Genetic structures and clinal variation of European red deer Cervus elaphus populations for two polymorphic gene loci

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SHORT COMMUNICATION

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Genetic structures and clinal variation of European red deer *Cervus elaphus* populations for two polymorphic gene loci

Sven Herzog & Thomas Gehle

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A study of nine enzyme systems in liver and kidney samples of red deer *Cervus elaphus* from three sites in North Germany and reanalysed allelic structures at two polymorphic gene loci (IDH, SOD) from eight sites in Germany, Scotland, France, Austria and Hungary (a total of 1,252 animals) have revealed two opposite genetic profiles. For IDH the presence of a biallelic major polymorphism is suggested, and for SOD a biallelic minor polymorphism. It is assumed that the three North German red deer populations at Harz, Lüneburger Heide and Solling descend from one former population. The comparison of the allelic structures at the SOD gene locus of German, French, Austrian and Hungarian red deer populations provides evidence for a clinal decrease of this rare allele from north to south as well as an analogous clinal differentiation within the populations. For the gene locus IDH the selection model of overdominance is probable, due to the viability advantage of heterozygote calves previously discovered by other researchers. The allelic distances found between the three collectives of North Germany approximately correspond to the geographical distance.

Key words: Cervus elaphus, clinal variation, genetic profiles, overdominance, red deer, wildlife management

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Due to densely populated landscapes and different hunting policies of different countries red deer *Cervus elaphus* habitats have been lost or fragmented in the past. This has led to a situation of several, partly isolated populations, concentrated on suboptimal forest habitats. To estimate the impact of this situation on genetic structures of populations of this large grazing mammal, we assess the genetic status of some populations on the basis

of a genetic inventory, and include the results of major previous studies in our study (Herzog 1988a,b, Pemberton, Albon, Guinness, Clutton-Brock & Berry 1988, Hartl, Willing, Lang, Klein & Köller 1990, Herzog 1991a, Herzog, Mushövel, Hattemer & Herzog 1991, Ströhlein, Lewalski, Hecht & Herzog 1991, Gehle & Herzog 1994).

Material and methods

Liver and kidney samples from a total of 136 red deer originating from three geographically isolated German populations at Harz (50), Lüneburger Heide (50) and Solling (36) were studied by means of starch gel electrophoresis in order to analyse genetic variation. All samples were taken during routine hunting, and were frozen immediately for transport at -20°C and stored at -60°C until further processing. The specific treatment and preparation of the samples for the electrophoretic separation is described by Herzog (1988a) and Gehle & Herzog (1994). Staining procedures were performed according to routine methods (Herzog 1988a).

Nine isoenzyme systems (alcohol dehydrogenase, lactate dehydrogenase, isocitrate dehydrogenase, glucose dehydrogenase, glucose-6-phosphate-dehydrogenase, glutamate dehydrogenase, NADH-diaphorase, superoxide dismutase and hexokinase were studied. Two of them, isocitrate dehydrogenase (IDH) and superoxide dismutase (SOD), have been found to be polymorphic. Therefore, the analysis was concentrated upon these two polymorphic enzyme systems. In the case of SOD the original sample size of 136 animals was enlarged by a sample of 84 animals previously collected by Herzog (1988a). The examination of homogeneity to genotypic structures showed no differences between the proportion of both samples.

To estimate genetic variation within populations, actual heterozygosity (H_a) as well as differentiation D_j (Gregorius & Roberds 1986) were applied. H_a was computed by direct counting. The measure of differentiation is based on the weighted average of the genetic distances (Gregorius 1974) between subpopulations and their complements. In contrast to other more commonly used measures, our measure fulfils all of the desirable conditions and has the additional advantage that its values are directly interpretable. For example, this measure fulfils the triangle inequity which *in praxi* means that e.g. the ranking of three or more populations according to their genetic distance becomes possible and meaningful. All measures applied in our study are described in detail by Gregorius (1978, 1985, 1987), Herzog (1988a) and Gehle & Herzog (1994).

For comparison with other European populations, allelic structures for the enzyme system SOD obtained in studies by Ströhlein et al. (1991; 196 animals) and Hartl et al. (1990; 686 animals) were reanalysed.

