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Genetic variability and conservation problems in Alpine ibex, domestic and feral goat populations (genus *Capra*)

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Abstract

Studied genetic variability in two Alpine ibex (*Capra ibex ibex*), and in domestic and feral goat (*Capra aegagrus hircus*) populations with multilocus enzyme electrophoresis. Ibex from the Gran Paradiso National Park (Italy), the “mother” population of all the present Alpine colonies, shows genetic variability lower than the Graubünden (Switzerland) colony. Feral goats from Montecristo Island (Italy) show genetic variability higher than domestic goats. Such results have been discussed taking into account the possibility of past interbreeding between ibex and domestic goat during the first stages of captive breeding and reintroduction in Switzerland, and of repeated introductions of domestic goats into Montecristo Island. Both Alpine ibex and Montecristo feral goats have been submitted to repeated bottlenecks and founding episodes, with consequent erosion of genetic variability. The opportunity to conserve genetic variability has been discussed within the framework of ibex reintroduction plans, and of conservation projects of small island goat populations.

Introduction

Allozyme variability could be an estimate of the average genetic diversity of individual genomes or populations, if variation at different kinds of genes should be, at least in part, correlated (SOULÉ et al. 1973). Optimal levels of heterozygosity (SCRIBNER et al. 1989) or linkage between particular allelic variants and other genetic systems, e.g. polygenes or regulatory genes (PEMBERTON et al. 1988), have been addressed as indicators of the genetic welfare of a population, and as determinants of the short-term fitness and evolutionary adaptation to varying environments (SOULÉ 1980). The genus *Capra* includes species of great ecological and economic importance, and offers several opportunities for biochemical and population genetics approaches to conservation problems. The geographic distribution and population size of several species have been heavily affected by the direct or indirect action of man. Goats have been domesticated before 7000 B.C. (MASON 1984). The Alpine ibex has a well documented population history (COUTURIER 1962; TOSI et al. 1986; GRODINSKY and STÜWE 1987) of man-caused bottlenecks, which drove the species near to extinction, and of successful reintroductions started in Switzerland in 1911 and still going on. Almost all the present colonies are managed, and many areas are potentially suitable for founding new colonies in the Alps. Population genetics data have been collected on a number of colonies from Switzerland, France and Austria (HARTL 1986; STÜWE and SCRIBNER 1989), and these data could be related to demographic and life history information to investigate the role of founder effect and genetic drift on the extent of genetic variability in the refounded colonies and its eventual relationships with their fitness.

Aims of this study are: 1. to estimate the extent of genetic variability in wild, domestic and feral populations belonging to the genus *Capra*, using multilocus protein electrophoresis; 2. to compare the genetic structure of the ibex population from the Gran Paradiso National Park, Italy, the “mother” colony of all the present Alpine ibex

populations, with a refounded Swiss population with a documented partial origin from captive reared animals; 3. to describe the genetic structure of the feral goat population of the Montecristo Island, Italy, an ancient population, whose origins are not historically documented. The integration of the goats into the fragile ecosystem of the island, now a Natural Reserve, is problematic and management efforts are needed.

Material and methods

Heart and liver tissue samples were obtained from the following populations:

1. Ibx (*Capra ibex ibex*) from the Gran Paradiso National Park (PNGP, Italy; $n = 20$) and from the Piz Albris colony (Graubünden, Switzerland; $n = 20$). Animals were collected after incidental dead (mainly avalanches) in winter, or shot. The PNGP has been the last colony surviving after the extermination of the ibex elsewhere in the Alps at the end of 18th century. The Piz Albris has been one of the first colonies refounded in the Swiss Alps, using some animals reared in captivity at the Peter and Paul and Harder (Interlaken) Zoological Parks (RAUCH 1941; DESAX 1978; GIACOMETTI 1988).
2. Montecristo feral goat (*Capra aegagrus hircus*, $n = 20$); the samples were collected during a selective culling campaign planned to control population density. Montecristo is a small Mediterranean Island, about 10 square km, belonging to the Tuscany Archipelago, Tyrrhenian Sea, Italy. Probably goats were repeatedly introduced into the Island, and, although no documented historical record is available, first introductions seem to be very ancient. Some goats were probably introduced into Montecristo as a game species during the second half of last century (BRUNO and SAULI 1976). Morphologic and eco-ethologic aspects of the Montecristo feral goat are described by SPAGNESI et al. (1986).
3. Domestic goat ($n = 20$); from an Alpine rural breed (Val Chiavenna, Italian Alps), obtained from a local abattoir.
4. An F1 hybrid male ibex \times female domestic goat specimen was obtained from the French southern Alps. This individual originated from a natural crossing in the wild. Hybridization between ibex and domestic goat has been reported both in captivity and in the wild (COUTURIER 1962).

