Genetic diversity of the class II major histocompatibility DRA locus in European, Asiatic and African domestic donkeys

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ARTICLE INFO

Article history:
Received 15 December 2010
Received in revised form 6 April 2011
Accepted 7 April 2011
Available online 14 April 2011

Keywords:
Domestic donkey
Major histocompatibility class II DRA gene
Genetic diversity
Theileria equi
Babesia caballi

ABSTRACT

The major histocompatibility complex (MHC) genes coding for antigen presenting molecules are the most polymorphic genes in vertebrate genome. The MHC class II DRA gene shows only small variation in many mammalian species, but it exhibits relatively high level of polymorphism in Equidae, especially in donkeys. This extraordinary degree of polymorphism together with signatures of selection in specific amino acids sites makes the donkey DRA gene a suitable model for population diversity studies. The objective of this study was to investigate the DRA gene diversity in three different populations of donkeys under infectious pressure of protozoan parasites, Theileria equi and Babesia caballi. Three populations of domestic donkeys from Italy (N = 68), Jordan (N = 43), and Kenya (N = 78) were studied. A method of the donkey MHC DRA genotyping based on PCR-RFLP and sequencing was designed. In addition to the DRA gene, 12 polymorphic microsatellite loci were genotyped. The presence of Theileria equi and Babesia caballi parasites in peripheral blood was investigated by PCR. Allele and genotype frequencies, observed and expected heterozygosities and Fst values were computed as parameters of genetic diversity for all loci genotyped. Genetic distances between the three populations were estimated based on Fst values. Statistical associations between parasite infection and genetic polymorphisms were sought. Extensive DRA locus variation characteristic for Equids was found. The results showed differences between populations both in terms of numbers of alleles and their frequencies as well as variation in expected heterozygosity values. Based on comparisons with neutral microsatellite loci, population sub-structure characteristics and association analysis, convincing evidence of pathogen-driven selection at the population level was not provided. It seems that genetic diversity observed in the three populations reflects mostly effects of selective breeding and their different genetic origins.

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1. Introduction

The amount of genetic diversity has been associated with the ability to adapt to environmental changes and with the potential to evolve (Reed and Frankham, 2003). Immune functions represent one of major components of an organism’s fitness and determine the potential for evolutionary interactions with pathogens or with other species (Lazzaro and Little, 2009). Diversity of genes important for immune functions may be associated with resistance and susceptibility to pathogens (Trowsdale and Parham, 2004; Tibayrenc, 2007). The major histocompatibility complex (MHC) is a cluster of linked genes playing a central role in the presentation of antigenic peptides to T lymphocytes (Klein, 1986). The MHC genes are the most polymorphic genes in the vertebrate genome. Their high polymorphism seems to be maintained by balancing selection, predating speciation events and reflecting the co-evolution of hosts with their pathogens (Bernatchez and Landry, 2003). The mechanisms maintaining the genetic diversity and the role of pathogens have not yet been completely clarified. Empirical evidence for pathogen-driven selection on MHC genes is based on the population diversity analysis and on associations with pathogens (Spurgin and Richardson, 2010). For this purpose, specific model populations living in specific areas and exposed to various pathogens can be studied.

The family Equidae is a suitable model for studying diversity, selection and evolution of the MHC genes (Janova et al., 2009). It is
a rapidly evolving and variable group composed of a single genus, Equus, with a relatively well-documented history of evolution (Bowling and Ruivinsky, 2000). Domestic, captive and free ranging equid populations are available for different types of studies. Domestication of wild asses occurred probably 6000 years ago in Northeastern Africa (Rossel et al., 2008). Analysis of mitochondrial DNA of modern donkeys revealed two highly divergent phylogenetic groups, suggesting existence of two maternal origins of the domestic donkeys from two distinct wild populations, the Nubian (Equus africanus africanus) and the Somali (Equus africanus somaliensis) wild asses (Beja-Pereira et al., 2004; Kimura et al., 2011). The domestic donkey is a suitable model equid species for diversity study. It exists in various populations in different geographical areas, often naturally exposed to infectious pathogens.

