Indigenous domestic breeds as reservoirs of genetic diversity: the Argentinean Creole cattle

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Summary

Contrary to highly selected commercial breeds, indigenous domestic breeds are composed of semi-wild or feral populations subjected to reduced levels of artificial selection. As a consequence, many of these breeds have become locally adapted to a wide range of environments, showing high levels of phenotypic variability and increased fitness under natural conditions. Genetic analyses of three loci associated with milk production (α_{S1}-casein, κ-casein and prolactin) and the locus *BoLA-DRB3* of the major histocompatibility complex indicated that the Argentinean Creole cattle (ACC), an indigenous breed from South America, maintains high levels of genetic diversity and population structure. In contrast to the commercial Holstein breed, the ACC showed considerable variation in heterozygosity (H_e) and allelic diversity (A) across populations. As expected, bi-allelic markers showed extensive variation in H_e whereas the highly polymorphic *BoLA-DRB3* showed substantial variation in A, with individual populations having 39–74% of the total number of alleles characterized for the breed. An analysis of molecular variance (AMOVA) of nine populations throughout the distribution range of the ACC revealed that 91.9–94.7% of the total observed variance was explained by differences within populations whereas 5.3–8.1% was the result of differences among populations. In addition, the ACC breed consistently showed higher levels of genetic differentiation among populations than Holstein. Results from this study emphasize the importance of population genetic structure within domestic breeds as an essential component of genetic diversity and suggest that indigenous breeds may be considered important reservoirs of genetic diversity for commercial domestic species.

Keywords *Bos taurus*, Creole cattle, genetic diversity, livestock diversity.

Introduction

Although livestock breeds are recognized as important components of world biodiversity (Hall & Ruane 1993; Hall & Bradley 1995), only a few studies have evaluated the importance of genetic diversity in animal domestic species (MacHugh *et al.* 1994; Moazami-Goudarzi *et al.* 1997). The importance of genetic diversity in domestic species is directly related to the necessity for genetic improvement of particular selected breeds as well as to facilitate rapid adaptation to potential changes in breeding goals (Notter 1999). Most selective regimes applied to livestock breeds tend, however, to reduce levels of genetic variation through two major processes. First, most domestic species are highly selected for a few economically important traits (e.g. milk or meat production), which decreases genetic diversity as a consequence of directional selection. Secondly, most populations within particular breeds tend to be genetically uniform as a result of high levels of gene flow among populations and artificial selection of some reproductive individuals (e.g. through assisted reproduction techniques such as artificial insemination and embryo transfer). The high levels of artificial selection through the intensive use of elite sires and assisted reproduction have greatly reduced the effective

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population size of commercial domestic breeds. For example, Georges & Andersson (1996) have estimated that the current USA Holstein population of about 10 million has an effective population size smaller than 1000. Therefore, it is clear that, in spite of the large populations of most commercial domestic breeds, livestock genetic diversity is compromised by the management strategies for massive production, which reduce the effective population size of most domestic breeds.

Contrary to the highly selected commercial breeds, indigenous domestic breeds (also known as native breeds) are composed of semi-wild breeds or feral populations subjected to reduced levels of artificial selection. Most indigenous breeds are unmanaged or managed through traditional husbandry (Bouzat *et al.* 1998a); therefore, they are subjected to the process of natural selection. As a consequence, these breeds have become locally adapted to a wide range of environments, showing high levels of phenotypic variability and increased fitness under natural conditions (Domestic Animal Diversity Information System; http://dad.fao.org/).

With the advent of molecular techniques an increasing number of studies have focused on the genetic characterization of domestic breeds through molecular genetic markers. These studies included comparisons of genetic variability among breeds (MacHugh *et al.* 1994; Moazami-Goudarzi *et al.* 1997), phylogenetic studies on the historical origin of domestic species (Loftus *et al.* 1994, 1999; MacHugh *et al.* 1997) and genetic studies on parental analyses (Heyen *et al.* 1997). Although the importance of population structure for the maintenance of genetic diversity has been widely addressed in studies of wild populations (Slatkin 1987), the lack of data addressing this issue on domestic species is surprising. Most studies on livestock diversity have focussed on comparisons of genetic variability among breeds (MacHugh *et al.* 1994; Moazami-Goudarzi *et al.* 1997), with only some exceptions addressing the importance of population structure within particular domestic breeds (Golijow *et al.* 1996; Blott *et al.* 1998; Kantanen *et al.* 2000).

