

Ammotragus lervia: a review on systematics, biology, ecology and distribution

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A revision on the current knowledge of the genus *Ammotragus* is provided. There is only one species, *A. lervia*, which is considered an ancestor of both *Ovis* and *Capra*. Six subspecies originally distributed in the North of Africa, but also introduced elsewhere, have been described. Particularly the study of the introduced wild ranging American populations, and recent research carried out on a captive population in Spain have expanded our knowledge on the species' social behaviour, reproduction, female fitness components, behavioural ecology, feeding habits and ecology. Native and introduced populations of arriuis are facing different problems; the former ones are generally threatened by human pressure, and the latter ones pose a serious risk to native ungulates and plants.

1. Short foreword

Ammotragus lervia is an African ungulate retaining some primitive and unique characteristics which makes it particularly interesting for research. It is also considered as a vulnerable species by IUCN (1996). The species was poorly known until its introduction to the United States of America in the late 1930s. This gave a beginning to ecological and management studies (e.g., Ogren 1965, Simpson 1980). Paradoxically, apart from few works mainly dealing with its distribution, research on this species has rarely been carried out in its natural, African, environment (e.g., Le Houérou 1992, Loggers *et al.* 1992, but see Clark 1964). Therefore, most of the knowledge we have about *Ammotragus* comes out from research on populations in European and American

zoos, or on American wild populations (e.g., Haas 1959, Simpson 1980, my own work). Herewith a review on the literature available and suggestion for future research are provided.

Common names for the species are: aoudad, audad, udad, uaddan, ouaddan, aroui, arui, aruii, Barbary sheep, Barbarian, mouflon africain, mouflon de Barbaris, muflón, muflón del Atlas, mouflon à manchettes, ruffed mouflon, Saharan mouflon, Mähnspringer, Mähnschaf, muflone berbere, Tassilin, Fechstal, Naded, Naddan, kebach, Kabsh Mai, Al Nakar, larrouy and bearded argali, among others (see e.g., Ogren 1965, Gray & Simpson 1980a, Shackleton 1997). Depending on the region, people and culture, we find a great diversity of common names for *Ammotragus*, some of them making an evident reference to its relationship with the genus *Ovis* (see below). Barbary sheep is the Eng-

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lish common denomination of the species; but, in order to prevent any taxonomic misinterpretation, I have preferred to use the Arabic name “arrui” in this review (*see* Valdez & Bunch 1980, and below).

2. Taxonomy

The genus *Ammotragus* Blyth, 1840, with only one species, *A. lervia* Pallas, 1777, has a commonly accepted taxonomic status:

Class: Mammalia
 Order: Artiodactyla
 Suborder: Ruminantia
 Infraorder: Pecora
 Family: Bovidae
 Subfamily: Caprinae
 Tribe: Caprini

However, the denomination of both genus and species has changed several times until reaching an accord (Gray & Simpson 1980a, Gray 1985):

Genus: *Ammotragus* Blyth, 1840
Aegoceros Heughlin, 1861
 Species: *Antilope lervia* Pallas, 1777
Ovis tragelaphus Afzelius, 1815
Ovis ornata I. Geoffroy Saint-Hilaire, 1827
Ammotragus lervia Thomas, 1902

Moreover, other taxonomic designations, which appeared between 1840 and 1902, may have contributed to creating a certain confusion in the taxonomy of the species (Gray & Simpson 1980a):

Ovis (Ammotragus) tragelaphus Blyth, 1840.
Ammotragus tragelaphus Gray, 1850.
Musimon tragelaphus Gervais, 1855.
Aries tragelaphus Lataste, 1887.
Ovis (Ammotragus) lervia Lydekker, 1898.
Ovis lervia Anderson and de Winton, 1902.

Finally, six subspecies have been described, mainly according to their distribution (*see* the section about the distribution of the species below):

Ammotragus lervia lervia Pallas, 1777.
Ammotragus lervia ornata I. Geoffroy Saint-Hilaire, 1827.
Ammotragus lervia sahariensis Rothschild, 1913.
Ammotragus lervia blainei Rothschild, 1913.
Ammotragus lervia angusi Rothschild, 1921.
Ammotragus lervia fassini Lepri, 1930.

3. Phylogeny: comparative morphology and biochemistry

Ammotragus still represents a challenge for evolutionists, since due to its particular morphology and behaviour, its phylogeny is a complicated and controversial subject.

Both goats (genus *Capra*) and sheep (genus *Ovis*) share a series of characteristics with arruis (*see* Table 1). Some authors even suggest that the latter should be included in one of these genera (e.g., Corbet 1978, *see* below). ‘*Ammotragus*’ means ‘sand goat’, probably in reference to its color, which is pale, tawny brown or rufous, grading to a whitish underside with dark brown areas around the head and forequarters (Valdez & Bunch 1980); variability in color tones, however, is notable among the subspecies. The general aspect resembles a robust goat, with a relatively long head, short and stocky legs, and a long, naked tail underneath. As a unique feature, a mane extends from under the throat down the front of the neck to the brisket, bifurcating then and continuing down the forelegs in mature animals, where it is named chaps. Arruis do not have a goatee, and like some sheep species (Geist 1971a, Delibes 1986), they have a haired chin and a short erect fringe on the back. True horns are elliptical and similar to those of mouflon (*Ovis musimon*). Unlike sheep, arruis lack preorbital, interdigital and flank glands, but they have sub-caudal glands. Their behaviour resembles that of sheep (Geist 1971a), although an ancestral pattern does predominate (Katz 1949, Haas 1959). Therefore, morphologically arruis show intermediate characteristics of sheep and goats (Geist 1971a, Schaffer & Reed 1972).

The chromosome number of the arrui ($2n = 58$) is identical to that of *Ovis vignei* (Nadler *et al.* 1974, Bunch *et al.* 1977). Besides, the seroprotein (Schmitt 1963) and immunoglobulin (Curtain & Fudenberg 1973) analyses show a close relationship to *Ovis*. However, the sequence of amino-acids of several hemoglobin chains (Manwell & Baker 1975) shows a closer relation to *Capra hircus*, and some unique characteristics. On the other hand, immuno-diffusion studies by Hight and Nad-

ler (1976) paradoxically establish a closer relationship between *Ovis* and *Capra* than between any of them and *Ammotragus*.

Some authors (Ansell 1971, Corbet 1978) place the arrui in the genus *Capra*, due to morphological similarities and because it may interbreed with goats and produce live hybrids (Petzsch 1957 in Geist 1971a). But Geist (1971a) discounted the ability of *Capra* to hybridize with *Ammotragus* as an indicator of a closer relationship, and hypothesized that reproductive barriers between *Ovis* and *Ammotragus* arose due to their sympatric distribution in North Africa during the Pleistocene, whereas arruis and goats were not sympatric.

Geist (1971a, 1985) hypothesized that the arrui is ancestral to the Palearctic sheep lineage. He related all the Eurasian mountain sheep by means of a cline based on the morphological characteristics

and geographic distribution of the species, the cline is named argali or *ammon* cline in reference to the Altai or Siberian argali, *Ovis ammon ammon*, which is placed in one end of the cline, while the arrui is in the other end. To determine in which direction sheep evolved, Geist (1971a) firstly compared all the species to ancestral forms to establish which is the evolutionary older form, and secondly he related the cline to the history of Pleistocene glaciations.