The horse major histocompatibility complex (ELA or Eqca) is located on the horse chromosome (ECA) 20. The equine and human MHCs have a similar genomic organization with class I, II and III regions (Gustafson et al., 2003). The class II genes of Equidae have been extensively characterized and high level of exon 2 sequence variation was observed (Albright-Fraser et al., 1996; Fraser and Bailey, 1998; Horin and Matiasovic, 2002; Brown et al., 2004; Janova et al., 2009). For population diversity studies, a reliable method of individual genotyping is needed. Due to the extensive variation in the class II DQA, DRB and DQB genes, individual genotyping of these genes in Equids is not available or it is of limited value (Fraser and Bailey, 1998; Diaz et al., 2001; Horin and Matiasovic, 2002; Janova et al., 2009).

While exon 2 DRA alleles generally exhibit if ever only small variation in mammalian species (e.g. Yuuki et al., 2003), extensive polymorphism even of DRA genes has been reported in Equidae. The sequence variations are mainly located in exon 2 coding for the extracellular antigen binding domain. Current knowledge of the donkey MHC is only fragmentary. The donkey MHC (Eqas) contains probably a single DRA locus with seven DRA alleles identified so far (Albright-Fraser et al., 1996; Brown et al., 2004; GenBank accession numbers FJ487912, HM165492). Effect of positive selection on exon 2 DRA sequences was reported (Janova et al., 2009).

Availability of various donkey populations living in different climatic conditions and with different levels of general and health care, relatively, but not extremely high level of polymorphism in a single locus, with signatures of selection in specific amino acid sites, makes the donkey DRA gene a suitable model for population diversity studies. Similarly to other equids, donkeys are affected by plethora of infectious diseases. Among them, the piroplasmids, apicomplexan intracellular protists represent valuable model pathogen, as they apparently co-evolved with their hosts and exhibit remarkable pathogenicity. Equine and donkey piroplasmosis is an often fatal, tick-borne disease of equids caused by Theileria equi and Babesia caballi (Bruning, 1996).

The objective of this study was to investigate, based on individual genotyping, the DRA gene diversity in three different populations of donkeys under infectious pressure of equine piroplasms.

2. Materials and methods

2.1. Animals

The genetic diversity was studied in three populations of domestic donkeys. Italian donkeys belonged to the Martina Franca breed. It is an ancient native breed of Apulia (southern Italy), characterized by extraordinary sturdiness, frugality and adaptation to rocky ground. The genetic uniqueness of this breed lies in its adaptation to enzootic tick-borne pathogens typically found in Apulia (Rizzi et al., in press). Unrelated donkeys selected from 12 farms (n = 68) were used in this study. Jordanian donkeys (n = 43) were sampled from several rural localities in western Jordan, characterized by hot semi-arid and arid climate; all sampled animals belonged to the local breed. The third population were local African donkeys owned by semi-nomadic pastoralists of Turkana and Samburu tribes living in an arid environment in Northern Kenya (n = 78). All donkeys were under permanent risk of infection by tick-transmitted piroplasmids. In contrast to Italian donkeys, where basic veterinary care is available, no therapeutic and/or prophylactic measures were ever taken in the Asian and African donkeys.

2.2. Assessment of genetic diversity

The MHC DRA genetic diversity was compared to diversity in 14 microsatellite loci. Distribution of genotype and allelic frequencies, expected heterozygosities within populations, population structure and associations with a common pathogen were investigated for both types of loci, i.e. DRA and microsatellites.

2.3. Genetic diversity within populations, neutrality tests

In all donkeys, individual genotypes were determined for the MHC DRA locus and the microsatellite loci. In all loci analyzed, genotype and allelic frequencies, expected, observed and unbiased expected heterozygosities and the corresponding P-values were computed using GENETIX v. 4.05 (http://www.genetix.univ-montp2.fr/genetix/genetix.htm) and Arlequin v. 3.11 (Excoffier et al., 2005; http://cmpg.unibe.ch/software/arlequin3/). Ewens-Watterson, Tajima’s D and Fu’s Fs tests were used for analyzing neutrality of the DRA locus by Arlequin.

