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RESEARCH ARTICLE

Effect of rams' social hierarchy upon scrotal circumference, semen quality, and copulation performance under arid land conditions

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ABSTRACT

Social hierarchies among animal species are based on the animal´s dominance-aggressiveness level aligned with the subordination of their mates. Social order is mostly defined by animal size, live weight, or age. This study aimed to evaluate the association between odor score (OS), horn presence (HP), horn size (HS), and body temperature on social rank hierarchy, scrotal circumference (SC), semen quality (SQ), and sexual drive (SD). Adult Dorper rams (n = 24) with similar live weight (LW), body condition score (BCS), and age (AG) were subjected to a behavioral test to define a success index (SI) based on male-to-male interactions. OS was highest ($P < 0.05$) for rams with high social rank (HSR; 2.5 ± 0.4) and lowest for rams with low social status (LSR; 0.75 ± 0.01). Scrotal circumference was highest ($P < 0.05$) for HSR rams (40.0 ± 3.5) and lowest for rams with medium social rank (MSR; 29.3 ± 1.20). Sperm cell concentration/mL was highest ($P < 0.05$) for HSR rams (3848 ± 187) and lowest for LSR (2660 ± 463). 80% of the HSR rams had horns, while 33.3 of the LSR rams were hornless. The percentage of rejection to mount an estrous ewe was 77.7 for LSR and 20% for HSR and MSR rams ($P < 0.05$). To conclude, the HSR rams presented the highest successful copulation, scrotal circumference, and sperm cell concentration compared to rams with lesser social rank scores.

Keywords: Horn presence; Seasonal reproduction; Sexual behavior; Sexual odor; Socio-sexual cues

INTRODUCTION

Various sensory systems, such as chemical, visual, auditory, postural, or a combination of these cues, have evolved among animal species to communicate and define social and sexual rank among animals (Fernald and Maruska, 2012; Fox et al. 2019). Regarding social dominance, animals exert such behavior to establish intrasexual competition for mates. In arid zones, the amount of feed resources tend to be limited and must be shared in some way among all members of the flock (Fernald and Maruska, 2012, Broom, 2002). Social rank is established through contests; such hierarchy is positively correlated with body size and body weight (Fernald and Maruska, 2012; Pelletier and Festa-Bianchet, 2006; Orihuela, 2014; Zuñiga-Garcia et al., 2020a, 2020b). These diverse social hierarchies occur among different animal species and production systems, based on the animal´s dominance-aggressiveness levels aligned with the level of subordination of others, which generates heterogeneous reproductive outcomes (Zuñiga-Garcia et al., 2020a, 2020b; Ceacero et al., 2012; Pelletier and Festa-Bianchet, 2006). Indeed, the greater sexual behaviors (DeYoung et al., 2006; Perkins and Fitzgerald, 1994) and reproductive outcomes (Ungerfeld and Lacuesta, 2010) are positively associated with higher-sexually ranked animals. Moreover, chemical cues such as odor (Boehm et al., 2005; Russell and Fernald, 2014), which emanate from the head, neck, and shoulders of males in a testosterone-dependent fashion (Keller and Levy, 2012), modulate reproduction by altering both physiology and behavior of receptive females (Petrulis, 2013).

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Also, in sheep, a positive interaction exists between serum testosterone concentration and follicular stimulating hormone, testicular size, and horn growth (Lincoln, 1998). Further, both the length and diameter of horns are linked with spermatogenic output in wildlife animals (Santiago-Moreno et al., 2007), while horned males have shown better reproductive outcomes (Rekik et al., 2012). Based on such findings, we hypothesized that Dorper rams with similar body weight, BCS, and age, both odor intensity, and horn presence/size, would increase socio-sexual status and testicular size, semen quality, and copulation success.

MATERIAL AND METHODS

General

All the experimental procedures, handling, and maintenance of the animals used in this study were based on the guidelines for ethical use, care, and welfare of animals in research at international (FASS, 2010) and national (NAM, 2010), with institutional approval reference number UAAAN/UL/1330-8241-2868.

Location and environmental conditions

The study was carried out during the spring (March-May) in northern Mexico (25° 51´ N, 103° 14´ W, 1,115 meters above sea level). The area is characterized by a dry and hot climate, with an average annual temperature of 23.1°C. The mean annual rainfall is 210 mm, the relative humidity oscillates from 12 to 61%, and the variations of light are from 13 h 41 min during the spring solstice (June) to 10 h 19 min in the winter solstice (December).

