Acta Theriologica, Suppl. 3: 145–155, 1995.
PL ISSN 0001–7051

Mitochondrial DNA differentiation in chamois (genus *Rupicapra*): implications for taxonomy, conservation, and management

Sabine HAMMER, Karl NADLINGER and Günther B. HARTL

Hammer S., Nadlinger K. and Hartl G. B. 1995. Mitochondrial DNA differentiation in chamois (genus *Rupicapra*): implications for taxonomy, conservation, and management. [In: Ecological genetics in mammals II. G. B. Hartl and J. Markowski, eds]. Acta Theriologica, Suppl. 3: 145–155.

Restriction fragment length polymorphisms (RFLPs) of mitochondrial (mt) DNA were used for investigating genetic differentiation in chamois (genus *Rupicapra*). Digestion of the mtDNAs of 58 individuals from 6 populations with a battery of 16 six-base cutting restriction endonucleases yielded a total of 67 restriction sites. Based on the presence and absence of these restriction sites a total of 8 haplotypes could be defined. Six of them served for assessing genetic diversity within and among 4 local populations of *R. rupicapra rupicapra*. Estimates of nucleotide divergence among those haplotypes ranged from 0.05% to 0.25%. One chamois from the High Tatra (subspecies *R. r. tatrica*) was examined and showed the standard haplotype found in *R. r. rupicapra*. MtDNA in chamois from Catalunya, belonging to *R. pyrenaica pyrenaica*, was polymorphic for two haplotypes not found in any population of *R. rupicapra*. Mean nucleotide divergence among haplotypes found in *R. rupicapra* and *R. pyrenaica* was 0.56% (SD = 0.16%). Based on this value, an estimated divergence time of about 280 000 years suggests that the mtDNA lineages of *R. rupicapra* and *R. pyrenaica* separated prior to the Riss glacial in the later Pleistocene.

Forschungsinstitut für Wildtierkunde und Ökologie der Veterinärmedizinischen Universität Wien, Savoyenstraße 1, A-1160 Vienna, Austria (SH); Institut für Haustierkunde der Christian-Albrechts-Universität zu Kiel, Olshausenstraße 40, D-24118 Kiel, Germany (KN, GBH).

Key words: *Rupicapra*, mtDNA, population genetics, taxonomy, conservation

Introduction

Apart from the maintenance of genetic variability within populations, the preservation of the integrity of locally well adapted gene pools is one of the major issues in conservation genetics (cf Templeton *et al.* 1986). Sound knowledge of systematic relationships in a given taxon, especially within the problematic range from geographically separated populations to closely related species, is thus essential for restocking operations, for promoting gene flow by translocation of animals, and for assessing priorities in the preservation of particular populations.

The systematics and taxonomy of chamois (genus *Rupicapra*) has been a controversial issue, both with respect to the relationship of chamois to other genera

of the Caprinae (cf Hartl *et al.* 1990) and to the subdivision of the genus into species and subspecies (cf Masini and Lovari 1988). Apart from Miller (1912) and Camerano (1914), earlier studies tended to consider all chamois one polytypic species, *Rupicapra rupicapra*. The classification of populations into various subspecies largely corresponded with their recent geographic distribution, restricted to mountain ranges on the Iberian peninsula, the Apennine peninsula, Central and Southeastern Europe, and Asia Minor. In his re-evaluation of the taxonomy of the Rupicaprini, Dolan (1963) recognized nine subspecies: *R. r. rupicapra* (Alps), *R. r. pyrenaica* (Pyrenées), *R. r. parva* (Cantabrian mountains), *R. r. ornata* (Apennines), *R. r. balcanica* (Balkan), *R. r. carpathica* (Carpathians), *R. r. cartusiana* (Massif de la Chartreuse), *R. r. caucasica* (Caucasus), and *R. r. asiatica* (Pontus, Taurus, Antitaurus). Apart from the identification of one more subspecies (*R. r. tatrica*, Tatra mountains), this classification at the subspecies level corresponds with the current taxonomic opinion (eg Knaus and Schröder 1983). However, based on a wealth of morphological and behavioural criteria summarized by Lovari (1987), and Masini and Lovari (1988), *R. r. pyrenaica*, *R. r. parva*, and