Tissues were homogenated in 0.01 M Tris/HCl, pH 7.5 (+0.001 M β -mercaptoethanol) buffer, centrifuged at 12,000 rpm for 15 min; supernatant was collected in Microtiter plates and stored at -80°C until usage. Vertical polyacrylamide gel (PAGE, 7.5% acrylamide concentration) and cellulose acetate membrane (CAM, Sartorius) electrophoresis was used to resolve 38 presumptive loci. The following electrophoretic conditions were used (multiple loci are numbered starting from the most anodal locus).

PAGE: 1. Discontinuous Tris/glycine, pH 8.3 (DAVIS 1964): malate dehydrogenase (MDH-1); superoxide dismutase (SOD-1, SOD-2); lactate dehydrogenase (LDH-1, LDH-2); fumarase (FUM); haemoglobin (HB-1, HB-2); albumin (ALB); non-enzymatic heart and liver proteins (H-PT and L-PT); malic enzyme (ME-1, ME-2); mannose phosphate isomerase (MPI); hexokinase (HK); glucose-6-phosphate dehydrogenase (G-6-PDH); α -glycerolphosphate dehydrogenase (α -GPDH); glutamate dehydrogenase (GLUD). 2. Discontinuous Tris/glycine, pH 8.5 (JOLLEY and ALLEN 1965): aspartate aminotransferase (AAT-1); phosphoglucose isomerase (PGI); phosphoglucomutase (PGM-2); glucose dehydrogenase (GDH-1, GDH-2). 3. Tris/borate, pH 8.9 (STUDIER 1973): α -naphthylacetate heart esterase (H-EST-1, -2, -3). 4. Lithium hydroxide, pH 8.6 (FERGUSON 1980): leucyl-alanine liver peptidase (L-PEP-1, -2, -3). CAM (GRÜNBAUM 1981): 1. Tris/maleate, pH 7.4: 6-phosphogluconate dehydrogenase (6-PGD). 2. Tris/glycine, pH 8.4: acid phosphatase (ACP). 3. Phosphate, pH 6.25: adenylate kinase (AK). 4. Citrate/phosphate, pH 7.0: isocitrate dehydrogenase (IDH-1, IDH-2). Staining recipes were adapted from HARRIS and HOPKINSON (1976) and from GRÜNBAUM (1981). Some serum samples (10 Montecristo goats; 10 PNGP ibexes; 1 F1 hybrid goat \times ibex) were used to study serum transferrin (TF) with the DAVIS (1964) discontinuous PAGE system.

Genotype frequencies were obtained by scoring the gels. The percentage of polymorphic loci (P), the observed (Ho) and the expected Hardy-Weinberg (He) heterozygosity, the mean number of alleles per locus (A) were computed at each polymorphic locus, and average values were obtained for all the studied loci. The program BIOSYS-1, release 1.7 (SWOFFORD and SELANDER 1989), was used to compute single locus chi-square test of Hardy-Weinberg equilibrium, F-statistics (WRIGHT 1978), contingency analysis of heterogeneity among populations (WORKMAN and NISWANDER 1972), and NEI (1978) and ROGERS (1972) genetic distances.