2.4. DRA genotyping

Blood for DNA extraction was collected by jugular venipuncture. Two methods for genomic DNA extraction were used, due to different methods of fixation of blood samples collected in different climatic conditions. In Italian donkeys, genomic DNA was extracted from EDTA-fixed peripheral blood, using the NucleoSpin blood kit (Macherey-Nagel, Duren, Germany). In Jordanian and Kenyan donkeys, a standard phenol–chloroform extraction from ethanol-fixed blood samples was used. Amplification of the 307 bp long product was carried out with standard primers Be3 and Be4 (Albright-Fraser et al., 1996). The extent of exon 2 DRA sequence variation in all populations was pre-screened by single strand conformation polymorphism analysis (SSCP) as described previously (Janova et al., 2009). Individual PCR-SSCP patterns were sequenced by 3730xl DNA analyzer (Applied Biosystems, Foster City, CA, USA). The sequences obtained were aligned by using the BioEdit sequence alignment editor (Hall, 1999) with known DRA alleles. A new E. asinus DRA allele (accession number HM165492, submitted to GenBank after we had completed the analysis, was not included. Heterozygote genotypes recognized based on double peaks were resolved manually by subtracting known alleles identified as specific SSCP patterns. No new allele was identified in the groups studied. The nomenclature suggested by Janova et al. (2009) was used for designing the DRA alleles.

Based on the exon 2 DRA sequences, a PCR-RFLP genotyping system was developed. Digestion of PCR products with restriction enzymes BsaI, NlaIII, AcI, and Cac8I produced fragments of different length (Table 1) that could be distinguished by capillary electrophoresis (MCE-202 MultiNA, Shimadzu Corporation, Kyoto, Japan). The combination of restriction sites allowed identification of four alleles, Eqas-DRA*0101, Eqas-DRA*0201, Eqas-DRA*0401 and Eqas-DRA*0501. The remaining alleles, Eqas-DRA*0301 and Eqas-DRA*0601, could be identified by subsequent sequencing and
2.5. Microsatellites

Fourteen microsatellites from the horse parentage test (Lee and Cho, 2006) were amplified in a standard multiplex PCRs using fluorescent-labeled primers and analyzed using automated sequencer ABI Prism310 (Applied Biosystems, Foster City, CA, USA) as described (Glowatzki-Mullis et al., 2006). 12 microsatellite loci, including one X-linked marker (Lex003), were polymorphic in the populations analyzed.

2.6. Population structure

Data obtained from previous research (Cho, 2006) were entered into Arlequin to compute the values of pathogen prevalence were 77.94; 26.19 and 88.46% in the three populations. Departure from H–W equilibrium due to the excess of heterozygotes/alleles was observed in the Jordanian population. As the recently reported allele Eqas-DRA*0701 could not be involved in the set-up, it could not be distinguished with this genotyping system.

2.7. Model pathogen: blood parasites Theileria equi and Babesia caballi

The blood parasites Theileria equi and Babesia caballi occurring in all three populations were selected as model pathogens for association studies. Both pathogens were diagnosed by PCR from DNA extracted from peripheral blood of all donkeys analyzed. Amplification of a specific fragment of the piroplasmid SSU rRNA gene was performed as described elsewhere (Sloboda et al., 2010). Based on the results of PCR, donkeys were classified as ‘double positive’, Theileria equi or Babesia caballi positive or negative. The values of pathogen prevalence were 77.94; 26.19 and 88.46% in the Italian, Jordanian and Kenyan donkeys, respectively.

2.8. Association analysis

Gene diversity indices were computed for six/five alleles identified in the respective populations, while for microsatellite loci; corrections for 12 polymorphic loci analyzed were made. The associations were analyzed within the three populations, while for Kenyan and Jordanian donkeys with the same allele pool.

2.9. Results

The numbers of DRA alleles and their frequencies, the values of heterozygosity found in the populations studied are shown in Table 2 and 3. In Jordanian and Kenyan donkeys, six DRA alleles were found, while in Italian donkeys the allele Eqas-DRA*0601 was missing. The highest value of expected heterozygosity was found in Jordanian donkeys, while their observed heterozygosity was lowest from the group. Department from H–W equilibrium due to the excess of DRA homozygotes was observed in the Jordanian population.

The data on microsatellite diversity are in Table 4. Two loci (MSI1 and ASB17) were monomorphic. In the remaining loci, numbers of alleles per locus ranged from 2 to 12. The numbers of alleles were smaller in Italian donkeys (average number per locus 4.42), while in Jordanian and Kenyan donkeys the numbers of alleles per locus were similar (6.83 and 6.75, respectively).

