Geographical partitioning of goat diversity in Europe and the Middle East

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Summary

Thirty microsatellite markers were analysed in 1426 goats from 45 traditional or rare breeds in 15 European and Middle Eastern countries. In all populations inbreeding was indicated by heterozygosity deficiency (mean $F_{IS} = 0.10$). Genetic differentiation between breeds was moderate with a mean F_{ST} value of 0.07, but for most (*c.* 71%) northern and central European breeds, individuals could be assigned to their breeds with a success rate of more than 80%. Bayesian-based clustering analysis of allele frequencies and multivariate analysis revealed at least four discrete clusters: eastern Mediterranean (Middle East), central Mediterranean, western Mediterranean and central/northern Europe. About 41% of the genetic variability among the breeds could be explained by their geographical origin. A decrease in genetic diversity from the south-east to the north-west was accompanied by an increase in the level of differentiation at the breed level. These observations support the hypothesis that domestic livestock migrated from the Middle East towards western and northern Europe and indicate that breed formation was more systematic in north-central Europe than in the Middle East. We propose that breed differentiation and molecular diversity are independent criteria for conservation.

Keywords *Capra hircus*, genetic diversity, goats, microsatellites, traditional breeds.

Introduction

The domestic goat (*Capra hircus*) has been an important livestock resource after its domestication 10 000 years ago in the Middle East (Pringle 1998). The species remains of great importance in many developing countries and several developed countries. With some exceptions, domestic goat populations exploit marginal agricultural resources, and in contrast to farmers who raise other types of domestic livestock, those involved in these production systems are frequently smallholders with little political influence. Selective breeding in goats is less advanced and systematic than in other livestock. Lack of parentage control and breed purity has facilitated a con-

tinuous gene flow. Because artificial insemination with frozen sperm is rarely practiced (FAO 2004), this gene flow is limited by distance and geography.

Therefore, phylogeographical structure may be more obvious than in other domestic ruminants, cattle or even sheep. On the other hand, local management may have led to genetic isolation, which reduces the effective population size.

Studies on genetic diversity of goats have so far focused on Swiss breeds (Saitbekova *et al.* 1999) and Asian breeds (Yang *et al.* 1999; Barker *et al.* 2001; Li *et al.* 2002; Li & Valenti 2004). However, populations from Europe and the Middle East account for 48% of the world's goat population (FAO 1999). The aim of this study was to examine patterns of microsatellite variation in domestic goat populations from Europe and the Middle East as part of the European ECONO-GENE project (http://lasig.epfl.ch/projets/econogene/), which aims to identify populations of high conservation priority and to correlate these populations with the socio-economic conditions of the regions of origin (Bruford & The ECONOGENE Consortium 2005).

Materials and methods

Sample collection

A total of 1426 goats belonging to 45 traditional and local breeds were sampled from 15 European and Middle Eastern countries. For each breed, a maximum of three unrelated goats per flock from an average of 10 flocks per breed were sampled. The geographical location of the breeds studied is shown in Fig. 1. One-third of the sampled goats were males. The 45 breeds, their acronyms, countries of origin, and the sample sizes are given in Table 1. Nine breeds are catalogued as endangered by the FAO (http://www.fao.org/

dad-is/), whereas 27 breeds were considered not at risk, and information on nine breeds was not available.

Microsatellite markers

Details of the 30 microsatellite markers, including sequences of polymerase chain reaction primers, are given in Table S1.

Statistical analysis

Unbiased estimates of gene diversity [expected or Hardy–Weinberg (H–W) heterozygosity] (Nei 1987), observed

1 Brava	**13** Valais Black Neck	**25** Girgentana	**37** Skopelos
2 Verata	**14** Grisons Striped	**26** Grigia Molisana	**38** Greek
3 Payoya	**15** Peacock	**27** Argentata dell'Etna	**39** Makeras
4 Florida	**16** German Alpine	**28** Polish Fawn Coloured	**40** Angora
5 Malagueña	**17** Sarda	**29** Dukati	**41** Hair
6 Guadarrama	**18** Corse	**30** Hungarian Native	**42** Abaza
7 Pyreneene	**19** Orobica	**31** Muzhake	**43** Gurku
8 Rove	**20** Camosciata (Alpine)	**32** Hasi	**44** Beeshi
9 French Alpine	**21** Bionda dell'Adamello	**33** Capore	**45** Najrani
10 Valdostana	**22** Thuringian Forest	**34** Liquenasi	
11 St. Gallen Booted	**23** Pinzgauer	**35** Mati	
12 Swiss Alpine	**24** Tauern Pied	**36** Carpathian	

Figure 1 Geographical position of 45 traditional and local goat breeds sampled in 15 countries. Three unrelated individuals were collected at each farm.