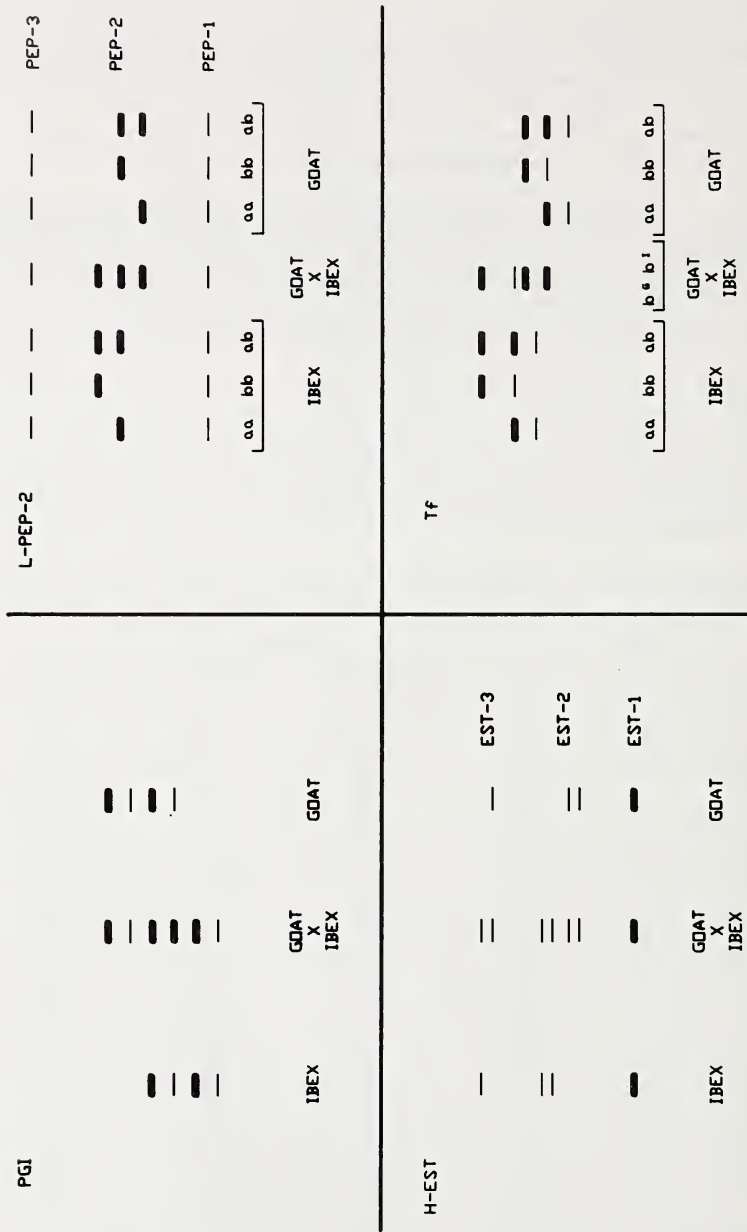
Results

Seven loci (LDH-1, PGM-2, H-PT-5, L-PT-7, L-PEP-2, ME-1, ME-2) were polymorphic in one or more populations, and four loci (PGI, H-EST-2, H-EST-3, and serum TF) showed fixed differences between ibex and goat (see Table and Fig.). Montecristo goat population showed the highest values of genetic variability ($P = 13.2$; $\bar{H} = 0.024$), while Gran Paradiso ibex showed the lowest ones ($P = 5.3$; $\bar{H} = 0.009$). Genetic variability was lower in the PNGP than in the Graubünden ibex. PNGP ibex showed also the lowest average number of alleles per polymorphic locus. The polymorphisms were heterogeneously distributed among the four populations: LDH-1 has been found polymorphic in ibex, but monomorphic in goat. Several loci were polymorphic only in goats (PGM-2; ME-1; ME-2; L-PT-7). Leucylalanine liver PEP-2 showed a widespread polymorphism both in goat and ibex populations, but the most frequent alleles were different in the two species (Fig.). Both average F_{ST} and contingency chi-square values at all the polymorphic loci were significant. Major differences between PNGP and Graubünden ibex were observed at H-PT-5 and L-PEP-2 ($\chi^2 = 8.8$, $p < 0.01$); between Montecristo and domestic goat at L-PEP-2 ($\chi^2 = 6.4$, $p < 0.01$); between Montecristo and domestic goat at L-PEP-2 ($\chi^2 = 6.4$, $p < 0.01$), ME-2 ($\chi^2 = 13.2$, $p < 0.01$), and ME-1 ($\chi^2 = 18.5$, $p < 0.01$). FIS values were generally low and nonsignificant, and deficiency of heterozygotes was observed only at ME-1 in the Montecristo goat and H-PT-5 in the Graubünden ibex. Expected and observed heterozygosities were similar, and chi-square tests of Hardy-

Allelic frequencies at ten loci polymorphic within populations and between ibex and goat

Locus	Allele	Populations			
		PNGP ibex	Graubünden ibex	Montecristo goat	Domestic goat
LDH-1	a	.050	.025	.000	.000
	b	.950	.975	1.000	1.000
PGI	a	1.000	1.000	.000	.000
	b	.000	.000	1.000	1.000
PGM-2	a	1.000	1.000	.974	1.000
	b	.000	.000	.026	.000
H-PT-5	a	1.000	.800	1.000	1.000
	b	.000	.200	.000	.000
L-PT-7	a	1.000	1.000	.975	1.000
	b	.000	.000	.025	.000
H-EST-2	a	.000	.000	1.000	1.000
	b	1.000	1.000	.000	.000
H-EST-3	a	.000	.000	1.000	1.000
	b	1.000	1.000	.000	.000
L-PEP-2	a	.000	.000	.950	.731
	b	.882	.559	.050	.269
	c	.118	.441	.000	.000
ME-1	a	1.000	1.000	.625	1.000
	b	.000	.000	.375	.000
ME-2	a	.000	.000	.000	.100
	b	1.000	1.000	.500	.750
	c	.000	.000	.500	.150
	\bar{n}	19.6	19.9	19.8	18.9
	\bar{A}	1.18	1.50	1.40	1.66
	P	5.3	7.9	13.2	5.3
	H_o	0.009	0.021	0.024	0.023

\bar{n} = mean sample size per locus; \bar{A} = mean number of alleles per polymorphic locus; P = percent of polymorphic loci (0.99 criterion); H_o = observed heterozygosity.