Paleontologists suggest that the caprids evolved from the Tribe Rupicaprinae (Thenius & Hofer 1960), which has four or six genera, according to various authors (Schaller 1977, Eisenberg 1981, Lovari & Perco 1982, MacDonald 1985). Two characteristic genera, the North American mountain goat, *Oreamnos*; and the serow, *Capricornis*; both share a great number of characteristics with the most

Table 1. Anatomical, chromosomal and blood protein differences between sheep, arruis and goats (from Valdez & Bunch 1980).

Phenotypic character	<i>Ovis</i>	<i>Ammotragus</i>	<i>Capra</i>
Preorbital gland	Present	Absent	Absent
Foot (interdigital) glands	Present	Absent	Absent
Inguinal glands	Present	Absent	Absent
Subcaudal glands	Absent	Present	Present
Chin beard	Absent	Absent	Present in males;
Horns	In males usually in spiral but sometimes bent backwards over the neck (supracervical)	Supracervical	usually scimitar-like or twisted and pointing up or bent backwards over the neck, with the tips pointing inwards and up
Tail length	Short (≤ 6.0 inches)	Long (≥ 6.0 inches)	Long (≥ 6.0 inches)
No. chromosomes (2n)	52 to 58	58	60
Transferrins (Tf)	I, A, G, B, C, D, M, E and F	Identical to D of sheep	A and B differ in mobility from A and B of sheep
Hemoglobins (Hb)	Normal adult hemoglobin A, B and D; with the exception of mouflon all wild sheep have Hb B	Amino acid sequencing has indicated several differences in the Hb B-chains from that of sheep and goats	Normal adult hemoglobin A, B, D and E; amino acid sequence of either α or β chains differ from sheep

primitive caprid, the thar, *Hemitragus*, which, on the other hand, clearly resembles *Ammotragus*. Therefore, this author concludes that the latter must be the most primitive species in the evolutionary argali cline (Geist 1971a). As for the second issue, according to the so-called 'Theory of Dispersion' (Geist 1971b, 1985), *Ammotragus* must also be the beginning of the cline. Firstly, it can be seen that the argali cline goes from North Africa, across Iran into Turkestan, then into the Pamir Mountains, and ends up in the Altai Mountains. This cline probably could not have existed during Pleistocene glaciations, for all the mountains inhabited by the argalis today, were then probably under ice (Frenzel 1968). This implies that the sheep found today in central Asia are of rather recent evolutionary origin, which surged from the unglaciated terrain into the mountain ranges after glacial withdrawal (Geist 1971a). After all this reasoning, Geist (1971a) concludes that *Ammotragus* should be placed in the origin of the argali cline, and discusses carefully all the morphological changes that have gradually taken place from arruis to argalis.

Ammotragus could also be an ancestor form of the genus *Capra*, at least of the round-horned goats (Geist 1971a). Disregarding its beard and mane, it is very similar to the young tur male (*Capra cylindricornis*) or the blue sheep (*Pseudois*). *Ammotragus* combines a number of goatlike characteristics and can be linked with intermediate forms not only to the argalis but also to the Siberian ibex (*Capra ibex sibirica*).

There is also a recent study on the phylogenetic relationships of nine genera of the Caprinae (*Capra*, *Ammotragus*, *Hemitragus*, *Pseudois*, *Ovis*, *Rupicapra*, *Oreamnos*, *Nemorhaedus* and *Capricornis*) based on the behaviours involved in courtship-mating and social status establishments (Kurt & Hartl 1994). The results obtained are in good agreement with biochemical-genetic data available.

4. Descriptive studies

4.1. Paleontology

In relation to fossil sheep remains recovered from superficial deposits in Europe at the end of XIX century, and which were referred to as several spe-

cies of *Ovis*, Lydekker (1912) commented that these 'sheep were akin to the modern arrui of North Africa'. Osborn (1910) mentioned a 'wild sheep (*Ovis paleotragus*) very similar to the existing Barbary sheep' when writing of the Pleistocene in North America. On the other hand, fossil remains of *Ammotragus* have been found in Libya, in a number of deposits which ranged in antiquity from about 85 000 to 2 000 years B.P. (McBurney 1967, Cremaschi & Di Lernia 1996), as well as in Quaternary deposits in Cyrenaican Libya (Bate 1955). Vaufrey (1955) noted the species among the Pleistocene fauna in the Maghreb, and Arambourg *et al.* (1934) recorded it at Beni Segoual, in Algeria.

This species was intensively exploited by Epipalaeolithic hunter-gatherers at the beginning of Holocene (Di Lernia & Cremaschi 1996), and a potential or incipient domestication might have occurred at that time (Saxon 1976, Smith 1992). Current surveys and excavations in the Libyan Sahara are providing new evidence about this issue (Cremaschi & Di Lernia 1996, Di Lernia 1998).

4.2. Anatomy and morphology

Bourdelle (1924) carried out a detailed study on the anatomical and osteological characteristics of *Ammotragus*. The cranial morphology was explained by Schaffer and Reed (1972), the vertebral formulae established by Lydekker (1913), and a first dental description made by Bourdelle (1924). Body measures were taken from individuals in New Mexico (McClellan 1955, Ogren 1965), Africa (Clark 1964), and Spain (Cassinello 1997a). The mean values obtained in a Spanish captive population show a strong sexual dimorphism in sexually mature individuals: mean body weight, 82.07 ± 6.29 kg (males, $N = 20$) vs. 41.34 ± 1.92 kg (females, $N = 42$); mean body length, 146.76 ± 4.66 cm (males, $N = 21$) vs. 128.14 ± 1.82 cm (females, $N = 44$) (Cassinello 1997a). The study of horn length and shape, as well as the analysis of their rings and annuli have originated a series of works trying to find a relationship with either body weight (Gray & Simpson 1979), or with the age of the individual (Gray & Simpson 1985). Sex and age classes can be identified by face and horn morphology (Gray & Simpson 1980b), although

a new and more reliable identification key has recently been published (Cassinello 1997b). Finally, a general description has already been provided above, when comparing *Ammotragus* with other caprids (*see* Section 3).

4.3. Biochemistry and genetics

The hemoglobin polypeptide chains were studied in detail (*see e.g.*, Huisman *et al.* 1958, Huisman 1974, Manwell & Baker 1975, 1977). Serum biochemical and hematological parameters (Schmitt 1963, Tumbleson *et al.* 1970, Brady & Ullrey 1975), and immunoglobulins (Curtain & Fudenberg 1973) were also analysed.

The species' karyotype was published by Heck *et al.* (1968), Schmitt and Ulbrich (1968), and Nadler *et al.* (1974); Buckland and Evans (1978a, 1978b) analysed in detail its characteristics. Other studies in the field of genetics were carried out by Schreiber and Prosi (1988), and Schreiber and Matern (1989).

4.4. Physiology

Ogren (1965) studied the reproductive tracts and sperm structure. Hormonal studies were carried out by Hamon and Heap (1990). In addition, the effects caused by some drugs have been reported by Nouvel *et al.* (1969), and Hampy (1978, in Gray & Simpson 1980a). Robbins and Robbins (1979) carried out a comparison of birth weight for various ungulates species in relation to the maternal reproductive effort.