The FIS values for DRA and microsatellite loci are also shown in Table 3. All FIS values were positive except the DRA locus in Kenyan donkeys. The FST pair-wise comparisons among populations for DRA and microsatellites are in Table 5. In both types of loci, the genetic distances between the Jordanian and Kenyan populations are smaller than distances between either of them and the Italian group. The FST values for DRA and microsatellites were comparable. In neutrality tests, only a significant Ewens–Waterston neutrality test P value for the Jordanian population was found (Fexp = 0.235, Fexp = 0.417, P = 0.041).

Marginal P values were found for associations of DRA-Beta with Theileria equi infection in the merged group of Jordanian and Kenyan donkeys (Table 6). A statistically significant difference (P < 0.004) in numbers of Theileria equi PCR-positive donkeys between Eqas-DRA*0401 and Eqas-DRA*0601 carriers was observed.

### Table 1

<table>
<thead>
<tr>
<th>DNA fragment size (bp) for PCR-RFLP detection of Eqas alleles.</th>
<th>BsaI</th>
<th>NlaIII</th>
<th>AciI</th>
<th>Cac8I</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eqas-DRA*01</td>
<td>73,228.6</td>
<td>128,119,60</td>
<td>157,150</td>
<td>184,123</td>
</tr>
<tr>
<td>Eqas-DRA*02</td>
<td>307</td>
<td>247,60</td>
<td>157,150</td>
<td>184,123</td>
</tr>
<tr>
<td>Eqas-DRA*03</td>
<td>73,228.6</td>
<td>247,60</td>
<td>157,150</td>
<td>307</td>
</tr>
<tr>
<td>Eqas-DRA*04</td>
<td>73,228.6</td>
<td>247,60</td>
<td>157,150</td>
<td>307</td>
</tr>
<tr>
<td>Eqas-DRA*05</td>
<td>73,228.6</td>
<td>247,60</td>
<td>307</td>
<td>184,123</td>
</tr>
<tr>
<td>Eqas-DRA*06</td>
<td>73,228.6</td>
<td>247,60</td>
<td>157,150</td>
<td>184,123</td>
</tr>
</tbody>
</table>

### Table 2

<table>
<thead>
<tr>
<th>Frequencies of DRA alleles.</th>
<th>N</th>
<th>Italy</th>
<th>Jordan</th>
<th>Kenya</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eqas-DRA*01</td>
<td>68</td>
<td>0.096</td>
<td>0.107</td>
<td>0.032</td>
</tr>
<tr>
<td>Eqas-DRA*02</td>
<td>42</td>
<td>0.199</td>
<td>0.381</td>
<td>0.468</td>
</tr>
<tr>
<td>Eqas-DRA*03</td>
<td>42</td>
<td>0.198</td>
<td>0.143</td>
<td>0.083</td>
</tr>
<tr>
<td>Eqas-DRA*04</td>
<td>78</td>
<td>0.007</td>
<td>0.083</td>
<td>0.244</td>
</tr>
<tr>
<td>Eqas-DRA*05</td>
<td>78</td>
<td>0.500</td>
<td>0.072</td>
<td>0.077</td>
</tr>
<tr>
<td>Eqas-DRA*06</td>
<td>78</td>
<td>0.000</td>
<td>0.214</td>
<td>0.096</td>
</tr>
</tbody>
</table>

### Table 3

<table>
<thead>
<tr>
<th>Comparison of genetic diversity of DRA locus and average values of 12 polymorphic microsatellite loci.</th>
<th>N</th>
<th>H exp.</th>
<th>H n.b.</th>
<th>H obs.</th>
<th>FST (CI 95%)</th>
<th>HWE P value/range of P values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Italy DRA</td>
<td>67</td>
<td>5.00</td>
<td>0.662</td>
<td>0.667</td>
<td>0.603</td>
<td>0.009 (0.972 to 0.206)</td>
</tr>
<tr>
<td>Jordan (N=63) DRA</td>
<td>63</td>
<td>6.60</td>
<td>0.765</td>
<td>0.774</td>
<td>0.548</td>
<td>0.295 (0.147 to 0.359)</td>
</tr>
<tr>
<td>Jordan (N=43) MSI</td>
<td>63</td>
<td>6.83</td>
<td>0.697</td>
<td>0.705</td>
<td>0.622</td>
<td>0.119 (0.038 to 0.155)</td>
</tr>
<tr>
<td>Jordan (N=78) DRA</td>
<td>78</td>
<td>6.00</td>
<td>0.699</td>
<td>0.703</td>
<td>0.769</td>
<td>-0.095 (0.176 to 0.012)</td>
</tr>
<tr>
<td>Jordan (N=78) MSI</td>
<td>78</td>
<td>6.75</td>
<td>0.691</td>
<td>0.695</td>
<td>0.645</td>
<td>0.072 (0.045 to 0.106)</td>
</tr>
</tbody>
</table>

