FACTORS MODIFYING FEMALE SOCIAL RANKS IN AMMOTRAGUS

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Short title: Female social ranks in Ammotragus

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Abstract

The Saharan arrui is characterised by an absolute dominance hierarchy, which is also near-linear and fairly stable, although female ranks may vary under some circumstances. Mating and parturition may cause an increase in the hierarchical status of females, while weaning of offspring and rank changes of the groupmates may lead to a lower status. Females ranks were related to age at the beginning of the study; whereas at the end, once some rank changes had occurred, the ranks were related to the current rank of the females' mothers. Ranks were not related to the physical condition (adult body weight and length). It seems plausible that female rank variation is related to proximal factors affecting social behaviour, because a female may then challenge her hierarchical status and acquire a higher social position. Finally, management implications and relevance captive populations of domestic sheep and goats are discussed.

Key words: Ammotragus, Social dominance, Ungulates, Captivity, Management.

Introduction

Empirical evidence shows that many social ungulates are characterised by stable, age-related dominance hierarchies (e.g. Rutberg 1983; Thompson 1993), but linearity is not always evident (Hass 1991; Alados & Escós 1992). Male rank variation is explained by the permanent challenges from other males that a dominant male experiences. Few studies, however, have focused on the proximate causes of female rank variation in societies based on relatively stable linear hierarchies. One exception is Espmark's (1964) study of female hierarchies in the reindeer (Rangifer tarandus), where pregnant females reach a higher position. The present paper analyses the factors underlying female rank variation in an African ungulate, the Saharan arrui (Ammotragus lervia sahariensis Rothschild, 1913), and explores some other aspects of social ranks, discussing possible implications for the management of captive populations.

Animals, Materials and Methods

The population of Saharan arrui that lives in captivity in the Estación Experimental de Zonas Áridas (EEZA), Almería, Spain, comes from three founder individuals, brought from Western

Sahara in 1975. Since then, and in spite of a high degree of inbreeding, the Saharan arrui has been breeding very successfully. At present, there are four herds and 156 individuals. During the years 1990, 1991 and 1992 I focused my study on one of the largest herds (the only one containing both sexes), made up by 17 males and 26 females at the beginning of the study (density=0.05 ind/m²), and by 33 males and 43 females at the end of it (density=0.08 ind/m²). The social ranks of all the 16 lactating females were calculated following the matrix method established by Scott (1980) and Lamprecht (1986). In these matrices the number of submissive responses (retreats) that occurred between the lactating females was recorded. Retreats were only noted as such, when there was no doubt that the animals responded to the approach and/or aggressive behaviour of another animal (the dominant one). Aggressive encounters not followed by a submissive response were not included in the analysis (Walker et al. 1983; Alados & Escós 1992; see also Kabuga et al. 1991), since this behaviour may sometimes be originated by stress or defensive responses, not being related to dominance status (Craig 1986). The rank given to a particular individual corresponds to the percentage of individuals that are situated in a lower hierarchical status. Measures of the dominance positions of the animals were based on observations in a particular herd, were taken daily and are normally distributed (see Beilharz & Zeeb 1982). During the sampling period, no recruitment of animals or human interference occurred, except for the collection of dead bodies, and capture of newborn and some adult individuals to be weighed; therefore, the animals were undisturbed most of the time. A data set in which adult body weights and lengths are registered is available for most of the population, the age is known for all the animals, and the mother's rank, i.e. the current rank held by the mother of the study females, for some of them (see Table 1).