Table 1. Genetic distances among (sub)species of the Caprini and the Rupicaprini. *n*I – sample of individuals (number of populations studied in parentheses), *n*L – sample of loci, *D* – genetic distance according to Nei (1972, 1978). Note that a judgement on the species or subspecies status of the respective taxa is quite arbitrary. For example, based on a *D*-value of about 0.09, Nascetti *et al.* (1985) considered *Rupicapra r. rupicapra* and *R. p. pyrenaica* separate species while Stüwe *et al.* (1992) considered *Capra i. ibex* and *C. i. nubiana* merely subspecies. Also the *D*-values between *Capra i. ibex* and *C. i. pyrenaica*, which are thought to be separate species, and between *Rupicapra r. rupicapra* and *R. r. cartusiana*, which are at best subspecies, are very similar. Generally, genetic distances between 0.0 and 0.1 are considerably influenced by the number of individuals as well as by the number and composition of loci investigated.

(Sub)species	*n*I	*n*L	*D*	References
Capra i. ibex/Capra i. nubiana	149/39	15	0.093	Stüwe *et al.* (1992)
	1/1	27	0.190	Hartl *et al.* (1990)
Capra i. ibex/Capra pyrenaica	3/20	52	0.023	Hartl *et al.* (1992)
Local populations of *Capra i. ibex*	149(8)	15	0.021	Stüwe *et al.* (1992)
	115(2)	33	0.006	Nascetti *et al.* (1987)
Capra aegagrus/Capra i. ibex	2/1	27	0.086	Hartl *et al.* (1990)
	43/115	33	0.228	Nascetti *et al.* (1987)
	40/40	38	0.110	Randi *et al.* (1990)
/Capra i. nubiana	2/1	27	0.129	Hartl *et al.* (1990)
/Capra falconeri	2/2	27	0.124	Hartl *et al.* (1990)
Capra falconeri/Capra i. ibex	2/1	27	0.173	Hartl *et al.* (1990)
/Capra i. nubiana	2/1	27	0.173	Hartl *et al.* (1990)
Rupicapra r. rupicapra/Rupicapra p. pyrenaica	43/25	25	0.096	Nascetti *et al.* (1985)
/Rupicapra p. ornata	43/18	25	0.121	Nascetti *et al.* (1985)
/Rupicapra r. cartusiana	32/7	55	0.013	Pemberton *et al.* (1989)
Rupicapra p. pyrenaica/Rupicapra p. ornata	25/18	25	0.009	Nascetti *et al.* (1985)
Local populations of *R. r. rupicapra*	32(4)	55	0.007	Pemberton *et al.* (1989)
	125(4)	42	0.010	Miller and Hartl (1987)

R. r. ornata are now believed to belong to a separate species, *R. pyrenaica*. Electrophoretic differentiation between *R. rupicapra* and *R. pyrenaica* was investigated by Nascetti *et al.* (1985), and the overall genetic distance of *D* (Nei 1972) 0.1 they obtained was interpreted as further evidence for separate species status of the latter taxon. However, as shown in Table 1, *D*-values among presumed species or subspecies of the Caprinae vary to an extent that does not allow to draw reliable taxonomic conclusions from a single genetic distance value in only one genetic system.

In the present study, restriction analysis of mitochondrial DNA (mtDNA) was used for examining genetic differentiation between *R. rupicapra* and *R. pyrenaica* in relation to genetic divergence among subspecies and local populations of *R. rupicapra*. The data obtained are compared with those of electrophoretic investigations available so far (Nascetti *et al.* 1985, Miller and Hartl 1986, 1987, Miller 1987, Pemberton *et al.* 1989), and are interpreted in the light of paleontological evidence on the colonization of Europe by chamois during the Pleistocene (cf Masini and Lovari 1988).

