Chapter 29
Conservation of Goat Populations from Southwestern Europe Based on Molecular Diversity Criteria

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Abstract Goat farming plays a key role in agricultural activity and in maintaining forest lands in Southwestern Europe. Remarkably, the Iberian Peninsula represents nearly 25% of the European goat census. Goat husbandry is often associated with low input production systems and uses selective breeding programs, which are less advanced than those employed in other livestock. Native goat breeds are very well adapted to produce in marginal areas under extensive conditions. Loss of their genetic diversity could have important economic, ecological and scientific implications as well as social consequences. Several methodologies have been developed to preserve the genetic diversity of single populations, but additional problems arise

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when a group of breeds, i.e., subpopulations, is considered in conservation programs. The conservation priority of a breed depends on its contribution to the overall genetic diversity of the species, in terms of the intrinsic genetic variation that it harbors and also of its relationship with other breeds. However, the estimation of the contributions of each of these two components to overall genetic diversity cannot be easily assessed. Besides, conservation goals in the short-term (avoidance of inbreeding) and long-term (adaptation to future environmental changes) should be considered when taking conservative decisions. A comprehensive analysis of Iberian goat breeds has been carried out to evaluate conservation priorities based on methodologies that account for within- or between-breed genetic diversity, or combinations of both. Based on genetic distinctiveness, breeds such as Palmera, Formentera, and Blanca Celtibérica were prioritized, whereas the maximum priority was assigned to Florida, Pirenaica, Retinta, and Moncaína breeds when focusing on within-breed diversity. Overall, combined approaches showed very little variation among breeds reflecting a history of extensive gene flow, partly due to transhumance and recent divergence. The main conclusion of our study is that these statistical analyses are useful, but conservation decisions must take into account other factors in addition to strict genetic diversity classification.

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29.1 Introduction

Domestic goats (*Capra hircus*) have traditionally played an important role in the animal husbandry sector of Portugal and Spain, producing high quality products under extensive conditions, often in marginal and forest lands. Even though goat numbers in both countries have declined sharply over the last decades, they still represent nearly 25% of the European goat census. Currently, there are 6 and 23 native breeds officially recognized in Portugal and Spain, respectively. In general, they are very well adapted to harsh local conditions, but their existence has been threatened by the progressive abandonment of agriculture in marginal areas and by uncontrolled crossbreeding with foreign transboundary breeds (Carolino et al. 2016; de Sierra et al. 2016). In Fig. 29.1 we show examples of individuals from two very distinct native goat breeds from Spain and Portugal, namely Palmera (top) from the Canary Islands and Preta de Montesinho (bottom) from the Northern region of Portugal, respectively.

Wild goats (*C. pyrenaica*) are also found in the Iberian Peninsula living in mountain areas. After decades of demographic decline due to severe population bottlenecks, the current risk status of this species is, according to the Red List criteria, the Least Concern, and the current population trend is increasing with about 50,000 individuals distributed in more than 50 subpopulations (http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T3798A10085397.en. Revised on May 10, 2017). Although hybridization between wild and domestic goats has been reported (Alasaad et al. 2012), a circumstance that represents an important issue for conservation purposes, major threats to Iberian wild goats are related to habitat fragmentation and poaching. Appropriate conservation polices could help to prevent further loss of emblematic populations, such as the extinction of the bucardo subspecies (*C. p. pyrenaica*), occurred in 2000.

Zooarchaeological and ancient DNA data suggest that the ancestor of domestic goats is the bezoar (*C. aegagrus*), which was domesticated approximately 10,000 years ago in at least two independent but contemporary Middle Eastern regions, i.e., the oriental Taurus and the Zagros mountains in Turkey and today's Iran, respectively, with substantial gene flow among European domestic goat populations since the Early Neolithic (Fernandez et al. 2006; Zeder 2008). Regarding domestic goats from the Iberian Peninsula, their origins and evolution are still under debate. It has been suggested that distinct goat populations from various geographic regions, namely from North Africa, have contributed to the Iberian gene pool (Pereira et al. 2005, 2009). In goats from the Canary Islands, an insular territory of Spain, autosomal DNA analysis supports an African influence at least for some breeds (Martínez et al. 2016). Genetic diversity and breed relationships based on microsatellite markers were reported for Portuguese native breeds by Bruno de Sousa et al. (2011), while Martínez et al. (2015) presented a comprehensive analysis of breeds from Portugal and Spain. Both studies revealed high levels of genetic diversity in Iberian goats and moderate differentiation among breeds, as expected given the historical migratory movements of small ruminants

Fig. 29.1 Individuals from two very distinct native goat breeds from Spain and Portugal, namely Palmera (top; provided by Juan Capote) from the Canary Islands and Preta de Montesinho (bottom; provided by António Sá, www.antoniosa.com) from the Northern region of Portugal, respectively

across the Iberian Peninsula associated with transhumance (Manzano and Casas 2010), a feature that promoted breed admixture.

The reduction in census and the corresponding increase in inbreeding in local goat populations have raised concerns about the best approaches to prevent genetic erosion, emphasizing the need for maintaining the genetic diversity that these breeds harbor as well as the unique adaptation features they have developed. When the goal is to maintain global genetic diversity and several breeds are candidates for conservation, priorities may have to be established based on the potential contribution of each breed to overall genetic diversity. Hence, the metapopulation is defined by the overall domestic goat population subdivided in breeds, i.e., subpopulations. Under this perspective, the contribution of a breed to both between- and within-breed genetic variation must be taken into consideration, when conservation decisions are implemented, and correctly weighted. However, to determine the relative weights of the within- and between-breed components of genetic variability is not simple at all, and several approaches have been proposed to address this issue (Toro and Caballero 2005).

Weitzman (1992) proposed a method where the marginal contribution of a breed to a metapopulation is assessed based on genetic distances among breeds, as the change in the expected diversity resulting from removing the breed from the metapopulation. In this case, only the contribution of the breed to the between-breed component of genetic diversity is considered and the conservation value will be likely assigned to geographically isolated breeds. To a certain extent, such assignment could be artifactual, being mainly due to founder effects, genetic drift or the accumulation of inbreeding. Thus, the need to further consider within-breed genetic diversity become clear, but it is not obvious which weights should be given to the between- and within-breed components of genetic diversity. Olivier and Foulley (2005) proposed an aggregate diversity procedure, where the fixation index F_{ST} and its complementary $(1-F_{ST})$ are used to weight the between- and within-breed components of genetic diversity, respectively. Other authors have suggested to assign arbitrary weights to these two components, for example attributing five times more weight to the between-breed genetic diversity (Piyasatian and Kinghorn 2003).

Alternative methods for establishing conservation priorities have been proposed, in an attempt to overcome the limitations of the procedures outlined above. These methods are known as the Core Set procedures, and they are designed to minimize global molecular coancestry in the metapopulation, by taking into account both the within- and between-breed kinship coefficients (Eding and Meuwissen 2001, 2003). Methodological variations of these procedures have also been proposed, e.g., using average molecular coancestries based on allele frequencies (Caballero and Toro 2002).

The multiple scenarios that can be envisaged when assessing the conservation value of breeds have been investigated in cattle (Cañon et al. 2011; Ginja et al. 2013) and pigs (Cortes et al. 2016), but no clear-cut conclusions were reached regarding the best combination of weights to be given to the between- and within-breed contributions to genetic diversity. Nonetheless, some of these approaches may be useful when investigating breed phylogenetic relationships and geographical patterns of genetic diversity distribution (Jordana et al. 2017). Besides genetic criteria, other aspects such as the environmental impact of a breed, as well as its social, cultural and historical role should also be taken into account when defining conservation priorities and strategies (Ruane 1999; Gandini et al. 2004).

In this chapter, we have selected a comprehensive sample of goat breeds from Portugal and Spain, including the Balearic and the Canary Islands (Spain), to evaluate different combinations of breed contributions to overall genetic diversity with the ultimate goal of establishing conservation priorities. We describe briefly the goat populations included in this analysis, and we also provide an overview of the methods available to prioritize these animal genetic resources for conservation. Finally, we discuss the results obtained with these different approaches, as well as their intrinsic limitations and outcomes.

