50 animals; present population size is about 150 ($n = 14$, 5 males and 9 females). The population at Fischamend also was founded within the last decade, but besides autochthonous individuals it also contains individuals from Hungary and Czechoslovakia. It is the only population examined which can be designated as mixed breed. The present population size is about 300 individuals ($n = 52$, 30 males and 22 females). For comparison seven specimens of domestic pig (mixed breed, German Edelschwein Landrace $\times$ Pirates) were screened. The pigs are from the same farm, but their degree of relationship was not known.

Tissues were frozen to -20°C by the hunters and sent to the laboratory together with information on sex, age, carcass weight, and condition of the specimen. Prior to electrophoresis, tissue extracts were prepared as described previously (Csaikl et al., 1980) using an Ultra Turrax TP 18-10. If not stated otherwise, liver and kidney were used for screening all enzymes. From a variety of buffer systems tested, four were found best for fast and effective screening of isoenzymes in wild boars: phosphate buffer (buffer system I) and a tris-malate buffer (buffer system II), both described in Csaikl et al. (1980), a tris-citrate buffer (buffer system III) described in Manlove et al. (1975), and a discontinuous histidine-sodium citrate buffer (buffer system IV) according to Brewer and Sing (1970). After electrophoresis gels were sliced and stained for: ADH, α -GPDH, SDH, LDH, MDH, ME, IDH, 6-PGD, G-6-PD, SOD, AAT, PGM, ADA, and GPI according to standard methods (see Csaikl et al., 1980); GDH and ACON according to Harris and Hopkinson (1976); XDH according to Selander et al. (1971); ACP, ES, HK, and CK according to Shaw and Prasad (1970); AK, MPI, and FH according to Siciliano and Shaw (1976); PEP according to Siciliano and Shaw (1976); using L-leucyl-L-alanine as substrate; GLUD and CAT according to Brewer and Sing (1970); and ACY-1 according to Qavi and Kit (1980). Genetic interpretation of electrophoretic patterns was based on principles described by Harris (1980) and Harris and Hopkinson (1976). Furthermore the list of enzyme quaternary structures published by Darnall and Klotz (1975) was used for interpretation of heterozygote banding patterns. Results were compared to homozygotes and heterozygotes of inbred strains of *M. musculus*. Loci and allele designations are according to Lyon (1977) and Staats (1980). The most common allele in wild boars of Eisenstadt was designated arbitrarily *a*.

RESULTS

The enzymes studied as well as the loci and alleles found are listed in Table 1. Screening of 28 enzyme systems representing 52 genetic loci revealed polymorphism in 12 isoenzymes: ME-1, 6-PGD, G-6-PD, PGM-2, PGM-3, ES-7, ES-8, ACP-2, PEP-1, ADA-1, and GPI-1. CAT and ES-4 seemed to be polymorphic as well, but it was impossible to score allelic frequencies. The electrophoretic banding patterns in wild boars and domestic pigs will be described in detail elsewhere. The frequency of the most common allele and heterozygosity at all polymorphic loci are given in Table 2. From the four populations studied, highest variability was found in Eisenstadt ($\bar{P}$, proportion of polymorphic loci, = 0.140, $\bar{H}$, average heterozygosity, = 0.050). Intermediate variability was found in Gaaden ($\bar{P}$ = 0.120, $\bar{H}$ = 0.035) and low variability in Fischamend ($\bar{P}$ = 0.080, $\bar{H}$ = 0.018) and Lainz ($\bar{P}$ = 0.060, $\bar{H}$ = 0.015). One polymorphism is shared by all populations (PGM-2), others by two or three of them (ME-1, ES-7, ES-8, PEP-1, ADA-1, and GPI-1). One variant, however, was found exclusively in Gaaden (G-6-PD). The loci for G-6-PD, PGM-2, ES-7, and GPI-1 segregated for the same variant alleles both in wild boars and domestic pigs. In the latter a $\bar{P}$ -value of 0.0143 and a $\bar{H}$ -value of 0.050 could be calculated from the data. In 6-PGD and ACP, variants were found exclusively in domestic pigs. In all monomorphic enzymes no difference in electrophoretic mobility of isoenzymes could be detected between wild boars and domestic pigs.

Based on 42 loci, average genetic identity ($\bar{I}$) and genetic distance ($\bar{D}$) between the wild boar populations and between wild boars and domestic pigs, respectively, was calculated according to Nei (1975). Detailed values are given in Table 3. The average $\bar{I}$ of wild boar populations was 0.9955 (± 0.0010); average $\bar{I}$ of wild boars and domestic pigs was 0.9748 (± 0.0011). Average $\bar{D}$ between wild boar populations was 0.0045 (± 0.0011), whereas that between wild boars and domestic pigs was 0.0255 (± 0.0042). A dendrogram (Fig. 1) constructed according to Nei (1975) shows genetic similarity among wild boar populations in relation to geographic distance.

