1 # Spatial association in a highly inbred ungulate

2 # population: Evidence of fine-scale kin recognition

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25 ABSTRACT

26

27 We present the first evidence of fine-scale kin recognition, based on a

28 continuous measure of relatedness, in ungulates. The spatial association

29 between herdmates of a captive population of aoudad (*Ammotragus lervia*),

30 where all the individuals are related, is analysed during resting time. Our goal is

31 to estimate which factors influence individuals' associations. The study

32 population is highly inbred, although it does not show serious deleterious effects

33 caused by consanguinity. It comprises a single captive herd, reproducing freely

34 and in good conditions for more than 10 years. It emerges that kin, measured

35 as the coefficient of relationship between two given herdmates, is the main

36 factor determining the spatial association (e.g., average distance) of male-male

37 and female-female dyads, as more-related individuals tend to rest closer to

38 each other than less-related ones. As for male-female dyads, individuals of a

39 similar age tend to stay closer. In order to rule out any familiarity confounding

40 effects, individuals' cohabitation time in the herd was added as a random factor

41 in the analyses. Concerning the type of dyad, mother-calf dyads are

42 characterized by higher proximity than others, particularly during the suckling

43 period, whereas males tend to stay closer to each other than females or male-

44 female dyads, being also more kin-related. Female social rank does not

45 influence spatial association between herdmates. These results are related to

46 group composition of the species in the wild, which are characterized by intense

47 mother-calf bonds and all-male groups that are probably kin-related. It is seen

48 that adult male-female associations are not related to kinship, but to age

49   similarity, which is in accord with the assumption that main familiy groups in the

50   wild are formed by matrilineal lines, whereas males are the dispersing sex.

51

52   INTRODUCTION

53

54   Individual discrimination and individual recognition are two cognitive abilities

55   evolved in animals, which allow them to recognise their conspecifics, according

56   to different classes, such as species, group member, sex, age or reproductive

57   status (Colgan 1983). Most animal societies are organized under dominance

58   hierarchies (Scott 1962; Drews 1993), which has led individual recognition to

59   reach a high level of accuracy, allowing individuals to discriminate the social

60   ranks of their group mates (Barnard & Burk 1979; Gheusi et al. 1994). Kin

61   recognition is the ability to identify relatives (see, e.g., Mateo 2003). It has been

62   widely reported in many species (Fletcher & Michener 1987; Hepper 1991), and

63   its adaptive significance is related to the practice of nepotism (a preferential

64   treatment of kin), which enhances inclusive fitness (Hamilton 1963; Griffin &

65   West 2002), and the prevention of undesirable matings with related

66   conspecifics, according to the inbreeding avoidance theory (Bengtsson 1978;

67   Harvey and Ralls 1986; Waser et al. 1986; Pusey & Wolf 1996). Although most

68   of the studies devoted to this issue have focused on the recognition of discrete

69   classes of kin, such as offspring or full siblings vs nonkin (see, e.g., Hepper

70   1991), the level of kin discrimination may be at a more refined level, as it has

71   been recently observed in mice (Ryan & Lacy 2003).

72

73   The ability to recognize individual conspecifics in ungulates has been

74   well acknowledged and described (see, e.g., Halpin 1991). It can be

75   accomplished by means of visual cues (Lindsay & Fletcher 1968; Alexander

76   1977; Wolski et al. 1980; Kendrick & Baldwin 1987; Kendrick 1991), hearing

77   and calls (Lindsay & Fletcher 1968; Espmark 1971; Poindron & Carrick 1976;

78   Alexander 1977), and olfactory signatures (Wolski et al. 1980; Gubernick

79   1981a; Porter et al. 1991). Most ungulate societies are strongly dependent on

80   the establishment and maintainability of dominance hierarchies, with well-

81   developed individual recognition abilities (e.g., Rutberg 1983; Thompson 1993;

82   Cassinello 1995).

83

84   The aoudad (*Ammotragus lervia*) is a North African caprid considered as

85   vulnerable in its native lands (Caprinae Specialist Group 1996), although it has

86   been successfully introduced in USA and Spain, where it is expanding its range

87   (Cassinello 1998). The species has been poorly studied in the wild, and apart

88   from a few studies carried out in USA, particularly in the 1980's (e.g., Simpson

89   1980), and more recently in Spain (Cassinello 2000; Cassinello et al. 2004,

90   2006), most of our knowledge of its behaviour comes from the same captive

91   population analysed in this study (see Methods). The aoudad is a mountain

92   caprid adapted to rugged terrains of the Saharan Desert and Sahel. Concerning

93   aoudad group composition and dynamics (Cassinello 2000), nursery groups

94   made up of adult females, subadults and calves, and male groups are common

95   throughout most of the year. Mixed groups of adult males and females are

96   basically formed in the mating season, although they can also be seen

97   throughout the year in some populations (J. Cassinello, pers. obs.). The

4

98   reproduction rate is relatively high, females usually giving birth to a single calf,

99   except for experienced, high-ranking and healthy females, which produce twins

100   and in rare occasions triplets (see Cassinello & Alados 1996). Populations tend

101   to expand their distribution when increasing in number, particularly in summer

102   time (Simpson et al. 1978; Dickinson & Simpson 1980).