Experimental animals and their management

Dorper rams (n=24) and ewes (n=10) were selected; animals of both sexes had an average age of 3 years (range 2 to 4 years). Animals were fed twice a day (1000 and 1800 h) with a mixed ration (forage-silage-grains; 2.9 Mcal ME/kg DM and 17% CP). Besides, the experimental units had free access to mineral salts and water. They were vaccinated against clostridium spp. (7-way Biobac bacterine, Biozoo, Jalisco, Mexico; 2.5 mL by subcutaneous route) and dewormed with Doramectina (Dectomax®, Bayer, Mexico; 1 mL by intramuscular route) against the main pathogenic agents in the region (like lungworms, gastrointestinal parasites and mange), three weeks before the start of the study, following routine herd management. The primary management practices and experimental activities are shown in Figure 1.

Evaluation of the social rank of Dorper rams: Behavioral tests

During the first phase of the study, the social rank and morphometric characteristics of Dorper rams were determined; also, the live weight and BCS (scale 0 to 5, where 0 = emaciated and 5 = very fat) were recorded (Phythian et al., 2012). The social rank of rams was assessed using ten estrogenized ewes. Females received 2 mg of estradiol cyprionate intramuscularly beginning on day –2 of the study. Rams were exposed to ewes in individual 2.5 x 2.5 m pens. In each behavioral evaluation, two males were exposed to each female for 30 min to evaluate the sexual behavior of rams. New pairs of rams were formed until each ram competed against the remaining nine rams. The social rank of rams was determined by the success index (SI) described previously (Alvarez et al., 2003; Barroso et al., 2000). The following male-to-male behaviors were considered: bumps, threats, shoves, chases, escapes, and evasions. A ram-to-ewe interaction was considered when a ram displayed dominant behaviors towards the other ram that declined the interaction (subordinated male). To define the success rate, the behavioral characteristics linked to success from the ram-to-ram competitions were considered; in sheep, the opportunity for male reproduction is primarily determined through paired-male rounds (Pelletier and Festa-Bianchet, 2006). The observations of the behavioral study (i.e., agonistic interactions) were made by a single person, and the information was recorded in a digital format. Then, the SI for each ram was quantified. SI was generated by dividing the number of events won by the number of lost events, thus determining three social ranks in the evaluated rams: low (LSR; SI= 0 to 0.33), medium (MSR; SI=0.34 to 0.66), and high (HSR; SI=0.67 to 1.0) as previously described (Barroso et al., 2000).

Skull-horn-body morphometric characteristics

The skull-horn morphometry characterization test of the rams (n=24) included 9 LSR, 10 MSR, and 5 HSR, quantifying the presence of horns (POH; %), distance between horns (DBH; cm), length of horns (LH; cm), size (SH, cm) and width (WH, CM) of the head. Besides, height to withers (HW, cm), thoracic circumference (TC), thoracic diameter (TD, cm), and scrotal circumference (SC, cm) was also recorded.

Evaluation of seminal characteristics, scrotal circumference, and odor score

Semen was collected with an artificial vagina for sheep (Artificial Vagina for Small Ruminants, IMV Technologies, L´Aigle, France) at 38° C, using one ewe in estrus to induce rams to mount. The semen collected was deposited in graduated tubes, which were immediately immersed in a container with water at 38°C and transported to the laboratory during the next 10 min after collection. Volume (mL) of ejaculate was directly quantified in the conical collection tube, with optically visible 0.1 mL intervals. The sperm cell concentration was assessed using a photometric analysis (Spermacue®, 12300/0500 Minitub, Landshut, Germany) as previously described (Olivera-Muzante et al., 2011), using undiluted semen, and expressed in 10^6 cells mL^{-1}. Mass motility (%) was assessed using an arbitrary scale from 1 to 5; where 1 = 25% and 5 = 100% motile sperm (Mahsud et al., 2013). Sperm motility was determined by contrast microscopy, 400X phase, using a preheated platform (37°C). Seminal pH was evaluated with a paper strip, adding 4 to 6 drops of semen to each strip, and the pH was subsequently determined according to the scale provided by the manufacturer. Scrotal circumference was measured with a flexible tape, and the odor score was determined by smelling the dorsum of the neck 10–15 cm behind the base of the horns and recording a score of 0 (neutral odor indistinguishable from ewes) to 3 (strong smell of rams) (Walkden-Brown et al., 1997). To avoid bias, a single experienced technician recorded the odor of each ram. Given that rams were not well-trained in the use of the artificial vagina, only 14 rams could ejaculate due to fear of some rams to the artificial vagina operator: LSR = 2, MSR = 8, and HSR = 4.

