High levels of inbreeding in captive *Ammotragus lervia* (Bovidae, Artiodactyla): Effects on phenotypic variables

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Short title: Inbreeding affecting phenotype in *Ammotragus*

Cassinello J. High levels of inbreeding in captive *Ammotragus lervia*
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Abstract

In this study, the analysis of variables that may affect birth weight and adult body weight/length in captive Saharan arrui has been carried out. Whenever enough data were available the following variables were considered: age, sex, type of parturition (single vs twins), birth weight, nursing status (single vs effective twinning), maternal age, and individual inbreeding coefficient. Previous considerations and the strong sexual dimorphism recommended a separate analysis for males and females. There was an expected positive relationship between age and growth. As adults, singleton females were larger than females who had a littermate, also, when reaching sexual maturity, females raised by older mothers were heavier. Birth weight, maternal age and individual inbreeding coefficient had no effect on adult phenotype. At birth there already appeared a significant sexual dimorphism, and singletons were heavier than twins. High inbreeding coefficients yielded lighter calves. Finally, birth weights increased with maternal age but were not affected by season of birth.

Introduction

Because of increasing human activities, wildlife habitats are being threatened and in many instances destroyed. Currently, long-term captive breeding programs are becoming the only hope for the preservation of many species, some of them living exclusively in zoos with all natural populations extinct. Accordingly, there has been great interest in the management and genetics of captive zoo populations (Soulé 1980; Frankel and Soulé 1981; Foose 1983; Ralls and Ballou 1983). The study of physical characteristics in captive animal populations may provide a first approach to evaluate the welfare of the individuals, as well as which variables influence a particular species' phenotype.

Particularly in zoos and captive populations, empirical evidence demonstrates that inbreeding may increase mortality in young animals and reduce fertility in adults (e.g. Ralls et al. 1979; Senner 1980; Hass 1989; MacNeil et al. 1989; Alados and Escós 1991; Ercanbrack and Knight 1991), resulting in the presence of inbreeding avoidance (e.g. Harvey and Ralls 1986; Ralls et al. 1986; Bollinger et al. 1991). Likewise, zoo reports show that mother-son and brother-sister matings are usually detrimental (Ralls and Ballou 1983). However, in some species, including humans, the existence of inbreeding tolerance may appear (e.g. Rao and Inbaraj 1977; Connor and Bellucci 1979; Cothran et al. 1984; Hoogland 1992). According to Templeton and Read (1983), the alternative breeding strategy of inbreeding tolerance may be adaptive when close relatives are the only potential mates available, or when dispersal costs exceed inbreeding costs (see also Waser et al. 1986; Motro 1991). Needless to say that in order to carry out a proper conservation programme, the inbreeding issue must be tackled very carefully during the management of captive populations of threatened species.

The captive population of Saharan arrui (*Ammotragus lervia sahariensis* Rothschild 1913) in Almería comes from only two specimens, resulting in a rapid increase of the inbreeding coefficient (see below). In a previous study (Cassinello and Alados 1996) it was stated that high inbreeding delays the age at first birth in female Saharan arrui. In this paper I shall test the possible deleterious effect of inbreeding on physical conditions, which may determine the viability of the individuals and, subsequently, their reproductive chances.

Materials and methods

1. The study population

The population of Saharan arrui living in captivity at the Estación Experimental de Zonas Áridas, EEZA (Higher Council for Scientific Research, CSIC), Almería, Spain, originates from two founder individuals that were collected from Western Sahara in 1975 (Alados and Vericad 1993). Since then, and in spite of a high degree of inbreeding (Alados et al. 1988), the Saharan arrui has been breeding very successfully (see Cassinello and Alados 1996). At the beginning of 1997 there were four herds and 145 individuals. The life history of the whole population, 241 individuals including those ones already dead, has been regularly recorded since it was established. The original distribution of the subspecies ranged across different localities in North Africa (see Gray 1985), but at present it is presumed extinct in the wild (Alados and Vericad 1993).