29.2 Iberian Goat Breeds Selected for Conservation Analyses

The Iberian Peninsula is considered as a biodiversity hotspot, with local native breeds representing important reservoirs of genetic diversity. Spanish goats included in our conservation analysis were the following 19 officially recognized breeds: Azpi Gorri, Moncaína, Pirenaica, and Blanca de Rasquera from the North and North Eastern regions; two ecotypes of the same breed Blanca Celtibérica and Celtibérica, del Guadarrama, Retinta, and Verata from the Central region; Murciano-Granadina, Malagueña, Payoya, Florida, Blanca Andaluza (or Blanca Serrana), and Negra Serrana from the Southern region; Mallorquina, and Pitiüsa or Ibicenca from the Balearic Islands; and Majorera, Palmera, and two ecotypes of Tinerfeña (North and South) from the Canary Islands (Fig. 29.2). Additionally, two

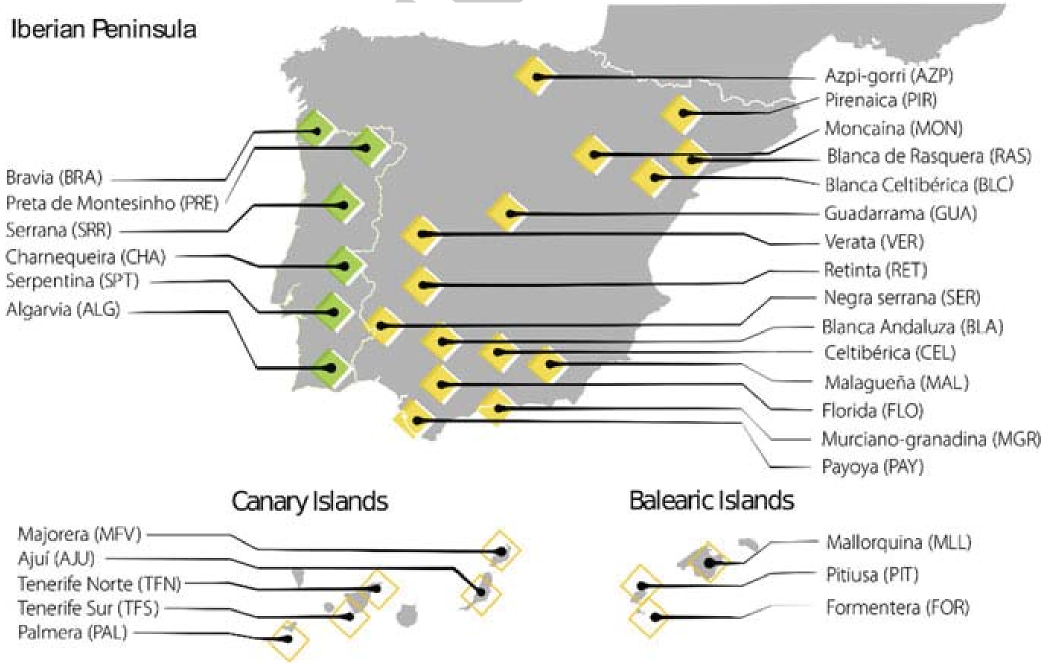

Fig. 29.2 Map showing the distribution of 29 native goat populations from Spain and Portugal

small isolated non-officially recognized goat populations were analyzed, namely Formentera and Ajuí from the Balearic and the Canary Islands, respectively. The populations Blanca Celtibérica and Celtibérica are two well-differentiated varieties of the same breed, each raised in different regions of the Iberian Peninsula (Fig. 29.2). The Northern and Southern ecotypes of the Tinerfeña breed are adapted to distinct climate conditions, i.e., while the former is raised in the humid and rainy areas of the Northern region of the Tenerife island, the latter is well adapted to the dry climate typical of the South (Martínez et al. 2006). The six Portuguese breeds analyzed here were the following: Bravia, Serrana and Preta de Montesinho from the Northern region; Charnequeira from the Central region; and Serpentina and Algarvia from the South of the country (Fig. 29.2).

Detailed information on the Iberian goat populations selected for conservation analyses is shown in Table 29.1, namely their geographic origin, breed names and acronyms, risk status as defined by the Food and Agriculture Organization of the United Nations—FAO, their census based on the number of breeding females (when available), and sample sizes. For comparison purposes, data on three transboundary commercial goat breeds, Saanen, Anglo-Nubian and Alpine, were also included in the analysis. A total of 970 goats were sampled by the BioGoat consortium (https://biogoat.jimdo.com/) according to recommended procedures for the collection of biological specimens (blood, semen or hair roots). Details on the sampling procedures and breed distributions were reported by Martínez et al. (2015). International and national regulations regarding experimental research on animals were strictly followed during collection procedures.

Considering the census of these breeds and the European Union regulation EC 445/2002, which establishes a number below 10,000 purebred breeding females as the threshold for classifying a goat breed as threatened of extinction, there are a total of 24 endangered Iberian native breeds (22 of which were included in our study; Table 29.1). Nevertheless, the majority of these goat populations are managed by well-organized breeder associations which keep and update herdbooks and carry out in situ conservation programs. Although Portugal and Spain have similar goat densities (5.8 animals per km^2), the origin of their caprine gene pools is quite different. In Spain, there are three million goats which belong almost entirely to native breeds or their crosses (de Sierra et al. 2016); while in Portugal the native goats represent only 12.5% of the national stock, and the majority of the animals has been crossed with transboundary commercial breeds (Carolino et al. 2016).

Iberian native breeds are traditionally raised in extensive agri-silvi-pastoral systems. Using poor natural pastures and marginal agroforestry lands, goats are able to optimize these resources thus contributing to the management of these ecosystems. Moreover, they play a crucial socio-economic role by contributing to the economic development of rural populations in less-favored regions. In general, Iberian native goat breeds have dual-purpose meat-milk abilities and they generate a large variety of cheese and meat products. Their certification by the European Union as quality products (http://ec.europa.eu/agriculture/quality/door/list.html) enhances the increased regional appreciation and commercial value of these breeds.

Table 29.1 Within-breed genetic diversity of 29 native goats from the Iberian Peninsula, the Balearic and Canary Islands, as well as three transboundary commercial breeds

Goat breed (acronym)	FAO risk status	Year	Census	n	$H_e \pm$ S.D.	$H_o \pm$ S.D.	MNA ± S.D.	Rt ± S.D.
Spain (continental part)								
Azpi Gorri (AZP)	Endangered	2016	1005^a	40	0.654 ± 0.041	0.634 ± 0.017	6.79 ± 2.76	3.10 ± 0.75
Blanca Andaluza (BLA)	Endangered	2016	7334^a	39	0.664 ± 0.042	0.628 ± 0.018	6.68 ± 2.69	3.18 ± 0.86
Blanca Celtibérica (BLC)	Endangered	2016	7288^a	30	0.646 ± 0.046	0.577 ± 0.021	6.58 ± 2.32	3.11 ± 0.88
Blanca de Rasquera (RAS)	Endangered	2015	4617^a	40	0.642 ± 0.051	0.588 ± 0.018	6.37 ± 2.95	3.07 ± 0.91
Celtibérica (CEL)	Endangered	2016	N.A.^{a}	40	0.657 ± 0.044	0.618 ± 0.018	7.21 ± 2.72	3.16 ± 0.85
Florida (FLO)	Not at risk	2016	$20{,}165^a$	40	0.695 ± 0.036	0.663 ± 0.017	7.47 ± 3.39	3.33 ± 0.77
Guadarrama (GUA)	Endangered	2016	7498^a	11	0.643 ± 0.056	0.580 ± 0.038	4.68 ± 2.11	3.09 ± 1.01
Malagueña (MAL)	Not at risk	2016	$39{,}420^a$	40	0.678 ± 0.043	0.623 ± 0.018	6.79 ± 2.95	3.24 ± 0.83
Moncaína (MON)	Endangered	2016	2809^a	29	0.688 ± 0.049	0.626 ± 0.021	6.89 ± 3.00	3.35 ± 0.97
Murciano-Granadina (MGR)	Not at risk	2016	$63{,}113^a$	40	0.650 ± 0.052	0.608 ± 0.018	6.53 ± 2.41	3.16 ± 0.89
Negra Serrana (SER)	Endangered	2016	4496^a	40	0.652 ± 0.039	0.598 ± 0.018	6.37 ± 2.69	3.06 ± 0.73
Payoya (PAY)	Endangered	2016	529^a	35	0.669 ± 0.042	0.677 ± 0.018	6.47 ± 3.20	3.19 ± 0.88
Pirenaica (PIR)	Endangered	2016	2117^a	18	0.690 ± 0.045	0.654 ± 0.027	6.58 ± 2.57	3.34 ± 0.87
Retinta (RET)	Endangered	2016	1884^a	15	0.688 ± 0.042	0.677 ± 0.029	5.61 ± 2.40	3.25 ± 0.84
Verata (VER)	Endangered	2016	8893^a	28	0.652 ± 0.048	0.539 ± 0.022	6.53 ± 2.61	3.10 ± 0.86
Balearic Islands								
Formentera (FOR)	Endangered	2016	$^{†,\ a}$	11	0.585 ± 0.052	0.541 ± 0.035	4.11 ± 1.59	2.77 ± 0.82
Mallorquina (MLL)	Endangered	2016	141^a	40	0.634 ± 0.046	0.596 ± 0.018	6.68 ± 2.67	3.02 ± 0.83
Pitiüsa (PIT)	Endangered	2016	124^a	40	0.647 ± 0.046	0.580 ± 0.018	6.63 ± 2.87	3.10 ± 0.85
Canary Islands								
Ajuí (AJU)	Endangered	–	1700^b	40	0.648 ± 0.029	0.620 ± 0.018	6.05 ± 2.30	2.99 ± 0.66
Majorera (MFV)	Endangered	2016	9664^a	40	0.635 ± 0.038	0.612 ± 0.018	6.53 ± 3.06	3.00 ± 0.75

