Journal of Veterinary Behavior 31 (2019) 82–91

Contents lists available at ScienceDirect

Journal of Veterinary Behavior

journal homepage: www.journalvetbehavior.com

Ovine Research

Social personality in sheep: Can social strategies predict individual differences in cognitive abilities, morphology features, and reproductive success?

Genaro C. Miranda-de la Lama [a,b,*], María Pascual-Alonso [a], Lorena Aguayo-Ulloa [c], Wilmer S. Sepúlveda [d], Morris Villarroel [e], Gustavo A. María [a]

[a] Department of Animal Production & Food Science, Agri-Food Institute of Aragon IA2 (University of Zaragoza and CITA), Zaragoza, Spain
[b] Department of Food Science, Metropolitan Autonomous University-Lerma, Lerma de Villada, Mexico
[c] Colombian Corporation of Agricultural Research, Agrosavia, CI Turipaná, Montería, Colombia
[d] GIAM-Z Research Group, Universidad Libre, Campus Majavita, El Socorro, Colombia
[e] Department of Animal Science, E.T.S.I.A. Polytechnic University of Madrid, Madrid, Spain

ARTICLE INFO

Article history:
Received 29 October 2018
Received in revised form
22 December 2018
Accepted 19 March 2019
Available online 30 March 2019

Keywords:
social personality
social strategies
cognitive abilities
reproductive success
sheep

ABSTRACT

Social personality can be key factor in evolution because of intraindividual consistency, heritable basis, and linkage with fitness. The aim of this study was to identify the existence of sheep personality profiles based on the use of social strategies and its associations on morphological, cognitive, and reproductive success. Fifty adult ewes, housed indoor, were studied in terms of social and maintenance behavior, stress response, morphological variables, and productive performance. The cognitive abilities of the ewes were also analyzed. A factor analysis was used to summarize the data of 7 social behavioral variables. Agonistic and nonagonistic behaviors were grouped in classes. The factors were extracted using principal components. A hierarchical cluster analysis was performed to identify clusters or profiles. The results demonstrated the existence of 4 personalities profiles (avoider, affiliative, aggressive, and pragmatic), determined by social behavior and the index of success. The study addresses the multidimensionality of personality, showing that sheep personality comprises several social and nonsocial dimensions. The data confirm that the use of social strategies and the index of success are a useful tool to predict individual differences or personalities in a flock.

Introduction

In animal personality research, many terms are used to explain individual differences in behavior, besides personality itself (i.e., behavioral syndromes, coping style, temperament, and social strategies) (Finkemeier et al., 2018). According to selection theory, personality traits within a population are maintained because of individual trade-offs between current and future fitness returns (Nawroth et al., 2017). Personality may explain individual differences in social rank, social bonds, coping, cognitive abilities, and physiology (Zidar et al., 2017). Therefore, personality represents an important biological trait because of its intraindividual consistency, heritable basis, and linkage with fitness (Sichova et al., 2014). Individuals adopt different behavioral strategies in response to changes in their environment, reducing competition with group members (Cardoso et al., 2015). Then, sociability may favor behavioral consistency and differentiation of behavioral types through social niche specialization, resulting in differences in personality trait levels within a social group (Bergmüller and Taborsky, 2010; Koski and Burkart, 2015). A social personality can be defined as a coherent set of social strategies to respond to the challenges of group life, which are consistent over time and characteristic of certain social groups (Boissy and Le Neindre, 1990; Miranda-de la Lama et al., 2011). Social strategies can be key factors in the evolution and development of consistent individual differences in the personality (Mülleder et al., 2003.). The social niche specialization hypothesis suggests that in group-living animals, the combination

* Address for reprint requests and correspondence: Department of Animal Production & Food Science, Agri-Food Institute of Aragon IA2 (University of Zaragoza and CITA), Miguel Servet 177, 50013 Zaragoza, Aragon, Spain. Tel: +34 876554150; Fax: +34 976 761 590.
E-mail addresses: genaro@unizar.es, g.miranda@correo.ler.uam.mx (G.C. Miranda-de la Lama).

https://doi.org/10.1016/j.jveb.2019.03.005
1558-7878/

of social conflicts and alternative behavioral strategies on how to deal with them are of key importance for the development and evolution of social personality (Von Merten et al., 2017).

Domestication is an evolutionary process during which the behavioral profile (comprising social and emotional behavior, cognitive abilities, as well as hormonal stress responses) is substantially reshaped (Kaiser et al., 2015). Sheep are highly social and have evolved to live in large groups within a home range. Social behavior determines their grazing activity, spatial distribution, and speed of movement or proximity to other group members (Michelena et al., 2004). The social group is part of the complex, dynamic environment of the individual, in which many strategies have evolved to enhance survival and maintain the viability of the group (Galindo et al., 2011; Doyle et al., 2016). However, the relationship animals have with their conspecifics can also be one of the largest sources of stress, especially when sheep production systems can be restrictive with respect to key resources such as self-grooming substrates, shade, feeding spaces, and dry and comfortable lying places. The acute elevation of glucocorticoids (cortisol) due to activation of the hypothalamic-pituitary-adrenal (HPA) axis and immunosuppression are key defining features of the stress response in sheep (Lepherd, et al., 2011). Cortisol secreted by the adrenal gland plays an important role in gluconeogenesis by stimulating the liver to convert fat and protein to intermediate metabolites that are ultimately converted to glucose for energy. Cortisol content in blood is generally considered to be a good index for the reaction of animals to any environmental challenge (Miranda-de la Lama et al., 2012). In this context, individual behavioral differences can influence the ability of animals to cope with the social stressors inherent to production systems and may, in part, explain why some animals adapt to this environment better than others (Rice et al., 2016). However, there are relatively few studies on the personality of domestic animals, and most have been concerned with understanding some aspects of individual differences in pigs (Reimert et al., 2014; Scheffler et al., 2014), cattle (Mülleder et al., 2003; Müller and Von Keyserlingk, 2006; Hedlund and Løvlie, 2015), goats (Miranda-de la Lama et al., 2011; Pascual-Alonso et al., 2013; Nawroth et al., 2017), and sheep (Sibbald et al., 2009; Qiu et al., 2016).