Statistical analyses

For LW, BCS, age, odor score, horn dimensions, head measurements, and other body measurements, a completely randomized design using the GLM procedure of SAS (SAS Institute, Cary, NC, USA) was performed, with three social ranks and five to ten replicates per group. The general model used was $Y_{ij} = \mu + A_i + e_{ij}$, where Y_{ij} is the dependent variable, μ is the overall mean, A_i is the effect of the ith social rank and e_{ij} is the random residual error. Rams within social rank were the experimental units. Means of treatments were compared for differences using the Fisher's MEANS TREATMENT/LSD option of SAS. Besides, pH, ejaculate volume, and sperm concentration mL^{-1} were analyzed using the GLM procedure of SAS. The significant differences between group means were compared using the PDIFF procedure of SAS. The data of microscopic characteristics of sperm cells were subjected to an ANOVA using the MIXED procedure of SAS for repeated measures across time. The sexual behavior variables had non-normal distribution according to the UNIVARIATE procedure of SAS. Therefore, these data were subjected to logarithmic transformation [log (X + 1)]. The transformed data were analyzed using the PROC GLM procedure of SAS to assess the effects of hierarchical status. Significant differences among groups were compared using the MEANS TREATMENT/LSD option of SAS. The GENMOD procedure of SAS was used to assess the effect of social rank (3 levels) on the percentage of mounts and rejection to mount estrous ewes. Group means were compared using the LSMEANS/PDIFF option of SAS. For all statistical analyses, differences were considered significant at $P < 0.05$.

RESULTS

Classification of the social rank and success index in Dorper rams

The proportion of rams in the different social ranks and the success index after win and lost events within rams, is presented in Table 1. MSR rams showed a higher proportion of animals, followed by LSR and HSR. HSR rams showed a greater ($P<0.05$) number of won events than the other rams. Likewise, HRS rams showed the lowest ($P < 0.05$) lost events compared with MSR and LSR rams. However, SI did not differ ($P>0.05$) among groups of rams.

Odor score, and skull-horn-body morphometric characteristics

Bodyweight and BCS, odor score, and some horn, skull, and body morphometric characteristics across experimental

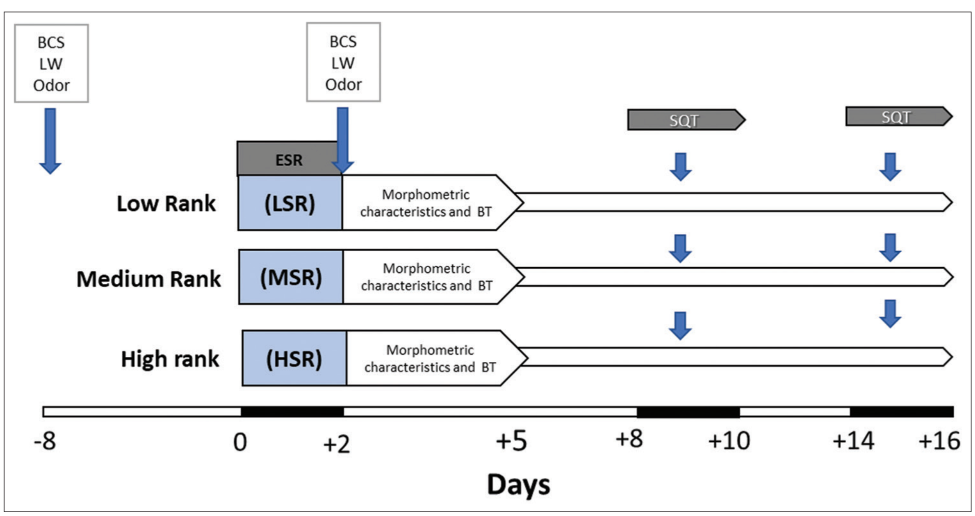

Fig 1. Experimental procedures depicting the timeline of actions. The evaluation of the social rank in Dorper rams (n= 24) was carried out during the non-breeding season (March-May) in northern Mexico (25° N) for two days (ESR). The morphometric characteristics were evaluated for five consecutive days. SQT = Seminal quality tests (dark gray bar). LSR = low social rank, MSR = medium social rank and HSR = high social rank.

