**Spatial association in a highly inbred ungulate
population: Evidence of fine-scale kin recognition**

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ABSTRACT

We present the first evidence of fine-scale kin recognition, based on a continuous measure of relatedness, in ungulates. The spatial association between herdmates of a captive population of aoudad (*Ammotragus lervia*), where all the individuals are related, is analysed during resting time. Our goal is to estimate which factors influence individuals' associations. The study population is highly inbred, although it does not show serious deleterious effects caused by consanguinity. It comprises a single captive herd, reproducing freely and in good conditions for more than 10 years. It emerges that kin, measured as the coefficient of relationship between two given herdmates, is the main factor determining the spatial association (e.g., average distance) of male-male and female-female dyads, as more-related individuals tend to rest closer to each other than less-related ones. As for male-female dyads, individuals of a similar age tend to stay closer. In order to rule out any familiarity confounding effects, individuals' cohabitation time in the herd was added as a random factor in the analyses. Concerning the type of dyad, mother-calf dyads are characterized by higher proximity than others, particularly during the suckling period, whereas males tend to stay closer to each other than females or male-female dyads, being also more kin-related. Female social rank does not influence spatial association between herdmates. These results are related to group composition of the species in the wild, which are characterized by intense mother-calf bonds and all-male groups that are probably kin-related. It is seen that adult male-female associations are not related to kinship, but to age

similarity, which is in accord with the assumption that main family groups in the wild are formed by matrilineal lines, whereas males are the dispersing sex.

INTRODUCTION

Individual discrimination and individual recognition are two cognitive abilities evolved in animals, which allow them to recognise their conspecifics, according to different classes, such as species, group member, sex, age or reproductive status (Colgan 1983). Most animal societies are organized under dominance hierarchies (Scott 1962; Drews 1993), which has led individual recognition to reach a high level of accuracy, allowing individuals to discriminate the social ranks of their group mates (Barnard & Burk 1979; Gheusi et al. 1994). Kin recognition is the ability to identify relatives (see, e.g., Mateo 2003). It has been widely reported in many species (Fletcher & Michener 1987; Hepper 1991), and its adaptive significance is related to the practice of nepotism (a preferential treatment of kin), which enhances inclusive fitness (Hamilton 1963; Griffin & West 2002), and the prevention of undesirable matings with related conspecifics, according to the inbreeding avoidance theory (Bengtsson 1978; Harvey and Ralls 1986; Waser et al. 1986; Pusey & Wolf 1996). Although most of the studies devoted to this issue have focused on the recognition of discrete classes of kin, such as offspring or full siblings vs nonkin (see, e.g., Hepper 1991), the level of kin discrimination may be at a more refined level, as it has been recently observed in mice (Ryan & Lacy 2003).

The ability to recognize individual conspecifics in ungulates has been well acknowledged and described (see, e.g., Halpin 1991). It can be accomplished by means of visual cues (Lindsay & Fletcher 1968; Alexander 1977; Wolski et al. 1980; Kendrick & Baldwin 1987; Kendrick 1991), hearing and calls (Lindsay & Fletcher 1968; Espmark 1971; Poindron & Carrick 1976; Alexander 1977), and olfactory signatures (Wolski et al. 1980; Gubernick 1981a; Porter et al. 1991). Most ungulate societies are strongly dependent on the establishment and maintainability of dominance hierarchies, with well-developed individual recognition abilities (e.g., Rutberg 1983; Thompson 1993; Cassinello 1995).