DISCUSSION

Few studies on the biochemical genetics of wild boars have been reported, and those were mostly restricted to one or a few loci (Glasnak et al., 1976; Skladanowski et al., 1979; Steinmann, 1976; Tanaka et al., 1980). However, for a detailed genetic analysis of population structure a large and randomly chosen sample of loci must be examined (Lewontin, 1974; Nei, 1978; Nei and Roychoudhury, 1972). As pointed out by Gorman and Renzi (1979), investigations give better information if restricted in sample size rather than in loci number. In their study on genetic variation in pigs, Smith et al. (1980) found only minor genetic variation in a small

TABLE 1.—List of enzymes, number of genetic loci and alleles found in wild boars (WB) and domestic pigs, (DP) and buffer systems routinely used for screening; n.s. = not studied; EI = Eisenstadt, F = Fischamend, LA = Lainz, GA = Gaaden.

E.C. number	Enzyme name (abbreviation)	Loci	Alleles found					B. f. system
			WB					
			EI	GA	FI	LA	DP	
1.1.1.1	alcohol dehydrogenase (ADH)	1	a	a	a	a	a	IV
		2	a	a	a	a	a	
1.1.1.8	α -glycerophosphate dehydrogenase (α -GPDH)	1	a	a	a	a	a	II
		2	a	a	a	a	a	
1.1.1.14	sorbitol dehydrogenase (SDH)	1	a	a	a	a	a	II
1.1.1.27	lactate dehydrogenase (LDH)	1	a	a	a	a	a	I
		2	a	a	a	a	a	
1.1.1.37	malate dehydrogenase (MDH)	1	a	a	a	a	a	II
		2	a	a	a	a	a	
1.1.1.40	malic enzyme (ME)	1	a/b	a	a/b	a	a	II
		2	a	a	a	a	a	
1.1.1.42	isocitrate dehydrogenase (IDH)	1	a	a	a	a	a	II
		2	a	a	a	a	a	
1.1.1.44	6-phosphogluconate dehydrogenase (6-PGD)	1	a	a	a	a	a/b	I
1.1.1.47	glucose dehydrogenase (GDH)	1	a	a	a	a	a	II
1.1.1.49	glucose-6-phosphate dehydrogenase (G-6-PD)	1	a	a/b	a	a	a/b	I
1.2.3.2	xanthine dehydrogenase (XDH)	1	a	a	a	a/b	a	II
1.4.1.3	glutamate dehydrogenase (GLUD)	1	a	a	a	a	a	II
1.11.1.6	catalase (CAT)	1	unscorable					I
1.15.1.1	superoxide dismutase (SOD)	1	a	a	a	a	a	I
		2	a	a	a	a	a	
2.6.1.1	aspartate amino-transferase (AAT)	1	a	a	a	a	a	I
		2	a	a	a	a	a	
2.7.1.1	hexokinase (HK)	1	a	a	a	a	n.s.	I
2.7.3.2	creatine kinase (CK)	1	a	a	a	a	n.s.	I
2.7.4.3	adenylate kinase (AK)	1	a	a	a	a	a	I
		2	a	a	a	a	a	
2.7.5.1	phosphoglucomutase (PGM)	1	a	a	a	a	a	I
		2	a/b	a/b	a/b	a/b	a/b	
		3	a	a	a/b	a	a	
3.1.1.1	esterases (ES)	1,2,3,5,6	a	a	a	a	a	I
		4	unscorable					
		7	a/b	a/b	a	a	a/b	
		8	a/b	a/b	a	a	a	
3.1.3.2	acid phosphatase (ACP)	1	a	a	a	a	a	I
		2	a	a	a	a	a/b	
3.4.11	peptidases (PEP)	1	a/b	a/b	a	a	n.s.	I
		2,3	a	a	a	a	n.s.	
3.5.1.14	aminoacylase-1 (ACY-1)	1	a	a	a	a	n.s.	I
3.5.4.4	adenosine deaminase (ADA)	1	a/b	a/b	a	a/b	a	I
		2	a	a	a	a	a	
4.2.1.2	fumarate hydratase (FH)	1	a	a	a	a	n.s.	I
4.2.1.3	aconitase (ACON)	1,2	a	a	a	a	a	I
5.3.1.8	mannose-6-phosphate isomerase (MPI)	1	a	a	a	a	a	I
5.3.1.9	glucosephosphate isomerase (GPI)	1	a/b	a	a/b	a/b	a/b	I
		2	a	a	a	a	a	

TABLE 2.—Genetic variability in wild boars and domestic pigs. Abbreviations: p = frequency of the most common allele of WBEI. H = observed heterozygosity, E = Hardy-Weinberg Equilibrium (level of significance of deviations from expected heterozygosity); $\bar{P}$ = proportion of polymorphic loci (99% criterion); H_o = observed average heterozygosity; n = sample size, L = number of loci scored.