Currently, research in farm animal welfare has focused on identifying consistent personality traits, when understood in the context of emotions, cognition, and social behavior can help improve animal welfare (Boissy and Erhard, 2014). Social stress caused by intensive production may disrupt cognitive processes like learning and memory (Proudfoot and Habing, 2015). Stress appears to affect the degree of attention and the speed of decision making, whereas chronic stress may affect cognitive abilities (Mendl, 1999). Animals with higher cognitive abilities should be more capable of producing new, modified, or innovative behaviors as this ability would allow them to cope better with unpredictable social and physical environmental changes, both in terms of improving survival and fitness and in terms of trying to achieve positive emotional states and avoid suffering (Wechsler and Lea, 2007). Experimental research has established that individuals within populations consistently vary in behavioral traits such as shyness, neophobia, exploration, aggressiveness, and sociability (Perals et al., 2017). In addition, with the increased use of cognitive indicators as inferred measures of personality, characterizing cognitive attributes of farm animal species may provide a basis for further developing practical measures of animal welfare under different husbandry and management settings (McBride et al., 2015). However, there are few studies on sheep and little is known about the relation between social personality and cognitive abilities. Thus, the aim of this study was to identify the existence of sheep personality profiles based on the use of social strategies and its possible associations with cognitive ability. In addition, the potential consequence of personality in morphological features and reproductive success of the ewes was evaluated.

Materials and methods

The study was carried out at the Animal Experimentation Service of the University of Zaragoza in the Autonomous Community of Aragon, Spain (41° 41 N). The area is located in the Ebro river depression, characterized by a dry Mediterranean climate with an average annual temperature of 15°C and mean annual rainfall of 317 mm. The study was conducted on a native breed; Chamarita sheep are a wool breed from La Rioja (Spain), included in the Official Catalogue of Spanish Livestock Breeds under Endangered Native Breeds. The Chamarita population size is about 10,000 sheep and it is officially recognized as an endangered breed to be preserved. Most herds are found in the mountains of lower La Rioja and in the Cidacos and Linares valleys. Animals are small in size (adult rams 55-65 kg, ewes 35-40 kg) and are mostly used for meat production.

Animals

The study involved 50 ewes, 5-8 years of age (7.5 average age), healthy, nonlactating, nonpregnant, multiparous, and housed in a 27×10 m pen (stocking density 5.4 m^2 per ewe) for six months before the behavioral observations were carried out (this was done to ensure a relatively stable flock social structure). The pen was equipped with a metallic water trough (1.5 m $\times$ 0.60 m), two metallic feeders (6 m $\times$ 0.50 m, 24 cm per ewe), and a lick stone for minerals. All animals were fed twice a day (at 08.00 and 15.00) with pellet concentrate (11.5 MJ ME/kg DM and 15.5% crude protein; approximately 0.3 kg per ewe), and *ad libitum* lucerne chaff (*Medicago sativa*). In addition, animals were provided with cereal straw as bedding on the floor and as forage in a fodder rake. No health problems or serious wounds/injuries were observed during the studies.

Study 1: phenotypic measurements

Maintenance and social behaviors measurements

All ewes were individually identified and marked with 30 cm–high numbers and letters painted on the sides and rump with washable spray paint (Peinture Marquage Mouton) for sheep marking. A platform with a seat at 3 m above the ground was used to observe the ewes from a distance. Direct observations, with a combination of instantaneous scan sampling (every 10 minutes) and continuous behavior sampling methods (between scans), were carried out to collect information on maintenance and social behavior, respectively (Martin and Bateson, 1993). All ewes were observed and recorded simultaneously 6 h daily, from 7:00 to 9:00, 11:00 to 13:00, and 16:00 to 18:00 pm for 16 consecutive days, making a total of 96 h of observations, and they are always recorded by the same trained observer. Within each observation period, data on maintenance behaviors were collected using an instantaneous scan sampling method at 10-minute intervals (576 samples per ewe) to estimate the proportion of time spent lying down (ewe resting with eyes open or closed), drinking (ewe with head inside the water trough), feeding (ewe with head inside the feeder trough), and walking (ewe moving from one place to another). For each ewe, the time spent performing nonsocial behaviors during the study was expressed as a proportion of observations calculated as follows: number of observations of a behavior/total number of scan samplings.

The continuous behavior sampling method was used between scan sampling episodes to record all events of agonistic and no-agonistic interactions. Agonistic interactions with contact included the following: butts (when a ewe used the front of her head to make contact with another ewe); pushes (when a ewe used other parts of her body to make contact with another ewe), and bites (when one ewe bit another ewe's body using her teeth). Agonistic interactions without contact included the following: threats (when a ewe turned toward or approached another individual with her head down and then lunged without making contact), or a chase (when a ewe actively moved toward another individual, causing the latter to walk or run away), and avoidance (when a ewe actively moved away from another individual as a result of a previous agonistic interaction). Nonagonistic interactions with contact included the following: licking (when a ewe passed her tongue over the body of another individual), or grooming (when a ewe groomed another ewe's body using her teeth). Non-agonistic interactions without contact included sniffing (when a ewe sniffed another ewe's body) and the flehmen response (when a ewe retracted the upper lip, wrinkled the nose, and bared the gums in the presence of another ewe). For each animal, the total number of times engaged in each of those social interactions was calculated. Indices of success were calculated using the data collected on interactive behaviors to reflect the social status of each ewe according to her experiences in agonistic interactions with any other member of the herd. The index of each ewe could therefore range from 0 to 1 and was calculated according to Mendl et al. (1992). Index of success = number of individual ewes she is able to displace/(number of individual ewes she is able to displace + number of individual ewes able to displace her). The ewes were then placed, as in the study by Miranda-de la Lama et al. (2011), into three ranking categories according to their index of success (IS): low (IS = 0.0-0.33), medium (IS = 0.34-0.66), and high rank (IS = 0.67-1.0). To substantiate the results obtained from the index of success, the index of displacement was also calculated as follows: the number of times an ewe displaces another ewe/(number of times it displaces another + number of times she is displaced).