The aoudad (*Ammotragus lervia*) is a North African caprid considered as vulnerable in its native lands (Caprinae Specialist Group 1996), although it has been successfully introduced in USA and Spain, where it is expanding its range (Cassinello 1998). The species has been poorly studied in the wild, and apart from a few studies carried out in USA, particularly in the 1980's (e.g., Simpson 1980), and more recently in Spain (Cassinello 2000; Cassinello et al. 2004, 2006), most of our knowledge of its behaviour comes from the same captive population analysed in this study (see Methods). The aoudad is a mountain caprid adapted to rugged terrains of the Saharan Desert and Sahel. Concerning aoudad group composition and dynamics (Cassinello 2000), nursery groups made up of adult females, subadults and calves, and male groups are common throughout most of the year. Mixed groups of adult males and females are basically formed in the mating season, although they can also be seen throughout the year in some populations (J. Cassinello, pers. obs.). The

reproduction rate is relatively high, females usually giving birth to a single calf, except for experienced, high-ranking and healthy females, which produce twins and in rare occasions triplets (see Cassinello & Alados 1996). Populations tend to expand their distribution when increasing in number, particularly in summer time (Simpson et al. 1978; Dickinson & Simpson 1980).

Aoudads seem quite tolerant of inbreeding, as practically no deleterious effects were found in this highly inbred population (Cassinello 1997a). A possible explanation may lie on the mountainous Saharan habitat the species has evolved. The aoudad lives in relatively isolated small herds, and although migration, particularly of males, is expected between familiar groups, the species has probably evolved under a certain genetic stress and developed some inbreeding tolerance (e.g., Waser et al. 1986; Crnokrak & Barrett 2002; see also Cassinello 2005). Given this, if yet high inbreeding levels may confer some disadvantages for the aoudad, we might expect the evolution of a mechanism to discriminate kin at a fine resolution in this species.

Resting or lying behaviour is the predominant activity in ungulates during the central part of the day, when rumination and sleeping take place (e.g., Pfeffer 1967). During resting, animals tend to stay closer to their herdmates, relatives or not, with whom they express a higher level of social association. Here we attempt to determine which factors affect spatial proximity, a measure of association (see Whitehead & Dufault 1999), in a highly inbred captive population of aoudads during resting time, and relate groups composition with group dynamics observed in the wild for the study species (Cassinello 2000).

We have focused our analysis on distances between individuals relative to a continuous measure of relatedness (Ryan & Lacy 2003), sex, age and social rank.

METHODS

The captive population of aoudads of this study has been subject to several behavioural studies since mid 1990's (Cassinello 1995, 1996; Cassinello & Alados 1996; Cassinello & Gomendio 1996; Cassinello 1997a, b, 2001, 2002). This population comes from just one male and one female captured in Western Sahara in 1975 and introduced at the Estación Experimental de Zonas Aridas (EEZA, CSIC), in Almería (Alados & Vericad 1993). Although the individuals' degree of inbreeding is extremely high in the study population, no severe deleterious effects have been apparent (Cassinello 1997a). 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, covered by rocky ground and bare soil used by the animals for sand bathing (see Haas 1959; Cassinello 2002). Apparently no resting place in the study enclosure provided advantages in terms of higher wind protection or less disturbance from the outside. The individuals were identified by means of colored plastic ear tags (Allflex Europe Ltd., Unit 6 - 8 Galalaw Business Park, Hawick, UK), some of them circular (Ø 28mm) and others rectangular (20x40mm). Birth date, sex, and identity of parents were known for each individual. The identity of the father was easily assessed, as there was only one reproductively active male in the herd (the

alpha male), and daily monitoring showed whether he was challenged and defeated by another male (e.g., Cassinello 1996). Social ranks were established for 16 adult females, which were the focal individuals used in previous behavioural studies (e.g., Cassinello 1995).

The exact knowledge of the study animals' kin relations, i.e., mother and fatherhood, allowed us to obtain the individuals' coefficients of inbreeding (F), calculated from the Additive Relationship method (Wright 1922; Ballou 1983), and the individuals' coefficients of relationship (COR, Falconer & Mackay 1996), calculated by means of a computer program (Pedigree © 1995-99 J.E. Seltzer). Individual F values in the study population are extremely high, ranging from 0.375 to 0.562. The COR of two given individuals is equivalent to the correlation between their breeding values. Its formulation is:

$$COR = \frac{2F_x}{\sqrt{(1 + F_y)(1 + F_z)}}$$

where F denotes the inbreeding coefficients of individuals x, y and z, being x the hypothetical offspring of individuals y and z. The COR is a measure of relationship that has a minimum value of zero and a maximum value of one. In the study population, it ranges from 0.57 to 0.85.