Table 1 Details of 30 microsatellite loci typed on 45 European and Middle Eastern goat breeds.

Breed name	Acronym	Country	n	H_e	MNA	F_{IS}	F_{ST}	Individuals correctly assigned (%)	Not assigned to pre-defined breed (%)
Capore	AlCAP	Albany	31	0.744	7.8	0.103	0.053	48.4	6.5
Dukati[1]	AlDUK	Albany	30	0.742	7.8	0.075	0.049	53.3	0.0
Hasi	AlHAS	Albany	31	0.739	8.0	0.096	0.050	51.6	6.5
Liqenasi	AlLIQ	Albany	31	0.752	7.9	0.091	0.070	64.5	3.2
Mati	AlMAT	Albany	30	0.712	7.9	0.100	0.045	53.3	3.3
Muzhake	AlMUZ	Albany	30	0.758	8.0	0.087	0.044	33.3	3.3
Pinzgauer[1]	AtPIZ	Austria	31	0.668	6.7	0.050	0.066	90.3	3.2
Tauern Pied[1]	AtTAS	Austria	31	0.658	5.3	0.045	0.104	100.0	0.0
Swiss Alpine	ChALP	Switzerland	62	0.648	7.3	0.096	0.083	87.1	4.8
Grisons Striped[1]	ChGRS	Switzerland	31	0.670	6.5	0.075	0.066	90.3	3.2
Peacock[1]	ChPCG	Switzerland	31	0.617	6.0	0.095	0.081	90.3	3.2
St. Gallen Booted	ChSGB	Switzerland	31	0.605	5.6	0.048	0.092	93.5	6.5
Valais Black Neck	ChVBN	Switzerland	31	0.602	5.2	0.113	0.119	100.0	0.0
Makeras	CyMAK	Cyprus	32	0.732	7.4	0.118	0.077	87.5	0.0
German Alpine	DeBDE	Germany	31	0.693	7.0	0.117	0.056	64.5	3.2
Thuringian Forest[1]	DeTWZ	Germany	31	0.664	6.1	0.049	0.091	96.8	3.2
Florida	EsFLR	Spain	31	0.688	7.3	0.078	0.074	77.4	6.5
Guadarrama	EsGDR	Spain	31	0.678	7.7	0.129	0.056	51.6	9.7
Malagueña	EsMLG	Spain	31	0.700	7.4	0.063	0.050	67.7	3.2
Payoya	EsPYY	Spain	30	0.676	6.8	0.109	0.071	83.3	6.7
Verata	EsVRT	Spain	31	0.650	6.9	0.147	0.071	77.4	3.2
French Alpine	FrALP	France	44	0.681	7.6	0.128	0.059	75.0	0.0
Corse	FrCOR	France	30	0.661	6.9	0.112	0.064	90.0	3.3
Pyreneenne	FrPYR	France	30	0.667	6.0	0.293	0.081	93.3	16.7
Rove	FrROV	France	31	0.634	6.5	0.098	0.078	96.8	6.5
Greek	GrGRG	Greece	30	0.746	8.7	0.104	0.040	23.3	0.0
Skopelos	GrSKO	Greece	31	0.696	6.7	0.080	0.065	93.5	3.2
Hungarian Native	HuNAT	Hungary	31	0.688	7.0	0.061	0.062	77.4	6.5
Argentata dell'Etna[1]	ItARG	Italy	31	0.741	8.2	0.077	0.051	61.3	6.5
Bionda dell'Adamello	ItBIO	Italy	31	0.682	6.6	0.110	0.055	71.0	3.2
Camosciata (Alpine)	ItCAM	Italy	30	0.658	6.1	0.096	0.065	80.0	3.3
Girgentana[1]	ItGIR	Italy	30	0.656	5.7	0.132	0.089	100.0	6.7
Grigia Molisana[1]	ItGMO	Italy	31	0.715	7.5	0.125	0.054	74.2	9.7
Orobica	ItORO	Italy	31	0.590	5.2	0.094	0.112	100.0	9.7
Sarda	ItSAR	Italy	31	0.699	7.4	0.122	0.059	71.0	6.5
Valdostana	ItVAL	Italy	31	0.651	6.0	0.105	0.088	93.5	6.5
Polish Fawn Coloured	PlBUK	Poland	31	0.683	6.9	0.111	0.063	67.7	0.0
Brava	PtBRA	Portugal	30	0.641	6.1	0.130	0.076	83.3	3.3
Carpathian	RoCAR	Romania	31	0.765	8.3	0.082	0.046	29.0	6.5
Beeshi	SaBES	Saudi Arabia	30	0.709	8.0	0.114	0.078	70.0	0.0
Najrani	SaNAG	Saudi Arabia	29	0.712	7.5	0.123	0.086	80.0	6.9
Abaza	TrABA	Turkey	31	0.772	9.1	0.117	0.067	54.8	3.2
Angora	TrANG	Turkey	31	0.750	7.9	0.072	0.066	80.6	6.5
Gurku	TrGUR	Turkey	31	0.751	8.1	0.083	0.078	71.0	6.5
Hair	TrHAI	Turkey	30	0.722	8.3	0.069	0.071	73.3	0.0
45 breeds		15 Countries	1426	0.690[2]	449	0.100[2]	0.069[2]	74.9[2]	4.5[2]