H exp., expected heterozygosity; H n.b., non-biased expected heterozygosity; H obs., observed heterozygosity.

* Number of individuals.

a Mean number of alleles per locus.
b 95% confidence interval.
**Table 4**

Genetic diversity of 11 autosomal microsatellite loci in three domestic donkey populations.

<table>
<thead>
<tr>
<th>Number of alleles</th>
<th>H exp.</th>
<th>H n.b.</th>
<th>H obs.</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Italy</td>
<td>Jordan</td>
<td>Kenya</td>
<td>Italy</td>
</tr>
<tr>
<td>AHT004</td>
<td>3</td>
<td>12</td>
<td>10</td>
<td>0.609</td>
</tr>
<tr>
<td>VHL020</td>
<td>3</td>
<td>3</td>
<td>5</td>
<td>0.642</td>
</tr>
<tr>
<td>AHT005</td>
<td>7</td>
<td>11</td>
<td>11</td>
<td>0.773</td>
</tr>
<tr>
<td>ASB023</td>
<td>5</td>
<td>5</td>
<td>6</td>
<td>0.662</td>
</tr>
<tr>
<td>HMS006</td>
<td>2</td>
<td>4</td>
<td>4</td>
<td>0.430</td>
</tr>
<tr>
<td>HTG006</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>0.254</td>
</tr>
<tr>
<td>CA425</td>
<td>4</td>
<td>9</td>
<td>7</td>
<td>0.515</td>
</tr>
<tr>
<td>HMS002</td>
<td>3</td>
<td>6</td>
<td>6</td>
<td>0.419</td>
</tr>
<tr>
<td>HMS003</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>0.640</td>
</tr>
<tr>
<td>HTG010</td>
<td>6</td>
<td>8</td>
<td>7</td>
<td>0.605</td>
</tr>
<tr>
<td>HTG007</td>
<td>7</td>
<td>10</td>
<td>10</td>
<td>0.620</td>
</tr>
</tbody>
</table>

H exp., expected heterozygosity; H n.b., non-biased expected heterozygosity; H obs., observed heterozygosity.

**Table 5**

Genetic distances (pairwise *F_{ST}* ) determined for MHIC-DRA/microsatellite loci.

<table>
<thead>
<tr>
<th></th>
<th>Italy</th>
<th>Jordan</th>
<th>Kenya</th>
</tr>
</thead>
<tbody>
<tr>
<td>Italy</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jordan</td>
<td>0.154/0.132</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Kenya</td>
<td>0.191/0.152</td>
<td>0.020/0.041</td>
<td>0</td>
</tr>
</tbody>
</table>

(Table 7). No associations of DRA alleles or genotypes with homozygosity/heterozygosity were found. No associations for microsatellite loci were found.

**4. Discussion**

The extent of *Equus* DRA polymorphism was primarily determined by sequencing. In Equids, individual DRA genotyping based on single strand conformation polymorphism analysis (PCR-SSCP) (Albright-Fraser et al., 1996), reference-strand-mediated conformational analysis (RSCA) (Brown et al., 2004) or pyrosequencing (Diaz et al., 2008) was reported. Our approach using PCR-RFLP and sequencing proved to be another feasible approach for assessing individual variation in the donkey DRA locus. It is rapid and efficient; there is no need for reference sequences like in RSCA and SSCP. However, pre-screening with PCR-SSCP was used for avoiding the risk of loss of non-recognized alleles potentially present in the populations studied.