The ACC is a hump-less bovine (*Bos taurus*) with long horns descendant of the cattle introduced into the Americas by Spanish conquerors during the first 50 years of the colonization. Entering into Argentina through Bolivia, Paraguay and Chile during 1555–1587, the breed rapidly spread and became adapted to a wide range of environments, from rainforest in the Northwest to the Patagonian steppe in the South (Fig. 1). Originally estimated in millions, the ACC suffered a severe reduction in population size during the end of the 19th and the beginning of the 20th centuries as a result of the introduction and massive production of highly selected European and Zebu commercial breeds (Bouzat *et al.* 1998a). As a consequence, the distribution of the ACC,

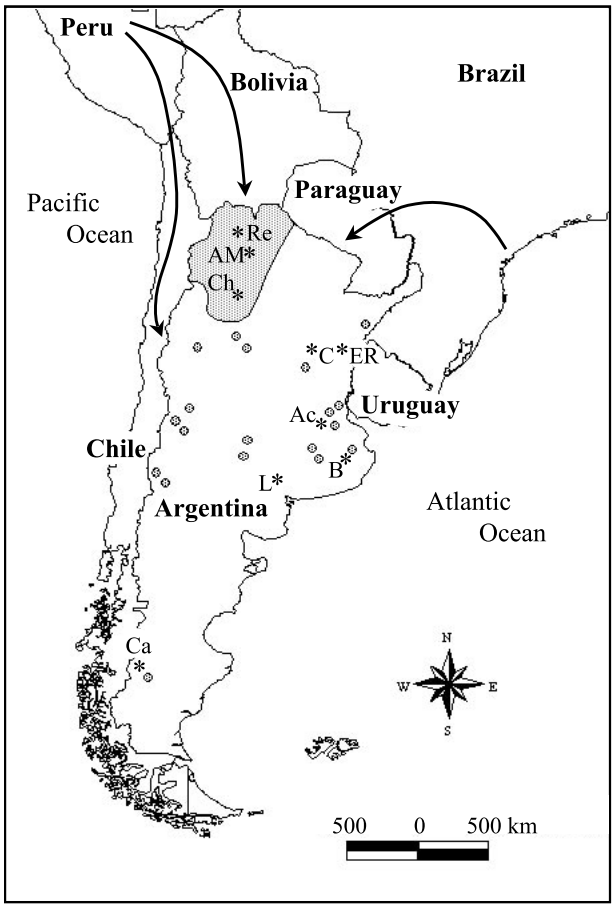

Figure 1 Geographic distribution of the Argentinean Creole cattle (ACC). Stars (*) indicate populations sampled for genetic analyses, which include Arroyo del Medio (AM), El Remate (Re), Chasquivil (Ch), Concordia (ER), Cruz de Guerra (C), Las Acacias (Ac), Balcarce (B), La Angelica (L) and Calafate (Ca). Arrows indicate the introduction routes that originated the ACC during 1555–1587.

which originally covered most of the Argentinean territory, became mainly restricted to marginal regions unsuitable for the production of commercial breeds. With an estimated size of about 300 000 individuals (data provided by the Society of ACC Breeders), the ACC is currently distributed in semi-isolated populations with relatively low number of individuals per herd, low levels of gene flow and geographical isolation.

Contrary to the highly selected commercial domestic breeds, the ACC has been bred since its origin in semi-wild conditions with low levels of artificial selection. Low levels of breeding management allowed the ACC to maintain a natural social structure upon which natural selection operated. As a consequence, this breed has become adapted to local environmental conditions resulting in high levels of phenotypic diversity (e.g. all coat colours described in cattle

are present in the ACC), high longevity and fertility and resistance to a number of endemic subtropical diseases including the tick *Bofilus microplus*, a common vector of numerous pathogens (Guglielmone *et al.* 1991).