2. Data collection and analysis

The data collection spans the period 1975-1992. Just after birth, each animal was marked with a plastic ear tag for individual identification. Concerning physical components, body weight and length (measured) at different ages were registered, whereas birth weights were periodically

collected from 1987. Body length was measured from the snout to the base of the tail, following the dorsal line of the body, and it is considered a reliable index of condition in *Ammotragus* since it directly influences longevity (Cassinello and Alados 1996). For the statistical analysis the following variables were taken into account:

- Sex of newborns: male (N=122) vs female (N=119).
- Parturition type: single (N=164) vs twins (N=74).
- Nursing status: presence of sibling (N=37) vs absence of sibling (N=201) during the first month of life. This variable is more reliable than parturition type (single vs twins) to assess maternal care, because when a twin calf dies a few days after birth, the variable parturition type does not reflect accurately the mother-offspring relationship in terms of maternal care, or maternal investment if applicable, as the surviving calf is receiving the whole care, like a single one. Furthermore, nursing status also considers instances of adoption¹. Effective twinning was used when a twin or an adoptive sibling survived at least the first month of life.
- Inbreeding coefficient: calculated from the Additive Relationship method (see Wright 1922; Ballou 1983). When used as a fixed factor in the Analysis of Variance, two groups were distinguished: < 0.4 and ≥ 0.4 , which is the median of its distribution (N=238). The identity of the father was easily known, as there was only one reproductively active male in each herd, and daily monitoring showed whether the alpha male was challenged and defeated by another male.
- Birth weight. N=165.
- Body weight (at different ages, one value per individual). N=84.
- Body length (at different ages, one value per individual). N=84.
- Age of the individual. N= 238.

¹ J Cassinello. Allosuckling in *Ammotragus*: A calves' strategy to obtain an extra source of resources? Submitted to Behavioural Processes.

- Season when the birth took place. This variable corresponds to the four seasons: Mar-May (N=101), Jun-Aug (N=29), Sep-Nov (N=17) and Dec-Feb (N=54).

- Maternal age when the birth took place. N=196.

Whenever possible parametric statistical tests were used. When the dependent variables did not follow a normal distribution the usual transformations were applied (Zar 1984). In some cases data from groups that differed from each other were pooled after the scores for each group were standardised. This converted the mean for that group to 0 with a standard deviation of 1. All the means are shown along with their standard error (SE). In the analyses, 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 response variables that the inter-group variance was not greater than the intra-group variance.

Results

1. Analysis of phenotypic variables in young and adult individuals

Body weights and lengths in the study population were recorded at very different ages (1.94 ± 0.17 years old, N=84). In order to see whether there is a stage from which no significant increase in body weight and length occurs, growth pattern of sexually mature arruis was analysed.

Successful matings have been recorded in 410 days old males (it was recorded in a herd where there was only one young male, the rest of the animals being females), and 270 days old females. Consequently, individuals from these ages may be regarded as sexually mature. The analysis of phenotypic characteristics of sexually mature males and females showed an evident sexual dimorphism, males being heavier and longer: mean body weight, 82.07 ± 6.29 kg (males, N=20) vs 41.34 ± 1.92 kg (females, N=42) (ANOVA: $F(1,60)=63.06$, $p<0.0001$); mean body length,

146.76±4.66 cm (males, N=21) vs 128.14±1.82 cm (females, N=44) (ANOVA: $F(1,63)=20.17$, $p<0.0001$). In addition, from Figure 1 it appears evident that sexually mature individuals continue growing for several years; also these growth logarithmic curves follow neat different patterns for both sexes.