Enzyme locus	Eisenstadt $n = 53$				Gaaden $n = 14$				Fischamend $n = 52$			
	p	H	E	n	p	H	E	n	p	H_o	E	n
Me-1	0.855	0.207	+	53	1.0	0.0		14	0.980	0.035	+	52
6-Pgd	1.0	0.0		53	1.0	0.0		14	1.0	0.0		52
G-6-pd	1.0	0.0		53	0.821	0.357	+	14	1.0	0.0		52
Xdh	1.0	0.0		53	1.0	0.0		14	1.0	0.0		52
Pgm-2	0.538	0.500	+	52	0.857	0.142	+	14	0.585	0.531	+	47
Pgm-3	1.0	0.0		52	1.0	0.0		14	0.877	0.204	+	49
Es-7	0.857	0.285	+	14	0.892	0.214	+	14	1.0	0.0		52
Es-8	0.750	0.500	+	14	0.755	0.420	+	14	1.0	0.0		52
Acp-2	1.0	0.0		53	1.0	0.0		14	1.0	0.0		52
Pep-1	0.673	0.461	+	52	0.535	0.642	+	14	1.0	0.0		52
Ada-1	0.692	0.576	— (**)	52	0.892	0.214	+	14	1.0	0.0		52
Gpi-1	0.839	0.320	+	53	1.0	0.0		14	0.923	0.153	+	52
$L = 50$	$\bar{P} = 0.140$	$H_o = 0.050$			$\bar{P} = 0.120$	$H_o = 0.035$			$\bar{P} = 0.080$	$H_o = 0.015$		

Enzyme locus	Lainz $n = 26$				All populations $n = 145$				E
	p	H	E	n	p	$\bar{p}$	H_o	$\bar{H}_o$	
Me-1	1.0	0.0		26	0.959	0.0035	0.061	0.0073	— (**)
6-Pgd	1.0	0.0		26	1.0	0.0	0.0	0.0	
G-6-pd	1.0	0.0		26	0.955	0.0060	0.059	0.0238	+
Pgm-2	0.840	0.320	+	26	0.705	0.0209	0.373	0.0243	+
Pgm-3	1.0	0.0		26	0.969	0.00025	0.051	0.0075	+
Es-7	1.0	0.0		26	0.973	0.0040	0.124	0.0162	+
Es-8	1.0	0.0		26	0.883	0.0136	0.230	0.0537	+
Acp-2	1.0	0.0		26	1.0	0.0	0.0	0.0	
Pep-1	1.0	0.0		26	0.802	0.0415	0.275	0.0801	+
Ada-1	0.740	0.250	+	26	0.831	0.0149	0.267	0.0424	+
Gpi-1	0.960	0.0	+	26	0.930	0.0035	0.118	0.0174	+
$L = 50$	$\bar{P} = 0.060$	$H_o = 0.015$			$\bar{P} = 0.150$		$H_o = 0.032$		

Enzyme locus	Domestic pigs $n = 7$			
	p	H	E	n
Me-1	1.0	0.0		7
6-Pgd	0.286	0.571	+	7
G-6-pd	0.500	1.0	— (**)	7
Pgm-2	0.928	0.142	+	7
Pgm-3	1.0	0.0		7
Es-7	0.714	0.0	— (**)	7
Es-8	1.0	0.0		7
Acp-2	0.714	0.571	+	7
Pep-1	not studied			
Ada-1	1.0	0.0		7
Gpi-1	0.857	0.285	+	7
$L = 42$	$\bar{P} = 0.143$	$H_o = 0.050$		

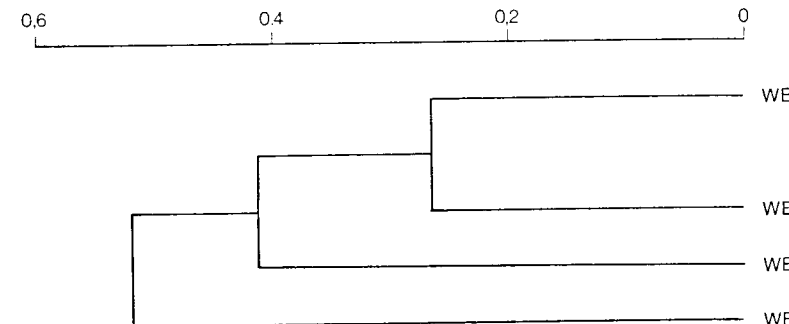
sample of European wild boars inhabiting the Great Smoky Mountains National Park (USA). Based on an investigation of 15 genetic loci they calculated a $\bar{P}$ -value of 0.067 and an H_o -value of 0.012. These authors also hypothesized that European wild boars might be characterized by "average or lower than average genetic variability" (Smith et al., 1980). Our results, based on the study of 52 loci (50 loci scored) screened in four different populations of European wild boars, indicate that this is not the case. Averaged over all populations we got a $\bar{P}$ -value of 0.105

TABLE 3.—Genetic identity ($\bar{I}$)—above the diagonal—and genetic distance ($\bar{D}$)—below the diagonal—between the wild boar populations studied and wild boars and domestic pigs, respectively.