Five DRA alleles seem to be equally common in donkeys analyzed so far. The sixth and seventh allele, Eqas-DRA*0601, Eqas-DRA*0701 were only recently added to GenBank (FJ487912, HM165492) and there is no information on their population frequencies. DRA frequencies observed by Brown et al. (2004) in 23 donkeys (origin not specified) were similar to those found in this study in the Jordanian group. Eqas-DRA*0601 and Eqas-DRA*0701 were not known at this time and they were not identified by the authors in the group analyzed. In two populations studied here, all known DRA alleles were found with exception of Eqas-DRA*0701. It could not be distinguished by the PCR-RFLP system used. However, we have observed no unexpected PCR-SSCP patterns in the groups analyzed and the sequence data have not suggested existence of additional alleles. We thus believe that if this allele was present in our populations, it must be very rare and could not influence the results obtained and their interpretation.

In the Italian group, where Eqas-DRA*0601 was not found, observed frequency of another allele, Eqas-DRA*0401, was also very low. This population thus seems to be less diverse in DRA than the two other groups. Similar results were found for expected DRA
heterozygosities. The Italian population showed lowest values of expected DRA heterozygosity. Calculations of expected and unbiased expected heterozygosities produced similar results due to the high numbers of donkeys. The most diverse in this parameter was the Jordanian group, showing at the same time the lowest values of observed DRA heterozygosity. The values of expected DRA heterozygosity observed in our donkeys (0.66–0.77) are higher than values observed for the same MHC class II locus in horses, 0.27–0.65 (Diaz et al., 2008), and roughly correspond to values for human HLA class I loci observed by Prugnolle et al. (2005) in populations living in environments with moderate level of pathogen-richness.

The differences observed can be explained by several different factors, including different origins of the populations under study, different approaches to selective breeding as well as by pathogen-driven selection. They suggest that populations living under “natural” conditions, i.e. with no selective breeding, virtually no veterinary care and no preventive measures, like vaccinations, are slightly more diverse in this MHC locus than the Italian breed, subject to selective breeding and elementary veterinary care. In Kenyan and Jordanian donkeys, no pedigree information was available, and random sample collection could not eliminate the risk of including relatives into the group analyzed. In Italian horses, pedigree data were available. Due to selective breeding, parental half-sibs could not be completely eliminated from the study. However, in terms of parentage, the group analyzed was a representative population sample.

Comparison with microsatellites showed that the Italian population was less diverse even in these neutral loci both in terms of heterozygosity values and especially of mean numbers of alleles (Table 3). In contrast to Equus, there was no evidence of significant differences between observed and expected heterozygosities in Jordanian donkeys. The reasons for the departure from H–W equilibrium and from neutrality observed for the DRA locus in the Jordanian population remain unclear. Due to the absence of pedigree data, excess of homozygotes in this population cannot be interpreted properly. The lower extent of genetic diversity in both types of loci seems to be due to selective breeding applied in Italian donkeys with controlled pedigree. The mean expected microsatellite heterozygosity values ranging between 0.57 and 0.71, similar to those reported in Spanish (0.66) and Croatian (0.66–0.70) domestic donkeys (Aranguren-Mendez et al., 2001; Ivanovkic et al., 2002) is in agreement with this assumption. In terms of neutral variation, genetic diversity of African and Arab donkeys studied was not strikingly different from the European domestic donkey populations. The two non-European populations were more similar to each other than to Italian donkeys in both types of loci as expressed by FST values.

MHC polymorphism can be maintained by balancing selection (Hedrick, 1999). Effects of pathogen-driven selection on the MHC locus can be observed at the population level as differences between MHC and neutral loci, population substructure and locus can be observed at the population level as differences (Hedrick, 1999). Effects of pathogen-driven selection on the MHC similarly to the results of neutrality tests for the donkeys (Aranguren-Mendez et al., 2001; Ivankovic et al., 2002) and infection were observed. This work was supported by the Czech Science Foundation project GA CR 523/09/172, partly by UVPs IGA 1230-IG10123 project and by the Apulian Regional Fund “ATZ 2008” administered by the Apulian Regional Office for Livestock Management.

Acknowledgments

This work was supported by the Czech Science Foundation project GA CR 523/09/172, partly by UVPs IGA 1230-IG10123 project and by the Apulian Regional Fund “ATZ 2008” administered by the Apulian Regional Office for Livestock Management.

References


Further reading (Web references)