n, sample size; F_{IS} and F_{ST}: Wright's F- statistics; H_e, expected heterozygosity; MNA, mean number of alleles.
[1]Listed by FAO as having endangered risk status.
[2]Unweighted mean values.

heterozygosity (Hedrick 1983) and the number of alleles per breed were calculated using the Microsatellite Toolkit (Park 2001). Version 2.9.3 of the program Fstat (http://www2.unil.ch/popgen/softwares/fstat.htm) was used for

calculating allelic richness (number of alleles in a sample of standardized size).

Genotypic frequencies were tested for H–W equilibrium using the GENEPOP computer package (Raymond & Rousset

1995), which performs a probability test using a Markov chain (dememorization = 5000, 100 batches and 1000 iterations per batch).

Wright's *F*-statistics (F_{IT}, F_{IS} and F_{ST}; Wright 1965) were calculated with the Genetix 4.0 (Belkhir *et al.* 2001) program. The significance of F_{IT} and F_{IS} was tested by 1000 permutations within the whole set of breeds and within each breed respectively. Significant deviation of F_{ST} from the null hypothesis was tested using random permutations of genotypes among samples.

Four approaches were used to analyse the genetic relationships among individuals and breeds. First, Nei's (Nei 1972) and Reynold's (Reynolds *et al.* 1983) distances were calculated using the Population Program v1.2.28 (http://www.pge.cnrs-gif.fr/bioinfo/populations/index.php) and used to the construction of trees or networks. Secondly, clustering of breeds and estimates of the proportions of the individual genomes that were derived from the respective inferred clusters were obtained using the model-based clustering program Structure (Pritchard *et al.* 2000). Estimated cluster membership coefficients of breeds were converted into genetic distances of breeds and represented in a neighbour-joining tree (Fig. S2). Thirdly, multivariate correspondence analysis (Lebart *et al.* 1984), which is analogous to principal component analysis with allele frequencies used to represent the breed position, was performed with the Genetix 4.0 program (Belkhir *et al.* 2001). Fourthly, a population assignment analysis was performed using the procedure proposed by Baudouin *et al.* (2004) and implemented in the GeneClass2 program (Piry *et al.* 2004). Posterior estimates of the allelic frequencies were obtained from the sample values with a Bayesian approach. These estimates were then used to simulate genotypes from the reference populations and derive an empirical probability distribution of the likelihood of genotypes belonging to their populations of origin. Bayes theorem was also applied to calculate the probability of an individual belonging to a certain population, given its genotype, as the quotient of the probability of finding its genotype given that it comes from that particular population, and the sum of the corresponding probabilities for all populations. A measure of the 'rarity' of an individual goat within its population was obtained in the form of an exclusion probability.