As a consequence of these sex differences, the analyses were carried out separately for males and females. Also, previous results obtained in the same population suggest that differing results in males and females may be expected (Cassinello 1996). Stepwise multiple regression analysis was used to assess which variables affect body weight and length; the independent variables included were age, birth weight, maternal age, inbreeding coefficient and nursing status. In a first series of analyses immature and mature individuals were included. Concerning body weight, age is the only variable included in the final step either for males (N=19, $R^2=0.86$, $p<0.0001$) or females (N=26, $R^2=0.78$, $p<0.0001$), the relationship is obviously positive. However, when the dependent variable was body length, not only age determined growth, but in females those ones who were raised alone became larger than twin ones (N=29, $R^2=0.74$, $p<0.0001$; males: N=21, $R^2=0.93$, $p<0.0001$). In a second analysis only sexually mature arruís were included, in order to see whether other effects can be detected in individuals that are reaching a more stable body size (particularly females). Using the same regression test and independent variables the results are as follows. Males: both body weight (N=11, $R^2=0.60$, $p=0.005$) and length (N=12, $R^2=0.69$, $p=0.0008$) are determined exclusively by age; females: whereas body length variability is simply explained by age (N=20, $R^2=0.46$, $p=0.001$), body weight not only increases in older individuals, but it decreases with increasing maternal age (N=18, $R^2=0.70$, $p=0.0001$).

2. Analysis of phenotypic variables in calves

The independent variables that characterise the offspring at birth are sex, parturition type and inbreeding coefficient. Using these variables as fixed factors and birth weight as dependent variable, the Analysis of Variance shows that the three factors have an effect on birth weight, no interaction being found (Table 1). Males are heavier than females at birth, single calves are heavier than twins, and inbreeding coefficients ≥ 0.4 produce lighter individuals at birth (Figure 2).

To test the relationship, if any, between birth weight and maternal age, a standard measure of birth weight was used in the regression; this eliminated the influences of sex and parturition type. The result points out a very significant positive relationship, although it explains only 7% of the variance ($N=164$, $R^2=0.07$, $p=0.0009$) (Figure 3).

Finally any seasonal effects on birth weight was analysed. The standard birth weight was used as in the former analysis, otherwise the ANOVA would be dealing with too many missing cells. Season of the year was the fixed factor now, and the ANOVA revealed no differences in birth weights ($F(3,161)=1.01$, $p=0.39$).

Discussion

1. Sexual dimorphism

The degree of sexual dimorphism of a species may be determined by reliable data of male and female body mass (Kappeler 1991). A positive correlation is usually found between body size and degree of sexual dimorphism in many taxonomic groups of birds and mammals (Ralls 1977; Alexander et al. 1979). Concerning ungulates, Alexander et al. (1979) used body length measures to assess sexual dimorphism, since body weight may vary due to nutritional state, welfare, age, season or gestation period (Moen 1978). Both variables were included in the analysis thereby disregarding

pregnant females. Differences in body size and weight between sexes were notable in the Saharan arrui, adult males being 72% heavier and 13% longer than adult females. The differences in body weight do emerge at birth, when males are 9% heavier than females; likewise, single calves were heavier than twin ones (for the relationship between birth weight and maternal social rank see Cassinello and Gomendio 1996).

The study of those factors that could affect phenotypic characteristics in arrui shows that females with no siblings tend to be slightly longer; and, when considering only sexually mature females, it appears that those ones raised by older mothers do not reach body weights so high as younger mothers' daughters do. These evidences may show that mothers allocate less resources towards daughters that have to share the lactating period with a sibling, and that older mothers, usually holding higher social ranks (Cassinello 1995), invest less in their female offspring (for a detailed study of the relationship between rank and frequency of twin births see Cassinello and Gomendio 1996). As no such differences have been found in males, this seems to support the evidence of a maternal investment biased towards males found in *Ammotragus* very recently (Cassinello 1996).