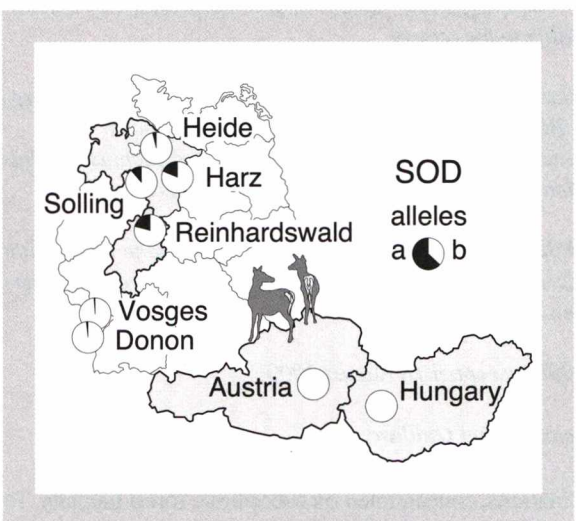

Figure 1. Clinal variation at gene locus SOD in red deer based on reanalysis of data from Herzog (1988a), Hartl et al. (1990) and Ströhlein et al. (1991).

Results

For each of the enzyme systems IDH and SOD three phenotypes have been found. As the most simple genetic hypothesis, we suggest the activity of one dimeric enzyme, encoded by one gene locus with two codominant alleles a and b. Analysis of three known matrilines (hind and calf) did not defeat this genetic hypothesis and it was consistent with results obtained in previous genetic analyses (Herzog 1988a,b).

The alleles a and b at locus IDH appear with about equal frequencies, but the SOD locus shows one allele (SOD^b) of relatively high and another (SOD^a) of relatively low frequency. Thus, the type of distribution at gene locus IDH is called a biallelic major polymorphism, at locus SOD analogously a biallelic minor polymorphism (Brown, Marshall & Albert 1975, Lewontin 1985).

In Europe, the highest frequency for the allele SOD^a is about 20%, obtained for the north of Germany (Reinhardswald and Harz). The frequency decreases with a latitudinal gradient towards the south (Fig. 1) up to the fixation on allele SOD^b in Austria and Hungary.

Figure 2 shows the current share of (actual) heterozygosity H_a.

Figure 2. Proportion of heterozygosity (actual heterozygosity H_a; ■) at the IDH and SOD gene loci for red deer populations. Values were calculated using our own data as well as reanalysed data from Herzog (1988a), Hartl et al. (1990) and Ströhlein et al. (1991). Y-axis: proportion of the rare (□) and common (■) alleles.

The relatively low values, especially for the SOD locus, in some populations is due to the type of polymorphism: the rareness of the allele SOD^a up to the fixation on allele SOD^b in Austria and Hungary (genetic profile is called monomorphism) may explain the low actual degrees of heterozygosity for this gene locus.

The differentiation D_j between the populations shows another aspect (Fig. 3): for IDH, the Harz population shows the lowest values, whereas the majority of the allelic variation occurs within the Solling and Lüneburger Heide populations; for SOD, an increasing proportion of common alleles in the sequence Lüneburger Heide-Harz-Solling is to be found. In the net diagram of differentiation the enclosed population at Reinhardswald with almost 15% of non-common alleles seems conspicuous. We have to take into account that for this population Ströhlein et al. (1991) found a significant surplus of heterozygote genotypes in relation to the corresponding Hardy-Weinberg-structure. A comparison with a collective outside this fence, namely the Reinhardswald population (50 animals; investigated by Herzog 1988a) is interesting, because it shows only average values of differentiation.