Results

Genetic variability

There was significant variation in the 30 microsatellites within this study, with 449 alleles in the 45 breeds, five to 43 alleles per locus and an average of 14.9 alleles (Table S2). Expected (H_e) and observed (H_o) heterozygosities per locus over all breeds ranged from 0.246 to 0.895 with an average of 0.69 and 0.62 respectively. The average expected heterozygosity over all loci ranged from 0.59 (Orobica)

to 0.77 (Abaza) per breed (Table 1). Positive F_{IS} values per locus and per breed with a mean value of 0.10 indicate inbreeding in all breeds. This was confirmed by the discrepancy between the observed and expected heterozygosities and by the difference between the observed and effective number of alleles (Table 1).

Microsatellites *DRBP1*, *P19* and *BM6444* were in H–W disequilibrium ($P < 0.005$) and were excluded from model-based clustering and correspondence analysis. *DRBP1* and *P19* are within the major histocompatibility complex (Schwaiger *et al.* 1993), which is under strong natural selection pressure (Hedrick & Kim 2000). Only two breeds (Pyreneenne and Abaza) had more than three loci in H–W disequilibrium. Twenty-four microsatellite markers were in H–W equilibrium in more than 90% of the breeds.

Genetic distances and clustering

All but one pairwise F_{ST} values were significantly positive ($P < 0.01$) and ranged from 0.004 (Greek to Mati) to 0.16 (Najrani to Valais Black Neck). However, the average genetic differentiation between breeds was moderate, with a mean F_{ST} of 0.07.

Comparison of genetic distances (Fig. S1) indicate that the Reynolds distances, which measure genetic drift, underestimate the divergence of eastern Mediterranean breeds (Saudi Arabia, Turkey, Albania and Cyprus) with a high heterozygosity. Model-based clustering (Pritchard *et al.* 2000) of the goat microsatellite genotypic values shows that the likelihood of the observed data increased with the predefined number of clusters (k), and reached a plateau at $k = 25$–30 (Fig. 2). This indicates that the most significant
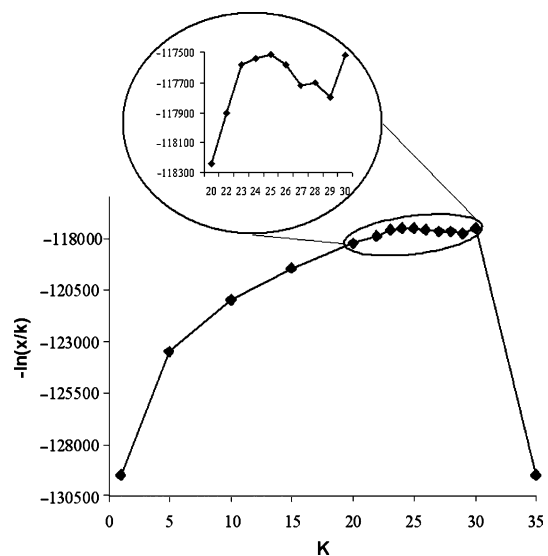

