Food access in captive *Ammotragus*:
The role played by hierarchy and mother-infant interactions

JORGE CASSINELLO

Departamento de Ecología Evolutiva,
Museo Nacional de Ciencias Naturales (CSIC)

Short title: Dominance and food access in *Ammotragus*

ADDRESS FOR CORRESPONDENCE:

Dr Jorge Cassinello

Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC)

C/José Gutiérrez Abascal 2, 28006 Madrid, Spain

Tel: +34 91 4111328, Fax: +34 91 5645078, e-mail: cass@mncn.csic.es

24

25

26 **Abstract**

27

28 An analysis of individuals' behavior when accessing a restricted food source (troughs)
 29 was carried out in a captive population of aoudad, *Ammotragus lervia*. Access to the
 30 troughs followed a strict hierarchical order, as higher ranking individuals fed before
 31 lower ranking ones. Unweaned male calves made use of the troughs from the age of two
 32 months, and female calves at the age of three months. Both fed from the troughs more
 33 frequently and for longer periods when their mother was present, which allowed them to
 34 make use of the troughs skipping the hierarchical order. Calves received fewer threats
 35 when in proximity to their mothers, particularly in high-ranking families. Mothers
 36 defended their calves from other herdmates more frequently when at the feeding area
 37 than in other areas of the herd; however, only sated mothers will let their calves feed
 38 freely from the troughs, as before that mothers showed an aggressive behavior even
 39 toward their calves. I conclude that maternal presence is necessary for aoudad calves to
 40 successfully feed from troughs, and that families holding higher social ranks benefit in
 41 getting access to this food source earlier in the day and are disturbed less than low-
 42 ranking families.

43 **Key words:** Access to Resources, Aoudad, Mother-Infant Relationships, Social Ranks,
 44 Ungulates

45

46 **Introduction**

47

48 In social species, when two or more individuals strive for the same resource (water,
 49 food, mates, resting place, shade...) conflicts of interest arise. These conflicts are solved

by means of agonistic-submissive encounters that are typically translated into dominance hierarchies, in which every individual in a group holds a social rank reflecting its position in the hierarchy [e.g., Scott, 1962]. Typically, high dominance status confers individuals preferential access to resources [e.g., Wrangham, 1981; Whitten, 1983; Cheney and Seyfarth, 1990]; thus, high-ranking individuals are expected to have higher reproductive success than low-ranking ones [e.g. Whitten, 1983; Gomendio, 1990; Cassinello and Alados, 1996; Cassinello and Gomendio, 1996; but see Packer et al., 1995].

It should be noted that when resources are patchily distributed dominant individuals can control access to them; thus, it is under highly restricted situations when social ranks become more evident [Harcourt 1987]. Under captive conditions, it is a common practice to provide food in a concentrated or limited space, i.e., by means of stalls or troughs filled periodically. This limited access to a food source causes a conflict of interests between the individuals living in a captive social group, so that a dominance hierarchy should show up [see Thouless, 1990].

In this paper, I investigated access to a restricted feeding source in a captive population of aoudad (*Ammotragus lervia*, Artiodactyla: Bovidae), paying particular attention to mother-infant interactions. This aoudad population has already been subject of previous studies on maternal investment and mother-infant conflict [see a review in Cassinello, 1998], as well as a recent comparison of suckling and grazing rates [Cassinello, 2001]; therefore it is an excellent choice to carry out a detailed study on mother-infant feeding behavior.

Ungulates are characterised by a strong mother-infant bond [Lent, 1974; Gubernick, 1981], which may last beyond weaning [e.g., Robbins et al., 1987; Green

and Rothstein, 1991; Rowell, 1991]. Weaned offspring may benefit from prolonged association with their mothers for protection against other herdmates and reduced intra-specific competition for food resources [Clutton-Brock et al., 1982; Green et al., 1989; Kojola, 1989].

Methods

Since 1975 an aoudad population has successfully bred in captivity at the Estación Experimental de Zonas Áridas (EEZA, CSIC), in Almería, south of Spain [Cassinello and Alados, 1996]. This population originated from just one male and one female captured in Western Sahara [Alados and Vericad, 1993]. Although intent of the EEZA is to eventually return this population to the wild, acute political difficulties in their historical range have precluded this.