(continued)

Table 29.1 (continued)

Goat breed (acronym)	FAO risk status	Year	Census	*n*	H_e ± S.D.	H_o ± S.D.	MNA ± S.D.	Rt ± S.D.
Palmera (PAL)	Endangered	2016	5949[a]	40	0.489 ± 0.040	0.493 ± 0.019	4.16 ± 1.68	2.34 ± 0.62
Tenerife North (TFN)	Not at risk	2016	11,625[a]	40	0.601 ± 0.038	0.575 ± 0.018	5.32 ± 2.36	2.80 ± 0.73
Tenerife South (TFS)				40	0.598 ± 0.038	0.583 ± 0.018	6.00 ± 2.69	2.84 ± 0.69
Portugal								
Algarvia (ALG)	Endangered	2016	4049[c]	30	0.677 ± 0.038	0.647 ± 0.020	6.37 ± 2.69	3.16 ± 0.75
Bravia (BRA)	Not at risk	2016	10,908[c]	39	0.628 ± 0.048	0.620 ± 0.018	6.05 ± 2.57	2.96 ± 0.78
Charnequeira (CHA)	Endangered	2016	4283[c]	29	0.683 ± 0.036	0.655 ± 0.020	6.37 ± 2.39	3.22 ± 0.77
Preta de Montesinho (PRE)	Endangered	2016	1107[c]	37	0.663 ± 0.045	0.563 ± 0.019	6.79 ± 2.86	3.15 ± 0.90
Serpentina (SPT)	Endangered	2016	4519[c]	30	0.666 ± 0.047	0.615 ± 0.020	6.89 ± 3.26	3.17 ± 0.91
Serrana (SRR)	Not at risk	2016	18,249[c]	29	0.669 ± 0.045	0.594 ± 0.021	6.95 ± 2.90	3.20 ± 0.84
Alpine (ALP)	Not at risk	–	N.A.	35	0.703 ± 0.048	0.683 ± 0.018	6.74 ± 2.84	3.39 ± 0.87
Anglo-Nubian (ANG)	Not at risk	–	N.A.	40	0.638 ± 0.030	0.606 ± 0.018	5.79 ± 2.23	2.94 ± 0.60
Saanen (SAA)	Not at risk	–	N.A.	36	0.641 ± 0.054	0.602 ± 0.019	6.63 ± 2.48	3.11 ± 0.90

Geographic origin, breed names and acronyms, FAO risk status, census, sample sizes (*N*), observed (*Ho*) and unbiased expected (*He*) heterozygosities, and mean number of alleles (MNA) are shown; *S.D.* standard deviation; *N.A.* not applicable

Census Spanish goat breeds at 31/12/2016 considering the number of registered animals (breeding females)

[a] https://aplicaciones.magrama.es/arca-webapp/flujos.html?_flowId=explotaDatosCensosRazaExcel-flow&_flowExecutionKey=e3s1

[b] https://aplicaciones.magrama.es/arca-webapp/flujos.html?_flowId=catalogoRazas-flow&_flowExecutionKey=e1s

[c] Census Portuguese goat breeds at 31/12/2016 considering the number of registered animals (breeding females)—http://dad.fao.org/

[†] Population registered in the same herdbook of Pitiüsa

29.3 Microsatellite Markers Suitable to Define Conservation Priorities in Goats

We used a microsatellite dataset previously generated by the BioGoat research consortium (Martínez et al. 2015; Ginja et al. 2017). A set of 19 short tandem repeat markers, recommended by the International Society for Animal Genetics (ISAG)/ Food and Agriculture Organization of the United Nations (FAO) Advisory Committee for genetic diversity studies in goats was genotyped, namely: *BM1329, BM6506, BM6526, BM8125, CRSM60, CSRD247, ETH010, ETH225, ILSTS011, INRA063, MAF065, MAF209, McM527, MM12, OarFCB048, OarFCB304, SPS115, SRCRSP08, and TGLA122*. Genotyping and allele standardization procedures have been validated and they were described in detail by Bruno de Sousa et al. (2011). Among the 19 markers, there was no evidence of null alleles segregating at high frequencies ($r > 0.2$) in any of the analyzed breeds (Bruno de Sousa et al. 2011; Martínez et al. 2015; Ginja et al. 2017). Although linkage disequilibrium was significant ($P < 0.0001$) for several short tandem repeat pairs, only the following three pairs appear to correspond to loci located in the same chromosome and thus are probably truly linked: *BM1329/SRCRSP08*, *BM8125/MAF209* and *BM8125/OarFCB048* (Ginja et al. 2017).

29.4 Brief Description of the Methods Used to Prioritize Animal Genetic Resources for Conservation Purposes

Conservation analysis depends on how the metapopulation is defined in order to investigate partial contributions of each sub-population to global genetic diversity. Furthermore, breed prioritization will vary considerably according to the relative importance of the within- and between-breed components of genetic diversity contributed by each breed, being the genetic relationships among breeds another important factor worth to mention. In this study, we included in a single metapopulation the 29 native goat populations from the Iberian Peninsula, the Balearic and the Canary Islands, as well as the three transboundary goat breeds. This allows to compare the impact on conservation estimates of prioritizing more diverse local goats *versus* highly selected commercial breeds.

For the conservation analyses, we followed the methods described by Cañon et al. (2011). Moreover, we categorized the different approaches as reported in Ginja et al. (2013), i.e., methods that aim at minimizing the overall kinship coefficient of the metapopulation (kinship-based methods); a method that reflects only the between-breed diversity component (Weitzman approach); and combined approaches that take into consideration both the within- and between-breed components of global genetic diversity.

Within-breed genetic diversity was characterized by using simple statistics obtained with GENETIX v. 4.05.2 (Belkhir et al. 1996–2004), namely observed (*Ho*) and unbiased expected (H_e) heterozygosities, and mean number of alleles (MNA) per breed. Additionally, FSTAT v. 2.9.3 (Goudet 2001) was used to estimate the *F* statistics per locus according to Weir and Cockerham (1984), and *P*-values were obtained based on 1000 randomizations. Allelic richness (R_t) over all loci for each breed was also calculated by rarefaction using this software and assuming a minimum of three animals per breed.

29.4.1 Minimizing Inbreeding of the Metapopulation: Kinship-Based Methods

We applied the Core Set methods of Eding et al. (2002) to investigate the population contributions to global diversity that account for within- and between-breed kinship coefficients by (1) minimizing the overall kinship coefficient of the metapopulation considered and (2) eliminating the genetic overlap between breeds included in the core set (Boettcher et al. 2010). Estimation of possible negative contributions by a given population is avoided through an iterative process that assigns a zero value to the lowest contribution and recalculates contributions after removal of that population.

In the absence of genealogical data, kinships were estimated from molecular data with different methods: (1) marker-estimated kinships (MEKs) obtained from individual genotypes, as described by Eding and Meuwissen (2001); (2) a variation of the MEK method based on log-linear regressions (Eding and Meuwissen 2003) obtained with the weighted log-linear model (WLM); (3) same as (2) but the log-linear regressions were obtained with the mixed model (WLMM); and (4) average molecular coancestries (*fm*) based on allele frequencies (Caballero and Toro 2002). MEKs were estimated with a macro function in Excel (Cañon et al. 2011), whereas the solutions for WLM and WLMM were obtained with matrices built with the MATLAB software (The MathWorks, Inc., USA). Average coancestry coefficients within (f_{ii}) and between (f_{ij}) each goat breed were calculated with the MOLKIN3 software (Gutierrez et al. 2005). Conservation analyses based on these similarity matrices (MEKs, WLM, WLMM and *fm*) were carried out with a FORTRAN program, as in Ginja et al. (2013). We derived pairwise kinship distances from the MEK coefficients following Eding et al. (2002) as: $d(i, j) = f_{ii} + f_{ij} - 2f_{ij}$. Kinship genetic distances were used to construct the neighbor-net phylogeny of the goat breeds with the SPLITSTREE4 4.12.6 software (Huson and Bryant 2006). Subsequently, breeds were sorted based on their genetic proximity to build contour plots of kinship coefficients (MEKs and *fm*) with the MATLAB software (The MathWorks, Inc., USA). In order to directly assess the importance of within-breed genetic diversity, partial contributions were also calculated as the proportional variation in the expected heterozygosity of the metapopulation after removal of each breed ($\mathrm{PC}_{\mathrm{He}}$).