Electrophoretic phenotypes at five loci showing diagnostic differences between ibex and goat, and phenotypes showed by an F1 hybrid goat x ibex

Weinberg equilibrium were nonsignificant for all the polymorphic loci. Serum TF was found to be polymorphic in Montecristo goat and PNGP ibex, but the alleles were different in the two species (Fig.).

Ibex and goat are well differentiated species with average Nei's genetic distance of 0.11. The genetic distances between the two ibex, as well as between the two goat populations are about one order of magnitude lower (0.01). At least four loci of the 38 screened showed clear fixed differences (PGI, H-EST-2, H-EST-3, serum TF), and L-PEP-2 showed very different allelic frequencies. The F1 hybrid ibex × goat showed hybrid (codominant) genotypes at all these loci (Fig.).

Two additional polymorphisms were found at PGM-1 and L-EST-1 loci in the Graubünden and in the two goat samples, but these loci did not stain clearly in the PNGP ibex. PGM-1 is the most anodal band we have found in our gels, and probably correspond to PGM-2 as indicated by HARTL (1986). This locus stained very faintly and was difficult to score in some specimens and in almost all the PNGP samples. For this reason we have not included PGM-1 and L-EST-1 in the comparison among the four populations.

Discussion

Wild and domestic populations of the genus *Capra* have so far been poorly investigated with biochemical genetic methods. Studies on domestic goat focused on finding genetic markers, mainly polymorphic blood enzymes, useful to the classification of different breeds, but not utilizable to obtain data of genetic variability at the population level (FESUS et al. 1983; BRABANCHO et al. 1984; TUÑON et al. 1987).

Somè Alpine ibex populations have been studied. STÜWE and SCRIBNER (1989) analyzed 53 ibexes belonging to 9 Swiss populations and obtained low average values of genetic variability ($\bar{H} = 0.007$, $P = 6.06$, $\bar{A} = 1.18$). Heterozygosity was lower than the value obtained by HARTL (1986) on 46 ibexes from the Piz Albris colony ($\bar{H} = 0.023$, $P = 5.30$), but a partially different set of loci was resolved and included in the computations. In the present study we have obtained genetic variability estimates that confirm the data previously reported. The Graubünden sample, from the same Piz Albris colony, showed higher variability ($\bar{H} = 0.021$, $P = 7.9$) than the PNGP ($\bar{H} = 0.009$, $P = 5.3$), but the set of studied loci was not quite coincident. HARTL (1986) found two polymorphisms: PGM-2 (our PGM-1) and ADA; STÜWE and SCRIBNER (1989) found polymorphic PEP-S, LDH-1, MPI, EST-2, and NP; ADA was monomorphic and PGM-2 was not scored. In the present study we have found polymorphic LDH-1, L-PEP-2 and a non-enzymatic heart protein. We did not score ADA and NP. PGM-1 (corresponding to HARTL's PGM-2) was apparently polymorphic in goats and Graubünden ibex, but impossible to score in the PNGP ibex. Different laboratories and partially different sets of loci could make it difficult to compare the data, but, notwithstanding, the Piz Albris ibex population seems to harbour a level of genetic variability higher than other Alpine ibex populations.

The PNGP ibexes constitute the "mother" population of all the present Alpine colonies (DESAX 1981; PERACINO and BASSANO 1986; TOSI et al. 1986). This colony now counts more than 4000 individuals, but was reduced to less than 100 during the first years of the 18th century. Due to the difficulty to obtain animals from the wild, starting from 1906, captive-breeding programs with ibexes belonging to the Gran Paradiso National Park, were undertaken in Switzerland to produce the founders for new ibex colonies. Bottlenecks and low population numbers, repeated foundings of new colonies starting from few animals, contributed to cause and to maintain a low genetic variability in ibex populations, as showed by electrophoresis results.