Material and methods

A total of 58 chamois from six populations (Fig. 1) were examined. In each specimen total mtDNA was prepared from frozen liver, purified, digested with restriction endonucleases, and screened by agarose gel electrophoresis as described in Hartl *et al.* (1993). The following 16 six-base cutting restriction endonucleases were used: ApaI, AsnI, BamHI, BclI, BglII, ClaI, DraI, EcoRI, EcoRV, HindIII, PstI, PvuII, SacI, SfuI, StuI, and XbaI. Fragment lengths were determined using Lambda phage DNA digested with HindIII as a size standard.

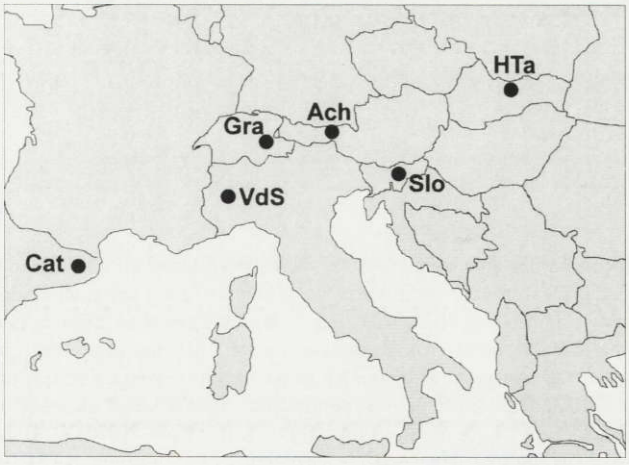

Fig. 1. Geographic location of the chamois populations investigated. Cat – Catalunya, Gra – Graubünden, Ach – Achenkirch, VdS – Val di Susa, Slo – Slovenia, HTa – High Tatra.

Table 2. Lengths (in kb, with a tolerance of ~5% measurement error) of fragments produced by the various restriction enzymes used for cutting mtDNA in chamois. The respective restriction types produced by each enzyme are marked by letters. [1] cutting site in type B different from that in type A, x.x – fragment length could not be exactly determined.

Enzyme	Type	Fragments											
ApaI	A	12.5	3.0	1.3									
AsnI	A		2.6		2.2	2.0	1.9	1.8	1.6	1.0	0.9	0.9	0.6
	B		2.6	2.5	2.2	2.0		1.8	1.6	1.0	0.9	0.9	
	C	3.5		2.5	2.2	2.0		1.8	1.6	1.0		0.9	
BamHI	A	5.1		3.5	3.0	2.6	1.4						
	B		4.0	3.5	3.0	2.6	1.4	1.1					
BclI	A	16.0											
	B		7.5	6.2	2.2								
BglII	A	16.0											
ClaI	A	16.0											
	B	16.0[1]											
DraI	A	6.9	4.5			1.6	1.4	0.8	0.7				
	B	6.9		2.6	1.9	1.6	1.4	0.8	0.7				
EcoRI	A	9.4	7.0										
	B	9.4			4.0	3.0							
	C		7.0	5.4	4.0								
EcoRV	A	8.7	7.4										
	B	8.6		4.8	3.6								
HindIII	A	13.3	1.9	1.4									
PstI	A	no cutting site											
PvuII	A		8.5	7.8									
	B	16.0											
SacI	A	16.0											
SfuI	A		7.2	2.9	2.9			1.6	1.6				
	B		7.2	2.9		2.1		1.6	1.6	0.8			
	C	x.x		2.9	2.9		x.x	1.6	1.6				
StuI	A	3.0	3.0	2.0	1.8	1.8	1.5	1.4	0.7	0.4			
XbaI	A		6.6		3.1	2.8	1.6	1.0	0.9				
	B		6.6	4.1		2.8	1.6		0.9				
	C	8.5			3.1	2.8		1.0	0.9				