29.4.2 Prioritizing Breed Differentiation: The Weitzman Approach

We calculated the partial contributions ($\mathrm{PC}_{\mathrm{Weitz}}$) of each goat breed to the total genetic diversity using the Weitzman method (Weitzman 1992). Here, Reynolds genetic distances (Reynolds et al. 1983) were used as a measure of between-breed diversity, while within-breed diversity was ignored. This approach estimates the reduction in length of the branches in a maximum likelihood phylogeny after removal of closely related populations, and $\mathrm{PC}_{\mathrm{Weitz}}$ were calculated with the FORTRAN program developed by García et al. (2005). Pairwise Reynolds genetic distances were calculated with the POPULATIONS 1.2.32 software (Langella 1999–2002) and used to obtain a neighbor-net phylogeny of the Iberian goat breeds with the SPLITSTREE4 4.12.6 software (Huson and Bryant 2006).

29.4.3 Accounting for Within- and Between-Breed Genetic Diversity: Combined Approaches

Ideally, analyses of conservation priorities should take into account both within- and between-population genetic variability in order to make more accurate management decisions. We used three approaches to calculate contributions that combine these two levels of the global diversity of the metapopulation: (1) aggregate diversity ($\mathrm{PC}_{\mathrm{Fst}}$) (Ollivier and Foulley 2005), which uses Wright's F_{ST} to and its complementary $(1 - F_{ST})$ to weight the between- and within-population components of diversity, respectively, i.e., $\mathrm{PC}_{\mathrm{Fst}} = \mathrm{PC}_{\mathrm{WEITZ}} * F_{ST} + \mathrm{PC}_{\mathrm{He}} * (1 - F_{ST})$; (2) the approach of Piyasatian and Kinghorn (2003), which assigns the between-population component an arbitrary weight, i.e., five times higher than within-breed genetic diversity, such that $\mathrm{PC}_{5:1} = \mathrm{PC}_{\mathrm{WEITZ}} * 0.833 + \mathrm{PC}_{\mathrm{He}} * (1 - 0.833)$; and (3) the method proposed by Caballero and Toro (2002) and Fabuel et al. (2004), which gives equal weights to within-population coancestries and genetic distances. In this case, Nei's minimum distances (Nei 1987) were used and calculations were carried out with the MOLKIN3 software (Gutierrez et al. 2005).

29.5 Results of the Different Conservation Approaches Applied to Iberian Goats

29.5.1 Within-Breed Diversity and Genetic Relationships of Iberian Goats

Summary statistics describing the genetic diversity of the Iberian goat breeds under analysis are shown in Table 29.1. Overall, genetic diversity was high ($H_o = 0.606 \pm 0.042$, $H_e = 0.648 \pm 0.041$, MNA = 6.29 ± 0.81, and $R_t = 3.08 \pm 0.20$), with Florida from south Spain showing the highest diversity ($H_o = 0.663 \pm 0.017$, $H_e = 0.695 \pm 0.036$, MNA = 7.47 ± 3.39, and $R_t = 3.33 \pm 0.77$). Endangered and isolated populations had the lowest diversities ($H_o < 0.550$, $H_e < 0.600$, MNA < 5.0, and $R_t < 2.8$), namely Palmera and Formentera from the Canary and Balearic Islands, respectively. Among the three commercial transboundary breeds analyzed, Saanen, Anglo-Nubian and Alpine, this latter had the highest diversity across all estimates ($H_o = 0.683 \pm 0.018$, $H_e = 0.703 \pm 0.048$, MNA = 6.74 ± 2.84, and $R_t = 3.39 \pm 0.87$). The levels of within-breed diversity can also be assessed using kinship coefficients with either the MEKs obtained from individual genotypes or average coancestries (*fm*) estimated from allele frequencies. In order to visualize both within- and between-breed kinships, contour plots were drawn by sorting populations according to their genetic proximity defined in the phylogenetic neighbor-net graph of kinship distances (Fig. 29.3, top). In the contour plots of Fig. 29.4, red areas represent highly inbred goat breeds i.e., Palmera (MEKs = 0.355 and *fm* = 0.517) and Formentera (MEKs = 0.268 and *fm* = 0.442). The Neighbor-Net of Reynolds genetic distances is shown in Fig. 29.3 (bottom). Goats from the Canary Islands grouped together in a tight net, with a possible influence from the transboundary Anglo-Nubian goats and more distant relationships with the remaining breeds. The Balearic goats were closely related to breeds from the Iberian Peninsula, but Formentera showed a more distant branch probably as a result of genetic drift. The Pirenaica and Moncaína breeds from the Pyrenees were entangled with the transboundary Saanen and Alpine goats. The remaining populations from Spain and Portugal showed weak differentiation, with a strong degree of interspersing, regardless of their geographical distribution, as previously described by Martínez et al. (2015).

29.5.2 Conservation Analyses in Iberian Goats

The results of the conservation analyses carried out for the set of breeds included in this study are shown in Tables 29.2 and 29.3. The kinship-based methods, namely MEKs, *fm* and WLM, resulted in a considerable number of goat breeds with a null contribution to overall genetic diversity, i.e., 27, 24 and 25 breeds, respectively (out of 32). In consequence, only highly prioritized breeds can be easily identified, i.e.,

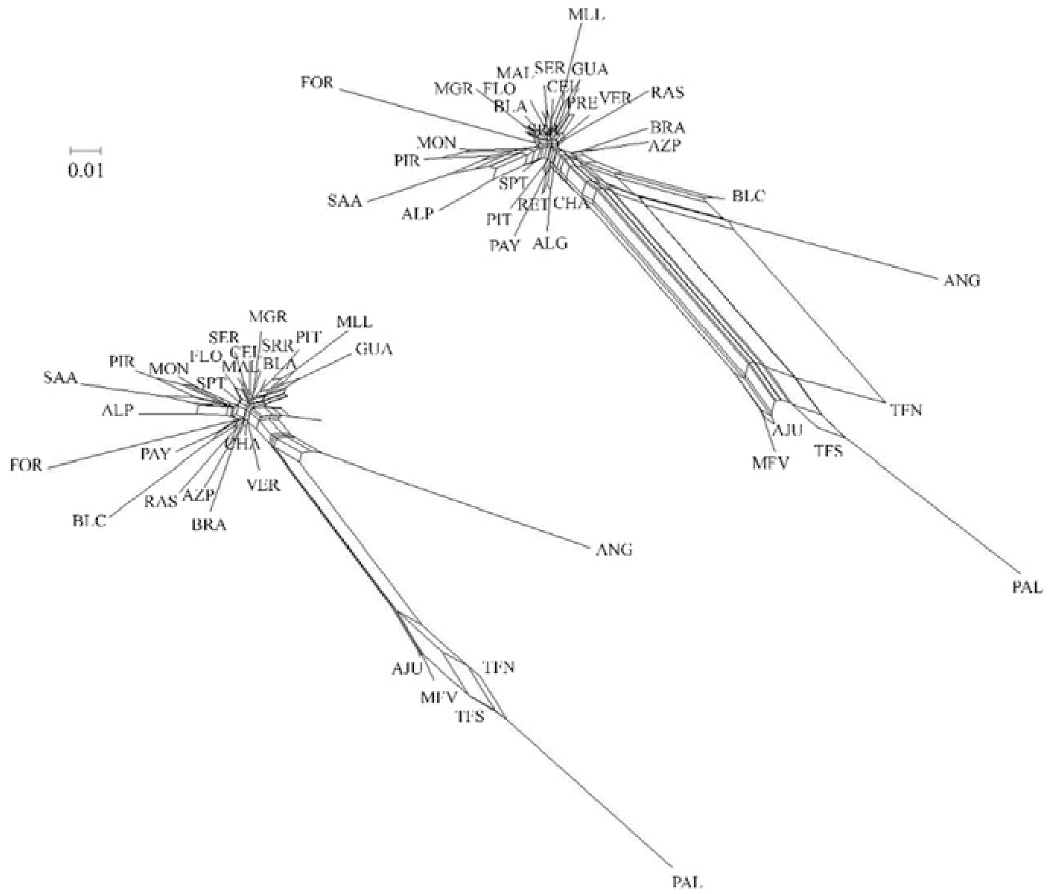

Fig. 29.3 Neighbor-net graph of kinship (top) and Reynolds (bottom) genetic distances depicting the relationships among 29 native goats from the Spain and Portugal, as well as three transboundary commercial breeds. Acronyms for breed names are defined in Table 29.1

Alpine, Ajuí, Anglo-Nubian, Pirenaica, Florida, Majorera, Moncaína, Blanca Celtibérica, and Retinta ($0.085 < \text{MEKs} < 0.281$, $0.014 < fm < 0.277$ and $0.0.010 < \text{WLM} < 0.234$) and the results were similar for the three methods. These results may reflect the high within-breed genetic diversity of these breeds, possibly as a result of crossbreeding. The WLMM method, which allows only one null contribution (in this case the Portuguese Bravia population), separated breeds more effectively and selected for conservation the breeds Anglo-Nubian, Alpine, Pirenaica, Majorera, Retinta, Ajuí and Moncaína goats ($0.56 < \text{WLMM} < 0.104$).

