**Offspring Grazing and Suckling Rates in a Sexually Dimorphic Ungulate
with Biased Maternal Investment (*Ammotragus lervia*)**

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Abstract

An analysis of resource gain is provided for *Ammotragus* calves during their first year of age. Both grazing and suckling rates are analysed and potential effects caused by age, sex, mother's rank and weaning period studied. During their first days of life, calves devote their time mainly to suckling, grazing starting at the second week of age and exceeding suckling rate from the fourth week on. When suckling rate reaches a significant decrease (at two months), male calves show a significantly higher grazing rate than female calves, suggesting a higher energetic demand for males at this age. When calves are one month old, sons of high-ranking mothers devote less time grazing than those of low-ranking ones, which is in accordance with the higher maternal investment they receive. Grazing rate shows distinctive values for the different weaning periods distinguished in this species, but the resumption of mothers' sexual activity, when a mother-offspring conflict occurs, does not affect grazing behaviour. These results are consistent with the biased maternal investment recently found in the same study population, and focus on the other side of the coin, i.e., grazing behaviour, which is determined by calves' own decisions.

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Introduction

Among polygynous mammals, variance in male reproductive success is greater than that of females, due to the fewer opportunities for poor quality males to mate and sire offspring. Under this premise, mothers with extra resources should bias their investment towards their offspring by adjusting sex ratio at birth and/or investing preferentially towards sons (Trivers & Willard 1973), provided that reproductive success of sons is mainly determined by maternal investment (Clutton-Brock & Albon 1982; Gomendio et al. 1990). Since this hypothesis was put forward, a series of studies have ratified it empirically in polygynous mammals from different taxa, such as rodents (e.g. Gosling et al. 1984; Clark et al 1990), primates (e.g. Paul & Thommen 1984; Symington 1987), marsupials (Austad & Sunquist 1986), seals (e.g. Kovacs & Lavigne 1986), or ungulates (reviewed by Hewison & Gaillard 1999); although other studies did not find any sex bias in maternal investment (see, e.g., for ungulates, *ibid.*).

The arrui or Barbary sheep (*Ammotragus lervia* Pallas, 1777) is a North African polygynous caprid which has been introduced in several other parts of the globe due to hunting interests. However, recent studies carried out in a Spanish captive population have allowed us to start understanding its behavioural ecology (see Cassinello 1998 for a comprehensive review on the species current knowledge). The species is now to be included among other polygynous and highly dimorphic mammals which accomplish Trivers & Willard's (1973) hypothesis on biased maternal investment (see Cassinello 1996; Cassinello & Gomendio 1996). In a previous study, I found that high-ranking mothers allocate their resources preferably towards their sons, as the average suckling rate is significantly higher in male calves than in female calves during their first month of life, when maternal investment reaches the highest values of the whole lactation period (Cassinello 1996).

However, no particular attention has been paid to the calves' complementary feeding source during the lactation period, i.e., grazing rate. An interesting question to be solved is thus to what extent calves manage to compensate an insufficient milk consumption by spending more time grazing, that is, do calves who suck for shorter periods show a higher grazing rate? Furthermore, given that we are dealing here with a species with a high degree of sexual dimorphism, a different feeding behaviour might be expected between sons and daughters due to their distinct energy demands.

In the present study, grazing behaviour is analysed during arrui calves' first year of age; the progressive change from milk consumption to foraging is studied taking into account calves' sex and mother's social rank, in order to test whether this behaviour is related to the different growth patterns of males and females (see Cassinello 1997a) and Trivers & Willard's (1973) hypothesis on maternal investment. The results obtained will also be placed under the context of weaning as well as the mother's resumption of her sexual activity, when conflicts of interests become more important (see Cassinello 1997b).

Methods

A population of arruis has successfully bred in captivity at the Estación Experimental de Zonas Áridas (EEZA), Almería, south of Spain, since 1975 (Cassinello & Alados 1996). This population originates from just one male and one female captured in the western Sahara lands, where the subspecies *A. l. sahariensis* is suspected to be extinct in the wild (Alados & Vericad 1993). Being the main policy of the EEZA to eventually return this population to the wild, it has not been accomplished so far, as their native lands are suffering from acute political difficulties which do not provide a safe environment for these animals.

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, and food and water were provided ad libitum. The

animals fed on standard fodder from a stall which was daily filled by the EEZA staff. Grazing behaviour analysed here included time devoting to feed from the stalls as well as grazing along the enclosure, when calves fed on scattered forage. A detailed information on sampling method and routine can be found in Cassinello (1996), although a general description has been added here.