Sampling was carried out from 1990 to 1992 in a herd made up of 17 males and 26 females at the beginning of the study, and 33 males and 43 females at the end of it. The study group was housed in a 950 m² enclosure (Fig. 1), covered by rocky ground and bare soil used by the animals for sand bathing [see Haas, 1959]. The individuals were identified by means of colored plastic ear tags. Birth date, sex, and identity of father and mother were known for each individual.

The animals fed on trusses of hay and standard cattle food pellets daily distributed by the EEZA staff in six rounded feeding troughs. The "feeding area" was defined as the area surrounding any of the six feeding troughs and from which an animal could access to them (around one meter distance) (Fig. 1). The feeding area also contained two drinking sources. An upper area was distinguished from a lower one,

both communicated by a middle area which consisted of a gradual slope (Fig. 1). Both food and water were provided ad libitum.

Feeding behavior analysed here included time devoted to feed from the troughs only, and not grazing on scattered forage along the enclosure [see Cassinello, 2001]. Sampling method have been described in detail elsewhere [e.g. Cassinello, 1996, 1997]. Focal sampling was used to record the behavior of mother-calf pairs during the evenings, when mothers and calves were more active [Altmann, 1974; Martin and Bateson, 1986]. Each sample being 20 min in duration. A "sampling period" consisted of all focal samples carried out on a given day, in average 6 samples. Every female which gave birth during 1990 and 1991 was sampled four times per week during her calf's first two months of life; during the rest of the lactation period (the average weaning age was 8.2 months), sampling was carried out 3 times in each 2-week period. All the interactions that took place between a mother and her calf were recorded, as well as any interaction between any of them and the other herdmates. The most conspicuous agonistic behaviors were: horn display, butting, horn pushing, horn clashing, rush-charge and subsequent withdrawal. More subtle behaviors included subtle horn displays and gazes along with subsequent retreats by the infant [see, e.g., Galef, 1981; Cassinello, 1996]. Feeding rate was measured as the proportion of time devoted to feeding per sampling period following Hass [1990] and Cassinello [2001]. Threats rate was defined as the percentage of visits by a given calf to the feeding area that resulted in a threat from herdmates other than their mothers. The data analysed here were obtained from the regular focal samples. Also, in those occasions when the fodder was provided in the evening, before the regular focal sampling started a continuous recording sampling allowed me to register all animals interactions when gathering at the feeding

troughs. The number of mother-calf pairs from which I have got information on their behavior at the troughs is 18. The analyses of feeding area use by unweaned calves included individuals up to six months of age in order to minimize any confounding effect of weaning [Cassinello, 1997]. The maternal social rank was calculated and monitored throughout the whole study, following a standard method used previously [e.g. Cassinello, 1995, 1996, 2001]. The rank given to a particular individual corresponded to the percentage of herdmates with a lower dominance status. Family rank was defined as the rank of a given mother in a mother-calf pair. Finally, in order to test whether the order of access to the troughs depended on the social rank, I differentiated up to seven rank classes, from 1 to 7: high, mid and low-ranking adult males, high, mid and low-ranking adult females, and juveniles.

Statistical analyses were two-tailed. Throughout the study parametric tests were preferably used and non-normal dependent variables transformed: frequencies into the form $\sqrt{(x+0.5)}$, rates into $\arcsin\sqrt{x}$, and age into its logarithm [see, e.g., Zar, 1984]. Data for different calves from the same mother were considered as independent, because a previous analysis of the intra and inter-group variance showed for all the behavioral variables that the inter-group variance was not greater than the intra-group variance [Cassinello, 1996, 1997, 2001].

Results

The high population density present in the study herd (0.05 ind/m² at the beginning of the study and 0.08 ind/m² at the end) was associated with a high frequency of interactions between all the individuals, and few chances for subordinates to escape

from aggression, although they were not involved in a higher number of aggressive encounters than dominant individuals (Simple regression analysis between frequency of aggression and social rank in adult females: $R^2=0.003$, $N=22$, $P=0.82$).