Here, we evaluated the population genetic structure of the Argentinean Creole cattle (ACC), a South American indigenous cattle breed, and compared it with that of Holstein as an example of a highly selected commercial breed. Genetic markers used to evaluate the genetic structure of these breeds included three genes involved in milk production (α_{S1}-casein, κ-casein and prolactin) as well as a gene of the major histocompatibility complex (*BoLA-DRB3*), which is related to the immune response of organisms against pathogens. Our general hypothesis is that because of their characteristic population structure with semi-isolated herds and their low levels of artificial selection, the ACC would present higher levels of genetic diversity and population genetic differentiation compared with other highly selected commercial breeds. The genetic evaluation of nine populations throughout the range of distribution of the ACC allowed us to address two specific questions related to the proposed hypothesis: (1) what patterns of genetic diversity exist within and among populations of the ACC? and (2) do levels of genetic diversity in the ACC differ from those of the commercial Holstein breed? Results from this study are discussed in the light of the importance of indigenous domestic breeds for the conservation of livestock genetic diversity.

Materials and methods

Studied populations

Blood samples from 339 adult animals were collected between 1992 and 1996 from nine populations throughout the range of distribution of the ACC (Fig. 1). When pedigree information was available, we selected individuals that have not shared a common ancestor for at least two generations. Studied populations included Arroyo del Medio ($n = 80$), El Remate ($n = 25$), Chasquivil ($n = 30$), Concordia ($n = 30$), Cruz de Guerra ($n = 39$), Las Acacias ($n = 30$), Balcarce ($n = 50$), La Angelica ($n = 30$) and Calafate ($n = 25$). These populations were distributed in four distinct habitats, including subtropical dry forest, highland steppe, grasslands and temperate forests. Population sizes ranged from 100 to 600 individuals, with considerable year-to-year variation as a result of rainfall patterns resulting in changes in water and food availability.

Allele frequencies from three Argentinean populations of Holstein were obtained from previous studies (Golijow *et al.* 1999). Holstein worldwide estimates were based on published data of up to 11 populations from Argentina, USA, Canada, Italy, Israel and Australia (McLean *et al.* 1984; Ng-Kwai-Hang *et al.* 1984; Lin *et al.* 1986; Gonyon *et al.* 1987; Aleandri *et al.* 1990; Poli & Antonini 1991; Ron *et al.* 1994; Dietz *et al.* 1997; Ojala *et al.* 1997; Sharif *et al.* 1998; Bobe *et al.* 1999).

DNA extraction and typing methods

Genomic DNA was isolated from lymphocytes using the DNAzol purification kit (Gibco Life Technologies, Rockville, MD, USA) following the manufacturer instructions. Genetic markers used in this study included genes encoding α_{S1}- and κ-casein, prolactin and *BoLA-DRB3*.

Allele typing for the α_{S1}-casein was performed using allele-specific oligonucleotides for the amplification of allele variants B and C (David & Deutch 1992). The remaining markers were genotyped by PCR-RFLP. Restriction patterns for κ-casein and prolactin were obtained by digestion with *Hind*III and *Rsa*I, respectively, following Agrawala *et al.* (1992) and Lewin *et al.* (1992). Genotyping of the *BoLA-DRB3* was performed using the restriction enzymes *Rsa*I, *BstY*I and *Hae*III (van Eijk *et al.* 1992). Restriction fragments of amplified products were discriminated by electrophoresis in 6% polyacrylamide gels and visualized with ethidium bromide under UV light.