Results

The Saharan arrui is characterised by an absolute dominance hierarchy (Wilson 1975), the rank being the same whatever the context (such as feeding, resting, etc.). The hierarchy was closely dependent on sex and maturity, since any male older than three years of age dominated all the females, whereas juveniles always held lower ranks than any adult. An effect due to parity was found in the female hierarchy, as primiparous females held lower ranks ($18.60 \pm$

5.73%, n=5) than multiparous ones ($67.91 \pm 6.13\%$, n=11), the difference being statistically significant ($F(1,14)=24.42$, $p=0.0002$). Another characteristic of the hierarchy is linearity; following Appleby (1983), a K value of linearity=0.63 was found ($\chi^2=75.75$, $df=23$, $p<0.001$). 44% of the females changed their rank during the study, and in all the cases there was always a particular event that led to these changes (see Table 2). Interactions between individuals in the group were very frequent every day, since the areas available to the herd are fairly small (950 m²); this fact allowed us to monitor quite accurately small changes in individual rank. Three circumstances may cause a change in a female's rank. Firstly, mating, since 42% of the females that changed their rank did so when they were mating with the dominant male; in all these instances the females acquired a higher-ranking position. Secondly, parturition, which coincided with 33% of the changes in rank, and which also increased the hierarchical status of the female who had just given birth. And thirdly, weaning of offspring, present at 25% of the cases, and which might cause lower ranks. A female's rank might also change when the rank of a previously subordinate groupmate increased. Only when a female was in a process of changing her social rank and interacted with another female, the transitive property could be broken. Namely, a series of encounters might arise between some females; in the beginning, the oestrus female might lose most of the encounters against the females holding higher ranks, but eventually she might challenge her status gradually, winning the majority of the encounters. Transitions between ranks did not occur suddenly, but it consisted in several interactions, where a non-ordered series of wins and losses took place until the new rank was established.

A simple regression analysis found no significant relationship between the phenotypic characteristics (adult body weight and length) and the ranks held at the end of the study (adult body weight vs rank: n=9, $R^2=0.08$, non-significant; adult body length vs rank: n=9, $R^2=0.007$, non-significant). A stepwise multiple regression analysis was carried out to assess any relationship between the rank and two other independent variables, age and mother's rank. Using the ranks obtained at the beginning of the study, a positive relationship between age and rank was found (n=7, $R^2=0.91$, $p=0.0009$). At the end of the study, however, this age effect vanished but a relationship with the mother's rank became evident (n=7, $R^2=0.64$, $p=0.03$).

92 Discussion

93 The general characteristics of arrui hierarchy coincide with Katz's (1949) observations of a
 94 captive arrui population at the New York Zoological Park. Rank variation in female Saharan
 95 arruis seems to be related to proximal factors affecting social life. From the empirical
 96 evidence, a strong relationship between female rank and mating with the dominant male
 97 became clear. An explanation might lie in the characteristic courtship of the species, with
 98 repetitive chases of the oestrus female by the dominant male, disturbing the whole herd (pers.
 99 obs.). During the courtship some encounters between the oestrus female and the other females
 100 of the herd may occur; and in some instances the oestrus female may challenge her
 101 hierarchical status, successfully winning encounters with females that were previously in a
 102 higher ranking position. This could be related to Espmark's (1964) findings in reindeer.
 103 Parturition and mother's rank improvement were also associated. Invariably during the few
 104 hours after birth, the newborn had to undergo aggressive encounters with most of the adult
 105 members of the herd, other than his/her mother and father. Under these circumstances the
 106 mother tended to defend her calf, acquiring in some instances a higher ranking status from that
 107 day on. A high social rank for mothers may be adaptive, in terms of access to feeding sites and
 108 protection of the newborn. The reduction of social rank at offspring weaning, when the mother
 109 resumed a single existence, may result from the less aggressive attitude by the mother towards
 110 her groupmates (pers. obs.). Contrary to Kondo & Hurnik's (1990) expectations, in this study
 111 population individuals holding lower social ranks had as many chances to change their status
 112 as middle-ranking individuals.