Our goal was to determine whether herdmates' associations while resting were related to COR, social rank, age similarity and/or sex. Sampling followed a routine detailed elsewhere, aimed at registering mother-infant behaviours (e.g., Cassinello 1996, 1997b). Thus, we visited the study site periodically from 17:00 and 20:00 h, when the activity of the animals was expected to be higher. In

those relatively few occasions that the whole herd was found at rest, animals' association was registered in detail. We established spatial proximity between individuals, a measure of association (for a review see Whitehead & Dufault 1999), by means of adult body-lengths. This measure is easy to estimate from the distance, regardless of the existence of reference points in the area (e.g., Lickliter 1984; Ralls et al. 1987; Weinrich 1991; Cassinello 1996). In order to estimate the average distance maintained between individuals, we distinguished up to 10 body-lengths. We also determined the percentage of occasions the dyads were registered at different distances: 0, 1, 2, and 3 or more body-lengths rates, the latter including all distances equal to or higher than 3 body-lengths, and referred to as 3+ distance rates later on. Merging of 3 and more body-lengths distances was done for convenience, because previous analyses showed that these distances give similar results to the analyses presented in this paper, and including more precise distances would lead to too many missing values. A total of 115 surveys were performed, in which 6,895 pair associations or dyads between 82 different individuals were registered (including individuals that died before the end of the study).

Animals' association in the study herd might also be caused by 'familiarity' or 'friendship' (e.g., Palombit et al. 1997), which is expected to be related to the time individuals live together. Thus, and to rule out any 'familiarity' effects on association causes, we calculated the time the two individuals of a given dyad have lived together in the study herd, and added this variable, cohabitation time, as a random effect on our analyses.

We used parametric, two tailed statistical tests (basically standard least squares models), and non-normal dependent variables were transformed following Zar (1984): values were log-transformed and proportions transformed into the arcsine of their square root. All R^2 shown are adjusted. To assess suckling/weaning differences and female social ranks effects, we calculated mean monthly distances for the individual dyads, and used the identity of dyads as a random effect in Mixed Analyses of Variance to prevent pseudoreplication (Hurlbert 1984). Dyads which had an individual in common were considered as independent, because previous analyses of intra and inter-group variation through one-way ANOVAs showed no significant differences for all the response variables (e.g., average distance: $F_{1,1312}=1.93$, $p=0.16$; 0 distance rate: $F_{1,1312}=1.36$, $p=0.24$). Non-significant results have been considered sufficiently powerful when they have been obtained from high sample sizes and yield high levels of probability of non-rejecting H_0 (see Johnsson 1996; cf. Thomas & Juanes 1996). The statistical package used was JMP 6.0.3 (SAS Institute Inc.).

RESULTS

Association distances according to the type of dyad

Firstly, we determined whether each type of dyad showed different average distances. The Analyses of Variance showed that mother-calf dyads tend to rest at the shortest distance, followed by male-male dyads; whereas no differences

were found between male-female and female-female dyads, which were registered at the longest distances (see Table 1 and Fig. 1).

Coefficient of Relationship, Age and Proximity

We tested whether COR values and age difference between the two individuals of a given dyad were related to individuals' association, measured as the average distances maintained by individuals while resting as well as 0, 1, 2 and 3+ distance rates. Cohabitation time between the individuals of the dyads was added in the model as a random effect to control for any 'familiarity' effect. Mother-infant dyads were excluded from the analyses.