Relationships among haplotypes were assessed as follows: Based on restriction sites (inferred from fragments given in Table 2) the mean number of base substitutions per nucleotide (p) was calculated using formulas 10 and 8 in Nei and Li (1979). The p-values were then used to generate an unrooted tree by means of the FITCH option in Felsenstein's PHYLIP-package (Felsenstein 1993). Relationships among haplotypes were also inferred by constructing a median graph according to Bandelt (1992). Genetic relationships among chamois populations that shared at least one haplotype were calculated from the respective frequencies of haplotypes using Nei's (1972) *D*. Based on the resulting distance matrix a Fitch-Margoliash tree was constructed (FITCH option in PHYLIP). Genetic diversity within populations was assessed by calculating haplotype diversity (h) and nucleotide diversity (π) according to Nei (1987). Genetic diversity among populations was estimated by calculating the pairwise net nucleotide diversity using the "NDBoots"-program of Tiedemann (1994).

Results

Digesting mtDNA of chamois with a battery of 16 six-base cutting restriction endonucleases yielded a total of 67 restriction sites. The restriction types produced by the various restriction enzymes applied are given in Table 2. Based on the composition of the respective restriction types a total of 8 haplotypes could be defined (Table 3). A matrix of pairwise nucleotide divergence (p) among haplotypes is given in Table 4. Relationships among haplotypes are displayed in a Fitch--Margoliash tree (Fig. 2) and in a median graph (Fig. 3). The geographic distribution of haplotypes is shown in Table 5. Pairwise genetic distances among

Table 3. MtDNA haplotypes detected in chamois. Letters refer to the restriction types defined in Table 2.

	Haplotypes							
Enzyme	1	2	3	4	5	6	7	8
ApaI	A	A	A	A	A	A	A	A
AsnI	B	B	A	A	A	A	C	C
BamHI	A	A	A	B	A	A	B	B
BclI	A	A	A	A	A	A	B	B
BglII	A	A	A	A	A	A	A	A
ClaI	A	A	A	A	A	A	B	B
DraI	A	A	A	A	A	A	B	B
EcoRI	A	A	A	B	A	A	C	C
EcoRV	A	A	A	A	A	A	B	B
HindIII	A	A	A	A	A	A	A	A
PstI	A	A	A	A	A	A	A	A
PvuII	A	A	A	A	A	A	B	B
SacI	A	A	A	A	A	A	A	A
SfuI	A	B	B	A	A	A	C	A
StuI	A	A	A	A	A	A	A	A
XbaI	A	B	B	A	A	C	A	A

Table 4. Matrix of pairwise nucleotide divergence (p, in per cent) among mtDNA haplotypes in chamois.

	Haplotypes							
	1	2	3	4	5	6	7	8
1	–							
2	0.10	–						
3	0.15	0.05	–					
4	0.15	0.25	0.20	–				
5	0.05	0.15	0.10	0.10	–			
6	0.10	0.20	0.15	0.15	0.05	–		
7	0.55	0.66	0.71	0.59	0.60	0.66	–	
8	0.50	0.61	0.66	0.54	0.55	0.61	0.05	–

populations, based on the frequencies of the respective haplotypes, and values of pairwise net nucleotide diversity are given in Table 6. Genetic relationships among populations are shown in a Fitch-Margoliash tree (Fig. 4). Haplotype diversity and nucleotide diversity within populations are shown in Table 7.

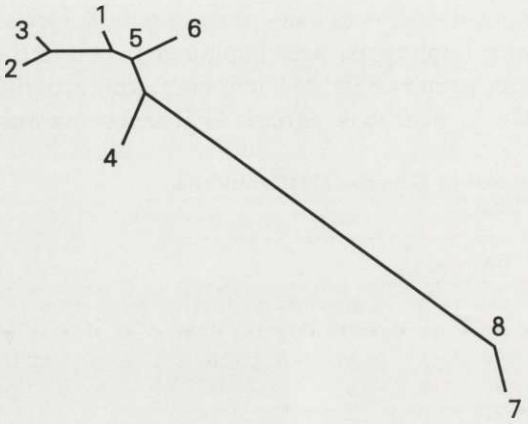

Fig. 2. Fitch-Margoliash tree showing phylogenetic relationships among mtDNA haplotypes in chamois. The tree is based on estimates of pairwise nucleotide divergence (Table 4). The distance (p) between haplotypes 7 and 8 is 0.05%.