4.5. Reproduction

Fourteen-months-old males and nine-months-old females can be regarded as sexually mature (Cassinello 1997a). Gestation and reproductive cycle was studied by several authors (*e.g.*, Brown 1936, Zuckerman 1953, Ogren 1965, Cassinello & Alados 1996). The mean gestation period is 5.5 months and mating season peak occurs from September to November, so that breeding season tends to be focused in spring. Cassinello and Alados (1996) analysed four components of female reproductive

success in captive Saharan arrui: longevity, fecundity, offspring one-month survival rate and the age at first birth. Longevity accounts for 69.9% of the variance of reproductive success, fecundity for 54.2%, offspring one-month survival rate for 29.8%, and the age at first birth for 10.4% (*see* Brown 1988). A detailed study of these components leads to the following conclusions: (a) longevity is higher in those individuals in better physical condition, (b) fecundity is related to age and social rank, (c) heavier offspring at birth have a higher probability of surviving during their first month of life, and (d) the age at first birth is delayed by high levels of population density, inbreeding coefficients, and birth weights. On the other hand, high-ranking females are characterized by shorter inter-birth intervals and give birth to a higher proportion of twins.

5. Factors affecting phenotypic traits

Following Cassinello (1997a), as adults, singleton females become larger than females who had a littermate, also, when reaching sexual maturity, females raised by older mothers are heavier. At birth, singletons are heavier than twins, but males are only heavier than females when their mother holds a high social rank. Furthermore, high-ranking mothers tend to produce heavier calves than low ranking ones (*see* Cassinello & Gomendio 1996). High inbreeding coefficients yield lighter calves. Finally, birth weights increase with maternal age (Cassinello 1997a).

6. Behavioural ecology

Pioneer studies on behavioural patterns in arrui, the so-called ethograms, were carried out by Katz (1949), and Haas (1959). Succeedingly, a series of works on the characteristic primitive agonistic behaviour of males, and on reproductive behaviour (arruis are polygynous and precocial mammals) have been published (*e.g.*, Ogren 1965, Schaffer 1968, Hamdy & Schmidt 1972 in Gray & Simpson 1980a, Schaffer & Reed 1972, Habibi 1987); as well as others on more general aspects of their behaviour (Solbert 1980, Gray & Simpson 1982a). A more detailed study carried out by Cas-

sinello (1995) on a captive Saharan arrui population in Spain shows that the species is characterised by an absolute dominance hierarchy, which is also near-linear and fairly stable. Females may change their hierarchical position under some circumstances: mating and parturition may cause a rank increase, and offspring weaning may lead to a lower status. Thus, 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. It is also postulated that females may present a variable social rank, related to age, at the beginning of their reproductive life, till they reach a fairly steady social status, in accordance with their reproductive experience and inherited family status.

According to a recent work (Cassinello 1996), high ranking females allocate their resources preferably towards their sons, according to Trivers and Willard's (1973) hypothesis. Cassinello and Gomendio (1996) also showed that litter size and sex ratio at birth are strongly influenced by the parity and maternal dominance rank at the time of conception in arrui. When females give birth for the first time they always produce a single offspring, while multiparous females produce both singletons and twins. As maternal rank increases, females tend to produce the following sequence: F-FF > M > MF > MM, which differs from Williams' (1979) prediction in that FF are produced by females of lower rank than M. This may be so, because of the strong sexual dimorphism of the species in which the differential costs of sons and daughters may be greater than in William's model, and in which dominant females have much to gain from producing exceptionally good males. Despite lower levels of investment in females, single females are more likely to survive than single males and twins.

Behavioural conflict between mother and offspring was investigated in the same captive population of Saharan arruis by Cassinello (1997c). Mothers that conceive in the following mating season accelerate the weaning process of their current offspring; furthermore, high-ranking females wean their male calves earlier. Behavioural conflict occurs during the resume of mother's sexual activity; however, no conflict appears to happen during weaning.

7. Ecology

The habitat selection was analysed in Africa (Rothschild 1921 in Gray & Simpson 1980a), America (Ogren 1965, Dickinson & Simpson 1980, Johnston 1980), and Europe (R. C. Bigalke, unpubl.). Arruis tend to inhabit rocky and precipitous areas, from the sea level up to the extent of snow-free areas at about 3 900 metres in their African endemic range. Johnston (1980) established the following habitat preference according to the season: woodlands during summer, grasslands during autumn and winter, and protective rocky slopes during spring, the main breeding season (*see above*). Research on population parameters were done in wild populations from Texas (Gray & Simpson 1983) and Murcia (R. C. Bigalke, unpubl.), the proportion of adults and juveniles being quite similar in all instances: approximately 30% juveniles, 20% adult males and 50% adult females. Concerning group dynamics, Gray and Simpson (1982b) verified that group leadership is ascribed to females when adults of both sexes are present, while group composition and size vary depending on the season. Six group types can be distinguished in the wild: solitary, nursery (females, calves and juveniles), mixed, all male, all female and all juveniles (Gray & Simpson 1982b). The knowledge of the feeding habits of the species is circumscribed to wild American (e.g., Ogren 1965, Bird & Upham 1980, Krysl *et al.* 1980, Simpson *et al.* 1980), and Spanish populations (Luengo & Piñero 1987, Piñero & Luengo 1992, R. C. Bigalke, unpubl.); but arruis are not selective at all and their diet may comprise shrubs, succulent forbs, forbs, creepers, dwarf shrubs and grasses, depending on season availability. Concerning territories size and population movements, Dickinson and Simpson (1980), and Simpson *et al.* (1978) provided some information, thus, the mean home range size ranges from 259 to 3 367 ha.; arruis' dispersal is particularly accentuated in summer. There are also studies on potential interspecific competition (Simpson *et al.* 1978) and parasites (e.g., Allen *et al.* 1956, Allen 1960, Yeruham *et al.* 1996), although arruis seem to be remarkably disease and parasite-free both in captivity and in the wild (e.g., Ogren 1965, J. Ortiz pers. comm., *see a review in* Pence 1980). Finally, a novel study on potential

energetic costs due to heat loss through the horn surface reached the conclusion that metabolic costs of possessing large horns in cold climates may impose constraints on morphology and sexual selection (Picard *et al.* 1994).

8. Distribution

Apart from its native distribution in Africa, the information on the arrui distribution in non-native lands, as a consequence of human introductions, has been collected mainly from the available bibliography and some few personal communications; but I have not intended to make an exhaustive listing of its presence in zoological gardens, and private game preserves. Undoubtedly, and because of the high reproductive rate and adaptability of the species (*see e.g.*, Ogren 1965, Simpson *et al.* 1978), it may be present in a great number of zoos and game preserves, particularly in temperate zones (south of Europe and USA). It follows the distribution of wild-ranging populations as well as the occurrence in zoos mentioned by the more relevant authors.