It seems problematic to explain why the Piz Albris colony consistently shows genetic variability higher than the Gran Paradiso "mother" population. Although sampling

limitations (both specimens and number of loci) and methodological details cannot be ruled out, another explanation is possible. During the first steps of captive-breeding and during the apparently unsuccessful first attempts to release ibexes in the wild, repeated crossbreeding with domestic goats are documented in Switzerland (GRODINSKY and STÜWE 1987). Although we have not found any "goat" gene in the Piz Albris specimens at the loci showing fixed differences between goat and ibex (the analysis of the F1 hybrid ibex \times goat showed in the figure supported that result), there is the possibility of an increase in genetic variability as consequence of crossing. This suggestion could be supported if the polymorphism at the PGM-1 locus that is present both in goat and in the Piz Albris samples, could be definitively excluded in the Gran Paradiso population.

The domestic goat population we have studied showed a level of heterozygosity ($\bar{H} = 0.023$) just slightly below the average value (0.029) computed for large mammals (NEVO et al. 1984). The Montecristo goats harbour higher levels of genetic variability, so it seems impossible that the population has been founded only once, starting with a few founders. The hypothesis that domestic animals were repeatedly introduced into the island (by sailors, fishermen and hunters), and that they have contributed to the present gene pool, is supported by our genetic findings.

In fact this is a closed population without gene flow, with probable natural selection acting to reconstruct a "wild" phenotype fitted to the hard environmental conditions of the island. The population is so inevitably subjected to an increase in inbreeding and to a decrease in genetic variation due to random drift (FRANKLIN 1980). This is the only Italian feral goat population and one of the few Mediterranean (SCHULTZE-VESTRUM 1963; NIEVERGELT and ZINGG 1986) so it has to be conserved in the island. It is therefore important to evaluate the effective population size (N_e) which has to be maintained to assure a low rate of inbreeding and a slow loss of genetic variability through the generations.

The actual population size (N_a) numbers about 400–450 animals. The sex ratio is near 1 : 1. The effective number of males and of females is lower than 200, because not all the individuals will mate with the same probability (e.g. full breeding activity is reached by males not before 2–3 years). Field observations of mating behavior (TOSO and TOSI unpubl.) suggest an approximate estimate of effective male number $N_{em} = 100$, and of effective female number $N_{ef} = 130$. The effect of sex ratio on effective population size is computed as $N_e = 4(1/N_{em}) + (1/N_{ef})^{-1}$ (LANDE and BARROWCLOUGH 1987), and it gives the value $N_e = 227$. The effects of variance in progeny number and overlapping generations are presently not evaluable, but they should lower further N_e to a value lower than $0.5 \times N_a$. We can roughly assume that N_e is in the range from 100 to 200. If we use $N_e = 100$ to compute the rate of inbreeding per generation $f = 1/2N_e$, we obtain $f = 0.5\%$, a value half of the threshold of 1% inbreeding per generation suggested by SOULÉ (1980) to permit the population to experience an eventual soft selection for inbreeding tolerance. The rate of loss of genetic variability per generation is $\Delta(\bar{H}) = \bar{H} - (1 - 1/2N_e)\bar{H}$ (WRIGHT 1931). Assuming $\bar{H} = 0.0300$ (including PGM-1 and L-EST-1 polymorphisms) in Montecristo goat population, then $\Delta(\bar{H}) = 0.0002$, corresponding to a loss of about 0.7% heterozygosity per generation.

Future conservation plans should evaluate the possibility to maintain a long-period $N_e = 100$ to be sure that Montecristo goat population is at low genetic risk for some 10s of generations.

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Zusammenfassung

Genetische Variabilität und Probleme ihrer Erhaltung bei Populationen von Alpensteinbock, Hausziege und verwilderter Hausziege (Genus Capra)

Durch Protein-Elektrophorese wurde die genetische Variabilität in zwei Populationen des Alpensteinbocks (*Capra ibex*), in einer Hausziegengruppe und bei den verwilderten Hausziegen (*Capra aegagrus hircus*) der Insel Montecristo geschätzt. Die Steinböcke aus dem Nationalpark Gran Paradiso in Italien zeigten eine geringere genetische Variabilität als die von ihnen abgeleiteten aus Graubünden in der Schweiz.

Die Ziegen von Montecristo sind genetisch stärker variabel als die Hausziegen, die aus menschlicher Haltung stammen. Dieses spricht dafür, daß Hausziegen zu verschiedenen Zeiten und mehrfach auf Montecristo eingeführt wurden. Eine Einkreuzung von Hausziegen in die Steinbock-Population von Graubünden konnte nicht nachgewiesen werden. Die für die Erhaltung der genetischen Variabilität auf Montecristo notwendige Mindestgröße der dortigen Population wird abgeschätzt.

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