groups are shown in Table 2. While the greatest (P<0.05) OS and SC were observed in the HSR-males, the lowest (P<0.05) value for POH occurred in the LSR-rams. The greater odor score (P<0.05) occurred in the HSR and MSR rams, vs. the LSR-group, with respective values of 2.5±0.4, 1.9±0.2, and 0.75±0.1 units. Besides, whereas 77.7 % of the LSR-rams were hornless, 80% of the HSR-group were horned, with intermediate values (50%) in the MSR rams. Moreover, the HSR-group showed the greatest scrotal circumference (40.0±3.5 cm; P<0.05), followed by the MSR-rams (29.3±1.2 cm) and the lowest (P<0.05) value occurring in the LSR-group. No differences (P>0.05) were observed regarding live weight (LW), body condition (CC), distance between horns (DBH), length of horns (LH), size of the head (SH), width of the head (WH), height at the withers (HW), thoracic circumference (TC), as well as thoracic diameter (TD, cm).

Consummatory sexual behavior and semen characteristics

Both mounts with ejaculation and seminal characteristics according to social rank are presented in Table 3. As for the number of mounts with ejaculation, while the HSR and MSR-rams showed the greatest response (80%), the LSR-rams exhibited the lowest performance (22%). Besides, the largest (P<0.05) rejection to ejaculate values was displayed by the LSR group. On the other hand, no differences in the other seminal characteristics occurred among social ranks; volume, motility, pH, and color (P>0.05). Nonetheless, both the HSR and MSR-rams showed the best performance regarding sperm concentration with respect to the LSR-rams (P<0.05).

DISCUSSION

Our working hypothesis stated that in Dorper rams with similar body weight, BCS, and age, odor intensity, horn size, and presence of horns would increase socio-sexual status and testicular size, semen quality, and successful copulation. Our results support this hypothesis. Dominance hierarchies are omnipresent in animal social systems; they are essential to defining social behaviors and to shape social relations (Fernald and Maruska, 2012). Certainly, hierarchies define social and sexual status, which are ubiquitous in the animal kingdom, and are communicated among animals via sensory systems (i.e., chemical, visual, auditory, or a combination of signal cues). This has evolved in diverse animal species assisting them to establish reproductive status. In our study, MSR rams were the most abundant, followed by the LSR and the HSR rams. Greater body weights, body sizes, or age have been closely related to socio-sexual status in both males and females (Pelletier and Festa-Bianchet, 2006; Orihuela, 2014; Zuñiga-Garcia et al., 2020a, 2020b). The most significant morphometric predictors of social rank in ungulates are body weight, muscle mass, and age (Pelletier and Festa-Bianchet, 2006; Fournier and Festa-Bianchet, 1995; Côte, 2000). Even under wild conditions, social rank has been highly associated with age in bighorn sheep populations (Pelletier and Festa-Bianchet, 2006; Hass and Jenni, 1991). Yet, in the present study, Dorper rams with similar body LW, size, BCS, and age, a socio-sexual hierarchy was clearly established, indicating that other signaling cues play a role in the establishment of socio-sexual ranks in rams.

Chemosignals, such as odor, can exert major effects on the physiology and behavior of diverse mammals. Physical, visual, auditory, and olfactory cues are differently amalgamated among individuals, leading to ritualized clashes or coercions, which are fundamental to decreasing unsafe fights (Boehm et al., 2005; Russell and Fernald, 2014). LSR-rams had the lowest odor score and had a low scrotal circumference, which was reflected in the lowest sperm cell concentration per mL and a high proportion of rejection to mount estrus ewes. This trend could be associated with lower blood testosterone levels because of the positive relationship between male odor score and serum testosterone concentrations in small ruminants, (Cruz-Castrejon et al., 2007; De-Santiago et al., 2018), although we were not able to quantify plasma testosterone, the previous studies helps to explain a possible scenario indicated by the LSR rams in this study. Additionally, there is a significant association between testosterone levels and social dominance in individual ungulates (Pelletier and Festa-Bianchet, 2006). A positive feedback loop exists between GnRH neurons and neurons, influencing both odor and pheromone processing (Boehm et al., 2005). In a previous study of our group, serum testosterone concentrations were positively related to successful copulation (Calderón-

Table 1: Least-square means ± standard error for of success index, wins and losses events according to social rank (independent variable) in Dorper rams managed under intensive conditions in northern Mexico in the non-breeding season.