Physiological measurements

Blood samples were taken by jugular venipuncture per ewe one day after behavioral observations ended (two 10-mL tubes were collected per animal, with and without anticoagulant, EDTA-K3). Approximately an hour before blood sampling, the site of venipuncture was clipped and covered with an anesthetizing cream to minimize the response to the initial puncturing of the skin. Restraint during blood sampling was kept to a minimum, and the total duration of the procedure did not exceed 1 minute. The handler grasped the halter with one hand and with the other groomed the ewe's neck to direct attention away from the blood sampling procedure. Samples were kept on ice for less than 1 hour and taken to the laboratory for routine hematological measurements. The EDTA plasma and serum were centrifuged at 3000 rpm for 10 minutes, and aliquots were frozen and kept at −30°C until analyzed.

An automatic particle counter (Microcell counter F-800 and auto dilutor AD-260, SysmexTM both) was used to count red blood cells and white blood cells (number per mm^3), hemoglobin (g/dL), and hematocrit (%). The leukocyte formula was estimated from blood swabs on clean slides. Staining was performed by the rapid panoptic method using dyes from *Química Clinica Aplicada Inc*. With an optic immersion microscope, we counted and identified 100 leukocytes per sample (neutrophils, lymphocytes, eosinophils, basophils, and monocytes). The neutrophil/lymphocyte ratio (N/L) was used as an indicator of chronic stress. Serum samples were used to determine the concentration of glucose (mg/dL, Ref. Glucose AE2-17), and the activity of creatinine kinase (UI/L) (Ref. CK.NAC AE1-13) using a multianalyzer ACE® (Clinical Chemistry System) and reagents from Alfa Wassermann (Woerden, the Netherlands). Serum concentration of nonesterified fatty acid levels was analyzed by a multianalyzer ACE® (Clinical Chemistry System of the Alfa Wassermann), with commercial kits (nonesterified fatty acid C Ref. 994-75409 of the Wako). The concentration of cortisol was determined from plasma (EDTA-K3) by enzyme immunoassay using an "in home-kit" (validated by Chacón et al., 2004). Each sample was determined in duplicate from 50 μl of plasma and the results were expressed in nmol/L, with the corresponding controls. Variation coefficients of the analysis, interassay and intra-assay, were 7% and 8%, respectively. The concentration of lactate was determined using a Sigma Diagnostic kit (lactate no. 735-10) and spectrophotometer Lambda 5 (Perkin Elmer, Waltham, MA).

Morphology, productivity, and fertility

Morphological traits were measured 1 day before blood sampling based on Miranda-de la Lama et al. (2011) using a measuring tape. Body measurements included body length; height at withers, and thorax circumference. In addition, each ewe was weighed using a portable digital weighing scale. Productivity and fertility traits were registered after behavioral observations ended. We registered lambing during 2 breeding seasons. Controlled natural mating was used. The lambs were kept together in the same pen with their mothers (8 m^2/sheep and lamb). All animals had *ad libitum* access to water and forage. The number of total lambs born from each ewe was registered. Lambs were weighed at birth (BW) and at weaning (WW). Preweaning average daily gain (ADG1) was estimated by the difference between WW and BW divided by the total milking period (30 days).

Study 2: cognitive abilities

This study used the same animals as study 1; we tested animals with T-maze validated for small ruminants built with 1.40 m high plastic panels (Pascual-Alonso et al., 2013). It consisted of a start box, isolation chamber (2 × 2 m) joined on one of its sides to a T-corridor (Figure 1). The start box was fully closed but large enough to enable an individual to move around. The T-corridor consisted of a 4 × 0.80 m path linked to two perpendicular arms (1.65 × 1.65 m each). A mirror (70 × 30 cm), loudspeaker, and plastic feeder (with feed pellets) were located in the target zone on the left arm. An observation platform was located on a 3-m high platform so as not to influence animal movement, adjacent to the T-maze apparatus. The apparatus was kept in a soundproof room (9 × 6 m) held at constant temperature and humidity during the trial.

The sounds used in the experiment were a playback of ewes and lamb vocalizations during short-term separation. We recorded at a distance of 50 cm from the noise source using a Handy Recorder H1 (Zoom Corporation Tokyo, Japan) numeric recorder (sampling rate: 44.1 kHz). Sounds were then imported into a computer at a sampling rate of 44.1 kHz and saved in WAV format at 16-bit amplitude resolution (Briefer and McElligott, 2012). We used Audacity® audio software (www.audacityteam.org; Boston, MA) to prepare sound sequences that were played back. A sample of each of these sounds was combined into a 5-minute segment and a random portion of this segment was played at each trial. The noise was played and measured using a Bioblock Scientific Sound Level Meter type 50517, at a set volume that ensured ewes were exposed to 81 dB of intensity through the majority of the T-maze. For each trial, the sounds were played back by a Handy Recorder H1 connected to a loudspeaker located at floor level in the left arm in the target zone. Each ewe underwent the cognitive test on 2 consecutive days. Each ewe entered the testing equipment twice in total, once on each day of test, without receiving prior training. Each animal stayed in the start box for 20 s before a guillotine door was lifted to allow