Food provisioning coincided with behavioral sampling on only 12 of 1565 sampling periods, so the analysis of access of feeding troughs was limited to these samples. In all cases the highest ranking males would always feed first and monopolise all the troughs, followed by mid and low-ranking adult males, then by high-ranking females, mid and low-ranking females, and finally by juveniles; as shown by a Spearman Rank correlation between the average rank class and the order of approach to the troughs: $\rho=1.00$, $N=7$, $P=0.01$. Calves did not follow this pattern as we will see later. Also, in the great majority (92%) of the 3610 encounters observed at the feeding troughs the subordinate individual let the dominant herdmate approach and feed, usually without direct confrontation.

Calves were seen feeding from the troughs from the age of 74 ± 8 days, which was positively related to the age when calves started to feed on solid food (20 ± 2 days; Simple regression: $R^2=0.28$, $N=18$, $P=0.02$). Male calves fed from the troughs at an earlier age (56 ± 4 days) than did females (92 ± 14 days; ANOVA: $F_{1,16}=7.29$, $P=0.02$). Maternal social rank had no influence on this behavior (Simple regression for all calves: $R^2=0.005$, $N=18$, $P=0.78$; Simple regression for males: $R^2=0.03$, $N=9$, $P=0.65$; Simple regression for females: $R^2=0.26$, $N=9$, $P=0.16$).

Calf visits to the feeding area were significantly longer when their mothers were present than when they were absent (mother absent: 0.09 ± 0.02 min.; mother present: 2.33 ± 0.15 min.; Paired t test: $t=20.06$, $df=17$, $P<0.0001$), and the average proportion of time spent feeding from the troughs was therefore higher when calves were in the

presence of their mothers (Paired t test: $t=26.63$, $df=17$, $P<0.0001$, Fig. 2).

Aggressive responses directed towards calves by other herdmates occurred almost every time the calves entered the feeding area in the absence of their mothers (99%); when mothers were present, the frequency of threats was much lower (67%) (Paired t test: $t=18.14$, $df=17$, $P<0.0001$). There was also a negative relationship between a calf's family social rank and threats rate received from herdmates (Simple regression: $R^2=0.25$, $N=18$, $P=0.03$; Fig. 3).

The frequency of responses by mothers to other herdmates' threats at the troughs or elsewhere in the herd did not vary; however, mothers tended to respond more often to threats directed at their infants in the feeding area than in other circumstances or areas of the enclosure (Paired t test: $t=3.30$, $df=14$, $P=0.005$, Fig. 4; 3 mother-calf pairs excluded due to insufficient data).

A detailed analysis of mother-calf interactions while feeding from the troughs showed that after accessing to the trough, calf's attempts to feed were usually followed by agonistic responses by the mother toward it; this aggressive or non-tolerant behavior decreased with time at the feeding trough, as shown in Fig. 5 (ANOVA: $F_{4,85}=46.69$, $P<0.0001$; Fisher's PLSD post hoc test showed significant differences, $P\leq 0.001$, for all pair comparisons except for minutes 4-5).

Discussion

Aoudad is highly gregarious and its herds are characterized by relatively fixed hierarchies, closely dependent on sex and maturity: any male older than three years of age dominates all the females, whereas juveniles always hold lower ranks than any adult

[Cassinello, 1995]. The high population density of the study herd allowed dominant individuals to easily control the feeding area. Under these circumstances, gaining access to food resources was always under hierarchical control. This was already reported by Katz [1949] in his pioneer work on the species. However, mother-calf pairs represent an exception to this rule, as infants in their mother's presence feed from the troughs even when higher ranking herdmates are still queueing and waiting for access. Similar findings on feeding behavior mediated by the hierarchical status have been found in other ungulate species, both when forced to compete for artificially concentrated food resources [red deer, *Cervus elaphus*: Appleby, 1980; Hall, 1983] and when feeding under natural conditions [woodland caribou, *Rangifer tarandus caribou*: Barrette and Vandal, 1985; red deer: Thouless, 1990].