The proportional contribution of each breed to the average heterozygosity of the metapopulation resulted in many negative values (15 breeds). If these breeds were removed, this would lead to a ‘gain’ in diversity. In accordance with their inbred status (high within-breed kinship coefficients, f_{ii}), Palmera, Formentera, Tenerife South, Tenerife North, and Bravia breeds had the most negative PC_{He} values (between −0.798 and −0.103). This method ranked breeds displaying greater H_e values at a higher level, such as Alpine, Florida, Pirenaica, Retinta, Moncaína ($0.191 < \text{PC}_{\text{He}} < 0.268$). In contrast, Charnequeira, Malagueña, Algarvia, Payoya,

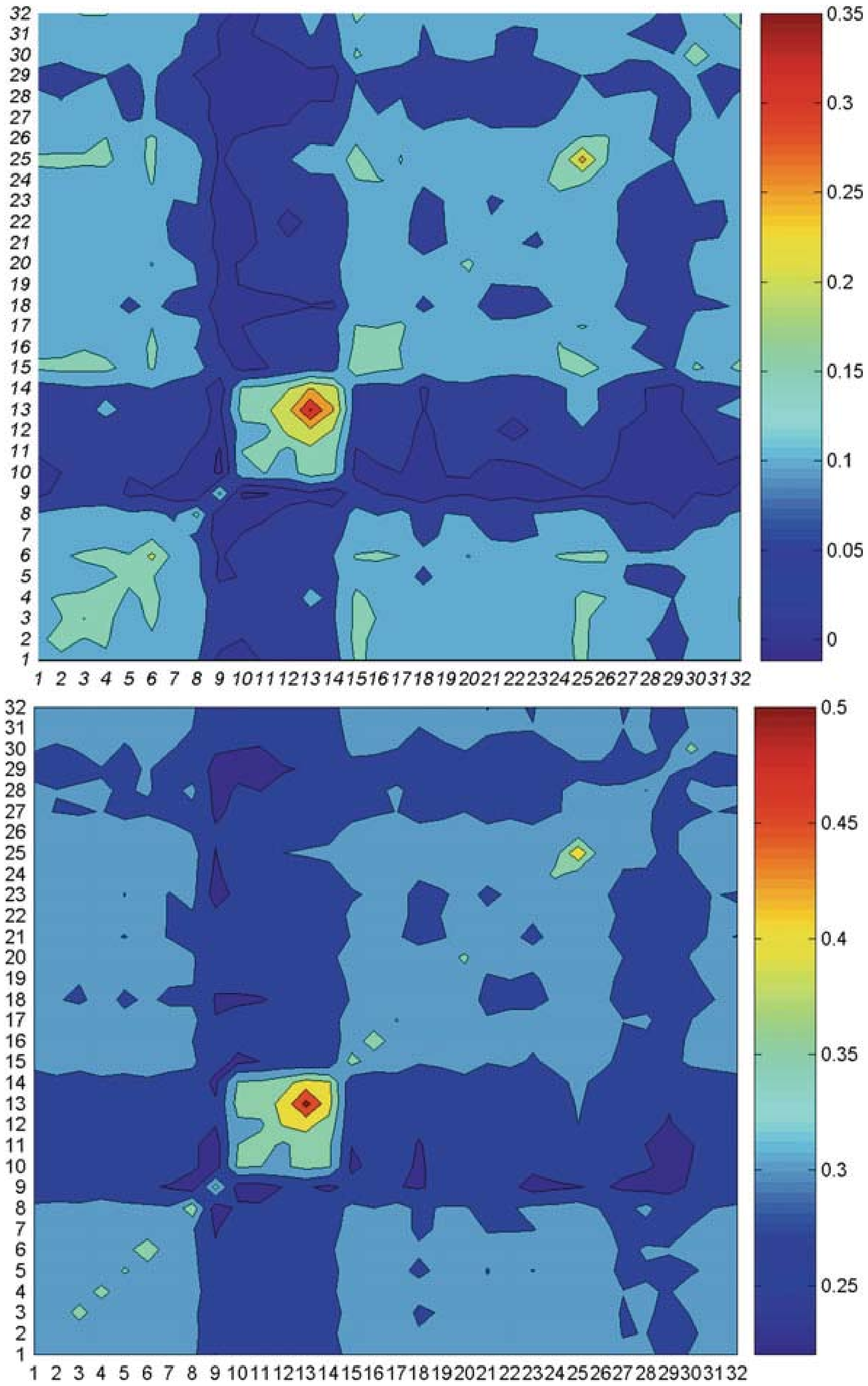

Fig. 29.4 Contour plots of marker-estimated kinships (MEKs; top) and average coancestries (*fm*; bottom) with goat breeds sorted according to their kinship phylogeny. Breed numbers correspond to the following: 1. Serrana, 2. Preta de Montesinho, 3. Blanca de Rasquera, 4. Verata, 5. Azpi Gorri, 6. Bravia, 7. Charnequeira, 8. Blanca Celtibérica, 9. Anglo-Nubian, 10. Ajuí, 11. Majorera, 12. Tenerife North, 13. Palmera, 14. Tenerife South, 15. Guadarrama, 16. Mallorquina, 17. Celtibérica, 18. Florida, 19. Malagueña, 20. Negra Serrana, 21. Algarvia, 22. Retinta, 23. Payoya, 24. Pitiüsa, 25. Formentera, 26. Serpentina, 27. Moncaína, 28. Pirenaica, 29. Alpine, 30. Saanen, 31. Blanca Andaluza, 32. Murciano-Granadina

Table 29.2 Contributions of 29 Iberian native and three commercial transboundary breeds to overall genetic diversity of goats according to: marker-estimated kinships (MEKs), average coancestries (*fm*), weighted log-linear model (WLM), weighted log-linear mixed model (WLMM), Weitzman formula (PC_{Weitz}), proportional variation of expected heterozygosity (PC_{He}), aggregate diversity (PC_{Fst}), and the Piyasatian and Kinghorn formula ($PC_{5:1}$)

Goat breed	Meks	*fm*	WLM	WLMM	PC_{He}	PC_{Weitz}	PC^{a}_{Fst}	$PC_{5:1}$
Azpi Gorri	0	0	0	0.016	0.024	2.50	0.225	2.09
Blanca Andaluza	0	0	0	0.014	0.074	1.15	0.161	0.97
Blanca Celtibérica	**0.085**	0.053	0	0.018	−0.018	**6.23**	**0.488**	**5.19**
Blanca de Rasquera	0	0	0	0.025	−0.035	3.08	0.218	2.56
Celtibérica	0	0	0	0.017	0.040	1.22	0.136	1.02
Florida	**0.099**	**0.110**	0	**0.040**	**0.227**	1.14	0.301	0.99
Guadarrama	0	0	0	0.003	−0.029	2.84	0.204	2.36
Malagueña	0	0	0	0.027	0.141	0.70	0.186	0.61
Moncaína	0	**0.058**	0.058	**0.056**	**0.191**	1.34	0.284	1.15
Murciano-Granadina	0	0	0	0.023	0.005	2.62	0.217	2.18
Negra Serrana	0	0	0	0.002	0.015	1.16	0.108	0.97
Payoya	0	0	0	0.044	0.100	2.79	0.318	2.34
Pirenaica	0	0.014	**0.187**	**0.070**	**0.202**	1.28	0.289	1.10
Retinta	0	0	**0.168**	**0.061**	**0.195**	0.76	0.240	0.67
Verata	0	0	0	0.009	0.014	2.05	0.179	1.71
Formentera	0	0	0	0.019	−0.320	**6.34**	0.220	**5.23**
Mallorquina	0	0	0	0.014	−0.074	3.03	0.178	2.51
Pitiüsa	0	0	0	0.015	−0.009	2.11	0.162	1.76
Ajuí	**0.281**	**0.202**	0.010	0.057	−0.007	0.68	0.049	0.57
Majorera	0	0.036	**0.169**	0.064	−0.072	1.20	0.031	0.99
Palmera	0	0	0	0.008	−0.798	**12.20**	0.255	**10.03**
Tenerife North	0	0	0	0.019	−0.239	2.99	0.023	2.45
Tenerife South	0	0	0	0.034	−0.254	1.65	−0.100	1.33
Algarvia	0	0	0	0.032	0.140	2.43	**0.325**	2.05
Bravia	0	0	0	0.000	−0.103	2.39	0.099	1.97
Charnequeira	0	0	0	0.015	0.166	1.17	0.248	1.00
Preta de Montesinho	0	0	0	0.024	0.070	0.95	0.142	0.80
Serpentina	0	0	0	0.018	0.082	0.90	0.148	0.76
Serrana	0	0	0	0.026	0.100	0.71	0.150	0.61
Alpine	**0.279**	**0.277**	**0.234**	**0.081**	**0.268**	3.00	**0.489**	2.54
Anglo-Nubian	**0.257**	**0.251**	**0.174**	0.104	−0.055	**11.51**	**0.882**	**9.58**
Saanen	0	0	0	0.043	−0.043	**5.07**	**0.371**	**4.22**