8.1. Endemic populations: Africa

The arrui is endemic to North Africa (*see* Brentjes 1980); and, in theory, it might be found in practically any rugged terrain or mountain chain throughout the whole northern part of the continent (*see* Gray 1985, Le Houérou 1992, Loggers *et al.* 1992, Shackleton 1997). There are six subspecies (Allen 1939), whose distribution is as follows:

— *Ammotragus lervia lervia*. Named Atlas arrui, it can be found in the mountains of Morocco (Aulagnier & Thévenot 1997) and Tunisia (de Smet 1997a), the northern part of Algeria (de Smet 1997b), and in the regions of Aïr and the Tibesti massif (*see* Aulagnier & Thévenot 1997). More than 30 years ago, it was approaching extinction in Algeria and Tunisia (Schomber & Kock 1960). Presumably, this is the subspecies that was imported to European zoological gardens at the end of last century, and from there to American zoos about 1900 (Ogren 1965). This subspecies also form the basis of free-ranging populations in the

United States of America (Gray 1985); and, according to Traweek (in Jones & Jones 1992), only in Texas there are currently more than 5 000 individuals. This could also be the subspecies introduced in the Sierra Espuña mountains of Murcia, in Spain (Gray 1985).

- *Ammotragus lervia ornata*. This subspecies is native to various desert areas in Egypt (*see* Gray 1985), but it may already be extinct (Heinemann 1972, Amer 1997). It is named Egyptian arrui.
- *Ammotragus lervia sahariensis*. It has a very large geographic distribution that, according to Gray (1985), includes parts of southern Morocco and the Western Sahara (*see* also Aulagnier & Thévenot 1997), the Sahara of southern Algeria (but *see* de Smet 1997b), southern Tunisia, southeastern Libya (*see* also Shackleton & de Smet 1997), Sudan, Mali (*see* also Lamarche 1997a), Niger, Mauritania (*see* also Lamarche 1997b), and the Tibesti Mountains. This is also the subspecies found in Chad (Mekonlaou & Daboulaye 1997, but *see* Alados *et al.* 1988), today probably restricted to the sandstone massifs in Ennedi (Mekonlaou & Daboulaye 1997). Named Saharan arrui, it has been introduced into the Estación Experimental de Zonas Áridas (EEZA) in Almería, Spain (Cano & Vericad 1983, Alados *et al.* 1988, Alados & Vericad 1993).
- *Ammotragus lervia blainei*. It used to be relatively widespread from western Sudan to the Red Sea coast, but currently it might be restricted to the Red Sea hills of eastern Sudan (Nimir 1997). It could also be found in the Ennedi and Uweinat mountains in Chad (Alados *et al.* 1988); but according to Mekonlaou and Daboulaye (1997), that is the subspecies *A. l. sahariensis*. In 1923, *A. l. blainei* was introduced into the Sabaloka reserve on the Sixth Cataract of the Nile (Gray 1985). It has also been reported in Libya (*see* Shackleton & de Smet 1997). It is named Kordofan arrui.
- *Ammotragus lervia angusi*. Named Aïr arrui, it inhabits the Aïr and Asben, in Niger (Magin & Newby 1997), west to the Adrar des Iforhas of Algeria (but *see* de Smet 1997b), and east to Tibesti in Chad (Alados *et al.* 1988, but *see* Mekonlaou & Daboulaye 1997).
- *Ammotragus lervia fassini*. It can be found in

Libya (Shackleton & de Smet 1997) and in the extreme southern part of Tunisia (Gray 1985, de Smet 1997a). There are no current population estimates. Likewise the Saharan arrui, this subspecies was introduced into the EEZA (Cano & Vericad 1983), but the whole population was moved into the Barcelona zoo in the late 1980s. It has been denominated Libyan arrui. The color of its fur is more pale than that of the Saharan arrui and it is characterized by a more tranquil and even-tempered mood (EEZA staff communication).

Currently, two main issues urge to be revised: first a more accurate definition of the subspecies, as from the distribution areas it may be inferred various possible hybridation zones (the regions of Air and the Tibesti massif, with three subspecies supposedly inhabiting, *A. l. lervia*, *A. l. angusi* and *A. l. sahariensis*); also, it remains unclear whether the populations found in the Western Sahara and Mauritania correspond with *A. l. sahariensis*, which type locality is sited in the Algerian Sahara (Gray 1985). A second issue would obviously be to carry out reliable surveys of the distribution of the species in Africa, although they may sadly be confronted with political and economic interests. Small groups scattered on large territories are the typical pattern of the distribution of the species in the wild (Savino di Lernia, accounting anonymous Tuareg informants), so that intense surveys would need to be done to test their presence.

8.2. Introduced populations

Unequivocally, arrui introductions in Europe and America have always been related to game interests. Captive populations in zoological gardens, on the other hand, might help to preserve the most threatened subspecies.

8.2.1. Europe

8.2.1.1. Germany

The arrui was introduced in two locations in the north, near Lopshorn in Lippe in 1883, and later in the Teutoburger Wald; none of these introduc-

tions was successful (*see* Gray 1985). However, the species is common in German zoos.

8.2.1.2. Italy

According to Zammarano (in Gray 1985), the species was introduced into some game preserves during the first half of this century. I do not know whether the introductions were successful.

8.2.1.3. Spain

Definitely, this is the European country where the arrui has been more successfully introduced, due in part to the mild climate and the geographic profile which, particularly in the south east of the country, resembles the native African lands. The current distribution of the Spanish arrui populations is difficult to assess accurately, as there are more and more private game preserves which are introducing the species, since it is easy to adapt to most of the environments and habitats, being practically a generalist (*see e.g.*, Ogren 1965, Simpson *et al.* 1978, Barrett & Beasom 1980, Dickinson & Simpson 1980, Johnston 1980, Luengo & Piñero 1987, R. C. Bigalke, unpubl.). However, those introductions carried out by public institutions into natural parks or reserves can be easily enumerated, such as Sierra Espuña in Murcia and the Parque Nacional de la Caldera de Taburiente, in La Palma, Canary Islands (*see* below). The arrui can be found in the following Spanish regions:

— Murcia: thirty-six arruis from the Frankfurt Zoo (Germany), and the Ain Sebad Zoological Park, in Casablanca (Morocco), were introduced in the Sierra Espuña Natural Park in 1970 (Ortuño & De la Peña 1979). The population expanded rapidly, reaching up to 2 000 individuals in 1991 which also inhabited the surrounding mountains, such as Sierra de las Cabras and Sierra del Burete (ARMAN-Murcia, unpubl.). Unfortunately, in 1992 a mange epidemic drastically diminished the arrui population (S. Eguia & P. Jimenez, unpubl.), and the most optimistic estimations established that scarcely 200 individuals survived (R. Sánchez pers. comm.). As a preventive measure, 63 arruis were kept in an enclosure, inside the Natu-

ral Park, in 1995 (DGMN-Murcia, unpubl.). Since then, the population has recovered again, and it is supposedly expanding once more and reaching nearby mountains (M. A. Sánchez pers. comm.). The arruis of Sierra Espuña probably belong to the subspecies *A. l. lervia* (see Gray 1985).