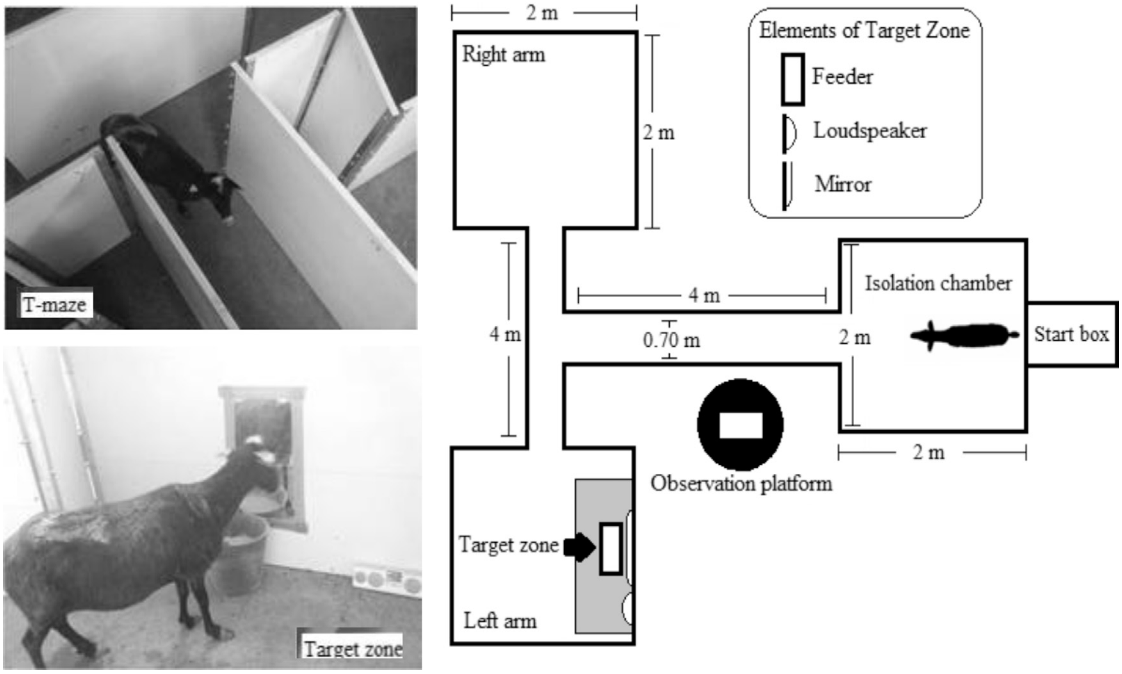

Figure 1. T-maze apparatus used to assess the cognition abilities in the study, all dimensions shown are in meters.

entrance into the maze. After the ewe left the start box, the guillotine door was quietly closed. At the same time, recorded playback was played and the test was started. The test was considered to be successfully passed when the individual found the target zone (which was always located in the left arm) where there was a mirror (self-image and possible social clue), the sound source (sound clue), and concentrate feed to reinforce behavior. Each animal was given a maximum time of 5 minutes to solve the T-corridor. No animal exceeded this time limit. The test was filmed and the time taken by each ewe to solve the T-corridor was recorded.

Statistical model

All statistical analyses were carried out with the software package SPSS, version 14.0. As an initial measurement, univariate analyses were carried out for all the variables studied to understand distribution data and to detect atypical data.

Factor analysis

A factor analysis was used to summarize the data of seven social behavioral variables and to understand their correlational structure. Agonistic and nonagonistic behaviors were grouped in the classes described in behavioral sampling to analyze them:

Number of times each ewe initiated an agonistic interaction with physical contact.

Number of times each ewe initiated an agonistic interaction without physical contact.

Number of times each ewe received an agonistic interaction with physical contact.

Number of times each ewe received an agonistic interaction without physical contact.

Number of times each ewe initiated a nonagonistic interaction with physical contact.

Number of times each ewe received a nonagonistic interaction with physical contact.

Number of times avoided another ewe.

The factors were extracted using principal components. The Kaiser-Meyer-Olkin index and Bartlett's test of sphericity were used as a measure of high correlation between variables. The criteria for the selection of the factors were that of eigenvalues ≥ 1. To gain a better understanding of the factors obtained, a Varimax method of orthogonal rotation was carried out. Accordingly, the factor scores in the analysis were estimated by the regression method and were consequently used for cluster analysis.

Cluster analysis

A hierarchical cluster analysis was performed to identify differences in social interactions. The cluster analysis enables segments of individuals to be identified, so that the characteristics of individuals that belong to the same group are as similar as possible, while, when compared with other groups, they are as different as possible. The distance used was the squared Euclidean distance and the Ward method was used for agglomeration. The variables used to calculate the squared Euclidean distances were the scores of the 3 factors obtained and the 2 variables (index of success and index of displacement) corresponding to commonly used measures of "social dominance." To reduce the effects of scale when forming the clusters, both groups of variables were standardized. The graphic solution used was the dendrogram (Figure 2). Once the membership to clusters variable had been created, they were then characterized using different variables such as index of success, classes of behavior (factorial scores), maintenance behavioral variables, physiological, morphological traits, and cognitive abilities. To select the most significant variables that would enable differentiation between clusters obtained, a nonparametric Kruskal-Wallis test and several nonparametric paired Mann-Whitney tests were carried out, bearing in mind the characteristics of the study and the variables. Based on group ranking, the Kruskal-Wallis test allows us to identify significant differences among more than two groups with respect to a quantitative variable. Nonetheless, it does not help to identify