2. Maternal age and season

The positive relationship found between birth weight and maternal age agrees with the results obtained in other ungulates, such as domestic sheep, *Ovis aries* (e.g. Lax and Brown 1967), red deer, *Cervus elaphus* (e.g. Blaxter and Hamilton 1980; Clutton-Brock et al. 1982), as well as in male calves of dama gazelle, *Gazella dama*, and Cuvier gazelle, *Gazella cuvieri* (Alados and Escós 1991); however, Hogg et al. (1992) did not find this relationship in bighorn, *Ovis canadensis*.

No relationship was observed between birth weight and season of the year. This result is expected under captive conditions, where a permanent and sufficient food supply is allocated to all the herds. In the wild differences would be expected in offspring mortality and, probably, in birth weights according to the seasonal period (see Green and Rothstein 1993, on the influence of birth date on growth and reproductive success in bison).

3. Deleterious effects of inbreeding

Empirical evidence points to the existence of deleterious effects of high inbreeding coefficients on birth weight in several species (e.g. Doney 1966; Lax and Brown 1968; Lamberson et al. 1982; MacNeil et al. 1989; Alados and Escós 1991). This effect was in the Saharan arrui, as calves with inbreeding coefficients higher than 0.4 were significantly lighter.

The lack of relationship between birth weight and adult physical characteristics would dismiss any possible influence of parturition type and inbreeding coefficient on adult phenotype (Bulger and Hamilton 1987; Feh 1990; Festa-Bianchet 1991; Alados and Escós 1992; although also see Clutton-Brock 1988). Furthermore, and although in some species of ungulates, adult body weight decreases with high inbreeding coefficients (see e.g. Doney 1957; Lax and Brown 1967; McCurley et al. 1984; Ryder 1987; Alados and Escós 1991), such a relationship has not been found in Saharan arrui.

According to the results obtained, the role of inbreeding on arrui physical conditions seems to be ambiguous. Without considering inbreeding influence on other biological aspects, such as reproductive performance, dispersal patterns, etc. (Moore and Ali 1984; for the relationship between inbreeding and fitness in arruis see Cassinello and Alados 1996), from the analysis of these data it is inferred that inbreeding

depression yields lighter individuals at birth (see also Ryder 1987; Alados and Escós 1991), but no deleterious effects have been found once they have grown up and become adults. However, the present findings on deleterious effects on birth weight are particularly significant, as the latter has a strong effect on offspring survival as well as on females' reproductive performance (Cassinello and Alados 1996).

Acknowledgements

I wish to thank J.R. Ginsberg, M. Festa-Bianchet and M. Gomendio for constructive comments on earlier drafts, and the staff of the EEZA for the management of the captive animals. During data collection the author enjoyed a predoctoral grant from MEC (PG89 27511603), being currently supported by DGICYT (PB 93-0186).

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Table 1. Factors affecting birth weight

	DF	F-VALUE	P-VALUE
SEX	1	7.28	0.008
PARTURITION	1	20.57	< 0.0001
SEX * PARTURITION	1	0.29	0.59
INBREEDING	1	9.24	0.003
SEX * INBREEDING	1	1.35	0.25
PART * INBREEDING	1	1.93	0.17
SEX * PART* INBREED	1	0.00064	0.98
Residual	157		

Analysis of variance carried out for the dependent variable birth weight in captive Saharan arrui.

The fixed factors are sex, parturition (single vs twin) and inbreeding (< and $\geq$ 0.4, the median of its distribution).

Figure captions

Figure 1. Male and female adult body weights (a) and lengths (b) at different ages in captive Saharan arrui. The fitted regression curves are also shown.

Figure 2. Mean birth weights (+ SE), according to sex, parturition type (single or twin) and inbreeding coefficient (< 0.4 , ≥ 0.4) in captive Saharan arrui. Sample size is shown.

Figure 3. Relationship between birth weights (standardised) and maternal age in captive Saharan arrui.

Figure 1a - J. Cassinello

Figure 1b - J. Cassinello

Figure 2 - J. Cassinello

Figure 3 - J. Cassinello