	LSR	MSR	HSR
Rank (%; n)	37.5% (9/24)[a]	41.6% (10/24)[a]	20.8% (5/24)[a]
Won events (%; n)	22.2% (48/216)[b]	43.3% (104/240)[b]	60.8% (73/120)[a]
Lost events (%; n)	77.7% (168/216)[a]	56.6% (136/240)[a]	39.1% (47/120)[b]
Success index (SI)	0.22±0.02[a]	0.42±0.01[a]	0.60±0.07[b]

[1] Social ranks: low (LSR), medium (MSR), or high (HSR).
[a,b,c]Least-square-means without a common superscript within variables in rows differ ($p < 0.05$).

Table 2: Least-square means ± standard error for age, liveweight, body condition score, odor score, horns, and head traits, body measurements, and scrotal circumference according to social rank (i.e., LSR, MSR and HSR), in Dorper rams (n = 24) managed under intensive conditions in Northern Mexico (March, 25° N)[1]

	Social rank of rams		
	LSW (n=9)	MSR (n=10)	HSR (n=5)
Age (yr)	3.17±0.1[a]	3.20±0.1[a]	3.70±0.1[a]
Liveweight (kg)	78.3±3.7[a]	75.6±5.4[a]	79.0±4.4[a]
Body condition (units)	3.89±0.4[a]	3.90±0.1[a]	3.90±0.1[a]
Odor score (units)	0.75±0.01[b]	1.9±0.2[a]	2.5±0.4[a]
Presence horns (%)	(3/9) 33.33[b]	(5/10) 50.0[ab]	(4/5) 80[a]
Distance horns (cm)	6.94±0.6[a]	7.98±0.5[a]	7.60±0.4[a]
Length of horns (cm)	85.1±2.6[a]	84.3±3.3[a]	90.7±4.7[a]
Head size (cm)	28.1±0.3[a]	28.7±0.8[a]	28.5±0.5[a]
Hight withers (cm)	10.1±0.2[a]	10.5±0.5[a]	10.0±0.2[a]
Head width (cm)	65.9±1.5[a]	67.4±1.7[a]	70.6±1.9[a]
Toracic circumference (cm)	105.2±1.8[a]	107.8±2.8[a]	105.8±4.6[a]
Toracic diameter (cm)	39.2±2.5[a]	43.4±3.4[a]	45.5±3.7[a]
Scrotal circumference (cm)	30.4±1.1[b]	29.3±1.2[b]	40.0±3.5[a]

LSR= low social rank, MSR= medium social rank, HSR= high social rank. [a,b]Least-square-means without a common superscript within variables differ ($p < 0.05$).

Table 3: Least-square means ± standard error regarding percentage of mounts, percentage of rejections, and semen characteristics according to social rank of Dorper rams (n = 24) under intensive conditions in northern Mexico in the non-breeding season

	Social Rank		
	LSR (n=9)	MSR (n=10)	HSR (n=5)
Mounts (%)	22.2% (2/9)[b]	80 % (8/10)[a]	80 % (4/5)[a]
Rejections (%)	77.7% (5/7)[a]	20 % (2/10)[b]	20 % (1/5)[b]
Ejavulates Volume (mL)	0.9±0.2[a]	1.0±0.1[a]	0.9±0.1[a]
Concentration (x10^6)	2660±463b	3687±101a	3848±187a
Motility (%)	1.8±0.7[a]	2.3±0.3[a]	2.8±0.4[a]
pH (1-14)	7.7±0.2[a]	7.6±0.1[a]	7.4±0.1[a]
Color (1-4)	1.8±0.6[a]	2.5±0.2[a]	2.6±0.2[a]

LSR= low social rank, MSR= medium social rank, HSR= high social rank. [a,b]Least-square-means without a common superscript within variables in rows differ ($p < 0.05$).