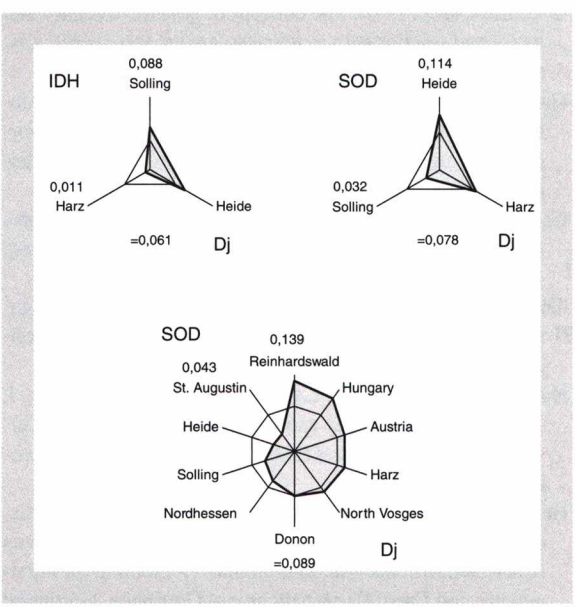

Figure 3. Differentiation between the demes Harz, Lüneburger Heide and Solling for the IDH and SOD gene loci and between these populations and, based on samples from Europe, the SOD gene locus (lower net diagram: reanalysis with data from Herzog (1988), Hartl et al. (1990) and Ströhlein et al. (1991).

Discussion

From the results, four trends can be derived: In all studies the two frequent alleles are indicating an allelic balance. In viability selection with advantage of heterozygote types both allele frequencies in actual infinite populations converge to one stable balance structure (safe polymorphism). Neutrality of the locus might be another possible explanation of the observed phenomenon. However, Pemberton et al. (1988) found a viability advantage of heterozygotes in calves (184 animals) of red deer. Only 40% of IDH homozygote calves survived, whereas 60% of heterozygote calves survived. However, homozygote calves survived with about equal frequencies for both alleles. There were no differences concerning viability carrying a specific allele. This situation, however, corresponds to the selection model of overdominance. For a sufficiently large community of reproduction, selection should conserve both alleles at gene locus IDH.

The suggested selection-model is by means of other studies neither to be confirmed nor to be rejected. On the one hand there is no uniform terminology between the studies; on the other hand the photographic representations of results or the information about observed genotypic structures are missing.

The frequency of the allele SOD^a is decreasing from

the north to the south (see Fig. 1). Red deer from France (Vosges) are almost fixed on the allele SOD^b. Animals from Austria and Hungary are monomorphic.

Beside other possible hypotheses, the clinal variation of SOD alleles could indicate an adaptation to a certain environment and would thus be the consequence of selection, resulting in a higher viability of the respective homozygote animals. Directional selection would then be the cause of the minor polymorphism.

The proportion of common alleles, separated for each enzyme, is highest between the demes Harz and Solling. The pairwise allelic distances between these two populations are two and three times further from the Lüneburger Heide collective. This fits perfectly with the geographical distance between the populations. The distance between the areas of Harz and Lüneburger Heide is about 60 km, and the distance from Solling or Harz to the area of Lüneburger Heide is about 120 km.

The distribution of heterozygosity has been tested on homogeneity for both gene loci. It shows that the collectives Harz, Lüneburger Heide and Solling may originate from one and the same population.

This assumption is supported by the short period of isolation in reference to genetically effective evolutionary time periods and by the number of deer migrations across rivers and highways. Male deer migrate about twice as far as the hinds with maximal distances of 40-50 kilometres (Ruhlé & Looser 1991, Drechsler 1991).

Our study shows no certain indication of a random loss of genetic variation, but a clinal variation. However, the fact that other studies on red deer found evidence also for genetic drift may be due to the anthropogenic subdivision and isolation (Herzog 1991b, Herzog et al. 1991). For the transferrin gene locus (Tf), Herzog et al. (1991) found no indication for a clinal variation. For most populations a biallelic minor polymorphism is suggested, but only in one natural as well as in one enclosed population, three alleles with frequencies of the third allele about 3 and 22% have been found. Thus, two populations differ significantly from other German wild and enclosed populations concerning their Tf gene locus.

So, both marker gene loci, SOD and Tf, indicate a genetic differentiation between demes. Whereas genetic differentiation at the SOD locus may be due to selective factors of different environmental situations over the range of the species, the differentiation at other loci as e.g. the Tf gene locus, exhibits no cline and may be caused by random effects, especially genetic drift. Thus, periodical genetic monitoring will be an indispensable tool to differentiate between selective and random impact on natural red deer populations. Moreover, future trends in changes of genetic structures will be observed only by systematic genetic inventories. Due to the low number of polymorphic isoenzyme gene loci, these inventories should take into account additional, e.g. molecular, genetic marker systems.