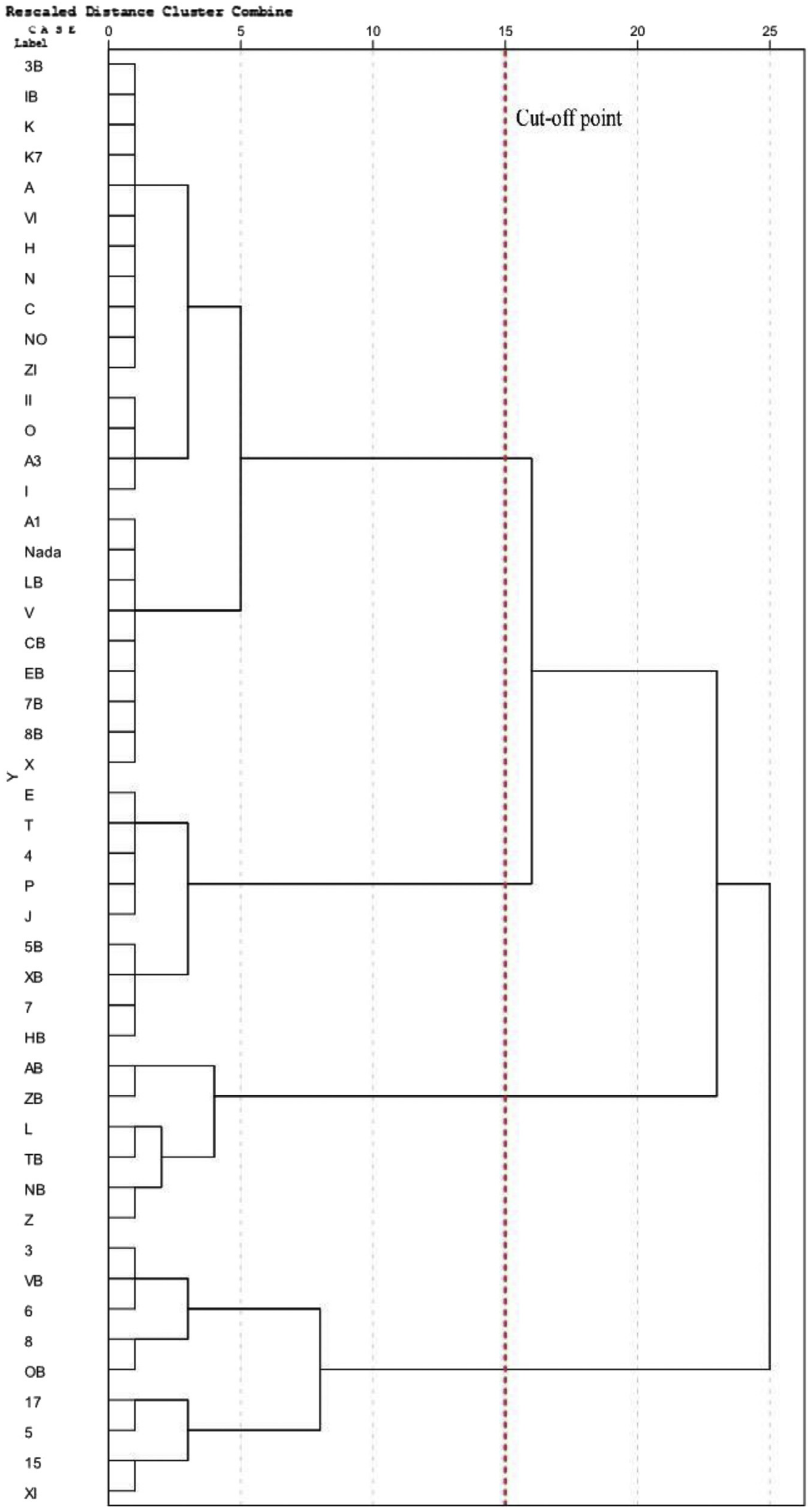

Figure 2. Dendrogram of hierarchical clustering of the studied ewes.

possible significant differences among each pair of groups that make up the group variable, as would occur with an ANOVA. For that reason, several Mann-Whitney *U* tests were carried out taking into account the variables that were more discriminant among the clusters after performing the Kruskal-Wallis test. Similarly, when using qualitative variables, we used the chi-squared test to identify the variables most associated with the groups. After the cluster analysis, it is common practice to develop bivariate tests to better

Table 1
Factor analysis results of ewe's social behavior (rotated component matrix)

Classes of behaviors	Factor 1 (avoidance)	Factor 2 (agonistic)	Factor 3 (nonagonistic)
No. of times avoiding another ewe	0.98[a]	−0.02	−0.08
No. of times each ewe receives an agonistic interaction with physical contact	0.95[a]	0.12	−0.10
No. of times each ewe receives an agonistic interaction without physical contact	0.91[a]	−0.17	0.15
No. of times each ewe initiates an agonistic interaction with physical contact	0.03	0.94[a]	−0.06
No. of times each ewe initiates an agonistic interaction without physical contact	−0.12	0.90[a]	0.22
No. of times each ewe receives a nonagonistic interaction	−0.16	−0.01	0.90[a]
No. of times each ewe initiates a nonagonistic interaction with physical contact	0.31	0.31	0.47[a]
Percentage of explained variance	40.5%	27.3%	14.9%

[a] Factor score coefficients are significant loadings of the variable on that factor (very significant loading ≥ 0.7).

describe the profiles of the segments based on the variables that are most discriminatory (Miranda-de la Lama et al., 2011).

Results

Factor analysis

Three factors were extracted, explaining 82.7% of the variance. The first factor accounted for 40.5% of the total variance and was characterized by 3 of the 7 variables that were used: number of times each ewe received an agonistic interaction with physical contact, number of times a ewe received an agonistic interaction without physical contact, and number of times it avoided another ewe. These variables had a very significant loading (≥0.9). This factor indicated recipient behavior, and both agonistic behavior and avoidance was labeled "avoidance factor." The second factor accounted for 27.3% of the total variance and was characterized by 2 variables, which had very significant loadings (≥0.9): number of times each ewe initiated an agonistic interaction without physical contact and number of times each ewe initiated an agonistic interaction with physical contact. Accordingly, factor 2 was labeled as the "agonistic factor." Factor 3 accounted for the remaining 14.9% of the total explained variance and was characterized by 2 variables: number of times each ewe initiated a nonagonistic interaction with physical contact and number of times each ewe received a nonagonistic interaction with physical contact. The first of these variables had a very significant loading (≥0.9) and this factor was labeled as the "nonagonistic factor" (Table 1).