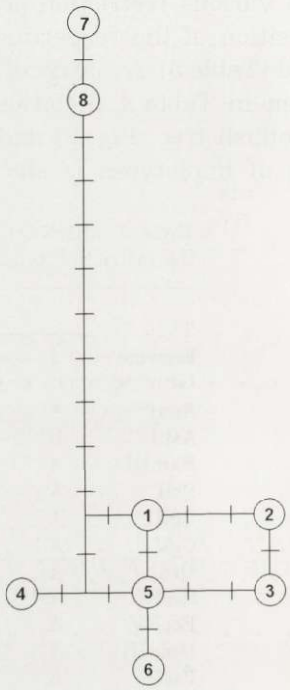

Fig. 3. Median graph showing phylogenetic relationships among mtDNA haplotypes in chamois. The small bars indicate the respective numbers of restriction site gains or losses.

Table 5. Geographic distribution of mtDNA haplotypes in chamois.

Area	*n*	Haplotypes							
		1	2	3	4	5	6	7	8
Catalunya	10	–	–	–	–	–	–	2	8
Graubünden	16	1	–	–	1	3	11	–	–
Achenkirch	8	–	–	–	–	8	–	–	–
Val di Susa	6	4	–	–	–	2	–	–	–
Slovenia	17	7	4	1	–	5	–	–	–
High Tatra	1	–	–	–	–	1	–	–	–
Total	58	12	4	1	1	19	11	2	8

Table 6. Net nucleotide diversity (in per cent) among all populations studied (above diagonal), and pairwise genetic distances according to Nei (1972) among populations sharing at least one haplotype (below diagonal). Cat – Catalunya, Gra – Graubünden, Ach – Achenkirch, VdS – Val di Susa, Slo – Slovenia, HTa – High Tatra.

	Cat	Gra	Ach	VdS	Slo	HTa
Cat	–	1.33	1.23	1.13	1.22	1.23
Gra	–	–	0.10	0.17	0.25	0.10
Ach	–	1.346	–	0.08	0.15	0.00
VdS	–	1.643	0.806	–	0.12	0.08
Slo	–	1.611	0.646	0.115	–	0.15
HTa	–	1.346	0.000	0.806	0.646	–

Table 7. Haplotype diversity (h) and nucleotide diversity (π, in per cent) in the chamois populations studied. Cat – Catalunya, Gra – Graubünden, Ach – Achenkirch, VdS – Val di Susa, Slo – Slovenia, n – sample size. Note that low estimates of h and π are not fully explained by small sample sizes.

Variable	Population				
	Cat	Gra	Ach	VdS	Slo
n	10	16	8	6	17
h	0.320	0.484	0.0	0.444	0.685
π	0.00	0.01	0.00	0.01	0.01

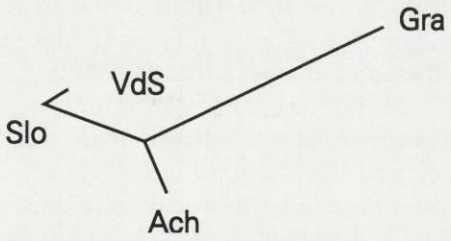

Fig. 4. Fitch-Margoliash tree showing genetic relationships among populations of *R. rupicapra rupicapra*. The tree is based on Nei's (1972) D, calculated from frequencies of mtDNA haplotypes. The distance (D) between VdS and Slo is 0.116. Gra – Graubünden, Ach – Achenkirch, VdS – Val di Susa, Slo – Slovenia.

Discussion

Especially due to the limited number of subspecies sampled the results of the present study are clearly preliminary. Yet several interesting conclusions can be drawn from our data.