Measures of genetic variability and statistical analysis

Estimates of genetic variability and statistical analyses were performed using GENEPOP, version 1.2 (Raymond & Rousset 1995) and ARLEQUIN, version 1.1 (Schneider *et al.* 2000) computer programs. Allele frequencies were determined for each population by direct counting. Levels of genetic variability were estimated using allelic diversity (A) and the unbiased expected heterozygosity (H_e), computed according to Nei (1987). The number of shared alleles between each possible pair of populations was calculated by direct counting. Regression analysis showed no significant effects of sample size on allelic diversity at the *BoLA-DRB3* locus ($r = 0.478$, $F = 2.07$, $P = 0.193$). Although estimates of allelic diversity using homogeneous sample sizes ($n = 30$) removed one or two rare alleles from the larger samples, the results did not alter our conclusions. Thus, reported values of allelic diversity are based on complete sample sizes.

Hardy–Weinberg equilibrium was evaluated using Wright's F_{IS} index (Wright 1951). Significant departures of F_{IS} from zero were tested using Guo & Thompson's (1992) test implemented in the ARLEQUIN software (Schneider *et al.* 2000). The Ewens–Watterson–Slatkin exact method (Slatkin 1996) was used to test the hypothesis of selective neutrality and population equilibrium against either balancing selection or the presence of advantageous alleles.

Table 1 Levels of genetic diversity (heterozygosity, H_e; and allelic diversity, A) estimated for nine populations of the Argentinean Creole cattle (ACC) and breed genetic diversity for the ACC and the commercial Holstein breed.

	α_{S1}-Casein		κ-Casein		Prolactin		*BoLA-DRB3*	
	H_e	A	H_e	A	H_e	A	H_e	A
ACC populations								
Balcarce	0.097	2	0.335	2	0.289	2	0.891	17
Arroyo del Medio	0.434	2	0.503	2	0.035	2	0.877	15
El Remate	0.510	2	0.476	2	0.078	2	0.874	12
Las Acacias	0.511	2	0.299	2	0.000	1	0.858	12
Cruz de Guerra	0.357	2	0.409	2	0.070	2	0.864	12
La Angelica	0.496	2	0.512	2	0.043	2	0.770	11
Concordia	0.443	2	0.487	2	0.226	2	0.811	9
Chasquivil	0.496	2	0.492	2	0.156	2	0.877	14
Calafate	0.157	2	0.491	2	0.048	2	0.731	10
Breed genetic diversity								
ACC	0.395	2	0.481	2	0.092	2	0.901	23
Holstein	0.148	2	0.456	2	0.227	2	0.922	24

Levels of genetic variation within and among populations of the ACC were estimated using an analysis of molecular variance (AMOVA) (Excoffier *et al.* 1992). Significance levels for variance components were computed by non-parametric permutation procedures, determining the probability of obtaining a more extreme variance component than the observed value by chance alone (1000 permutations).

Levels of genetic differentiation among populations were estimated using Wright's F_{ST} index (Wright 1951). Significance levels for this index were calculated using the chi-square statistic $\chi^2 = 2NF_{ST}(k–1)$ as defined by Chesser (1983), where N indicates the total number of individuals analysed and k the number of alleles. Significance levels for the ACC and Holstein worldwide were also estimated through probability tests or Fisher exact tests using non-parametric permutation approaches, as described by Excoffier *et al.* (1992) and Raymond & Rousset (1995). In both cases, chi-square significances were concordant to those estimated through non-parametric tests.

Indirect estimates of gene flow were calculated according to Slatkin & Barton (1989). The effective number of migrants (Nm) was estimated, assuming the n-island model of population structure, on the basis of the relationship $F_{ST} = 1/[4Nmd/(d–1) + 1]$, where d is the number of demes exchanging genes (Slatkin & Barton 1989).

Results

Our results did not show significant differences in the heterozygosities averaged across loci between the ACC ($H_e = 0.467$) and Holstein ($H_e = 0.438$) breeds. Estimates at each individual locus showed no significant differences between the ACC and Holstein for κ-casein ($t = 2.212$, $P > 0.05$), prolactin ($t = 2.536$, $P > 0.05$) and the *BoLA-DRB3* ($t = 2.037$, $P > 0.05$; Table 1). However, the ACC had significantly higher levels of H_e than Holstein at the α_{S1}-casein locus ($t = 7.626$, $P < 0.05$).