- Canary Islands: 16 individuals from Sierra Espuña were introduced close to the Caldera de Taburiente National Park in La Palma in June 1972 (Luengo & Piñero 1987, Piñero & Luengo 1992). They expanded successfully since then on, inhabiting nowadays the most remote and mountainous regions. The population increased without an effective management (anon. comm.). Gray (1985), erroneously, quoted this introduction as a failed one.
- Andalusia: there are some populations of arrui in private game preserves in Cádiz (Gray 1985), Málaga and Granada (anon. comm.). I do not know the origin of these private introductions and, in consequence, which subspecies they are composed of. Libyan arruis can be found at a zoological garden in Córdoba. Finally, there is a captive population of the subspecies *A. l. sahariensis* at the EEZA, in Almería (e.g., Alados *et al.* 1988), originated from two individuals which were shipped from the western Sahara in 1975.
- Castile-La Mancha: according to Gray (1985), there are some private herds of arruis in the provinces of Ciudad Real and Toledo.
- Catalonia: at least there is a population of Libyan arruis at the Barcelona zoo (see above).

8.2.2. America

8.2.2.1. United States of America

According to Ogren (1965), the arrui apparently has been present in the USA since about 1900; all known imports being from European zoos. And by 1965, nearly every sizeable zoo had acquired the species. The species is present in six main regions:

- California: according to Barrett (1980), the species, which is commonly known as aoudad in this state, has been a common animal in zoos for decades. In 1953, the Hearst Zoo at

San Simeon was disbanded and consequently 85 arruis began a wild existence. This population expanded to over 500 within 10 years (see also Gray 1985).

- New Mexico: according to Ogren (1965), in 1950, 57 arruis from private ranches were released at Old Mills Canyon and on a state game refuge near the Canadian River Gorge. Thus, the Canadian River arrui population stems from these animals. Apart from this population, the Picacho herd is also known to be the source of other arrui populations in central and southern New Mexico. Finally, 21 individuals were planted in Canyon Largo by the San Juan County Wildlife Federation in 1956 (Ogren 1965). Furthermore, periodic escapes of arruis from the McKnight game enclosure have resulted in a another wild breeding population in the Guadalupe Mountains National Park (Dickinson & Simpson 1980). As a whole, there may be about 5 000 individuals in the state (B. Morrison, pers. comm. quoted by Gray 1985).
- Texas: in December 1957, 31 arruis were released in Palo Duro Canyon (DeArment 1971 in Gray 1985). According to Gray (1985), another 13 individuals were liberated in Briscoe County in February 1958. This author also comments the dispersal of this species throughout the state. The arrui population at Palo Duro seemed to be as high as about 2500 animals in the late 1970s (Simpson *et al.* 1978). A series of releases and escapes from private enclosures have resulted in some small free-ranging populations of the species since 1960's (Decker 1978, Simpson & Krysl 1981). Free-ranging herds now exist on caprock along much of the eastern edge of Llano Estacado, in the rough country of Trans-Pecos, and on parts of Edwards Plateau (Jones & Jones 1992). The total population in the wild exceeds 5 000 (Traweek 1985).
- Oklahoma: arrui sightings have been reported occasionally, probably as a result of dispersal from the populations already mentioned (Simpson & Krysl 1981, Gray 1985).
- Colorado: sporadic reports of sightings (Ogren 1965, Simpson & Krysl 1981, Gray 1985). Gray (1985) doubted that any populations had become established.

8.2.2.2. Mexico

Rangel-Woodyard and Simpson (1980) document the release of arruis in three localities: in the Sierra Morena Ranch, Sierra Pájaros Azules and in San Luis Potosí; these releases were not designed to supplement the endemic fauna for sport-hunting purposes as it was in some areas of the USA, but they were made to fulfill the interests of individuals in a private collection of exotics. On the other hand, Gray (1985) was informed by the Universidad Nacional Autónoma in Mexico on the release of the species on Espíritu Santo Island, in the Sea of Cortez, but heavy hunting extirpated eventually not only this population but also the other three ones released in Mexico, so that currently there seems to be no longer any free-ranging population anywhere in the country.

9. Management and conservation prospects

African populations of *Ammotragus* are generally threatened due to a combination of overgrazing by domestic livestock, deforestation and habitat destruction, and poaching (*see* Loggers *et al.* 1992, Shackleton 1997). The general conservation programmes of each country where the species occurs are summarized in Shackleton (1997).

From a purely hunting perspective, the arrui is of great interest (*see e.g.*, Ogren 1965, Ortuño & De la Peña 1979, Christian 1980), but unfortunately the introductions carried out in the past did not take into account the potential costs for the environment that an opportunistic species like this may cause. Careful management and control of introduced populations are needed in order to prevent any potential risks on autochthonous species, such as interspecific competition with other ungulates (Simpson *et al.* 1978) or feeding on native flora (Luengo & Piñero 1987, Piñero & Luengo 1992). There is no recorded instance of direct competition between arruis and other ungulate species; but, following Simpson *et al.*'s (1978) reasoning, a real threat against the desert bighorn (*Ovis canadensis*) might occur in those American sites where both species show close home ranges. These authors point out the immense dispersal capacities of arruis and their ability to survive in virtually

any rugged terrain. They also evaluated that out of 49 desert bighorn food plants, 37 were recorded so far as eaten by arruis, and that if both species would happen to share their home ranges, in winter, when both are feeding predominantly on grasses, competition should be hard, to the detriment of the desert bighorn (Simpson *et al.* 1978). On the potential risk on native or endemic flora, arruis are generalists, and their wrong introduction in valuable zones, such as the Caldera de Taburiente National Park, in La Palma island (Canary Islands; *see* above), has shown the presence of endemic plants in their diet (Luengo & Piñero 1987, Piñero & Luengo 1992). An uncontrolled increase in arrui introduced populations has always been observed (*e.g.*, Barrett & Beasom 1980, R. C. Bigalke, unpubl.), so that a proper monitoring should be one of the priorities in any management project of the species.

Concerning conservation prospects, apart from the management of already-introduced populations which are to be maintained, the re-introduction of the subspecies *A. l. sahariensis* in Western Africa is desirable, as a viable population is kept in captivity in Spain (*e.g.*, Alados *et al.* 1988). Proper surveys urge to be tackled in arrui's original sites in Africa in order to know the actual distribution and abundance of the species, which is mostly indeterminate (*see* Shackleton 1997), and to carry out pertinent management policies if necessary. But a series of logistical and even political problems make it particularly difficult to carry out proper protection actions in the native lands of *Ammotragus* (*see* also Alados & Shackleton 1997).

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References

- Alados, C. & Shackleton, D. M. 1997: Regional Summary. — In: Shackleton, D. M. (ed.), Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae: 47–48. IUCN, Gland, Switzerland.