Restriction profiles of mtDNA in chamois yield clear phylogeographic patterns that can be utilized for inferring phylogenetic relationships among populations (cf Avise *et al.* 1987). Among medium-sized and larger mammals this is not always the case. For example, in a large-scale study on genetic differentiation in the brown hare *Lepus europaeus*, Hartl *et al.* (1993, 1994) detected a total of seven different haplotypes. However, in all populations examined one and the same standard haplotype predominated, while the other haplotypes, each differing from the standard type by but one restriction site gain or loss, respectively, yielded population genetic information only through their geographic distribution.

On the whole, patterns of mtDNA differentiation in the chamois are in accordance with the geographic distribution of the populations studied, both with respect to relationships among haplotypes and their respective occurrence. In the *R. rupicapra rupicapra* populations, haplotypes 1 and 5 seem to be the basic types from which haplotypes 2, 3, 4 and 6 are derived (Fig. 3). In accordance with this interpretation both of them are present in almost all samples. Haplotypes 4 and 6, separated by several restriction site gains or losses (Fig. 3), are found exclusively in Graubünden while 2 and 3, being very similar to one another (Figs 2 and 3), are confined to the Slovenian samples. The pattern of differentiation among rare haplotypes corresponds to some extent with differences of their frequencies in the various populations (Figs 3 and 4, Table 5). This is reflected by estimates of nucleotide diversity. They are highest in populations with a high haplotype diversity (Table 7), suggesting that populations tend to be polymorphic for related haplotypes, respectively. In terms of haplotype frequencies, the populations located south of the main crest of the Alps are clearly separated from those in the north (Table 5, Figs 1 and 4). The population in Graubünden appears to be genetically most isolated from the other chamois colonies investigated. The presence of only the standard haplotype (5) in Achenkirch may be due to local genetic depletion. Indeed, low mtDNA variation in Achenkirch is paralleled by comparatively low estimates of polymorphism and heterozygosity obtained from electrophoretic allozyme analyses (Rubin 1992).

As far as mtDNA differentiation among subspecies is concerned, the single specimen from the High Tatra, belonging to the presumed subspecies *R. r. tatrica*, showed the standard haplotype (5) detected in the *R. r. rupicapra* populations. On the one hand this result confirms the basic status of haplotype 5. On the other hand, it indicates that the chamois population in the High Tatra shares at least one haplotype with the chamois populations from the Alps. Clearly more individuals from the High Tatra need to be investigated to assess the extent of mtDNA differentiation between *R. r. tatrica* and *R. r. rupicapra*. However, both at the population and the subspecies level chamois appear to be somewhat less differentiated than the European red deer, where even local populations were found monomorphic for different haplotypes (cf Hartl *et al.* 1995).

In the population from Catalunya, belonging to the species *R. pyrenaica*, only two haplotypes (7, 8) were found, which are not present in the populations

belonging to *R. rupicapra* (Table 5) and are different from those detected in the latter taxon by a minimum of 10 restriction site gains or losses (Fig. 3). This degree of mtDNA differentiation is higher than that detected among presumed subspecies in red deer (cf Hartl *et al.* 1995). Although this result, or any of that kind, cannot be considered positive proof for separate species status of *R. rupicapra* and *R. pyrenaica* for a number of reasons (see eg Cronin 1993, Avise 1994), it does not support any objection against this classification. In fact, if nucleotide divergence among haplotypes (p, Table 4) is converted into estimates of divergence time (t) among mtDNA lineages (assuming that p = 2% roughly corresponds to t = 1 million years, Wilson *et al.* 1985), the time divergence between the haplotypes found in *R. rupicapra* and *R. pyrenaica* amounts to approximately 280 000 years. This estimate roughly matches the schedule of divergence times given by Masini and Lovari (1988). Based on paleontological evidence, they hypothesized that the chamois or its direct ancestor reached the European region as a late immigrant from Asia during the early and middle Pleistocene, and that *R. rupicapra* and *R. pyrenaica* separated some time prior to the Würm glacial.

Given the comparatively low extent of electrophoretic differentiation among local populations of *R. r. rupicapra* (Miller and Hartl 1986, 1987, Miller 1987, Pemberton *et al.* 1989), in future studies mtDNA is likely to reveal phylogenetic differentiation among chamois populations much more clearly than allozymes.