Sex composition of dyads significantly interacted with COR and age difference on proximity, and post-hoc analyses showed that the effect of these factors differed for male-female in relation to the rest of sex associations. According to this, we repeated the analyses pooling male-male and female-female dyads. Standard least squares models revealed that high COR values are associated to short distances in male-male and female-female dyads (see Figure 2), whereas male-female dyads closeness depends on age similarity (see Table 2).

Motherhood and Proximity

Mother-calf dyads stay significantly closer to each other in comparison to other dyad types ($F_{1,1312} = 73.28$, $p < 0.0001$; see also Table 1). Zero distance rate

was significantly higher in mother-calf dyads, too ($F_{1,1312} = 168.24$, $p < 0.0001$). No differences were found between dyads in 1 distance rate ($F_{1,1312} = 1.46$, $p = 0.23$). Both 2 and 3+ distance rates were lower in mother-calf dyads than in the other dyads ($F_{1,1312} = 8.39$, $p = 0.004$, and $F_{1,1312} = 14.99$, $p = 0.0001$, respectively). No calf sex differences were appreciated.

Regarding mother-calf dyads during and after suckling period, it appeared that weaned calves no longer show such close bond to their mothers, as they stayed at a further mean distance ($F_{1,105.8} = 32.15$, $p < 0.0001$, where the individual dyads were entered as a random factor in the model).

Female Social Rank and Proximity

In female-female dyads of known social ranks, we tested whether rank similarity influences spatial association. No significant result was obtained; e.g., simple regression with average distance: $n = 516$, $R^2 = 0.04$, $F_{1,156.2} = 0.91$, $p = 0.34$. In adult male-female dyads of known female social ranks, we tested whether higher ranks are related to spatial association. No significant result was obtained; e.g., simple regression with average distance: $n = 96$, $R^2 = -0.36$, $F_{1,83.27} = 0.27$, $p = 0.60$. Finally, in mother-infant dyads, we neither found differences in spatial association patterns according to maternal rank and the sex of the offspring (ANCOVA for average distance: calf sex as factor, $F_{1,13.59} = 0.002$, $p = 0.96$; maternal rank as covariant, $F_{1,20.53} = 0.49$, $p = 0.49$; interaction term, $F_{1,20.53} = 0.15$, $p = 0.71$); however, this last analysis should be taken with caution, due to the small sample size and values obtained for effect size and

confidence intervals (see Thompson 2002; Nakagawa & Foster 2004). When carrying out these analyses, the individual dyads identification was used as a random factor to prevent pseudoreplication (Hurlbert 1984).

DISCUSSION

This study deals with factors determining individual spatial associations in a captive population of aoudads, subject to a high degree of inbreeding. Despite all the herdmates being genetically related, it emerges that individuals organize in the space through familiarity and kin bonds, which suggests that individuals are able to discriminate close relatives at a very small scale.

We have investigated individuals' spatial association while the study herd was at rest because that was the only occasion when we were able to identify all the individuals properly, and calculate distances maintained between them at a given time. Our previous knowledge of the behaviour of the study population, where focal samples were carried out periodically, indicates that individuals' association does not vary essentially in other contexts (J. Cassinello, unpub. data), such as feeding behaviour, when social groups were clearly identified (Cassinello 2002), resembling the associations also identified in this study.

It is also interesting to note that, given that no resting place in the study enclosure provided apparent advantages for the animals, and therefore no costs would be associated to resting places, we might postulate that when costs and benefits become weaker, the expected fitness benefits of bond associations

would temper and the associations observed would not reflect individuals bonds as stronger as in other contexts, where costs and benefits are clearly involved, such as foraging in the troughs. This might, perhaps, account for the low variance explained in our results, which can also be a consequence of the low range of COR values in the study population, only a 28% of the maximum range (see, e.g., Lane 2007 on interpreting variance explained).