113 The relationship between rank and age is consistent with the literature and with the
 114 characteristics of arrui's rank, such as its relationship with parity. Once the females had some
 115 reproductive experience, however, other factors seemed to show up, such as the mother's
 116 social status. The apparent inheritance of mother's rank could be related to the formation of
 117 matrilinear kin groups, which characterises free-ranging arrui populations (pers. obs.). It is not
 118 clear why social ranks were related to age at the beginning of the study, but related to mother's
 119 rank at the end of it. I postulate that female Saharan arruis may present a variable social rank,
 120 related to age, at the beginning of their reproductive life, till they reach a fairly steady social
 121 status, in accordance with their reproductive experience and inherited family status (mother's

rank). Finally, the lack of any relationship between rank and physical status might be a characteristic of the conditions in captivity, since all the animals had plenty of food daily and free access to the stalls. Nevertheless, high-ranking females may share a series of benefits, such as less stress and feeding order preference (Cassinello, unpublished data). On the other hand, high-ranking females did not engage in a higher proportion of aggressive encounters (Cassinello 1994), which suggests that the herd structure (dimensions, density) was satisfactory from a welfare perspective, and allowed the high-ranking animals to keep their status without extra energetic costs. Dominant animals may have been aggressive in the past to obtain their dominant positions, as Beilharz & Zeeb (1982) suggest, but this is an issue to be considered in the context of rank changing processes, not once a particular social status is reached.

The management of captive animals can be more properly conducted under a fair knowledge of their behaviour. In social species the characterisation of hierarchies will allow us to carry out fine studies on reproductive behaviour as well as to establish the proper structure of the herds (number of individuals, sex ratio, dimensions of the enclosures), in order to develop successful captive breeding programmes. Among other different names, the arrui is also called Barbary sheep, although it is not a sheep, but a very close relative, and most behavioural, taxonomic, genetic and hormonal studies treat it as an ancestor of both Ovis and Capra genera (see a revision in Cassinello 1994). Thereby, we should be very cautious when extrapolating the results of the management of captive populations of Ammotragus. Furthermore, a clear distinction should be made between captive herds which undergo frequent changes in its composition and/or human interference, and those which are kept mostly undisturbed; since there may be crucial differences in behavioural responses, depending on the level of stress present in these populations (see e.g. Baldock & Sibly 1990; Hargreaves & Hutson 1990).

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Table 1. Data for the 16 females included in the study. Rank 1 refers to the social ranks held at the beginning of the sampling period, whereas Rank 2 refers to the ones held at the end of it. Social ranks are measured as the percentage of subordinate individuals.

Female	Parity	Age (years)	Weight (kg)	Length (cm)	Rank 1 (%)	Rank 2 (%)	Mother's Rank (%)
17	Multiparous	7.36	52.30	143	100	100	-
21	Multiparous	6.63	51.00	134	93	93	-
26	Multiparous	5.95	43.80	123	73	73	-
28	Multiparous	5.94	-	-	80	80	-
31	Multiparous	5.62	36.75	125	60	33	-
33	Multiparous	5.47	28.50	118	27	53	-
35	Multiparous	5.45	27.00	112	47	0	-
36	Multiparous	5.45	34.00	127	67	47	-
37	Multiparous	5.45	-	-	53	27	-
38	Multiparous	5.45	27.00	119	87	87	100
46	Multiparous	4.65	12.75	88	40	67	93
63	Multiparous	3.64	-	-	20	20	87
64	Multiparous	3.63	-	-	33	60	73
65	Multiparous	3.63	-	-	13	13	53
93	Primiparous	2.82	-	-	7	40	73
96	Primiparous	2.82	-	-	0	7	47

Table 2. Changes in hierarchical status on female Saharan arrui which took place during the sampling period. Social ranks are measured as the percentage of subordinate individuals.

Female	Change of rank	Cause	Date
33	from 27% to 67%	Parturition	3/4/90
31	from 53% to 67%	Mating	12/9/90
64	from 27% to 40%*	Mating	2/12/90
46	from 27% to 60%	Parturition	31/12/90
31	from 67% to 47%	Weaning	5/2/91
93	from 7% to 27%	Parturition	1/3/91
64	from 33% to 40%*	Parturition	2/5/91
35	from 20% to 0%	Weaning	7/6/91
64	from 40% to 60%	Mating	6/8/91
26	from 73% to 93%	Mating	9/9/91
93	from 27% to 40%	Mating	17/9/91
26	from 93% to 73%	Weaning	4/11/91

(*) Sequentially, ranks do not coincide for some females due to changes caused in other ones, which were previously situated in a lower hierarchical position.