In the ACC, most populations revealed the same allelic diversity (A) for the three bi-allelic systems studied (α_{S1}-casein, κ-casein and prolactin). Most populations showed the two alleles characteristic of all bovine domestic breeds (Table 1). The exception was prolactin in population Las Acacias, which revealed fixation for one allele. On the other hand, H_e values varied considerably among populations as a result of significant differences in allele frequencies. The ACC showed H_e values ranging from 0.097 to 0.511 for α_{S1}-casein, 0.299–0.512 for κ-casein and 0.000–0.289 for prolactin (Table 1). This contrasts with the relatively uniform H_e observed for the same markers in different populations of Holstein. For example, estimated H_e of α_{S1}-casein for five Holstein populations worldwide ranged from 0.015 to 0.148.

Analysis of the multi-allelic system *BoLA-DRB3* exhibited a different pattern. The ACC revealed relatively high levels of H_e (0.901) and A (23) for this particular system (Table 1). Levels of H_e are similar to those reported for Holstein (Table 1). However, the number of alleles and the frequency distributions within populations of the ACC differed from those observed in other domestic breeds. For example, different Holstein herds presented the same alleles with similar frequencies, whereas individual populations of the ACC had 39–74% of the total number of alleles characterized for this breed (Table 1). In addition, individual populations revealed unique alleles at considerable frequencies, an unusual situation for commercial breeds. For example, the average number of shared alleles among populations of the ACC (7.17) was significantly smaller than that observed among Holstein populations from USA

Locus	Variance among populations (%)	Variance within population (%)	F_{ST}	*P*-value	*Nm*
BoLA-DRB3	6.64	93.36	0.064	<0.0001	3.25
κ-Casein	8.08	91.92	0.081	<0.0001	2.52
α_{S1}-Casein	8.08	91.92	0.081	<0.0001	2.53
Prolactin	5.32	94.68	0.053	<0.0001	3.97

Table 2 Percentage variance components of genetic diversity estimated by an AMOVA of nine populations of the Argentinean Creole cattle, levels of genetic differentiation as measured by the Wright's F_{ST} index with their significance values (*P*) based on non-parametric permutation tests and average estimates of gene flow (*Nm*).

and Argentina, which shared 18 alleles. Similar trends were observed in four highly polymorphic microsatellite markers (data not shown). It is noteworthy that two *BoLA-DRB3* alleles described in the ACC were never detected in other highly selected European breeds. Interestingly, these two alleles were reported in African indigenous breeds that have contributed to the origin of the Iberian cattle ancestral to the ACC (Cymbron *et al.* 1999).

All ACC populations were at Hardy–Weinberg equilibrium. Average F_{IS} across loci were not significantly different from zero in all studied populations. Individual tests per locus showed that only 2 out of the 36 tests performed revealed significant departures from Hardy–Weinberg (κ-casein and *BoLA-DRB3* in La Angelica and Concordia populations, respectively). Ewens–Watterson–Slatkin exact tests indicated that all studied loci were selectively neutral in most populations. The exception was κ-casein in La Angelica population, which showed a tendency towards balancing selection ($P = 0.010$).

The AMOVA revealed that 91.9–94.7% of the total observed variance in the ACC was explained by differences within populations whereas 5.3–8.1% was the result of differences among populations (Table 2). Variance components among populations were highly significant for all studied loci. Accordingly, genetic differentiation estimated by the F_{ST} index revealed significant levels of population structure (Table 2). Average F_{ST} values were highly significant for all the studied markers ($P < 0.0001$, based on 1000 permutations). The milk proteins α_{S1}- and κ-casein showed similar levels of genetic differentiation ($F_{ST} = 0.081$), while prolactin and the *BoLA-DRB3* exhibited slightly reduced but highly statistically significant F_{ST} values (Table 2). Pair-wise F_{ST} for the highly polymorphic *BoLA-DRB3* consistently showed that Calafate, a feral geographically isolated population representative of the original Patagonian Creole, was the most differentiated population. F_{ST} values between Calafate and each of the remaining populations were consistently higher ($F_{ST} > 0.120$) than any other pair-wise F_{ST} considered (F_{ST} ranging from 0.000 to 0.102).