Figure 2 Plot of data likelihoods for several values of k: ln Pr($X|k$) vs. k. Mean values of five independent runs are plotted with Monte Carlo Markov Chain iterations ranging from 250 000 (50 000 burn-in length) for $k = 10$ to 500 000 (150 000 burn-in length) for $k = 35$ (see http://pritch.bsd.uchicago.edu/structure.html).
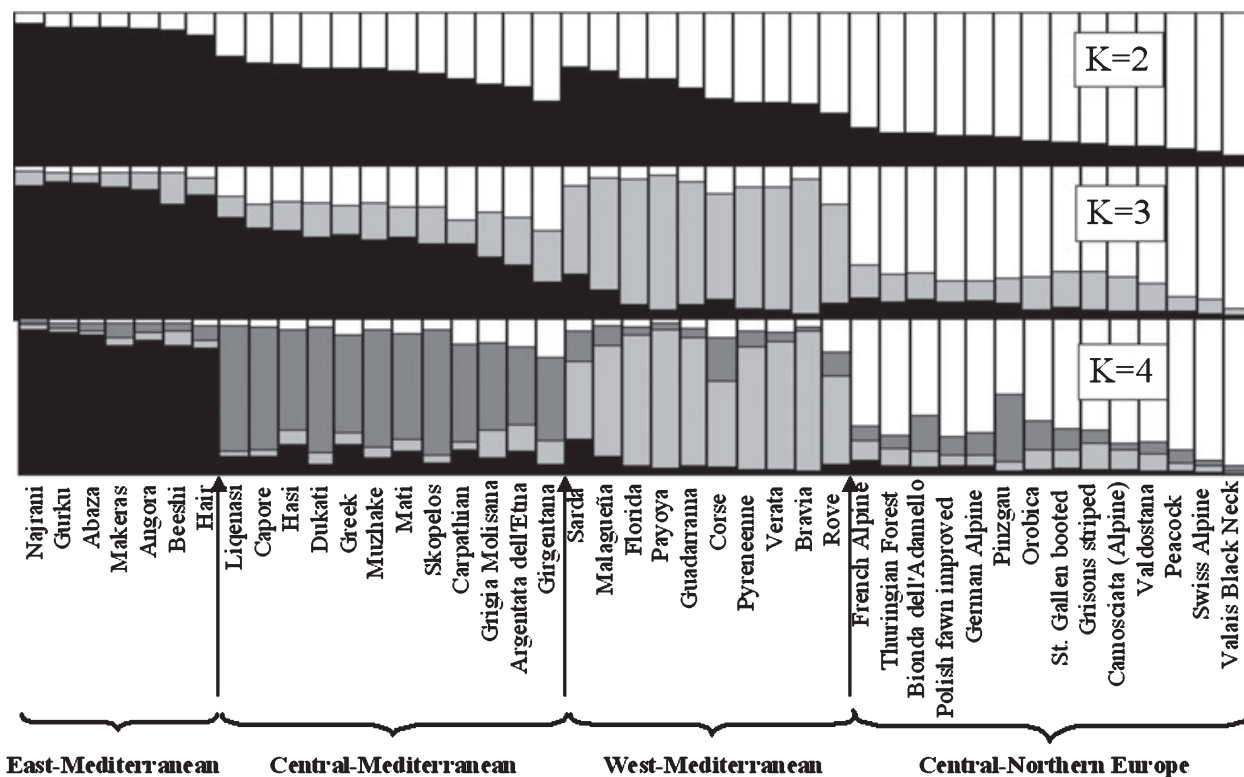
Figure 3 Estimated membership fractions of goat breeds for each of the *k* inferred clusters with *k* = 2–4. Each breed is represented by a stacked column broken into *k* white, grey or black segments, indicating the proportion of membership of each breed to the *K* clusters. The highly inbred Tauern Pied and the Hungarian native were omitted.
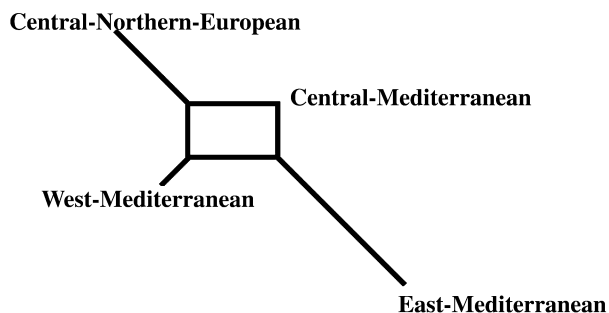

Figure 4 Neighbour-network of F_{ST} distances of the four main clusters.

Table 2 Diversity parameters for the four major clusters of European goat breeds.

	Allelic richness[1]	H_o	H_e	F_{ST}	F_{IS}
East Mediterranean	7.9[a]	0.663[a]	0.737[a]	0.033	0.10[a]
Central Mediterranean	7.3[ab]	0.658[a]	0.726[a]	0.040	0.10[a]
West Mediterranean	6.8[bc]	0.584[b]	0.671[b]	0.051	0.13[b]
Central-north European	6.1[c]	0.594[b]	0.654[b]	0.069	0.10[a]

The highly inbred Tauern Pied and Hungarian Native without clear cluster assignment were excluded from this analysis. Values with the same superscript letters are not significantly ($P < 0.05$) different. H_e, expected heterozygosity; H_o, observed heterozygosity.

subdivision was at the level of breeds or of groups of closely related breeds. Analysis at lower *k*-values may indicate a subdivision of the goat population (Rosenberg *et al.* 2002) that preceded breed formation. In the analysis shown in Fig. 3, we omitted the relatively inbred and allele-poor Tauern Pied (Table 1), which confounded the analysis by an apparent relation to central Mediterranean breeds, and the Hungarian native, which behaved like a composite of other breeds with large inferred components of all clusters. As shown in Fig. 3, results for *k* = 2 indicate a Near East to north-central European transition. Setting *k* = 3 generated a cluster of western Mediterranean populations. The clearest subdivision appeared at *k* = 4 with the following clusters

of breeds: eastern Mediterranean, central Mediterranean, western Mediterranean and central/northern European. Clustering at higher *k*-values mainly led to a further division of the north-central breeds with a tendency of inbred breeds to group together or to form their own cluster (see Fig. 4).