Acknowledgements: The authors are indebted to Dr B. Chovancova, Tatra National Park, to Dr I. Marco Sanchez, University of Barcelona, to Dr P. G. Meneguz, University of Turin, and to Dr P. Ratti, Forstinspektorat Graubünden, for providing samples for the present study. Prof S. Lovari kindly reviewed a previous version of the manuscript. This research was supported by the Austrian Research Foundation (project P09660-BIO, granted to G. B. Hartl).

References

Avise J. C. 1994. Molecular markers, natural history and evolution. Chapman and Hall, New York, London: 1–511.

Avise J. C., Arnold J., Ball R. M., Bermingham E., Lamb T., Neigel J. E., Reeb C. A. and Saunders N. 1987. The mitochondrial DNA bridge between population genetics and systematics. Annual Review of Ecology and Systematics 18: 489–522.

Bandelt H.-J. 1992. Generating median graphs from Boolean matrices. [In: L_1-statistical analysis. Y. Dodge, ed]. North-Holland, Elsevier: 305–309.

Camerano L. 1914. Ricerche intorno ai camosci (Parte Ia, IIa, IIIa). Memorie della Regia Accademia di Scienze di Torino (Classe Scienze Fisiche Matematiche Naturali) 64(4): 1–82, 64(12): 1–88, 65(14): 1–82.

Cronin M. A. 1993. Mitochondrial DNA in wildlife taxonomy and conservation biology: cautionary notes. Wildlife Society Bulletin 21: 339–348.

Dolan J. M. 1963. Beitrag zur systematischen Gliederung des Tribus *Rupicaprini* Simpson 1945. Zeitschrift für zoologische Systematik und Evolutionsforschung 1: 311–407.

Felsenstein J. 1993. PHYLIP (Phylogeny Inference Package), version 3.5c. Department of Genetics, University of Washington, Seattle.

Hartl G. B., Burger H., Willing R. and Suchentrunk F. 1990. On the biochemical systematics of the Caprini and the Rupicaprini. Biochemical Systematics and Ecology 18: 175–182.

Hartl G. B., Meneguz P. G., Apollonio M., Marco-Sanchez I., Nadlinger K. and Suchentrunk F. 1992. Molecular systematics of ibex in western Europe. Proceedings of the International Congress on the genus *Capra* in Europe, 20– 22.10.1992, Ronda (in press).

Hartl G. B., Nadlinger K., Apollonio M., Markov G., Klein F., Lang G., Findo S. and Markowski J. 1995. Extensive mitochondrial-DNA differentiation among European red deer (*Cervus elaphus*) populations: implications for conservation and management. Zeitschrift für Säugetierkunde 60: 41–52.

Hartl G. B., Suchentrunk F., Nadlinger K. and Willing R. 1993. An integrative analysis of genetic differentiation in the brown hare *Lepus europaeus* based on morphology, allozymes, and mitochondrial DNA. [In: Ecological genetics in mammals. G. B. Hartl and J. Markowski, eds]. Acta Theriologica 38, Suppl. 2: 33–57.

Hartl G. B., Willing R. and Nadlinger K. 1994. Allozymes in mammalian population genetics and systematics: Indicative function of a marker system reconsidered. [In: Molecular ecology and evolution: Approaches and applications. B. Schierwater, B. Streit, G. P. Wagner and R. DeSalle, eds]. Birkhäuser, Basel, Experientia, Suppl. 69: 299–310.

Knaus W. and Schröder W. 1983. Das Gamswild. Paul Parey, Hamburg und Berlin.

Lovari S. 1987. Evolutionary aspects of the biology of chamois, *Rupicapra* spp. (*Bovidae*, *Caprinae*). [In: The biology and management of *Capricornis* and related mountain antelopes. H. Soma, ed]. Croom-Helm, London: 51–61.

Masini F. and Lovari S. 1988. Systematics, phylogenetic relationships and dispersal of the chamois (*Rupicapra* spp.). Quaternary Research 30: 339–349.