- Alados, C. L., Escós, J. & Vericad, J. R. 1988: Captive populations of northwest African Antilopinae and Caprinae at the Estación Experimental de Zonas Áridas. — In: Dixon, A. & Jones, D. (eds.), Conservation and biology of desert antelopes: 199–211. — Christopher Helm Ltd., Kent.
- Alados, C. L. & Vericad, J. R. 1993: Aoudad. *Ammotragus lervia* from Western-Sahara. International Studbook. — Bol. Inst. Est. Almer. Ciencias 11/12: 65–97.
- Allen, G. M. 1939: A checklist of African mammals. — Bull. Mus. Comp. Zool. 83: 548.
- Allen, R. W. 1960: Diseases and parasites of Barbary and bighorn sheep in the Southwest. — Trans. Desert Bighorn Council 4: 17–22.
- Allen, R. W., Becklund, W. W. & Gilmore, R. E. 1956: Parasites of the Barbary sheep. — J. Parasitol. 42: 19.
- Amer, M. 1997: Egypt. — In: Shackleton, D. M. (ed.), Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae: 21–26. IUCN, Gland, Switzerland.
- Ansell, W. F. H. 1971: Order Artiodactyla. — In: Meester, J. & Setzer, H. W. (eds.), The mammals of Africa, an identification manual: 1–84. Smithsonian Institution Press, Washington.
- Arambourg, C., Boule, M., Vallois, H. & Verneau, R. 1934: Les grottes paléolithiques des Beni Segoual, Algérie. Institut de paléontologie humaine, Paris. — Archives, Mém. 13: 1–242.
- Aulagnier, S. & Thévenot, M. 1997: Morocco (including Western Sahara). — In: Shackleton, D. M. (ed.), Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae: 34–38. IUCN, Gland, Switzerland.
- Barrett, R. H. 1980: History of the Hearst Ranch Barbary sheep herd. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 46–50. Texas Tech. Univ. Press, Lubbock.
- Barrett, R. H. & Beasom, S. L. 1980: Research needs for management of Barbary sheep in the future. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 106–107. Texas Tech. Univ. Press, Lubbock.
- Bate, D. M. A. 1955: Vertebrate faunas of Quaternary deposits in Cyrenaica. — In: McBurney, C. B. M. & Hey, R. W. (eds), Prehistory and Pleistocene geology in Cyrenaican Libya: 274–291. Cambridge University Press, Cambridge.
- Bird, W. & Upham, L. L. 1980: Barbary sheep and mule deer food habits of Largo Canyon, New Mexico. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 92–96. Texas Tech. Univ. Press, Lubbock.
- Bourdelle, E. 1924: Quelques caractères anatomiques du Mouflon à manchettes. — Revue Hist. Nat. Appl. 5: 129–140.
- Brady, P. S. & Ullrey, D. E. 1975: Protein requirement of weaned aoudads (*Ammotragus lervia*). — J. Zool. Anim. Med. 6: 24–28.
- Brentjes, B. 1980: The Barbary sheep in ancient North Africa. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 25–26. Texas Tech. Univ. Press, Lubbock.
- Brown, C. E. 1936: Rearing wild animals in captivity, and gestation periods. — J. Mammal. 17: 10–13.
- Brown, D. 1988: Components of lifetime reproductive success. — In: Clutton-Brock, T. H. (ed.), Reproductive success. — The University of Chicago Press, Chicago: 439–453.
- Buckland, R. A. & Evans, H. J. 1978a: Cytogenetic aspects of phylogeny in the Bovidae. I. G-banding. — Cytogenet. Cell. Genet. 21: 42–63.
- Buckland, R. A. & Evans, H. J. 1978b: Cytogenetic aspects of phylogeny in the Bovidae. II. C-banding. — Cytogenet. Cell. Genet. 21: 64–71.
- Bunch, T. D., Rogers, A. & Foote, W. C. 1977: G-band and transferrin analysis of aoudad-goat hybrids. — J. Hered. 68: 210–217.
- Cano, A. & Vericad, J. R. 1983: Rapport des recherches en faune saharienne de la “Estación Experimental de Zonas Áridas” (Almería, Espagne). — Symposium on international conservation and gestion faune sauvage méditerranéenne, Fez (Maroc), 16–17 March 1983.
- Cassinello, J. 1995: Factors modifying female social ranks in *Ammotragus*. — Appl. Anim. Behav. Sci. 45: 175–180.
- Cassinello, J. 1996: High ranking females bias their investment in favour of male calves in captive *Ammotragus lervia*. — Behav. Ecol. Sociobiol. 38: 417–424.
- Cassinello, J. 1997a: High levels of inbreeding in captive *Ammotragus lervia* (Bovidae, Artiodactyla): Effects on phenotypic variables. — Can. J. Zool. 75: 1707–1713.
- Cassinello, J. 1997b: Sex and age classes in Spanish populations of arrui (*Ammotragus lervia*). Relationship with the management of free-ranging populations. — Bol. Inst. Est. Almer. Ciencias 14: 171–178. [In Spanish with English summary.]
- Cassinello, J. 1997c: Mother-offspring conflict in the Saharan arrui. Relation to weaning and mother’s sexual activity. — Ethology 103: 127–137.
- Cassinello, J. & Alados, C. L. 1996: Female reproductive success in captive *Ammotragus lervia* (Bovidae, Artiodactyla). Study of its components and effects of hierarchy and inbreeding. — J. Zool., Lond. 239: 141–153.
- Cassinello, J. & Gomendio, M. 1996: Adaptive variation in litter size and sex ratio at birth in a sexually dimorphic ungulate. — Proc. Roy. Soc. Lond., B 263: 1461–1466.
- Christian, T. T. 1980: Development and economic role of Aoudad hunting in a cattle ranching operation. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 104–105. — Texas Tech. Univ. Press, Lubbock.
- Clark, J. L. 1964: The great arc of the wild sheep. — University of Oklahoma Press, Norman.
- Corbet, G. B. 1978: The mammals of the Palaearctic region: a taxonomic review. — Cornell University Press, Ithaca.
- Cremaschi, M. & Di Lernia, S. 1996: Current research on