A subdivision in four major clusters of cluster is also supported by the following observations:

1 Clustering at the *k*-value that maximized the likelihood of the data yielded membership coefficients of 25 inferred clusters. If these values were converted into genetic distances, the resulting neighbour-joining tree of distances reproduced the four main clusters (Fig. S2a).

2 A neighbour-joining tree on the basis of D_S distances (Fig. S2b) also showed the four clusters as well as the relationships of breeds from the same region.

3 In a correspondence analysis (Fig. S3), the first axis accounts for 12% of the total inertia and separated the eastern Mediterranean, central Mediterranean plus western Mediterranean and north-central Europe clusters. The second axis accounted for 6.6% of the total inertia and separated the central and the western Mediterranean clusters.

Breeds from the eastern Mediterranean cluster were the most variable in terms of allelic richness and heterozygosity (Table 2). However, F_{ST} values indicated that the genetic differences among the eastern Mediterranean breeds were relatively low. In contrast, north-central European breeds had a lower diversity but a higher degree of breed differentiation.

A Bayesian approach (Baudouin & Lebrun 2000) assigns individuals to the population that has the highest likelihood for the individual genotype. The mean percentage of individuals correctly assigned for all breeds (Table 1), correlated with F_{ST} and with expected heterozygosity, was higher for north-central breeds (64.5–100%) than for eastern Mediterranean breeds (23.3–87.5%). Percentage of excluded individuals (Cornuet *et al.* 1999) is given in the last column of Table 1. Rejection of the assignment to its own breed was higher than 10% only in the French Rove goats.

Discussion

The goat breeds studied in this paper had considerable genetic diversity. The mean number of 14.9 alleles per breed was also found in 10 European sheep breeds (14.9 alleles/breed; Byrne *et al.* unpublished results), but it is higher than for 14 cattle breeds from different continents (11.4 alleles/breed; Loftus *et al.* 1999) or 16 European local beef-cattle breeds (6.5 alleles/breed; Cañón *et al.* 2001). Three of the four Turkish breeds had relatively high heterozygosity values (≥ 0.75), but the Abaza breed combined a high genetic variability with an above-average inbreeding value. The lowest genetic variability was observed in several Alpine breeds with heterozygosity values around 0.6 as reported earlier for eight Swiss goat breeds (Saitbekova *et al.* 1999). A positive correlation ($r \sim 0.35$) was detected between population size and heterozygosity (data not shown).

The values for inbreeding obtained in this work (mean F_{IS} 0.10) were between the values of 0.23 reported for 11 Asian goat populations in an analysis of 25 microsatellites (Barker *et al.* 2001) and of 0.03 reported for 12 Chinese indigenous goat populations in an analysis of 26 microsatellites (Li *et al.* 2002). Because many loci contribute to these average values, an effect of null alleles or selection is not likely. An effect of the sampling strategy is more plausible because the data were collected from 10 flocks per breed. If mating of related animals occurred, positive F_{IS} values would reflect the Wahlund effect of a genetic subdivision within breeds.

A typical feature of the genetic constitution of livestock is the existence of distinct breeds genetically isolated and subject to the systematic selection of animals conforming to breeding objectives. The levels of breed differentiation were relatively low given that these animals were sampled from a very large area. The average F_{ST} value of 0.069 was lower than the values of 0.14 recorded for Asian goats (Barker *et al.* 2001) and of 0.17 for Swiss goat breeds (Saitbekova *et al.* 1999). A similar value (0.10) was reported for a set of Chinese goat populations (Li *et al.* 2002). All pairwise F_{ST} values were significant ($P < 0.01$) except for the geographically close Greek and Albanian Mati goats.