Cluster analysis

This multivariate analysis suggests the existence of 4 clusters or personality types that explain their association with behavioral traits, morphological traits, cognitive abilities, and fertility rates. The distribution of animals by strata was not homogeneous (cluster 1 = 9; cluster 2 = 24; cluster 3 = 9, and cluster 4 = 6). Given the social behavioral dimensions that were found in each cluster, the number 1 was termed "Avoider," number 2 "Affiliative," number 3 "Aggressive," and number 4 "Pragmatic," according to the social strategy preferentially used for each personality type (Table 2). There were no differences in any of the maintenance behaviors studied. However, all the morphological traits were significantly different between clusters as well as the total time needed for the cognitive test in the second trial. No significant differences were found in physiological stress response variables with the exception of cortisol and lactate, which was higher in the aggressive profile compared to the rest of clusters (Table 3). The birth live weight and the weekly weights of the lambs born from ewes of each cluster were similar in all cases as well as the average daily gain for the whole milking period (Table 4). On the other hand, there were

Table 2
Characterization of clusters obtained from dominance, social and maintenance behavior, morphological and cognitive traits

Variables	Avoider (n = 9)	Affiliative (n = 24)	Aggressive (n = 9)	Pragmatic (n = 6)	P[d]
Social behavior					
Dominance					
Index of success	0.41[a]	0.48[a]	0.56[b]	0.60[b]	0.000
Index of displacement	0.30[a]	0.50[a]	0.61[bc]	0.78[c]	0.000
Factors					
Avoidance	1.76[a]	−0.51[b]	−0.24[b]	−0.22[b]	0.000
Agonistic	−0.28[ab]	−0.51[a]	0.31[b]	1.99[c]	0.000
Nonagonistic	0.16[a]	0.25[a]	−1.36[b]	0.79[a]	0.000
Maintenance behavior					
Drinking (%)	0.20	0.35	0.25	0.40	N.S.
Feeding (%)	36.29	34.49	39.05	34.16	N.S.
Resting (%)	25.39	28.54	24.07	28.77	N.S.
Walking (%)	38.12	36.63	36.63	36.67	N.S.
Morphological measures					
Body length (cm)	69.44[a]	72.94[b]	74.83[b]	74.92[b]	0.015
Height at withers (cm)	62.50[a]	66.06[b]	68.39[b]	66.00[b]	0.007
Thorax circumference (cm)	100.44[a]	104.69[b]	107.94[b]	102.42[ab]	0.005
Body weight (Kg)	39.50[a]	44.42[b]	49.72[b]	46.25[b]	0.012
Cognitive ability					
Total time to solve on first-day exposure (s)	97.89	106.00	65.44	123.50	N.S.
Total time to solve on second-day exposure (s)	18.56[ab]	27.79[a]	13.67[b]	57.50[c]	0.036

The superscripts a, b, and c were used to identify whether there are significant differences ($P < 0.05$) or not ($P \geq 0.05$) among each pair of group comparisons after applying several Mann-Whitney U tests.
Different letters (a, b, c) indicate significant differences between groups.
[d] P is the P-value corresponding to the Kruskal-Wallis test; N.S., $P \geq 0.05$.

Table 3
Characterization of clusters obtained from physiological variables

Variables	Avoider (n = 9)	Affiliative (n = 24)	Aggressive (n = 9)	Pragmatic (n = 6)	P^d
WBC (103/mm^3)	7.80	8.93	7.61	6.46	N.S.
RBC (106/mm^3)	9.09	8.62	9.17	8.89	N.S.
HG (g/dL)	9.59	9.06	9.73	9.20	N.S.
HTC (%)	29.36	28.14	30.67	28.32	N.S.
PT (103/mm^3)	222.00	299.83	321.78	394.00	N.S.
MCV (um^3)	32.44	32.70	33.22	31.80	N.S.
MCH (pg)	10.58	10.53	10.61	10.38	N.S.
MCHC (g/dL)	32.71	32.265	31.86	32.50	N.S.
CK (UI/L)	128.00	119.87	128.44	143.60	N.S.
Cortisol (nmol/L)	19.15^a	27.65^a	45.30^b	17.11^a	0.005
Glucose (mg/dL)	81.56	71.57	67.89	74.80	N.S.
Lactate (mg/dL)	11.28^a	21.27^b	25.44^b	10.82^a	0.017
NEFA (mmol/L)	0.09	0.09	0.07	0.05	N.S.
Ratio N/L	0.77	0.85	0.77	0.62	N.S.

CK, creatine kinase; NEFA, nonesterified fatty acid; ratio N/L, neutrophil/lymphocyte ratio; WBC, white blood cell; RBC, red blood cell; HG, hemoglobin; HCT, hematocrit; PT, platelets; MCV, mean corpuscular volume; MCH, mean corpuscular hemoglobin; MCHC, mean corpuscular hemoglobin concentration.
The superscripts a, b, and c were used to identify whether there are significant differences ($P < 0.05$) or not ($P \geq 0.05$) among each pair of group comparisons after applying several Mann-Whitney *U* tests.
Different letters (a, b, c) indicate significant differences between groups.
[d] P is the *P*-value corresponding to the Kruskal-Wallis test; N.S., $P \geq 0.05$.

significant differences in the percentages of ewe fertility and prolificacy (Table 5).

The avoider profile was characterized by individuals with a low index of success (0.41), high avoidance strategy factor, and a positive but much lower value of the nonagonistic strategy. These animals were the smallest and leanest ones in the social groups. The live weights of animals in that group were significantly different than in the other clusters (−12.4%, −25.8%, and −17% for affiliative, aggressive, and pragmatic groups, respectively; $P < 0.05$). Those animals also showed the lowest values of height at withers (−5.6%, −9.4%, and −5.6% compared to the affiliative, aggressive, and pragmatic groups, respectively; $P < 0.05$). In the case of the body length, they only showed significant differences with the pragmatic profile (-7.8%; $P < 0.05$). The thorax circumference of the avoiders was significantly smaller than the affiliative or aggressive profiles (−4.7% and −7.9%, respectively; $P < 0.05$). From the cognitive point of view, the avoiders used 20% of the time of the first round in solving the test, demonstrating a significantly greater capacity than the affiliative and pragmatic individuals, being similar to the aggressive ones. The avoider showed significantly lower hematological responses than the aggressive profile (≈40% lower lactate and cortisol), but similar to the affiliative or pragmatic profiles. Avoiders presented a medium fertility rate (lower than affiliative and aggressive profiles, but higher than the pragmatics). However, the prolificacy of this profile was higher than affiliative and aggressive, and lower than pragmatics. No significant differences were observed for the other productive traits.