- the prehistory of the Tadrart Acacus (Libyan Sahara). Survey and excavations 1991–1995. — Nyame Akuma 45: 50–59.
- Curtain, C. C. & Fudenberg, H. H. 1973: Evolution of the immunoglobulin antigens in the Ruminantia. — *Biochem. Genet.* 8: 301–308.
- Decker, E. 1978: Exotic. — In: Schmidt, J. L. & Gilbert, D. L. (eds.), *Big game of North America: ecology and management*: 229–256. Wildlife Management Institute, Stackpole Books, Harrisburg, PA.
- Delibes, M. 1986: *Ammotragus lervia* (Pallas, 1777), Mänschaf. — In: Niethammer, G. (ed.), *Handbuch der Säugetiere Europas*: 423–431.
- de Smet, K. 1997a: Tunisia. — In: Shackleton, D. M. (ed.), *Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae*: 45–47. IUCN, Gland, Switzerland.
- de Smet, K. 1997b: Algeria. — In: Shackleton, D. M. (ed.), *Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae*: 17–19. IUCN, Gland, Switzerland.
- Dickinson, T. G. & Simpson, C. D. 1980: Home range movements, and topographic selection of Barbary sheep in the Guadalupe Mountains, New Mexico. — In: Simpson, C. D. (ed.), *Symposium on ecology and management of Barbary sheep*: 78–86. Texas Tech. Univ. Press, Lubbock.
- Di Lernia, S. & Cremaschi, M. 1996: Taming Barbary sheep: wild animal management by Early Holocene hunter-gatherers at Uan Afuda (Libyan Sahara). — *Nyame Akuma* 46: 43–54.
- Di Lernia, S. 1998: Cultural control over wild animals during the early Holocene: the case of Barbary sheep in central Sahara. — In: Di Lernia, S. & Manzi, G. (eds.), *Proceedings of the Workshop Before food production in North Africa. Questions and tools dealing with resource exploitation and population dynamics at 12000–7000 B.P.* XIII UISPP Congress, ABACO-CIRSA, Forlì. [In press].
- Eisenberg, J. F. 1981: The mammalian radiations. An analysis of trends in evolution, adaptation, and behaviour. — The Athlone Press, London.
- Frenzel, B. 1968: The Pleistocene vegetation of northern Eurasia. — *Science* 161: 637–648.
- Geist, V. 1971a: Mountain sheep. A study in behaviour and evolution. — The University of Chicago Press, Chicago.
- Geist, V. 1971b: On the relation of social evolution and dispersal in Ungulates during the Pleistocene, with emphasis on the old-world deer and the genus *Bison*. — *Quaternary Research* 1: 283–315.
- Geist, V. 1985: On evolutionary patterns in the Caprinae with comments on the punctuated mode of evolution, gradualism and a general model of mammalian evolution. — In: Lovari, S. (ed.), *The biology and management of mountain ungulates*: 15–30. — Croom Helm, London.
- Gray, G. G. 1985: Status and distribution of *Ammotragus lervia*: a worldwide review. — In: Hoefs, M. (ed.), *Wild sheep. Distribution, abundance, management and conservation of the sheep of the world and closely related mountain ungulates*: 95–126. Northern Wild Sheep and Goat Council, Whitehouse, Yukon, Canada.
- Gray, G. G. & Simpson, C. D. 1979: Weight estimation of Barbary sheep from horn length. — *Wildl. Soc. Bull.* 7: 285–288.
- Gray, G. G. & Simpson, C. D. 1980a: *Ammotragus lervia*. — *Mammal. Species* 144: 1–7.
- Gray, G. G. & Simpson, C. D. 1980b: Identification of Barbary sheep sex and age classes in the field. — In: Simpson, C. D. (ed.), *Symposium on ecology and management of Barbary sheep*: 63–65. Texas Tech. Univ. Press, Lubbock.
- Gray, G. G. & Simpson, C. D. 1982a: Aspects of behaviour in free-ranging Barbary sheep (*Ammotragus lervia*). — *The Prairie Naturalist* 14: 113–121.
- Gray, G. G. & Simpson, C. D. 1982b: Group dynamics of free-ranging Barbary sheep in Texas. — *J. Wildl. Manage.* 46: 1096–1101.
- Gray, G. G. & Simpson, C. D. 1983: Population characteristics of free-ranging Barbary sheep in Texas. — *J. Wildl. Manage.* 47: 954–962.
- Gray, G. G. & Simpson, C. D. 1985: Horn growth and aging of free-ranging Barbary sheep (*Ammotragus lervia*). — *Mammalia* 49: 85–91.
- Haas, V. G. 1959: Untersuchungen über angeborene Verhaltensweisen bei Mähnspringern (*Ammotragus lervia* Pallas). — *Z. Tierpsychol.* 16: 218–242.
- Habibi, K. 1987: Behaviour of aoudad (*Ammotragus lervia*) during the rutting season. — *Mammalia* 51: 497–513.
- Hamon, M. H. & Heap, R. B. 1990: Progesterone and estrogen concentrations in plasma of Barbary sheep (*Aoudad*, *Ammotragus lervia*) compared with those of domestic sheep and goats during pregnancy. — *J. Reprod. Fertil.* 90: 207–211.
- Heck, H., Wurster, D. & Benirschke, K. 1968: Chromosome study of members of the subfamilies Caprinae and Bovinae, family Bovidae; the musk ox, ibex, aoudad, Congo buffalo, and gaur. — *Z. Säugetierk.* 33: 172–179.
- Heinemann, D. 1972: Barbary sheep, tahr, and blue sheep. — In: Grzimek (ed.), *Grzimek's animal life encyclopedia* 13. — Von Nostrand Reinhold, New York: 492–496.
- Hight, M. E. & Nadler, C. F. 1976: Relationships between wild sheep and goats and the aoudad (*Caprini*) studied by immuno-diffusion. — *Comp. Biochem. Physiol.* 54B: 265–269.
- Huisman, T. H. J. 1974: Structural aspects of fetal and adult hemoglobins from nonanemic ruminants. — *Ann. New York Acad. Sci.* 241: 392–410.
- Huisman, T. H. J., Van Vliet, G. & Sebens, T. 1958: Haemoglobin types in different species of sheep. — *Nature* 182: 172–174.
- IUCN 1996: The red list of threatened animals. — IUCN Publications Service, Cambridge.