Our results show that spatial proximity between two given individuals in the aoudad is determined by the coefficient of relationship, provided dyads are of the same sex (male-male and female-female), and by the age difference in male-female dyads. The higher their relatedness and age similarity, the smaller the individuals' proximity. To our knowledge, this is the first evidence of fine-scale kin recognition, based on a continuous measure of relatedness, in ungulates. Indeed, most of the empirical studies dealing with kin recognition in animals have distinguished a few discrete classes of relatedness (Herper 1991), e.g., first order relatives (offspring, siblings), second order relatives (aunts/uncles, half-siblings), and non-relatives (the rest of the population). There are also a few studies on kin recognition dealing with first-cousins (e.g., Bateson 1982; Keane 1990). Recently, Ryan & Lacy (2003) carried out a fine study in oldfield mice (*Peromyscus polionotus*) using a continuous measure of kinship, as we have done here. These authors found that male mice are able to bias their behaviour towards conspecifics according to very small differences in their kinship (Ibid.).

320 This high ability of the aoudad to discriminate between close relatives,
321 even under a marked degree of inbreeding, may reflect that their social units in
322 the wild are mainly driven by genetic relatedness, being also genetic units (see
323 Archie et al. 2006). The species shows practically an absence of phenotypic
324 evidence of inbreeding depression (Cassinello 1997a), which might result from
325 a history of purging of genetic load, where local populations are small and
326 undergo disequilibrium gene dynamics (Duarte et al. 2003). It could also be the
327 case that the study population is able to cope with a certain degree of
328 inbreeding, while attaining an optimal level of inbreeding-outbreeding (Hoogland
329 1992).

330
331 It is interesting that male-female dyads, on the contrary, stay closer
332 depending exclusively on their age similarity, and not on their genetic
333 relatedness. This might be related to the fact that, in the wild, it is assumed that
334 male aoudad is the dispersing sex (Barrett 1980; Dickinson & Simpson 1980),
335 whereas philopatric family groups are probably formed by related females, a
336 group dynamic observed in various ungulate species (e.g., Clutton-Brock et al.
337 1982; Green et al. 1989), and which in the aoudad would be supported by a
338 hypothesized inheritance of maternal rank by daughters (Cassinello 1995).
339 Under such a behavioural pattern, kin-related spatial association between
340 males and females would not have evolved in the study species.

341
342 As expected, and on average, mother-calf dyads stay closer than other
343 dyad types. This relates to the distinctive strong bonds occurring between
344 mothers and infants in ungulates during the lactating period (Lent 1974;

Gubernick 1981b). Once weaning has taken place, mother-calf attachment loosens (Cassinello 1997b), and it is also reflected here, as weaned calves stay at a further mean distance from their mothers than lactating ones. No calf sex differences have been found, i.e., both sons and daughters show similar strong maternal bonds in terms of spatial association. This measure of association could be considered a form of maternal care with no apparent costs, which happens not to be related either to maternal rank nor calf sex, contrary to the sex-biased maternal investment observed in this species (Cassinello 1996).

Our results also show that male-male dyads are characterized by a higher spatial association than female-female and male-female ones. This might resemble the bachelor groups than can be seen in the wild, probably made up of related adult males in search of new territories, while leaving apart their parental herds (Dickinson & Simpson 1980). There are a series of costs associated with dispersal, such as moving to unfavourable habitats or increasing predators encounters (Greenwood 1980; Waser & Jones 1983; Pusey & Packer 1987). Thus, if dispersing groups are made up of related individuals, reciprocal cooperation may be favoured (see Trivers 1971; Axelrod & Hamilton 1981), which would confer inclusive fitness advantages to the members of the group. It would be interesting to test this in the field, comparing the behaviour of dispersing aoudad groups of dissimilar kinship.

The hierarchical status of the adult females does not relate to spatial association in the aoudad. Although these analyses were made using a small sample size, it is not surprising that resting behaviour was not ruled by social

ranks. A high social status confer priority access to limited or critical resources (e.g., Appleby 1980; Drews 1993), however, to our view, the study enclosure did not have any particularly protected or more comfortable resting sites, which would be appealing to the animals and, thus, prone to be controlled by high-ranking individuals. Finally, as mature males (older than 3 years) show a higher social status than any adult female (Cassinello 1995), we tested whether adult male-female association is relaxed according to female rank. No relationship was found, evidencing that high social status in females does not confer closer spatial association with adult males in the aoudad.