Gene flow among most breeds has probably been restricted by geographical isolation rather than adherence to pedigree or the use of herd-books, which for goat breeds are either lacking or were only recently established. A geographical restriction of genetic contacts of population may cause geographical clines or maintain clines that predate breed formation. Examination of population structure using the model-based clustering method (Pritchard *et al.* 2000) yielded at least four clusters that correlated with different regions: east Mediterranean, central Mediterranean, west Mediterranean and central/northern Europe. The same clusters were found by the hierarchical neighbour-joining tree algorithm and by analysis of correspondence. Other clusters defined at higher *k*-values corresponded to breeds with a relatively high level of inbreeding or were non-hierarchical. For instance, clustering at $k = 10$ defined an exclusive Spanish cluster, but at higher *k*-values the Florida and Malagueña breeds from the eastern Spanish coast were clustered with the French and Italian breeds of Corsica and Sardinia.

If the four major geographical clusters, instead of breeds, are considered for partitioning genetic variability, the proportion of variability attributable to variation among clusters is 2.83% ($F_{ST} = 0.0283$), which is almost half (41%) of the variability attributable to breed origin ($F_{ST} = 0.069$).

Genetic distances between the major clusters were visualized in a neighbour-net representation (Huson & Bryant 2006). This suggests a transition from the Asian breeds via the Balkan breeds to those of Alpine Europe, but also indicates a more direct link of Middle Eastern and Spanish breeds. In addition, genetic radiation resulted in a high level of genetic and phenotypic differentiation in north-central breeds, but reduced the number of microsatellite alleles (Tables 1 and 2, Fig. S2b). Similar observations have been made for sheep (Lenstra & The ECONOGENE Consortium 2005) and cattle (European Cattle Genetic Diversity Consortium, unpublished data; Medjugorac *et al.* 1994; Loftus *et al.* 1999; Cymbron *et al.* 2005). These patterns with clear south-east to north-west gradients provide additional support for the hypothesis that people living in the eastern Mediterranean developed goat domestication, which spread to south-eastern and then to west-central and northern Europe. The relative short distance between Spanish and Middle Eastern breeds suggests a relatively fast migration

along the Mediterranean coast. This has also been proposed for cattle by Cymbron *et al.* (2005). The loss of alleles is probably the consequence of repeated founder effects during migration events (Cymbron *et al.* 2005).

The proportion of correct assignments of individuals to their breeds of origin correlated with the F_{ST} value ($r = 0.79$) and was negatively correlated with heterozygosity ($r = -0.76$). However, the influence of heterozygosity on assignment success is not as clear in previous reports. Blott *et al.* (1999) found little influence, while Estoup *et al.* (1998) and Manel *et al.* (2002) suggest that higher heterozygosity provides better assignment performance.

In conclusion, values of heterozygosities and allelic richness indicate that Middle Eastern breeds are a reservoir of goat diversity, whereas a high level of breed differentiation exists in the more developed populations. We propose that both resources of genetic variability are relevant for conservation strategies because of their impact on adaptive and economic traits.

Acknowledgements

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Supplementary Material

The following supplementary material is available online at http://www.blackwell-synergy.com:

Figure S1 Plot of the pair-wise Nei (D_S) standard genetic distances vs. Reynolds (D_R) genetic distances by geographical origin. These genetic distances can be related through

$$E(D_s) = \frac{E(D_R)H_0}{(1 - H_0)}$$

(Laval *et al.* 2002), where H_0 is the founder heterozygosity.

Figure S2 (a) Neighbour-joining tree with equalized branch lengths of genetic distances based on estimated membership coefficients $q_k(i)$ of breed i for cluster k via

$$d_s(i,j) := \sum_{k=1}^{K} |q_k(i) - q_k(j)| \frac{q_k(i) + q_k(j)}{2}.$$

Distances were averaged over five different runs at $k = 25$ and represented in a neighbour-joining tree by the algorithm implemented in the SplitsTree program (Huson & Bryant 2006). (b) Neighbour-joining tree of D_S distances of breeds.

Figure S3 Correspondence analysis of allele frequencies of 27 loci typed in 45 local goat populations.

Table S1 Details of the 30 microsatellite markers included in the analysis.

Table S2 Number of alleles, range of allele sizes and expected and observed heterozygosities for 30 microsatellite markers in 45 European and Middle Eastern goat breeds.