- Johnston, D. S. 1980: Habitat utilization and daily activities of Barbary sheep. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 51–58. Texas Tech. Univ. Press, Lubbock.
- Jones, J. K. Jr. & Jones, C. 1992: Revised checklist of recent land mammals of Texas, with annotations. — Texas J. Sci. 44: 53–74.
- Katz, I. 1949: Behavioural interactions in a herd of Barbary Sheep (*Ammotragus lervia*). — Zoologica 34: 9–18.
- Krysl, L., Simpson, C. D. & Gray, G. G. 1980: Dietary overlap of sympatric Barbary sheep and mule deer in Palo Duro Canyon, Texas. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 97–103. Texas Tech. Univ. Press, Lubbock.
- Kurt, F. & Hartl, G. B. 1994: Socio-ethogram of adult males versus biochemical–genetic variation in assessing phylogenetic relationships of the Caprinae. — Acta Theriol. 53: 183–197.
- Lamarche, B. 1997a: Mali. — In: Shackleton, D. M. (ed.), Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae: 32–33. IUCN, Gland, Switzerland.
- Lamarche, B. 1997b: Mauritania. — In: Shackleton, D. M. (ed.), Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae: 33–34. IUCN, Gland, Switzerland.
- Le Houérou, H. N. 1992: Outline of the biological history of the Sahara. — J. Arid Environ. 22: 3–30.
- Loggers, C. O., Thévenot, M. & Aulagnier, S. 1992: Status and distribution of Moroccan wild ungulates. — Biol. Conserv. 59: 9–18.
- Lovari, S. & Perco, F. 1982: Los animales. Gran enciclopedia ilustrada. Tomo II. — Editorial Delta S.A., Barcelona.
- Luengo, J. L. R. & Piñero, J. C. R. 1987: Datos preliminares sobre la alimentación del arrui (*Ammotragus lervia*) (Bovidae) en La Palma. Islas Canarias. — Vieraea 17: 291–294.
- Lydekker, R. 1912: The sheep and its cousins. — Ballantyne, Hanson & Co., Edinburgh.
- Lydekker, R. 1913: Catalogue of the ungulate mammals in the British Museum (Natural History). — British Museum, London 1: 1–249.
- MacDonald, D. (ed.). 1985: The encyclopaedia of mammals: 2. — George Allen & Unwin, London.
- Magin, C. D. & Newby, J. 1997: Niger. — In: Shackleton, D. M. (ed.), Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae: 38–40. IUCN, Gland, Switzerland.
- Manwell, C. & Baker, C. M. A. 1975: *Ammotragus lervia*: Progenitor of the domesticated sheep or specialized offshoot of Caprine evolution? — Experientia 31: 1370–1371.
- Manwell, C. & Baker, C. M. A. 1977: *Ammotragus lervia*: Barbary sheep or Barbary goat? — Comp. Biochem. Physiol. 58B: 267–271.
- McBurney, C. B. M. 1967: The Haua Fteah (Cyrenaica) and the stone age of the South-East Mediterranean. — Cambridge Univ. Press, Cambridge.
- McClellan, J. 1955: Preliminary report on the Barbary sheep of New Mexico. — Proc. Western Assoc. State Game Fish Comm. 35: 167–176.
- Mekonlaou, M. & Daboulaye, B. Y. 1997: Chad. — In: Shackleton, D. M. (ed.), Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae: 19–21. IUCN, Gland, Switzerland.
- Nadler, C. F., Hoffmann, R. S. & Woolf, A. 1974: G-band patterns, chromosomal homologies, and evolutionary relationships among wild sheep, goats and the aoudad. (Mammalia, Artiodactyla). — Experientia 30: 744–746.
- Nimir, M. B. 1997: Sudan. — In: Shackleton, D. M. (ed.), Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae: 40–45. IUCN, Gland, Switzerland.
- Nouvel, J., Chauvier, G. & Strazielle, L. 1969: Effects de quelques tranquillisants et anesthésiques sur les animaux sauvages. — Zool. Garten 37: 114–116.
- Ogren, H. 1965: Barbary sheep. — New Mexico Department of Game and Fish Bulletin 13, Santa Fe.
- Ortuño, F. & De la Peña, J. 1979: Reservas y cotos nacionales de caza. 4. Región mediterránea. — Ed. Incafo. Colección Naturaleza Española, 5. Madrid.
- Osborn, H. F. 1910: The age of mammals in Europe, Asia and North America. — MacMillan, New York.
- Pence, D. B. 1980: Diseases and parasites of the Barbary sheep. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 59–62. Texas Tech. Univ. Press, Lubbock.
- Picard, K., Thomas, D. W., Festabianchet, M. & Lanthier, C. 1994: Bovid horns. An important site for heat-loss during winter. — J. Mammal. 75: 710–713.
- Piñero, J. C. R. & Luengo, J. L. R. 1992: Autumn food-habits of the Barbary sheep (*Ammotragus lervia* Pallas 1777) on La Palma Island (Canary Islands). — Mammalia 56: 385–392.
- Rangel-Woodyard, E. & C.D. Simpson, C. D. 1980: Status of Barbary sheep in Mexico. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 30–32. Texas Tech. Univ. Press, Lubbock.
- Robbins, C. T. & Robbins, B. L. 1979: Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. — Am. Nat. 114: 101–116.
- Saxon, E. C. 1976: The evolution of domestication: a reappraisal of the Near Eastern and North African evidence. — In: Higgs, E. (ed.), Origine de l'élevage et de la domestication: 180–226. Colloque XX, IX Congress UISPP, Nice.
- Schaffer, W. M. 1968: Interspecific combat and the evolution of the Caprini. — Evolution 22: 817–825.
- Schaffer, W. M. & Reed, C. A. 1972: The co-evolution of social behaviour and cranial morphology in sheep and goats (Bovidae, Caprini). — Fieldiana 61: 1–62.
- Schaller, G. B. 1977: Mountain monarchs. Wild sheep and goats of the Himalaya. — The University of Chicago Press, Chicago.

- Schmitt, J. 1963: Ammotragus lervia Pallas, Mähenschaf oder Mähnenziege? — Z. Säugetierk. 28: 7–12.
- Schmitt, J. & Ulbrich, F. 1968: Die Chromosomen verschiedener Caprini Simpson, 1945. — Z. Säugetierk. 28: 7–12.
- Schomber, H. W. & Kock, D. 1960: The wild life of Tunisia: Part 2. Some larger animals. — African Wild Life 14: 277–282.
- Schreiber, A. & Matern, B. 1989: Genetic investigations and pedigree analysis in captive Barbary sheep (Ammotragus lervia, Pallas 1777). — Zoo Biol. 8: 253–264.
- Schreiber, A. & Prosi, F. 1988: Evidence of loss of a suggested genetic-polymorphism in the blood potassium contents of zoo-living Barbary sheep Ammotragus lervia (Pallas 1777). — Comp. Biochem. Physiol. 89A: 75–77.
- Shackleton, D. M. (ed.) 1997: Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae. — IUCN, Gland, Switzerland.
- Shackleton, D. M. & de Smet, K. 1997: Libya. — In: Shackleton, D. M. (ed.), Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae: 30–32. IUCN, Gland, Switzerland.
- Simpson, C. D. (ed.) 1980: Symposium on ecology and management of Barbary sheep. — Texas Tech. University Press, Lubbock.
- Simpson, C. D. & Krysl, L. J. 1981: Status and distribution of Barbary sheep in the southwest United States. — Desert Bighorn Council Trans. 25: 9–15.
- Simpson, C. D., Krysl, L. J. & Dickinson, T. G. 1980: Food habits of Barbary sheep in the Guadalupe Mountains, New Mexico. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 87–91. Texas Tech. Univ. Press, Lubbock.
- Simpson, C. D., Krysl, L. J., Hampy, D. B. & Gray, G. G. 1978: The Barbary sheep: a threat to desert bighorn survival. — Desert Bighorn Council Trans. 22: 26–31.
- Smith, A. B. 1992: Pastoralism in Africa. Origins and development ecology. — Hurst & Company, London.
- Solbert, A. G. K. 1980: Social organization and behaviour of aoudad (Ammotragus lervia Pallas) in Texas. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep: 66–72. Texas Tech. Univ. Press, Lubbock.
- Thenius, E. & Hofer, H. 1960: Stammesgeschichte der Säugetiere. — Springer Verlag, Berlin.
- Traweek, M. S. 1985: Statewide census of exotic big game animals. — Texas Parks Wildlife Dept., Fed. Aid Proj., W-109 (job no. 21).
- Trivers, R. L. & Willard, D. E. 1973: Natural selection of parental ability to vary the sex ratio. — Science 179: 90–92.
- Tumbleson, M. E., Middleton, C. C. & Wallach, J. D. 1970: Serum biochemic and hematologic parameters of adult aoudads (Ammotragus lervia) in captivity. — Lab. Anim. Care 20: 242–245.
- Valdez, R. & Bunch, T. D. 1980: Systematics of the Aoudad. — In: Simpson, C. D. (ed.), Symposium on ecology and management of Barbary sheep. — Texas Tech. Univ. Press, Lubbock: 27–29.
- Vaufrey, R. 1955: Préhistoire de l'Afrique. I. Le Maghreb. — Publ. Inst. Hautes Etudes Tunis, Masson, Paris 4: 1–435.
- Williams, G. C. 1979: The question of adaptive sex ratio in outcrossed vertebrates. — Proc. Roy. Soc. Lond., B 205: 567–580.
- Yeruham, I., Rosen, S., Hadani, A. & Nyska, A. 1996: Sarcoptic mange in wild ruminants in zoological gardens in Israel. — J. Wildl. Diseases 32: 57–61.
- Zuckerman, S. 1953: The breeding seasons of mammals in captivity. — Proc. zool. Soc. Lond. 122: 827–949.