Miller C. 1987. Populationsgenetische Untersuchungen an Alpengams. Unpublished Ph D thesis, Ludwig-Maximillians-Universität München: 1–277.

Miller C. and Hartl G. B. 1986. Genetic variation in two alpine populations of chamois (*Rupicapra rupicapra* L.) Zeitschrift für Säugetierkunde 51: 114–121.

Miller C. and Hartl G. B. 1987. Genetische Variation bei Gemsen der Alpen (*Rupicapra rupicapra rupicapra* L.). Zeitschrift für Jagdwissenschaft 33: 220–227.

Miller G. S. 1912. Catalogue of the mammals of Western Europe (Europe exclusive of Russia). British Museum (Natural History) Publications, London: XVI+1–1019.

Nascetti G., Lanfranchi P., Ratti P., Peracino V., Mattiucci S., Meneguz P. G., Rossi L. and Bullini L. 1987. Studi elettroforetici sulla variabilita e divergenza genetica di *Capra ibex ibex* e *Capra aegagrus hircus* delle Alpi. [In: Lo stambecco delle Alpi: Realta attuale e prospettive. T. Balbo, D. DeMeneghi, P. G. Meneguz and L. Rossi, eds]. Universita di Torino, Torino: 11–15.

Nascetti G., Lovari S., Lanfranchi P., Berducou C., Mattiucci S., Rossi L. and Bullini L. 1985. Revision of *Rupicapra* genus III. Electrophoretic studies demonstrating species distinction of chamois populations of the Alps from those of the Apennines and Pyrenees. [In: Biology and management of mountain ungulates. S. Lovari, ed]. Croom-Helm, London: 57–62.

Nei M. 1972. Genetic distance between populations. American Naturalist 106: 283–292.

Nei M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583–590.

Nei M. 1987. Molecular evolutionary genetics. Columbia University Press, New York: 1–512.

Nei M. and Li W.-H. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. Procedings of the National Academy of Sciences, USA 76: 5269–5273.

Pemberton J. M., King P. W., Lovari S. and Bauchau V. 1989. Genetic variation in the Alpine chamois, with special reference to the subspecies *Rupicapra rupicapra cartusiana* Couturier 1938. Zeitschrift für Säugetierkunde 54: 243–250.

Randi E., Tosi G., Toso S., Lorenzini R. and Fusco G. 1990. Genetic variability and conservation problems in Alpine ibex, domestic and feral goat populations (genus *Capra*). Zeitschrift für Säugetierkunde 55: 413–420.

Rubin A. 1992. Untersuchungen über einen Zusammenhang zwischen Alloenzym-Polymorphismen und Kupfergehalten von Leber und Niere bei Wildwiederkäuern. Unpublished Diploma Thesis, University of Vienna: 1–53.

Stüwe M., Scribner K. T. and Alkon P. U. 1992. A comparison of genetic diversity in Nubian ibex (*Capra ibex nubiana*) and Alpine ibex (*Capra i. ibex*). Zeitschrift für Säugetierkunde 57: 120–123.

Templeton A. R., Hemmer H., Mace G., Seal U., Shields W. M. and Woodruff D. S. 1986. Local adaptation, coadaptation, and population boundaries. Zoo Biology 5: 115–125.

Tiedemann R. 1994. Taxonomische und populationsgenetische Untersuchungen an der mitochondrialen DNA von Eiderenten (*Somateria mollissima* L. 1758) und Watvögeln der Familien *Haematopodidae*, *Charadriidae* und *Scolopacidae*. Unpublished Ph D Thesis, Christian-Albrechts--Universität zu Kiel: 1–173.

Wilson A. C., Cann R. E., Carr S. M., George M., Gyllensten U. B., Helm-Bychowski K. M., Higuchi R. G., Palumbi S. R., Prager E. M., Sage R. D. and Stoneking M. 1985. Mitochondrial DNA and two perspectives on evolutionary genetics. Biological Journal of the Linnean Society 26: 375–400.

Received 7 August 1995, accepted 1 September 1995.