The animals were identified by means of coloured plastic ear tags. Birth date, sex, identity of father and mother, and inbreeding coefficient were known for each individual. A previous analysis of the species' daily activity showed that night activity is lacking or scarce, early in the morning the most active individuals are the adult males, but from 9:00 h the animals spend their time mostly resting until late in the afternoon, when the main activity starts to take place. Therefore, sampling was performed between approximately 17:00 and 20:00 h, when the adult females and calves were more active (D. Morgan pers. comm., pers. obs.). Focal sampling was used to record mother-calf pairs behaviour (Altmann 1974; Martin & Bateson 1986), each sample being 20 min of duration. A sampling period was the total number of focals carried out on a given day. Every female which gave birth during 1990 and 1991 was sampled four times a week during her calf's first two months of life; during the rest of the lactation period (for the weaning process see Cassinello 1997b) sampling was carried out 3 times in each 2-week period. All mother-calf interactions between them and the other groupmates were recorded. Suckling events were sampled *ad libitum*.

Suckling and grazing rates corresponded to the proportion of time devoted to these activities per sampling period (Hass 1990; Cassinello 1996). A total of 26 mother-calf pairs were sampled, although I have not one-year samples of all of them, being that the reason why the sample size in the analyses varies and decreases down to 15 at the time of weaning. Also, comparisons between oestrus/non-oestrus periods were only possible in a few mother-calf pair bonds and at different lactation stages; data from one to six months old calves were included. I determined the rates differences between maternal non-oestrus and oestrus periods, and the percentage increase or decrease.

The mothers' social rank was calculated and monitored throughout the whole sampling period, following the matrix method established by Scott (1980) and Lamprecht (1986). Only submissive interactions were considered when building the matrix; aggressive

behavior by itself is not a reliable indicator of dominance status as it may sometimes be caused by stress or defensive responses (Craig 1986). Retreats were only noted when there was no doubt that the individuals responded to the approach and/or aggressive behaviour of another individual. The rank given to a particular individual corresponds to the percentage of individuals with a lower dominance status (see Cassinello 1995).

When parametric tests were used (Student t tests, ANOVAs and simple regressions), non-normal dependent variables (grazing/suckling rates and social ranks) were transformed into the form $\arcsin\sqrt{x}$, and then tested for normality (see, e.g., Zar 1984). Data of 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 behavioural variables that the inter-group variance was not greater than the intra-group variance (Cassinello 1996, 1997b).

Results

During calves' first year of age (from month 1 to 12) both suckling and grazing rates followed opposite directions, the former decreasing steadily and ceasing at weaning (see Cassinello 1997b) and the latter increasing up to reaching an asymptotic level (1st-2nd month: $df=19$, $t=-5.07$, $p<0.0001$; 2nd-3rd month: $df=12$, $t=-2.81$, $p=0.02$; no significant pair-months differences were found from then on; see Figure 1). The differences between suckling and grazing rates were statistically significant except during the first month (1st month: $df=24$, $t=-0.14$, $p=0.89$; 2nd month: $df=19$, $t=-7.92$, $p<0.0001$; same p value from then on). Analysing in more detail this pattern, it appeared that during their first week, calves significantly suckled more frequently than grazed ($df=13$, $t=6.72$, $p<0.0001$); in fact, grazing did not occur until calves reached 20 ± 2 days of age (range 9-35 days). It was not until the fourth week when grazing did occur at a significantly higher rate than suckling (2nd week: $df=18$, $t=1.81$, $p=0.09$; 3rd week: $df=18$, $t=1.63$, $p=0.12$; 4th week: $df=18$, $t=-3.90$, $p=0.001$; see Figure 2).

When taking into consideration calf sex, no differences in grazing rate were seen during the first year of age, except for the second month, precisely

when a highly significant increase was reached (see above). At this age male calves grazed at a higher rate than female calves ($F(1,18)=4.45$, $p=0.049$; see Figure 3). As far as suckling rate is concerned, no sex differences were found at any age.

The mother's social rank might play a role in calves grazing behaviour (for a relationship between hierarchy and suckling see Cassinello 1996), but no relationship was found in the general grazing rate pattern. However, when data were split into sex, differences arose during the first month of calves' life. It appeared that the higher the mother's rank, the lower the time devoted to graze by her male calves ($N=10$, $R^2=0.51$, $p=0.02$); no relationship was found with daughters though ($N=11$, $R^2=0.009$, $p=0.78$); see Figure 4.

By distinguishing the three weaning periods established in a previous work (Cassinello 1997b), before (b), during (d) and after (a) weaning, again an inverse pattern was found between suckling and grazing rates (see Figure 5), the differences between the weaning periods being statistically significant (suckling: b vs d, $df=15$, $t=3.99$, $p=0.001$; d vs a, $df=15$, $t=9.33$, $p<0.0001$; grazing: b vs d, $df=15$, $t=-2.27$, $p=0.04$; d vs a, $df=15$, $t=-3.92$, $p=0.001$); along with the differences between suckling and grazing rates in the three periods (before: $df=15$, $t=-6.69$, $p<0.0001$; during: $df=15$, $t=-16.11$, $p<0.0001$; after: $df=15$, $t=-10.52$, $p<0.0001$).