Aoudad calves start to alternate milk consumption with grazing early in life [Cassinello, 2001]. At about two and a half months of age they start feeding from the troughs, which is precisely when suckling rates substantially decline [Cassinello, 1996]. Moreover, males start using the feeding area at an earlier age than females, which is in accordance with the greater time spent grazing by males at the age of two months [Cassinello, 2001]. This is not surprising considering the higher energetic demand of unweaned males compared to females in a highly sexually dimorphic species such as this [see Clutton-Brock, 1991].

Mother's presence and behavior had a significant effect on calf visits to the troughs. Calves spent more time feeding from the troughs when their mother was present, calves received fewer threats when their mother was present (especially if their mother was high-ranking), and mothers tended to react before agonistic behaviors addressed to their calves at a higher frequency when at the troughs than in other

circumstances/locations. It is worth pointing out that the existence of a mother's response to a threat did not necessarily imply that the encounter was won by her, instead, it is a measure of the mother's willingness to defend her calf. Mother-infant pair bonds are very strong in ungulates [e.g. Green et al., 1989], and calves tend to synchronize their activities to those of their mothers as they mature [Lickliter, 1987], especially "follower" species [e.g. Estes and Estes, 1979], such as aoudads. This could partly explain why calves follow their mothers to the troughs, but a more evident benefit obtained is the lower rate of threats suffered by calves when escorted by their mothers. An interesting finding is importance of social dominance: high-ranking families suffered from a lower rate of aggressions in the feeding area. This, along with their higher priority of access to the feeding troughs, confers obvious advantages. Similarly, Deutsch and Lee [1991] reported that high-ranking females of rhesus monkeys (*Macaca mulatta*) are threatened less frequently while feeding than subordinates.

The onset of a behavioral conflict between mother and infant under a feeding context has been widely studied in primate species [e.g. Rosenblum and Sunderland, 1982]. Apart from conflicts related to the amount of maternal investment (lactation) allocated to the infant [Barrett et al., 1995], when foraging conditions are demanding, mothers tend to agonistic responses or reject more frequently their offspring during feeding time [Rosenblum and Sunderland, 1982; Andrews et al., 1993]. Here, I have registered a progressively decreasing agonistic behavior of the mothers towards their calves, which seems to corresponds with a satiety process after several minutes feeding from the troughs.

These results may help in understanding the complex relationships within ungulate family groups, namely, maternal effects, offspring requirements and

hierarchical roles played under limited resources. It should also help in establishing adequate housing conditions, which is a priority for any successful captive breeding program.

Conclusions

1.- Access to concentrated food resources in captive aoudads is determined primarily by the hierarchical status of the individuals.

2.- Maternal presence is necessary for unweaned aoudad calves to successfully feed from these resources, as threats directed to them decrease, enabling them to spend more time feeding.

3.- Families holding high social ranks benefit by getting access to concentrated feeding sources earlier and with fewer disturbances than low-ranking families.

Acknowledgements

The author wishes to thank two anonymous referees for their useful comments on a previous version of the manuscript and EEZA staff for access to their facilities. During data collection the author enjoyed a predoctoral fellowship awarded by MEC (PG89 27511603), and is currently supported by Dirección General de Investigación Project REN2000-1470 GLO.