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572

573 Table 1. Analyses of variance for the average distance and four distance rates
574 maintained by herdmates, according to the type of dyad. The comparison for
575 each pair was accomplished by a Student's t test. Dyad type key: MC = mother-
576 calf, MM = male-male, MF = male-female, FF = female-female. Dyad type
577 differences are shown in a decreasing order, with significant differences
578 denoted by a 'higher than' (>) sign, and no differences by an 'equal' (=) sign.
579 Sample size is n = 1314 dyads.

Dependent variable	F value	p value	Dyad type differences	Pair comparison p values
Average distance	$F_{3,1310} = 34.95$	< 0.0001	(FF = MF) > MM > MC	< 0.0001
0 distance rate	$F_{3,1310} = 59.87$	< 0.0001	MC > MM > (MF = FF)	< 0.006
1 distance rate	$F_{3,1310} = 3.40$	0.02	MM > (FF = MF = MC)	< 0.04
2 distance rate	$F_{3,1310} = 4.28$	0.005	(FF = MF = MM) > MC	< 0.02
3+ distance rate	$F_{3,1310} = 10.47$	< 0.0001	(FF = MF) > MM > MC	< 0.01

580

581

Table 2. Summary of standard least squares models for the average distance and four distance rates maintained by herdmates (dyads), according to two independent variables, their Coefficients of Relationship (COR) values and age difference in the study aoudad population. Herdmates' cohabitation time in the enclosure was added as a random effect. Male-female dyads were differentiated from male-male and female-female dyads. Sample size is n = 1291 dyads. ns = non-significant relation.

Male-female dyads					
Dependent variable	R ²	Independent variables	F value	p value	Relation sign
Average distance	0.056	COR	F _{1,588} = 0.01	0.92	ns
		Age difference	F _{1,587.8} = 12.31	0.0005	Positive
0 distance rate	0.041	COR	F _{1,586.8} = 2.75	0.10	ns
		Age difference	F _{1,588} = 14.64	0.0001	Negative
1 distance rate	0.005	COR	F _{1,455.3} = 1.38	0.24	ns
		Age difference	F _{1,547.2} = 1.41	0.24	ns
2 distance rate	0.010	COR	F _{1,584.1} = 0.52	0.47	ns
		Age difference	F _{1,587.6} = 2.58	0.11	ns
3+ distance rate	0.050	COR	F _{1,587.9} = 1.18	0.28	ns
		Age difference	F _{1,587.6} = 3.23	0.07	ns

Male-male and female-female dyads					
Dependent variable	R ²	Independent variables	F value	p value	Relation sign
Average distance	0.067	COR	F _{1,696.9} = 29.48	< 0.0001	Negative
		Age difference	F _{1,692.8} = 1.95	0.16	Ns
0 distance rate	0.030	COR	F _{1,695.3} = 7.54	0.01	Positive
		Age difference	F _{1,680} = 2.89	0.09	Ns
1 distance rate	0.017	COR	F _{1,696.2} = 5.38	0.02	Positive
		Age difference	F _{1,686.3} = 0.18	0.67	Ns
2 distance rate	-0.001	COR	F _{1,559.1} = 0.02	0.90	Ns
		Age difference	F _{1,290.4} = 0.26	0.61	Ns
3+ distance rate	0.054	COR	F _{1,697} = 19.89	< 0.0001	Negative
		Age difference	F _{1,694.1} = 1.43	0.23	ns

FIGURE LEGENDS

Figure 1. Average ($\pm$ SE) distance (in body-lengths) and average ($\pm$ SE) distances rates maintained by the different dyad types included in the analyses.

Figure 2. Relationship between average distance and COR values for male-male and female-female dyads.

FIGURE 1

FIGURE 2