Values for the five breeds with the highest contributions are shown in bold

[a] Aggregate diversity was calculated as: $PC_{Fst} = PC_{WEITZ} * 0.081 + PC_{He} * 0.919$

Table 29.3 Average coancestries (f_{ii}) and Nei's genetic distances (D_{Nei}), contributions to global coancestry (f) and to average Nei's distance (D), global coancestry (GDT|i) and proportional loss or gain in genetic diversity after removing each breed, proportional contributions (PC) to a pool of maximum genetic diversity weighted and unweighted by sample sizes

Goat breed	f_{ii}	D_{NEI}	Contribution to f^a	Contribution to D^a	GDT|i	loss/gain (%)[a]	$PC^a_{weighted}$	$PC^b_{unweighted}$
Azpi Gorri	0.354	0.056	0.011	0.026	0.702	0.049	3.69	3.12
Blanca Andaluza	0.341	0.046	0.011	0.025	0.703	0.090	3.61	3.13
Blanca Celtibérica	**0.383**	0.077	0.009	0.019	0.702	−0.021	2.74	3.08
Blanca de Rasquera	0.366	0.060	0.011	0.026	0.703	0.066	3.65	3.08
Celtibérica	0.352	0.049	0.011	0.026	0.703	**0.110**	3.67	3.10
Florida	0.314	0.049	0.010	**0.027**	0.701	−0.104	**3.87**	**3.27**
Guadarrama	0.368	0.065	0.003	0.007	0.702	0.004	1.01	3.10
Malagueña	0.331	0.047	0.011	0.026	0.702	0.031	**3.76**	3.18
Moncaína	0.328	0.058	0.007	0.020	0.701	−0.085	2.78	**3.24**
Murciano-Granadina	0.358	0.055	0.011	0.026	0.703	0.084	3.66	3.10
Negra Serrana	0.358	0.051	0.011	0.026	0.703	**0.135**	3.64	3.08
Payoya	0.340	0.057	0.009	0.023	0.702	−0.033	3.30	3.18
Pirenaica	0.352	0.067	0.005	0.012	0.702	−0.041	1.69	3.18
Retinta	0.333	0.050	0.004	0.010	0.702	−0.004	1.41	3.19
Verata	0.365	0.52	0.008	0.018	0.703	**0.103**	2.53	3.05
Formentera	**0.442**	0.090	0.004	0.007	0.702	0.038	0.94	2.88
Mallorquina	0.374	0.063	0.011	0.026	0.703	0.075	3.63	3.07
Pitiüsa	0.361	0.054	0.011	0.026	0.703	**0.102**	3.65	3.08
Ajuí	0.360	0.088	0.010	**0.027**	0.700	−0.228	**3.82**	**3.23**
Majorera	0.372	**0.092**	0.010	**0.027**	0.701	−0.206	**3.78**	3.20
Palmera	**0.517**	**0.145**	**0.014**	0.023	0.702	0.025	3.30	2.79
Tenerife North	**0.405**	**0.094**	**0.012**	0.025	0.702	−0.045	3.62	3.06

(continued)

Table 29.3 (continued)

Goat breed	f_{ii}	D_{NEI}	Contribution to f^a	Contribution to D^a	GDT|i	loss/gain (%)^a	$PC^a_{weighted}$	$PC^b_{unweighted}$
Tenerife South	**0.409**	**0.094**	**0.012**	0.025	0.702	−0.025	3.60	3.04
Algarvia	0.333	0.055	0.008	0.020	0.702	−0.044	2.85	3.21
Bravia	0.379	0.059	**0.012**	0.025	0.703	**0.148**	3.49	3.02
Charnequeira	0.328	0.046	0.008	0.019	0.702	0.012	2.74	3.19
Preta de Montesinho	0.348	0.048	0.010	0.024	0.703	0.093	3.40	3.11
Serpentina	0.345	0.047	0.008	0.019	0.703	0.070	2.77	3.12
Serrana	0.344	0.047	0.008	0.019	0.703	0.060	2.68	3.12
Alpine	0.311	0.061	0.008	0.024	0.701	−0.210	3.45	**3.33**
Anglo-Nubian	0.368	**0.115**	0.009	**0.028**	0.698	−0.514	**3.93**	**3.32**
Saanen	0.368	0.074	0.010	0.024	0.702	−0.071	3.34	3.14

Values for the five breeds with the highest contributions are shown in bold, except for contributions to f and D for which only the two highest values are in bold

[a] average coancestries weighted by sample sizes; [b] average coancestries estimated by ignoring sample sizes; mean coancestry within-breeds, $f = 0.363$; mean Nei's minimum distance in the metapopulation, $D = 0.066$; mean coancestry in the metapopulation, $f = 0.298$; global genetic diversity of the metapopulation, GDT = 0.702

and Serrana breeds were associated with intermediate contributions ($0.100 < PC_{He} < 0.166$).

The Weitzman approach prioritizes highly differentiated breeds (i.e., those with displaying large genetic distances with regard to their counterparts) based only on their contribution to between breed genetic diversity. In this case, breeds with the highest contributions ($5.07 < PC_{Weitz} < 12.20$) were Palmera, Anglo-Nubian, Formentera, Blanca Celtibérica, and Saanen followed by Blanca de Rasquera, Mallorquina, Alpine, Tenerife North, Guadarrama, Payoya, Murciano-Granadina, Azpi Gorri, Algarvia, Bravia, Pitiüsa, and Verata ($2.05 < PC_{Weitz} < 3.08$). The Preta de Montesinho, Serpentina, Retinta, Serrana, Malagueña and Ajuí breeds had the lowest contributions amongst all breeds (<1%).

The combined approach of Ollivier and Foulley (2005) (PC_{Fst}), which takes into account both within- and between-breed components of the genetic diversity, seems to provide more balanced solutions. In this case, the between-breed component (i.e., PC_{Weitz}) was weighted by the overall F_{ST} value of 0.081 obtained for the metapopulation of goat breeds. The PC_{Fst} approach prioritized breeds that also ranked high with the PC_{He} and the kinship-based methods (i.e., with high within-breed diversity), namely Alpine, Algarvia, Florida, Pirenaica and Moncaína ($0.284 < PC_{Fst} < 0.489$). Nevertheless, several breeds prioritized by PC_{Weitz} (i.e., with greater genetic distances) also had high PC_{Fst} estimates, particularly Anglo-Nubian ($PC_{Fst} = 0.882$), Blanca Celtibérica ($PC_{Fst} = 0.488$) and Saanen ($PC_{Fst} = 0.371$) and Payoya ($PC_{Fst} = 0.318$), while goat breeds Palmera, Charnequeira, Retinta, Azpi Gorri, Formentera, Blanca de Rasquera, Murciano-Granadina, and Guadarrama had intermediate conservation values ($0.200 < PC_{Fst} < 0.260$). Overall, the $PC_{5:1}$ method gave similar results, in terms of breed ranking for conservation, with regard to those obtained with the Weitzman approach, implying that higher between-breed genetic diversity was favored.

The results of the combined approach of Caballero and Toro (2002) and Fabuel et al. (2004) are shown in Table 29.3. The isolated Palmera breed from the Canary Islands made the greatest contribution to global coancestry (f, 0.014) because its within-breed coancestry was quite high ($f_{ii} = 0.517$). The Tenerife South, Bravia, and Tenerife North breeds made high contributions to f (0.012) as a consequence of their high f_{ii} values (~ 0.400) and also to their relatively low within-breed genetic diversity ($H_e \approx 0.600$). Although the Formentera, Blanca Celtibérica, Guadarrama, and Anglo-Nubian breeds had high f_{ii} values (between 0.368 and 0.442), their mean genetic distances were also large (between 0.065 and 0.115). Thus their contributions to f, obtained from the difference between f_{ii} and D_{Nei}, were less significant (between 0.003 and 0.009). Proportional contributions to genetic diversity were identical across goat populations ($PC_{weighted} \approx 3$), with only Formentera, Guadarrama, Retinta and Pirenaica ranking low ($PC_{weighted} < 2$). Nevertheless, lower estimates can be biased as a consequence of the rather small sample size of these populations ($N < 18$). Indeed, when the proportional contributions to genetic diversity are estimated by ignoring sample sizes ($PC_{unweighted}$), only the Formentera breed maintains its low ranking. The proportional contribution of each breed to a pool of maximum genetic diversity showed very little variation among goat breeds

(~0.700), but removal of the Anglo-Nubian, Ajuí, Alpine, and Majorera breeds from the metapopulation of goats caused the greatest loss in total genetic diversity (between −0.5 and −0.2%).