	WBEI	WBCA	WBLA	WBF1	DP
WBEI	—	0.9945	0.9949	0.9947	0.9701
WBCA	0.0055	—	0.9972	0.9952	0.9800
WBLA	0.0051	0.0025	—	0.9964	0.9753
WBF1	0.0053	0.0048	0.0036	—	0.9739
DP	0.0303	0.0202	0.0250	0.0264	—

and an H_o -value of 0.031. These values are somewhat higher than those for red deer (Gyllen et al., 1983) and Scandinavian moose (Ryman et al., 1980), the most extensively studied large mammals in Europe, and similar to those given by Baccus et al. (1983) for large mammals for mammals in general. Furthermore the variability found in averaging $\bar{P}$ and $\bar{H}$ over all v

GENETIC DISTANCE



GEOGRAPHIC DISTANCE

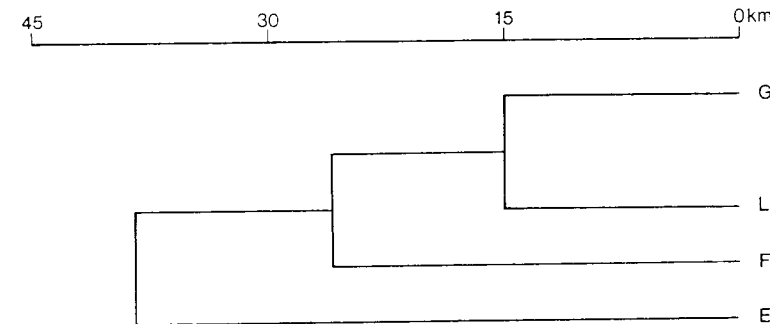


FIG. 1.—Genetic similarity between the wild boar populations studied in relation to geographic distance. The dendrograms are constructed according to Nei (1975). The values of genetic distance ($100 \times \bar{D}$) calculated over 42 loci. WB = wild boars. EI = Eisenstadt, GA = Gaaden, LA = Lainz, FI = Fischamend.

boar populations studied is an underestimate of the total variability of the species. Recall that all populations investigated were founded by fencing a small number of wild-living individuals from a relatively small geographic area. Therefore it seems likely that all polymorphisms detected are present within the natural population and the comparatively large genetic diversity between the artificial populations is due to a loss of genetic variability by genetic founder effects and the heavy hunting pressure in the absence of gene flow. However, because of the close similarity of genetic and geographic distance (Fig. 1) the possibility of a cline in allelic frequencies within the natural population must be considered.

To have reliable values for comparisons with other large mammals we would prefer to estimate $\bar{P}$ for *Sus scrofa ferus* by summing up all polymorphic loci over all populations. This calculation gives higher values than averaging the $\bar{P}$ -values found from each population and gives in our opinion a better estimation of the genetic variability of this species in our region. If in wild boars all polymorphic loci are considered (and even 6-PGD is assumed to be polymorphic in this species according to Steinmann, 1976) the $\bar{P}$ -value rises to 0.200. In all studies on large mammals, a different number of loci (15 up to 42) was screened. According to several authors (see Nevo, 1953; Selander, 1976; Ward, 1977; Zouros and Hertz, 1984, for reviews) there are differences in the extent of polymorphism between enzymes of different structure, metabolic function, or substrate specificity. For comparison of genetic variability only enzymes should be considered which have been studied simultaneously in all populations or species (Baccus et al., 1983). The most variable species in their study was the white-tailed deer ($\bar{P} = 0.355$, $\bar{H} = 0.074$). Variability in all other species was far below this level. If we take the same set of enzymes (albumin data were taken from Steinmann, 1976) for our study, $\bar{P}$ of wild boars rises to 0.269 and $\bar{H}$ to 0.049. Ignoring the fact that polymorphic loci may not be exactly the same in all studies because of a different nomenclature for the multilocus enzymes ES, ME, GPI, PGM, and PEP, *Sus scrofa* is one of the most variable of large mammals yet studied, this result is in good agreement with the remarkable morphological plasticity of wild boars throughout Europe (Herre, pers. comm.). High genetic variability may have been a prerequisite for successful domestication of this species.

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