References

- 266 Alados CL, Vericad JR. 1993. Aoudad. *Ammotragus lervia* from Western-Sahara.
267 International Studbook. Bol Inst Est Almerienses, Ciencias 11/12: 65-97.
- 268 Altmann J. 1974. Observational study of behaviour: sampling methods. Behaviour 49:
269 227-267.
- 270 Andrews MW, Sunderland G, Rosenblum LA. 1993. Impact of foraging demand on
271 conflict within mother-infant dyad. In: Mason WA, Mendoza SP, editors. Primate
272 social conflict. Albany: SUNY Press. p 229-252.
- 273 Appleby MC. 1980. Social rank and food access in red deer tags. Behaviour 74: 294-
274 309.
- 275 Barrett L, Dunbar RIM, Dunbar P. 1995. Mother-infant contact as contingent behaviour
276 in gelada baboons. Anim Behav 49: 805-810.
- 277 Barrette C, Vandal D. 1985. Social rank, dominance, antler size, and access to food in
278 snow-wound wild woodland caribou. Behaviour 97: 118-146.
- 279 Cassinello J. 1995. Factors modifying female social ranks in *Ammotragus*. Appl Anim
280 Behav Sci 45: 175-180.
- 281 Cassinello J. 1996. High-ranking females bias their investment in favour of male calves
282 in captive *Ammotragus lervia*. Behav Ecol Sociobiol 38: 417-424.
- 283 Cassinello J. 1997. Mother-offspring conflict in the Saharan arrui, *Ammotragus lervia*
284 *sahariensis*: Relation to weaning and mother's sexual activity. Ethology 103: 127-
285 137.
- 286 Cassinello J. 1998. *Ammotragus lervia*: a review on systematics, biology, ecology and
287 distribution. Ann Zool Fennici 35: 149-162.
- 288 Cassinello J. 2001. Offspring grazing and suckling rates in a sexually dimorphic
289 ungulate with biased maternal investment (*Ammotragus lervia*). Ethology 107: 173-

- 290 182.
- 291 Cassinello J, Alados CL. 1996. Female reproductive success in captive *Ammotragus*
 292 *lervia* (Bovidae, Artiodactyla). Study of its components and effects of hierarchy and
 293 inbreeding. J Zool, Lond 239: 141-153.
- 294 Cassinello J, Gomendio M. 1996. Adaptive variation in litter size and sex ratio at birth
 295 in a sexually dimorphic ungulate. Proc R Soc Lond B 263: 1461-1466.
- 296 Cheney DL, Seyfarth RM. 1990. How monkeys see the world. Chicago: University of
 297 Chicago Press. 377 p.
- 298 Clutton-Brock TH. 1991. The evolution of parental care. Princeton, New Jersey:
 299 Princeton University Press. 352 p.
- 300 Clutton-Brock TH, Guinness FE, Albon SD. 1982. Red deer. Behaviour and ecology of
 301 two sexes. Edinburgh: Edinburgh Univ. Press. 378 p.
- 302 Deutsch JC, Lee PC. 1991. Dominance and feeding competition in captive rhesus
 303 monkeys. Inter J Primatol 12: 615-628.
- 304 Estes RD, Estes RK. 1979. The birth and survival of wildebeest calves. Z Tierpsychol
 305 50: 45-95.
- 306 Galef BG. 1981. The ecology of weaning: parasitism and the achievement of
 307 independence by altricial mammals. In: Gubernick DJ, Klopfer PH, editors. Parental
 308 care in mammals. New York: Plenum Press. p 211-241.
- 309 Gomendio M. 1990. The influence of maternal rank and infant sex on maternal
 310 investment trends in rhesus macaques: birth sex ratios, inter-birth intervals and
 311 suckling patterns. Behav Ecol Sociobiol 27: 365-375.
- 312 Green WCH, Griswold JG, Rothstein A. 1989. Post-weaning association among bison
 313 mothers and daughters. Anim Behav 38: 847-858.