The affiliative profile comprised animals of medium success index (0.48), with high values for the nonagonistic strategy. They were medium-sized animals, significantly bigger and heavier than the avoiders. However, no significant differences were observed for this profile in comparison with the aggressive or pragmatic animals for live weight or body size. From the cognitive point of view, the animals of this profile were similar to avoiders. Regarding physiological stress variables, they presented higher lactate levels along with the aggressive profile. However, the cortisol values were similar to the avoiders and pragmatics but significantly lower than the aggressive. In relation with productive traits, the ewes of this profile presented the highest fertility rate, but the lowest prolificacy values. No significant differences were observed for the other productive traits.

The aggressive profile was formed by individuals with a medium index of success (0.56) with a preponderant agonistic strategy. This group was composed of medium-sized animals, significantly bigger and heavier than the avoiders. However, no significant differences were observed for this profile in comparison with the aggressive or pragmatic animals for live weight and body size measures. The aggressive profile was the fastest (along with the avoiders), to solve the T-maze on the second trial, showing significant differences with the pragmatic profile (solving it 4 times faster) and also with the affiliative profile (twice as fast). The physiological stress variables of the aggressive animals were characterized by high lactate levels, along with the affiliative profile, and higher cortisol levels compared to the rest of the profiles. For productive traits, the ewes of this profile had a higher fertility rate, and medium prolificacy. No significant differences were observed for the other productive traits.

The pragmatic personality was made up of individuals with the highest index of success (0.60; similar to aggressive profile). These

Table 4
Characterization of clusters obtained from productive traits of lambs born from ewes of each cluster

Variables	Avoider (n = 9)	Affiliative (n = 24)	Aggressive (n = 9)	Pragmatic (n = 6)	P^a
Birth live weight (Kg)	3.13	3.75	3.69	3.10	N.S.
Weight in the second week (Kg)	4.33	4.80	5.30	4.20	N.S.
Weight in the third week (Kg)	5.55	6.14	6.66	5.95	N.S.
Weight in the fourth week (Kg)	6.60	7.72	8.47	6.35	N.S.
Weight in the fifth week (Kg)	8.20	9.26	10.04	7.90	N.S.
Weight in the sixth week (Kg)	9.53	10.93	10.95	8.90	N.S.
Weaning live weight (Kg)	11.98	12.22	12.94	11.25	N.S.
Average daily gain during the milking period	0.20	0.23	0.25	0.18	N.S.

[a] P is the *P*-value corresponding to the Kruskal-Wallis test; N.S., $P \geq 0.05$.

Table 5
Characterization of clusters obtained from reproductive performance

Variables	Avoider (n = 9)	Affiliative (n = 24)	Aggressive (n = 9)	Pragmatic (n = 6)	P[a]
Pregnancy					
Pregnant	55.6%	91.3%	77.8%	33.3%	0.015
Nonpregnant	44.4%	8.7%	22.2%	66.7%	
Type of delivery					
Single	60.0%	76.2%	57.1%	0.0%	0.040
Twin	40.0%	23.8%	42.9%	100.0%	

[a] P is the *P*-value corresponding to the chi-squared test.

animals use a combination of agonistic and nonagonistic strategies in the social group, which led us to call them "pragmatic" animals. They were heavier than the avoiders, but similar to the affiliative and aggressive profiles. Morphologically, they were also bigger than the avoiders, but similar to the other 2 profiles. The individuals of this profile were the slowest to solve the T-maze on the second trial, showing significant differences with all the other profiles. Regarding physiological stress variables, they presented lower lactate and cortisol levels than the affiliative or aggressive profiles, but similar to the avoiders. Finally, in relation with productive traits, the ewes of this profile presented the lowest fertility rate but the highest prolificacy rate. No significant differences were observed for the other productive traits.

Discussion

Significant variation exists in how individuals behave and respond to their environment, which can have important welfare and production implications for production animals (Hedlund and Løvlie, 2015). Under the conditions of our study, the results suggest the existence of at least 4 personality profiles (avoider, affiliative, aggressive, and pragmatic), determined by analyzing social behavior and the index of success of displacement. In addition, those profiles were associated with some morphological, reproductive, and cognitive variables. We did not detect differences in maintenance behavior among profiles, possibly because they are less affected by the social environment and have a stronger and more uniform innate base, compared to social behaviors that are more plastic. This finding could imply that the use of different social strategies in a stable group of sheep (with enough pen surface and feeding space) does not affect individual maintenance behavior. Variation in sheep personality within populations results from selection caused by social interactions, if divergent behavior types provide higher fitness prospects than intermediate strategies. It is possible that personality is affected by breed, the production system (intensive vs. extensive), and the productive goals (dairy systems are more restrictive than meat systems). According to previous work in goats, the profiles can be relatively different between breeds and production systems; however, aggressive, affiliative, passive, and evasive profiles still appear (Miranda-de la Lama et al., 2011; Pascual-Alonso et al., 2013). This process leads to multimodal phenotype distributions and has been studied extensively in the context of alternative behavioral and reproductive tactics (Bergmüller and Taborsky, 2010).

In sheep, hierarchies are often bidirectional and nonlinear so that rank obtained for "social dominance" of 1 sheep over another is not absolute (Lynch et al., 1992). In our study, confirming this hypothesis, we found the existence of 2 levels of social dominance with a threshold located around a success index of 0.50 (below and above 0.50), grouping 2 types of profiles each. Avoider and affiliative are in the lower category, whereas the aggressive and pragmatic are in the upper category. Aggressive and pragmatic animals have in common the use of agonistic behaviors as a stable social strategy. Pragmatics also use, albeit to a lesser extent, nonagonistic or affiliative behaviors in the social context, whereas avoider and affiliative animals use the nonagonistic behaviors as a predominant social strategy (Mülleder et al., 2003). Avoiders also use evasion as the main strategy in the social group. Taking into account that the social stability and welfare of a group depends on the cohesion between its individual members, the pragmatic profile characteristics suggest that a combination of agnostic and nonagonistic behaviors may result in a more efficient social strategy to monopolize and control social relationships in the group. This feature may facilitate the duration of the association and fission of the group, an important characteristic in a gregarious species like sheep (Broom and Fraser, 2015).