Another consequence of the present study for wildlife management is the need for sufficiently large reproduction demes. At present, this should be the primary aim of wildlife management efforts on European red deer.

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References

Brown, A.H.D., Marshall, D.R. & Albert, L. 1975: Profiles of electrophoretic alleles in natural populations. - Genetic Research (Cambridge) 25: 137-143.

Drechsler, H. 1991: Über das Raumverhalten des Rotwildes im Harz. - Zeitschrift für Jagdwissenschaft 37: 78-90. (In German).

Gehle, T. & Herzog, S. 1994: Genetische Variation und Differenzierung von drei geographisch isolierten Rotwildpopulationen (Cervus elaphus L.) in Niedersachsen. - Zeitschrift für Jagdwissenschaft 40: 156-174. (In German).

Gregorius, H-R. 1974: Genetischer Abstand zwischen Populationen. I. Zur Konzeption der genetischen Abstandsmessung. - Silvae Genetica 23: 22-27. (In German).

Gregorius, H-R. 1978: The concept of genetic diversity and its formal relationship to heterozygosity and genetic distance. - Mathematical Biosciences 41: 253-271.

Gregorius, H-R. 1985: Measurement of genetic differentiation in plant populations. - In: Population Genetics in Forestry. Lecture Notes in Biomathematics No. 60. Berlin, Heidelberg [u.a.], Springer-Verlag Berlin, pp. 276-285.

Gregorius, H-R. 1987: The relationship between the concepts of genetic diversity and differentiation. - Theoretical and Applied Genetics 74: 397-401.

Gregorius, H-R & Roberds, J.H. 1986: Measurement of genetical differentiation among subpopulations. - Theoretical and Applied Genetics 71: 826-834.

Hartl, G.B., Willing, R., Lang, G., Klein, F. & Köller, J. 1990: Genetic variability and differentiation in red deer (Cervus elaphus L) of Central Europe. - Genetics Selection Evolution 22: 289-306.

Herzog, S. 1988a: Cytogenetische und biochemisch-genetische Untersuchungen an Hirschen der Gattung Cervus (Cervidae, Artiodactyla, Mammalia). - Abteilung für Forstgenetik und Forstpflanzenzüchtung. Göttingen, Göttingen Research Notes in Forest Genetics 10: 1-139. (In German).

Herzog, S. 1988b: Polymorphism and genetic control of erythrocyte 6-phosphogluconate dehydrogenase in the genus Cervus. - Animal Genetics 19: 291-294.

Herzog, S. 1991a: Genetic analysis of erythrocyte superoxide dismutase polymorphism in the genus Cervus. - Animal Genetics 21: 391-400.

Herzog, S. 1991b: Management implications of genetic differentiation in red deer (Cervus elaphus LINNÉ) populations. - In: University of Agricultural Sciences, Gödöllö, Hungary (Eds.); Proceedings of the XXth Congress of the International Union of Game Biologists, Gödöllö, Hungary, August 21-26th, pp. 816-821.

Herzog, S., Mushövel, C., Hattemer, H.H. & Herzog, A. 1991: Transferring polymorphism and genetic differentiation in Cervus elaphus L. (European red deer) populations. - Heredity 67, 231-239.

Lewontin, R.C. 1985: Population genetics. - Annual Review on Genetics 19: 81-102.

Pemberton, J.M., Albon, S.D., Guinness, F.E., Clutton-Brock, T.H. & Berry, R.J. 1988: Genetic variation and juvenile survival in red deer. - Evolution 42: 921-934.

Ruhlé, Ch. & Looser, B. 1991: Ergebnisse von Untersuchungen über die Wanderung von Rothirschen (Cervus elaphus L.) in den Kantonen St. Gallen und Graubünden (Schweiz) und der Nachbar-Kantone sowie im Land Vorarlberg (Österreich) und im Fürstentum Liechtenstein. - Zeitschrift für Jagdwissenschaft 37: 13-23. (In German).

Ströhlein, H., Lewalski, H., Hecht, W. & Herzog, A. 1991: Elektrophoretische Untersuchungen der Superoxiddismutase-Isoenzyme beim hessischen Rotwild (Cervus elaphus L). - Zeitschrift für Jagdwissenschaft 37: 35-39. (In German).