Finally, I was interested in seeing whether grazing and suckling rates were affected by mothers' sexual activity. The analysis of the percentage increase in grazing rate during maternal oestrus vs the decrease showed no statistically significant differences ($N=12$, Mann-Whitney $U=16$, $U'=19$, $p=0.81$); when considering the suckling rate no significant differences were obtained either, although there is a somewhat surprising tendency towards a higher suckling rate when the mother is in oestrus ($N=6$, Mann-Whitney $U=0$, $U'=8$, $p=0.06$).

Discussion

As a complementary study of the recent findings on mothers' biased investment in *Ammotragus*, which determined that high-ranking females addressed their investment preferably towards their sons (Cassinello 1996), the grazing behaviour was investigated in the same arrui population. This behaviour shows calves' own decisions in order to acquire the available resources which will complement the investment received by their mothers, milk intake, and prepare them for a long weaning process (Cassinello 1997b). Therefore, some sort of relationship between maternal investment and calf grazing behaviour should be expected.

Let us note firstly that suckling rate in arruis does reflect the actual maternal investment addressed to calves, as it is strongly related to the interval of time to the next birth (Cassinello 1996:418-419); therefore, this measure is out of the current controversy on suckling behaviour as a reliable predictor of milk intake (see Cameron et al. 1999).

Not surprisingly, the pattern followed by grazing somewhat matches that of suckling but in the opposite direction; nevertheless, the percentage of time devoted to both activities does not reflect equivalent energy intakes, as milk provides more nutrients to calves than forage. Calves suckle more than graze during their first week, from the second to the third weeks both rates do not differ significantly, but from then on grazing will be the preferential activity of calves (Figure 2). When suckling rate reaches a significant decrease (at two months; see Cassinello 1996), male calves show a significantly higher grazing rate than female calves, suggesting a higher energetic demand at this age in males (see a review in Clutton-Brock 1991), as this species is strongly sexually dimorphic in body size, and male growth rates are exceptionally high compared to those of females in order to attain the required body size which, in turn, will

205 determine male reproductive success (e.g., Clutton-Brock 1988; see also
206 Cassinello & Gomendio 1996).

207 Male calves from higher ranking mothers graze at a lower rate than those
208 from lower ranking mothers; this is in accordance to previous findings on the
209 same arrui population which showed that male calves from high-ranking
210 mothers suckle at a higher rate than female calves (Cassinello 1996) and are
211 weaned at an earlier age too (Cassinello 1997b), findings which relate to Trivers
212 & Willard's (1973) hypothesis of differential investment in polygynous
213 mammals. The first month of age is crucial during the lactation period, as that is
214 the age at which calves receive the majority of milk resources (Cassinello
215 1996); here it is seen that low-ranking mothers' sons devote more time grazing,
216 probably in order to compensate a comparatively poor investment received from
217 their mothers. In one of my previous works (ibid.) it was shown that grazing rate
218 increases as a function of mother-calf distance, and also that low-ranking
219 mothers spend more time close to their daughters than to their sons; all this is in
220 accord with the fact that male calves of low-ranking mothers graze at a higher
221 rate, as shown here (see Figure 4). Finally, as no evidence of biased investment
222 addressed towards daughters was found in low-ranking mothers (ibid.), no rank-
223 associated differing grazing rate was expected in this sex, as it has been seen
224 here.

225 As expected, grazing rate increases with age, and the analysis of the
226 weaning periods showed clear differences, also with the suckling rate.
227 Previously, I found that during the resumption of sexual activity by the mother
228 there appears to be a conflict between mother and offspring (Cassinello 1997b);
229 but this conflict does not cause any effect either in grazing or suckling rates. A
230 somewhat surprising tendency towards a higher suckling rate when the mother
231 is in oestrus was obtained, but the small sample size should make us be cautious
232 about it. Therefore, the mother-offspring conflict which occurs when the mother

is in oestrus seems to be solely translated into agonistic behavioural responses against calves (ibid.).

In sum, as suckling behaviour is basically controlled by the mother (see Hogg et al. 1992; Cassinello 1996), up to a certain degree calves would have to compensate for an insufficient maternal investment by changing their grazing rate according to their energetic and growing demands. The results found in relation to mothers' rank and differential growth rate in both sexes, as expected in sexually dimorphic species, support this view.

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Figure Legends

Figure 1. Mean $\pm$ SE suckling (S) and grazing (G) rate during the first year of age of arrui calves. The small plot in the upper right corner compares both rates during the first month of age, when no significant differences were found.

Figure 2. Mean $\pm$ SE suckling and grazing rate during the first four weeks of age of arrui calves. Asterisks denote significant differences.

Figure 3. Mean $\pm$ SE grazing rate during the first year of age of male and female calves. Significant differences only arose in two months old individuals.

Figure 4. Relationship between calves' grazing rate and their mother's social rank during the first month of age. The continuous regression line refers to male calves (white circles), whereas the discontinuous one to female calves (black circles).

Figure 5. Mean $\pm$ SE suckling and grazing rate during the three weaning periods (according to Cassinello 1997b). All means differences were statistically significant.

FIGURE 1

FIGURE 2

FIGURE 3

FIGURE 4

FIGURE 5