In contrast to the ACC, F_{ST} values for α_{S1}- and κ-casein and the highly polymorphic *BoLA-DRB3* estimated for Holstein populations from Argentina were not significantly different from zero (Table 3). In addition, the ACC breed consistently showed higher F_{ST} values than those estimated for Holstein populations worldwide, which included populations from three different continents (Table 3). Indirect estimates of gene flow indicated significant differences in the effective number of migrants (*Nm*) among populations of the ACC and that among populations of Holstein worldwide. *Nm* estimated among populations of the ACC was smaller than four individuals per generation (Table 2). This contrasts with the estimated *Nm* among Holstein populations. For example, the *Nm* estimate based on the κ-casein F_{ST}, which included 11 Holstein populations worldwide, was more than five times higher ($Nm > 22$) than that of the ACC.

Discussion

Our results showed that the ACC has relatively high levels of genetic diversity. Increased levels of genetic variability in indigenous breeds might have resulted from recent admixture with other commercial breeds such as Zebu. Although previous studies have shown male-mediated introgression of *Bos indicus* genes in Brazilian and Bolivian Creole breeds (Giovambattista *et al.* 2000), analysis of the Y chromosome in the ACC did not reveal evidence of genetic introgression in any of the populations included in this study. Thus, the pattern of genetic diversity present in the ACC is unlikely to be the result of recent admixture between ACC and Zebu.

	α_{S1}-Casein			κ-Casein			*BoLA-DRB3*		
Bovine breed	*N*	F_{ST}	*P*	*N*	F_{ST}	*P*	*N*	F_{ST}	*P*
ACC	9	0.081	<0.001	9	0.081	<0.001	9	0.064	<0.001
Holstein Argentina	3	0.011	<0.500	3	0.014	<0.250	3	0.011	>0.100
Holstein worldwide	5	0.010	<0.001	11	0.013	<0.001	3	0.020	<0.001

Table 3 The F_{ST} and chi-square significance values (*P*) estimated for α_{S1}-casein, κ-casein and the *BoLA-DRB3* genes for the ACC and the commercial domestic breed Holstein. *N* indicates the number of populations considered for the calculation of the F_{ST} index at each locus.

Differences in H_e in the bi-allelic systems α_{S1}-casein, κ-casein and prolactin resulted from variations in allele frequencies rather than the presence/absence of particular alleles. The presence of a predominant allele in all populations for the marker prolactin is consistent with results observed in other Creole cattle (e.g. Bolivian Creole) and in the Iberian breed Retinta, which showed the same predominant allele (Lirón *et al.* 2000).

The highly polymorphic *BoLA-DRB3* showed a more homogeneous H_e among populations. This is not unexpected because, in multi-allelic systems, changes in allele frequencies in different populations may have compensating effects on average H_e and the loss of rare alleles may not affect H_e substantially. Allelic diversity has been shown to be a better estimator of genetic diversity in systems with a large number of alleles (Bouzat *et al.* 1998b; Lukiart & Cornuet 1998). In the ACC, individual allele variants and frequencies varied considerably among the studied populations. In contrast, Holstein breeds exhibited high homogeneity in allelic variants and their frequencies, with the majority of the alleles being shared among all populations.

Two major processes may explain the observed patterns of genetic diversity in the ACC. First, natural selection may have favoured particular alleles or allele combinations in different environments. The wide range of environments to which the ACC is adapted (from rainforest to grasslands) may have facilitated the overall retention of different genetic variants and frequencies. This could explain the observed differences in allele frequencies in the bi-allelic systems and the differences in both allele combinations and frequencies in the *BoLA-DRB3* locus. Adaptation through natural selection could play an important role in the maintenance of genetic diversity in genes such as the *BoLA-DRB3* (Hedrick 1994). As a member of the *MHC* gene family, this gene participates in the immune response of organisms against pathogens. Although our results did not show evidence for either balancing selection or the presence of advantageous alleles at each individual marker studied, we cannot discard the possibility that selective forces may be favouring gene combinations for particular quantitative traits.