Leyva et al., 2018). Rams with low libido (i.e., LSR-males) showed fewer mounts with ejaculation and displayed many rejections to mount estrous ewes. In the present study, the greater mounts with ejaculation occurred in the MSR and HSR rams.

Moreover, a positive relationship was observed between sperm concentration, testicular size, and social rank, the highest the social rank, the largest the testis size, and the greatest the semen concentration. In seasonal breeder mammals, androgens exert a crucial role in the modulation of aggressiveness, with a seasonal shift of androgen concentration between the breeding and non-breeding seasons, thru the involvement of other environmental (i.e., photoperiod) and endocrine cues (i.e., thyroid hormones and steroids) (Hood and Amir, 2018). In the present study, a set of signaling cues may have affected not only the establishment of the highest social hierarchy but also possibly activated accelerated spermatogenesis, generating, in turn, an increased spermatic output, positively linked to odor score. A key player triggering such a response could be the serum testosterone concentration (Keller and Levy, 2012; Recabarren et al., 2017), as this hormone is highly correlated with scrotal circumference as well as ejaculatory volume in bulls (Sajjad et al., 2007). Testosterone is also correlated with aggression (Muller and Wrangham, 2004), male social dominance (Koren et al., 2002; Muller and Wrangham, 2004), and courtship (Ungerfeld et al., 2019). The last physiological and behavioral scenario requires further experimental substantiation.

There are other individual characteristics in males that can give competitive advantages when establishing social hierarchies (Pelletier and Festa-Bianchet, 2006). Early studies demonstrated that larger body size, testicular dimensions, augmented odor scores, and blood androgen concentrations were linked to large horn development, which greatly enhances male competitiveness, sexual maturity, physical growth, social hierarchies, and reproductive success (Lincoln, 1998; Santiago-Moreno et al., 2007; Rekik et al., 20012; Coltman et al., 2002; Eberhard, 2006). In the Dorper breed, horns may be present, but selection for hornless animals may improve management (Milne, 2000). When evaluating blood testosterone levels in hornless and horned Dorper rams under extensive conditions, hornless rams exhibited the highest values (Fourie et al., 2005). Also, a positive correlation exists among body measurements and scrotal circumference (Akpa et al., 2021). Such differences in scrotal circumference may arise between production systems since nutritional status positively affected scrotal circumference (Murray et al., 1991).

Moreover, the size of antlers and horns plays a vital role in establishing social hierarchies (Coltman et al., 2002; Hass, 1991); in the present study, rams with the smaller horns concentrated in the LSR-group. Yet, since the percentage of horned rams was similar in both the MSR and HSR, brain mechanisms that shape socio-sexual supremacy could be implicated in interrmale aggression to establish social rank (Stagkourakis et al., 2018). Besides, the LSR group of rams had the highest proportion of hornless rams and horns with less thickness. Both horn presence and horn length have been positively related to testicular size. This scenario may be related to higher sexual and reproductive success (Preston et al., 2003). Indeed, while horn quality was firstly associated with sperm motility in wild sheep (Santiago-Moreno et al., 2007), improved reproductive outcomes also arose in horned bucks (Rekik et al., 2012).

Interestingly, highly expressed genes for horn development were greatly co-expressed in bone, nerve tissue, and testis growth (Wang et al., 2019).

Along with the presence and size of horns, another fundamental trait for establishing social dominance is aggressiveness, a behavior with a relatively similar neurophysiological circuitry and function among vertebrates, where testosterone is the main trigger (Giammanco et al., 2005; Shargal et al., 2008). From our perspective, it is suggested a genomic approach to help to understand our main findings; activation of specific genes that promote intensity of sexual behavior. In this respect, aggressiveness is a fundamental issue to quantify the SI when defining social status.

CONCLUSIONS

Our results shown that while size and thickness of horns play an essential role in establishing social hierarchies, chemosignals, such as odor, are also crucial cues modulating sexual behavior. This study demonstrates that social rank in Dorper rams is a complex trait influenced by factors other than horns or horn characteristics. HSR and MSR rams showed a higher mount with ejaculation and a higher sperm concentration than the LSR rams. Social rank was a strong determinant of copulatory capacity, scrotal circumference, and semen quality for mature Dorper rams, so sexual selection should favor high social rank rams. Further studies are required in order to determine the levels of testosterone and other hormones in the establishment of social rank in rams.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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