In mammals where female competition is unusually intense, females often show physiological, morphological, and behavioral adaptations that increase their competitive abilities as they do in a wide range of other animals (Clutton-Brock and Huchard, 2013). There is evidence in the literature that demonstrates that some corporal features play an important role in the establishment of social rank and strategies (Öst et al., 2015). Corporal features may be honest signals that communicate a certain genetic value (Smith et al., 2009). Avoider ewes were clearly the smallest and lightest of the 4 profiles. These evasive animals also have a low success rate, which would indicate that they are the weakest link in terms of social success of the group. Miranda-de la Lama et al. (2011) highlighted the relationship between small size and low social status as an adaptive advantage, which makes animals more efficient when they are exposed to scarce resources, needing less energy and being metabolically more efficient. On the other hand, pragmatic ewes seem to be the most skillful and "dominant" individuals in the group. It is possible that the thoracic circumference of these animals is an optimal measure in comparison with the aggressive profile. The data suggest that the animals with largest thorax are not always the most successful in the social group.

We found that interindividual variation (expressed by 4 profiles) in learning and memory ability could be attributable, at least in part, to differences in personality (i.e., White et al., 2017). Variations in personality styles are often associated with consistent behavioral traits for learning and cognition (Nawroth et al., 2017). The results of learning in the T-maze test were interpreted as the ability to learn from specific stimuli, actions, and results to be able to solve a challenge (Pascual-Alonso et al., 2013). Some personality traits may affect learning simply because they increase probabilities or rates of exposure to the to-be-learned experimental contingencies (Guillette et al., 2017). Our result indicates that the fastest animals in solving the test were the avoiders and affiliative profiles (low rank dominance). It is possible that the low-dominance animals need to learn quickly how to relate socially to avoid aggressions, suggesting a kind of "survival" learning (Croney and Newberry, 2007). Traditionally, low social status animals have been considered to have a higher level of stress compared to those with a higher social status (McBride et al., 1967). However, from our results, the animals with the lowest social status were the least stressed, indicating that the maintenance of a high social status carries an important energetic cost and demands a high activity of the HPA axis. Results here suggest that personality may influence learning and cognition, and the significance of this finding across domestic animals and production systems will be a fruitful line of future research.

Sociability is an important part of social dynamics and has been shown to relate to personality differences in a wide range of animal taxa (Von Merten et al., 2017). Sheep live in complex environments that can change over time. When changes in their environment are potentially harmful, ewes adjust by generating stress responses (Ralph, and Tilbrook, 2016). These neuroendocrine responses involve activation of the HPA axis and secretion of cortisol or other associated metabolites. When an animal perceives a stimulus to be a threat (i.e., social challenge) and the HPA axis is activated, it also experiences basic emotions such as fear (Sapolsky et al., 2000). Stress responses can differ markedly between individuals (Guimont and Wynne-Edwards 2006). It has been suggested that different stress responses in animals may be associated with different personalities (Cockrem, 2007). As we mentioned previously, our results suggest that the aggressive profile had the highest stress response when compared to the rest of the profiles, indicating that higher social dominance using aggressive strategies does not imply a lower stress response or better animal welfare, which may affect their productivity in the flock.

Variation in animal personality is related to traits relevant for production, including fertility (Hedlund and Løvlie, 2015). Estimates of personality and investigation of links with production traits are therefore of relevance to animal production (Adamczyk et al., 2013). Nevertheless, despite current interest and potential implications, the origin and consequences of personality variation are still poorly understood. Our results effectively indicate the existence of a relationship between numerical productivity and personality profiles. The affiliative animals (low social dominance) presented the highest fertility rates among the 4 profiles detected. However, they also had the lowest prolificacy. We did not observe a relation between personality of ewes and individual productivity of their lambs. A possible simple explanation for the lack of productive variables could be related to the small size of the sample. It is noteworthy that the pragmatic (more socially dominant) and apparently more socially skilled animals had the lowest fertility, but the highest rates of prolificacy. In conclusion, ewes that achieved higher social dominance (as defined by displacement of others) did not enhance their fecundity, nor the numeric productivity and performance of their lambs. Indeed, there is evidence in the scientific literature indicating the weak relationship between social dominance and fertility (Sarova et al., 2017). One possible explanation for this phenomenon is that more socially dominant animals may have hormonal profiles that predispose them to a higher rate of ovulation, but that does not correspond with improved embryonic survival, as was suggested by Biro and Stamps (2008). In this sense, there is evidence suggesting that high levels of stress do not favor embryonic survival (Von Borell et al., 2007). Social stress may reduce embryo competence by shifting blood flow away from the reproductive system as part of the classic “fight or flight” response, and methods to reduce social stress, can improve pregnancy success (Meldrum et al., 2016). However, more specific studies in sheep are required regarding the relation between personality characteristics and reproduction.

Conclusions

Under the conditions of our study, the results suggest the existence of 4 personalities (avoider, affiliative, aggressive, and pragmatic). The use of social strategies and the index of success as a determinant of social personality is a suitable way to detect personalities in a stable flock. It is likely that these personality traits are evolutionarily stable and related to certain morphological, physiological, cognitive, and reproductive characteristics. From the 4 profiles detected, the pragmatic profile that uses a combination of agonistic and nonagonistic behavioral strategies may be more socially efficient to cope up with the environment, favoring group cohesion. Following the current trend of modern concepts of animal welfare that involve returning to an individualized treatment of animals, our results provide useful information for the decision making of the managers of the production system who aim to optimize the welfare of the animals using personality as a selection criteria.

Acknowledgments

This research was financed by the Spanish Ministry of Economy and Competitiveness, Project AGL-2009/10794. The authors also want to acknowledge Aragonese Agency for Research and Development (ARAID) and Aragon Government for funding Miranda-de la Lama’s incorporation to the IA2.

Ethical considerations

All studies and procedures were performed with the approval of the Animal Care and Ethics Committee of the University of Zaragoza and were raised according to current regulations of the European Community Commission (1986) for Scientific Procedure Establishments.

Conflict of interest

The authors declared that they have no conflicts of interest with respect to their authorship and/or the publication of this article.

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