The second process is related to the population structure of the ACC, which may maintain overall levels of genetic diversity among populations as a result of reduced levels of gene flow. Significant differences among populations in the allele frequencies of the studied loci as well as the detection of private alleles in the *BoLA-DRB3*, suggest that connectance among populations of the ACC is restricted. Population structure and limited gene flow may facilitate local adaptation and increase the effects of stochastic processes such as genetic drift. As a consequence, these processes may lead to increased levels of genetic differentiation among populations. Overall, the ACC consistently showed higher levels of genetic variation among populations (5–8%) than those observed in Holstein (1–2%). In contrast to Holstein populations from Argentina, the ACC showed highly significant F_{ST} for each of the studied markers (Table 3). Furthermore, the ACC breed showed F_{ST} values consistently higher than those estimated for Holstein populations worldwide. The consistent trends in both the F_{ST} values and the allele frequency distributions observed among the studied loci strongly suggest that the ACC has higher levels of genetic differentiation.

The Holstein breed represents an extreme example of the genetic uniformity present in most commercial domestic cattle. It is noteworthy that populations of the ACC, which are separated by no more than 3000 km, revealed higher levels of genetic differentiation than Holstein populations from different continents. We think this is a clear consequence of differences in management and breeding strategies between the ACC and other commercial breeds. The use of assisted reproduction techniques such as artificial insemination and embryo transfer and elite sires for the selection and massive production of commercial breeds facilitate genetic homogenization among herds within particular breeds. This may explain the increased difference between the effective and total population sizes characteristic of commercial domestic species (Georges & Andersson 1996). Indirect estimates of gene flow reported in this study are consistent with this idea. The relatively small levels of gene flow reported for the ACC ($Nm < 4$), compared with those of Holstein ($Nm > 22$), may have prevented genetic homogenization among local populations of the ACC inhabiting different environments.

Implications for the conservation of genetic diversity

Results from this study suggest that indigenous domestic breeds may be useful as reservoirs of genetic diversity for commercial domestic species. As shown by the genetic analyses of the ACC, indigenous breeds may possess unique genes and gene combinations currently absent in highly selected European breeds. The detection in the ACC of two allelic *BoLA-DRB3* variants shared with other indigenous breeds, but never reported in European commercial herds, is an example of unique variants that may have been lost through the intense selective management of commercial breeds.

The characteristic population structure of indigenous breeds may also provide a mechanism for preserving adaptive genetic diversity. While in most commercial breeds artificial selection is directed towards economically important traits, natural selection operating on native domestic breeds favours multi-locus quantitative traits directly associated with the fitness of individuals in their local environments. Therefore, indigenous breeds are more likely to

preserve adaptive genetic variation, an essential component for livestock genetic improvement and/or potential changes in breeding goals.

Indigenous domestic breeds should be considered important resources of economic value for agriculture in the future. The massive expansion of some commercial livestock breeds worldwide has increased dramatically the number of domestic breeds threatened with extinction. For example, Loftus & Scherf (1993) have estimated that about one-third of the 3213 currently extant domestic breeds are endangered. Replacement or interbreeding of native domestic breeds with foreign commercial breeds may eliminate valuable locally adapted populations. The N'Dama breed, a native breed from West Africa, which is highly resistant to Trypanosome infections, is a clear example of the potential detrimental effects of these processes. The increasing introgression of imported breeds into N'Dama has decreased the number of individuals resistant to *Trypanosoma*, thus, threatening the persistence of an important local resource (Bradley *et al*. 1994).

Our study also emphasizes the importance of considering population genetic structure within breeds as an essential component for assessing genetic resources. In contrast to studies on wild species, which commonly emphasize levels of population genetic structure, most studies on domestic species focus on genetic variability at the breed level, disregarding levels of genetic variation among populations within any particular breed. This study revealed distinct patterns in the partitioning of genetic diversity within and among populations of the ACC and the highly selected Holstein breed.

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