29.6 Limitations and Outcomes of Different Conservation Approaches When Prioritizing Iberian Goats

Organized programs for the conservation of Iberian goat breeds exist in Portugal and Spain, nonetheless goat populations have declined in both countries and most breeds are currently classified as endangered in the Domestic Animal Diversity Information System hosted by the FAO (http://dad.fao.org/). Ideally, a conservation program should target several breeds even though financial resources are limited. For this reason, conservation priorities need to be established. Factors that should be considered when defining such priorities include the importance of a breed in terms of genetic uniqueness but also its own genetic diversity, and other aspects such as adaptation to specific environments, display of unique phenotypes, cultural and historical value, contribution to environmental sustainability, etc. (Ruane 2000). Once priorities have been established, different conservation strategies can be applied, namely in situ or ex situ in vivo preservation, and cryoconservation, which differ in their ability to capture and maintain genetic diversity as well as to address the different aspects considered in the rationale for conservation (FAO 2012a). Knowledge of the population structure of a livestock species in terms of distribution of genetic variability within and between breeds is a key factor for establishing conservation priorities and strategies (Caballero and Toro 2002) aiming to maintain genetic diversity for the benefit of the future generations (Notter 1999).

Previous studies confirmed that Iberian goat breeds have retained high levels of genetic diversity and, with the exception Canarian goats, they are weakly differentiated as a consequence of extensive gene flow due to transhumance and common ancestry (Cañon et al. 2006; Bruno de Sousa et al. 2011; Martínez et al. 2015). It has also been claimed that long-distance cyclic migrations, the great mobility of goats, and recent divergence are the main causal factors that explain the poor phylogeographic structure detected with mitochondrial markers in the Iberian Peninsula (Azor et al. 2005; Pereira et al. 2005) and at a worldwide scale (Luikart et al. 2001; Fernandez et al. 2006). In order to preserve breed identities, reduce inbreeding, and maintain overall biodiversity when prioritizing breeds for conservation it is important to characterize both within- and between-breed genetic variability. For example, genetic substructure has been identified in several goat breeds from the Iberian Peninsula, such as the Spanish dairy goat Murciano-Granadina breed and the Portuguese Serrana breed (Martínez et al. 2015). While in the first case substructure results from breeding decisions to keep separate herds, the latter is associated with ecotypes raised in distinct geographic regions. Because several of these ecotypes may harbor specific adaptive traits, it is relevant that management strategies for breed conservation take into account the existence of weak population structure as well as the specificities of breed demographic histories (Cañon et al. 2011). As expected, conservation priorities of the goat populations analyzed here depended on whether the method used to set them placed more emphasis on the contribution of each breed to the within- or the between-breed components of genetic diversity. Thus, if the focus was on breed distinctiveness, priority was given to breeds such as Palmera, Anglo-Nubian, Formentera, Blanca Celtibérica, and Saanen, whereas if the focus was on within-breed diversity, priority was given to Alpine, Florida, Pirenaica, Retinta, and Moncaína breeds. Finally, the contribution to genetic diversity based on average coancestries combined with genetic distances showed very little variation among goat breeds (Table 29.3). This feature probably reflects the extensive levels of admixture observed across these breeds, in a way that all breeds made similar contributions to the overall genetic diversity of the metapopulation.

The difficulties and challenges associated with the choice of the best method to prioritize breeds for conservation decisions have been broadly discussed (Toro et al. 2009; Meuwissen 2009; Caballero et al. 2010; Cañon et al. 2011; Bruford et al. 2015). For instance, previous studies focused on cattle indicated that breeds with a small census, which are often inbred, will be selected for conservation when the emphasis is placed on the between-breed component of genetic diversity (Bennewitz et al. 2006; Consortium 2006; Ginja et al. 2013). This outcome invalidates the use of the Weitzman approach, which is based on genetic distances, as a single criterion for breed prioritization. In contrast, higher ranking will be given to large, and possibly crossbred, populations when the emphasis is placed on the within-breed component (Meuwissen 2009). This pattern of genetic variation distribution is typical of subdivided populations in which the global genetic diversity of the species is maintained at the cost of a loss in the genetic variability of the subpopulations. Overall, the choice of the most appropriate method to prioritize breeds for conservation decisions is determined by whether it is important to maintain genetic diversity in either the short- or long-terms. For example, if the focus is on short-term objectives, the emphasis should be placed on maintaining high levels of heterozygosity, while if the goal is focused on long-term goals, the main stress should be placed on allelic richness and breed differentiation (Medugorac et al. 2011). In several goat breeds, selection for adaptation to specific environments has played a major role in their genetic composition. Thus, maintaining high levels of allelic diversity is a key element for the long-term preservation of these breeds as well as for ensuring their ability to cope and adjust to future environmental changes. Maximizing heterozygosity may be a wrong approach, as highly crossbred breeds are often valued for conservation under these circumstances. Statistical analyses aimed at making conservation decisions are useful but they should be considered carefully, since there is a risk of ignoring certain breeds or breed groups in conservation programs. Thus, such decisions must take into account additional factors, including the results of other population genetics methods such as cluster and admixture analyses as well as other factors in addition to strict genetic diversity priorities.

The establishment of conservation decisions exclusively based on ‘neutral’ genetic markers, such as microsatellites, can fail to take into account important genetic information associated with phenotypic variation (e.g. morphology or production traits), disease resistance, and other adaptive traits. Whole-genome approaches using next-generation sequencing have been developed for livestock species, including goats, which allow for the identification of genomic regions under selection (Song et al. 2016; Dong et al. 2015; Wang et al. 2016). Because a high number of genetic markers (e.g., SNPs) in coding and non-coding genomic regions can be used in population genomics, these approaches can provide more reliable estimates of inbreeding coefficients, particularly when pedigree information is lacking, as well as more accurate measures of the genetic diversity and of the conservation value of the breeds under study (Hall et al. 2012). Nonetheless, it is necessary to carefully evaluate the usefulness of the analyses described here to define conservation priorities on the basis of whole-genome SNP data. This is even more important when prioritizing genetically distinct native breeds, because commercial SNPs may not be informative as these breeds were not considered when the marker arrays were developed (FAO 2012b). Additionally, genome sequencing will be extremely useful to identify genomic regions under selection in Iberian goats as well as in other breeds.

29.7 Concluding Remarks

Prior to the large scale application of the conservation principles discussed here, it is essential to reach a consensus on the specific criteria to be used in the definition of such priorities. Besides factors directly associated with genetic diversity, which have been the main subject of our discussion, other aspects such as the contribution of a breed to food security and economic return, demography and risk status, the existence of unique traits or specific adaptation features, historical and cultural values, the contribution to sustainable development and environmental balance, etc., should be also taken into account when defining conservation priorities (Ruane 2000). The final outcome may be an index combining the different ranking criteria weighted appropriately in order to establish conservation priorities, as outlined by the FAO (2012a, b). Moreover, high-throughput genetic markers, such as SNPs, may detect additional genetic factors related to breed differentiation, especially those underlying adaptation and production traits, and they should be further investigated for their potential applications in conservation genetics.

Recently and as a result of the last conference of the European Science Foundation Genomic Resources program (https://livestockgenomics.wordpress.com/2014/04/15/home/), several problems and challenges for the effective conservation of livestock genomic resources until 2020 were summarized in a publication (Bruford et al. 2015). One of the major conclusions was the following: “Despite the fact that the livestock sector has been relatively well-organized in the application of genetic methodologies to date, there is still a large gap between the current state-of-the-art in the use of tools to characterize genomic resources and its application to many non-commercial and local breeds, hampering the consistent utilization of genetic and genomic data as indicators of genetic erosion and diversity" (Bruford et al. 2015).

In any case, the consensus is that the best way to ensure the survival of a breed is to make it profitable and appealing to producers. The development of sustainable utilization and organized mating programs of goat breeds, and the added value resulting from their products, could make a major contribution towards their survival in the future.