- 314 Green WCH, Rothstein A. 1991. Sex bias or equal opportunity? Patterns of maternal
315 investment in bison. *Behav Ecol Sociobiol* 29: 373-384.
- 316 Gubernick DJ. 1981. Parental and infant attachment in mammals. In: Gubernick DJ,
317 Klopfer PH, editors. *Parental care in mammals*. New York: Plenum Press. p 243-
318 289.
- 319 Haas VG. 1959. Untersuchungen über angeborene Verhaltensweisen bei
320 Mährenspringern (*Ammotragus lervia* Pallas). *Z Tierpsychol* 16: 218-242.
- 321 Hall MJ. 1983. Social organisation in an enclosed group of red deer (*Cervus elaphus* L.)
322 on Rhum. I. The dominance hierarchy. *Z Tierpsychol* 61: 250-262.
- 323 Harcourt AH. 1987. Dominance and fertility among female primates. *J Zool, Lond* 213:
324 471-487.
- 325 Hass CC. 1990. Alternative maternal-care patterns in two herds of bighorn sheep. *J*
326 *Mammal* 71: 24-35.
- 327 Katz I. 1949. Behavioural interactions in a herd of Barbary Sheep (*Ammotragus lervia*).
328 *Zoologica* 34: 9-18.
- 329 Kojola I. 1989. Mother's dominance status and differential investment in reindeer
330 calves. *Anim Behav* 38: 177-185.
- 331 Lent PC. 1974. Mother-infant relationships in ungulates. In: Geist V, Walther F, editors.
332 *The behaviour of ungulates and its relation to management*. Vol. 1. Morges,
333 Switzerland: I.U.C.N. p 14-55.
- 334 Lickliter RE. 1987. Activity patterns and companion preferences of domestic goat kids.
335 *Appl Anim Behav Sci* 19: 137-145.
- 336 Martin P, Bateson P. 1986. *Measuring Behaviour. An Introductory Guide*. Cambridge:
337 Cambridge Univ. Press. 200 p.

- 338 Packer C, Collins DA, Sindimwo A, Goodall J. 1995. Reproductive constraints on
339 aggressive competition in female baboons. *Nature* 373: 60-63.
- 340 Robbins CT, Oftedal OT, O'Rourke KI. 1987. Lactation, early nutrition, and
341 handrearing of wild ungulates, with special reference to deer. In: Wemmer CM,
342 editor. *Biology and management of the Cervidae*. Washington: Smithsonian Inst. Press.
343 p 429-442.
- 344 Rosenblum LA, Sunderland G. 1982. Feeding ecology and mother-infant relations. In:
345 Hoffman LW, Gandelman R, Schiffman HR, editors. *Parenting: its causes and*
346 *consequences*. Hillsdale: Erlbaum. p 75-110.
- 347 Rowell TE. 1991. Till death us do part: long-lasting bonds between ewes and their
348 daughters. *Anim Behav* 42: 681-682.
- 349 Scott DK. 1980. Functional aspects of the pair bond in winter in Bewick's swans
350 (*Cygnus columbianus bewickii*). *Behav Ecol Sociobiol* 7: 323-327.
- 351 Thouless CR. 1990. Feeding competition between grazing red deer hinds. *Anim Behav*
352 40: 105-111.
- 353 Whitten PL. 1983. Diet and dominance among female vervet monkeys (*Cercopithecus*
354 *aethiops*). *Am J Primatol* 5: 139-159.
- 355 Wrangham RW. 1981. Drinking competition in vervet monkeys. *Anim Behav* 29: 904-
356 910.
- 357 Zar JH. 1984. *Biostatistical Analysis*. Second edition. Englewood Cliffs, New Jersey:
358 Prentice-Hall, Inc. 718 p.
- 359

Figure Captions

Figure 1. Diagram of the 950 m² enclosure inhabited by the study aoudad population. Three promontory levels are distinguished: upper, middle and lower, with an unevenness (wall) of 1.5 m between upper and lower levels. Middle level actually refers to a gradual slope area from lower to upper.

Figure 2. Average (+SE) feeding rate (proportion of time feeding per sample period) of six months-old aoudad calves (N=18) observed inside the feeding area, in the presence or absence of their mothers.

Figure 3. Relationship between mothers' social rank and threats rate (threats per sample period) addressed to their calves while in the feeding area.

Figure 4. Average (+SE) frequency of mother's responses to herdmates threatening her calf inside the feeding area and in other locations of the enclosure (N=15).

Figure 5. Average (+SE) number of mothers' agonistic responses towards their calves while both were feeding from the troughs for feeding bouts which lasted 5 or more minutes (N=18).

FIGURE 1 - J. CASSINELLO

FIGURE 2 - J. CASSINELLO

FIGURE 3 - J. CASSINELLO

FIGURE 4 - J. CASSINELLO

FIGURE 5 - J. CASSINELLO