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References

Alasaad S, Fickel J, Rossi L et al (2012) Applicability of major histocompatibility complex DRB1 alleles as markers to detect vertebrate hybridization: a case study from Iberian ibex x domestic goat in southern Spain. Acta Vet Scand 54:56. https://doi.org/10.1186/1751-0147-54-56

Azor PJ, Monteagudo LV, Luque M et al (2005) Phylogenetic relationships among Spanish goats breeds. Anim Genet 36(5):423–425

Belkhir K, Borsa P, Chikhi L, et al (1996–2004) GENETIX: logiciel sous Windows TM pour la génétique des populations. 4.02 edn. Laboratoire Génome, Populations, Interactions, CNRS, Université de Montpellier II, Montpellier, France

Bennewitz J, Kantanen J, Tapio I et al (2006) Estimation of breed contributions to present and future genetic diversity of 44 North Eurasian cattle breeds using core set diversity measures. Genet Sel Evol 38(2):201–220

Boettcher PJ, Tixier-Boichard M, Toro MA et al (2010) Objectives, criteria and methods for using molecular genetic data in priority setting for conservation of animal genetic resources. Anim Genet 41:64–77

Bruford MW, Ginja C, Hoffmann I et al (2015) Prospects and challenges for the conservation of farm animal genomic resources, 2015–2025. Front Genet 6:314. https://doi.org/10.3389/Fgene.2015.00314

Bruno de Sousa C, Martínez A, Ginja C et al (2011) Genetic diversity and population structure in Portuguese goat breeds. Livest Sci 135(2–3):131–139

Caballero A, Rodriguez-Ramilo ST, Avila V et al (2010) Management of genetic diversity of subdivided populations in conservation programmes. Conserv Genet 11:409–419

Caballero A, Toro MA (2002) Analysis of genetic diversity for the management of conserved subdivided populations. Conserv Genet 3:289–299

Cañon J, García D, Delgado JV et al (2011) Relative breed contributions to neutral genetic diversity of a comprehensive representation of Iberian native cattle. Animal 5(9):1323–1334

Cañon J, García D, García-Atance MA et al (2006) Geographical partitioning of goat diversity in Europe and the Middle East. Anim Genet 37(4):327–334

Carolino N, Bruno de Sousa B, Carolino I et al (2016) Biodiversidade caprina em Portugal. In: Vargas Bayona JE, Zaragoza Martínez L, Delgado Bermejo JV et al (eds) Biodiversidad caprina Iberoamericana. Universidad Cooperativa de Colombia, Bogotá, pp 57–74

Consortium ECGD (2006) Marker-assisted conservation of European cattle breeds: an evaluation. Anim Genet 37(5):475–481

Cortes O, Martínez AM, Cañon J et al (2016) Conservation priorities of Iberoamerican pig breeds and their ancestors based on microsatellite information. Heredity 117(1):14–24

de Sierra GEF, Belmonte SA, Camacho Vallejo ME et al (2016) Biodiversidad caprina en España. In: Vargas Bayona JE, Zaragoza Martínez L, Delgado Bermejo JV et al (eds) Biodiversidad caprina Iberoamericana. Universidad Cooperativa de Colombia, Bogotá, pp 13–56

Dong Y, Zhang XL, Xie M et al (2015) Reference genome of wild goat (*capra aegagrus*) and sequencing of goat breeds provide insight into genic basis of goat domestication. BMC Genom 16(1):431. https://doi.org/10.1186/S12864-015-1606-1

Eding H, Crooijmans RP, Groenen MA et al (2002) Assessing the contribution of breeds to genetic diversity in conservation schemes. Genet Sel Evol 34(5):613–633

Eding H, Meuwissen TH (2001) Marker-assisted estimates of between and within population kinships from genetic marker data for the construction of core sets in genetic conservation schemes. J Anim Breed Genet 118:141–159

Eding H, Meuwissen THE (2003) Linear methods to estimate kinships from genetic marker data for the construction of core sets in genetic conservation schemes. J Anim Breed Genet 120 (5):289–302

Fabuel E, Barragan C, Silio L et al (2004) Analysis of genetic diversity and conservation priorities in Iberian pigs based on microsatellite markers. Heredity 93(1):104–113

FAO (2012a) Cryoconservation of animal genetic resources. Animal production and health guide, vol 12. Food and Agriculture Organization of the United Nations, Rome, Italy

FAO (2012b) Draft guidelines on in vivo conservation of animal genetic resources. Comm Genet Resour Food and Agric, vol 7. Food and Agriculture Organization of the United Nations, Rome, Italy

Fernandez H, Hughes S, Vigne JD et al (2006) Divergent mtDNA lineages of goats in an Early Neolithic site, far from the initial domestication areas. Proc Natl Acad Sci USA 103 (42):15375–15379

Gandini GC, Ollivier L, Danell B et al (2004) Criteria to assess the degree of endangerment of livestock breeds in Europe. Livest Prod Sci 91(1–2):173–182

García D, Corral N, Cañon J (2005) Combining inter- and intrapopulation information with the Weitzman approach to diversity conservation. J Hered 96(6):704–712

Ginja C, Gama LT, Cortés O et al (2013) Analysis of conservation priorities of Iberoamerican cattle based on autosomal microsatellite markers. Genet Select Evol 45:35. https://doi.org/10.1186/1297-9686-45-35

Ginja C, Gama LT, Martínez A et al (2017) Genetic diversity and patterns of population structure in Creole goats from the Americas. Anim Genet 48(3):315–329

Goudet J (2001) FSTAT a program to estimate and test gene diversities and fixation indices. Version 2.9.3. Available at: https://www2.unil.ch/popgen/softwares/fstat.htm

Gutierrez JP, Royo LJ, Alvarez I et al (2005) MolKin v2.0: a computer program for genetic analysis of populations using molecular coancestry information. J Hered 96(6):718–721

Hall SJG, Lenstra JA, Deeming DC et al (2012) Prioritization based on neutral genetic diversity may fail to conserve important characteristics in cattle breeds. J Anim Breed Genet 129 (3):218–225

Huson DH, Bryant D (2006) Application of phylogenetic networks in evolutionary studies. Mol Biol Evol 23(2):254–267

Jordana J, Goyache F, Ferrando A et al (2017) Contributions to diversity rather than basic measures of genetic diversity characterise the spreading of donkey throughout the American continent. Livest Sci 197:1–7

Langella O (1999–2002) POPULATIONS 1.2.28. 1.2.28 edn. CNRS UPR 9034, France

Luikart G, Gielly L, Excoffier L et al (2001) Multiple maternal origins and weak phylogeographic structure in domestic goats. Proc Natl Acad Sci USA 98(10):5927–5932

Manzano P, Casas R (2010) Past, present and future of trashumancia in Spain: nomadism in a developed country. Pastoralism 1:72–90

Martínez A, Manunza A, Delgado JV et al (2016) Detecting the existence of gene flow between Spanish and North African goats through a coalescent approach. Sci Rep 6:38935. https://doi.org/10.1038/srep38935

Martínez AM, Acosta J, Vega-Pla JL et al (2006) Analysis of the genetic structure of the canary goat populations using microsatellites. Livest Sci 102:140–145

Martínez AM, Gama LT, Delgado JV et al (2015) The Southwestern fringe of Europe as an important reservoir of caprine biodiversity. Genet Sel Evol 47:86. https://doi.org/10.1186/s12711-015-0167-8

Medugorac I, Veit-Kensch CE, Ramljak J et al (2011) Conservation priorities of genetic diversity in domesticated metapopulations: a study in taurine cattle breeds. Ecol Evol 1(3):408–420

Meuwissen T (2009) Towards consensus on how to measure neutral genetic diversity? J Anim Breed Genet 126(5):333–334

Nei M (1987) Molecular evolutionary genetics. Columbia University Press, New York, NY, USA

Notter DR (1999) The importance of genetic diversity in livestock populations of the future. J Anim Sci 77(1):61–69

Ollivier L, Foulley JL (2005) Aggregate diversity: new approach combining within- and between-breed genetic diversity. Livest Prod Sci 95:247–254

Pereira F, Pereira L, Van Asch B et al (2005) The mtDNA catalogue of all Portuguese autochthonous goat (*Capra hircus*) breeds: high diversity of female lineages at the western fringe of European distribution. Mol Ecol 14(8):2313–2318

Pereira F, Queirós S, Gusmão L et al (2009) Tracing the history of goat pastoralism: new clues from mitochondrial and Y chromosome DNA in North Africa. Mol Biol Evol 26(12):2765–2773

Piyasatian N, Kinghorn BP (2003) Balancing genetic diversity, genetic merit and population viability in conservation programmes. J Anim Breed Genet 120:137–149

Reynolds J, Weir BS, Cockerham CC (1983) Estimation of the coancestry coefficient: basis for a short-term genetic distance. Genetics 105(3):767–779

Ruane J (1999) A critical review of the value of genetic distance studies in conservation of animal genetic resources. J Anim Breed Genet 116(5):317–323

Ruane J (2000) A framework for prioritizing domestic animal breeds for conservation purposes at the national level: a Norwegian case study. Conserv Biol 14(5):1385–1393

Song S, Yao N, Yang M et al (2016) Exome sequencing reveals genetic differentiation due to high-altitude adaptation in the Tibetan cashmere goat (*Capra hircus*). BMC Genom 17:122. https://doi.org/10.1186/s12864-016-2449-0

Toro MA, Caballero A (2005) Characterization and conservation of genetic diversity in subdivided populations. Philos Trans R Soc Lond B Biol Sci 360(1459):1367–1378

Toro MA, Fernandez J, Caballero A (2009) Molecular characterization of breeds and its use in conservation. Livest Sci 120(3):174–195

Wang XL, Liu J, Zhou GX et al (2016) Whole-genome sequencing of eight goat populations for the detection of selection signatures underlying production and adaptive traits. Sci Rep 6:38932. https://doi.org/10.1038/srep38932

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38(6):1358–1370

Weitzman ML (1992) On diversity. Q J Econ 107(2):363–405

Zeder MA (2008) Domestication and early agriculture in the Mediterranean Basin: origins, diffusion, and impact. Proc Natl Acad Sci USA 105(33):11597–11604