103

104   Aoudads seem quite tolerant of inbreeding, as practically no deleterious

105   effects were found in this highly inbred population (Cassinello 1997a). A

106   possible explanation may lie on the mountainous Saharan habitat the species

107   has evolved. The aoudad lives in relatively isolated small herds, and although

108   migration, particularly of males, is expected between familiar groups, the

109   species has probably evolved under a certain genetic stress and developed

110   some inbreeding tolerance (e.g., Waser et al. 1986; Crnokrak & Barrett 2002;

111   see also Cassinello 2005). Given this, if yet high inbreeding levels may confer

112   some disadvantages for the aoudad, we might expect the evolution of a

113   mechanism to discriminate kin at a fine resolution in this species.

114

115   Resting or lying behaviour is the predominant activity in ungulates during

116   the central part of the day, when rumination and sleeping take place (e.g.,

117   Pfeffer 1967). During resting, animals tend to stay closer to their herdmates,

118   relatives or not, with whom they express a higher level of social association.

119   Here we attempt to determine which factors affect spatial proximity, a measure

120   of association (see Whitehead & Dufault 1999), in a highly inbred captive

121   population of aoudads during resting time, and relate groups composition with

122   group dynamics observed in the wild for the study species (Cassinello 2000).

123 We have focused our analysis on distances between individuals relative to a

124 continuous measure of relatedness (Ryan & Lacy 2003), sex, age and social

125 rank.

126

127   METHODS

128

129 The captive population of aoudads of this study has been subject to several

130 behavioural studies since mid 1990's (Cassinello 1995, 1996; Cassinello &

131 Alados 1996; Cassinello & Gomendio 1996; Cassinello 1997a, b, 2001, 2002).

132 This population comes from just one male and one female captured in Western

133 Sahara in 1975 and introduced at the Estación Experimental de Zonas Aridas

134 (EEZA, CSIC), in Almería (Alados & Vericad 1993). Although the individuals'

135 degree of inbreeding is extremely high in the study population, no severe

136 deleterious effects have been apparent (Cassinello 1997a). Sampling was

137 carried out from 1990 to 1992 in a herd made up of 17 males and 26 females at

138 the beginning of the study, and 33 males and 43 females at the end of it. The

139 study group was housed in a 950 m^2 enclosure, covered by rocky ground and

140 bare soil used by the animals for sand bathing (see Haas 1959; Cassinello

141 2002). Apparently no resting place in the study enclosure provided advantages

142 in terms of higher wind protection or less disturbance from the outside. The

143 individuals were identified by means of colored plastic ear tags (Allflex Europe

144 Ltd., Unit 6 - 8 Galalaw Business Park, Hawick, UK), some of them circular (Ø

145 28mm) and others rectangular (20x40mm). Birth date, sex, and identity of

146 parents were known for each individual. The identity of the father was easily

147 assessed, as there was only one reproductively active male in the herd (the

148   alpha male), and daily monitoring showed whether he was challenged and

149   defeated by another male (e.g., Cassinello 1996). Social ranks were established

150   for 16 adult females, which were the focal individuals used in previous

151   behavioural studies (e.g., Cassinello 1995).

152

153   The exact knowledge of the study animals' kin relations, i.e., mother and

154   fatherhood, allowed us to obtain the individuals' coefficients of inbreeding (F),

155   calculated from the Additive Relationship method (Wright 1922; Ballou 1983),

156   and the individuals' coefficients of relationship (COR, Falconer & Mackay 1996),

157   calculated by means of a computer program (Pedigree © 1995-99 J.E. Seltzer).

158   Individual F values in the study population are extremely high, ranging from

159   0.375 to 0.562. The COR of two given individuals is equivalent to the correlation

160   between their breeding values. Its formulation is:

161
$$COR = \frac{2F_x}{\sqrt{\left(1+F_y\right)\left(1+F_z\right)}}$$

162   where F denotes the inbreeding coefficients of individuals x, y and z, being x the

163   hypothetical offspring of individuals y and z. The COR is a measure of

164   relationship that has a minimum value of zero and a maximum value of one. In

165   the study population, it ranges from 0.57 to 0.85.

166

167   Our goal was to determine whether herdmates' associations while resting

168   were related to COR, social rank, age similarity and/or sex. Sampling followed a

169   routine detailed elsewhere, aimed at registering mother-infant behaviours (e.g.,

170   Cassinello 1996, 1997b). Thus, we visited the study site periodically from 17:00

171   and 20:00 h, when the activity of the animals was expected to be higher. In

172 those relatively few occasions that the whole herd was found at rest, animals'

173 association was registered in detail. We established spatial proximity between

174 individuals, a measure of association (for a review see Whitehead & Dufault

175 1999), by means of adult body-lengths. This measure is easy to estimate from

176 the distance, regardless of the existence of reference points in the area (e.g.,

177 Lickliter 1984; Ralls et al. 1987; Weinrich 1991; Cassinello 1996). In order to

178 estimate the average distance maintained between individuals, we

179 distinguished up to 10 body-lengths. We also determined the percentage of

180 occasions the dyads were registered at different distances: 0, 1, 2, and 3 or

181 more body-lengths rates, the latter including all distances equal to or higher

182 than 3 body-lengths, and referred to as 3+ distance rates later on. Merging of 3

183 and more body-lengths distances was done for convenience, because previous

184 analyses showed that these distances give similar results to the analyses

185 presented in this paper, and including more precise distances would lead to too

186 many missing values. A total of 115 surveys were performed, in which 6,895

187 pair associations or dyads between 82 different individuals were registered

188 (including individuals that died before the end of the study).

189

190   Animals' association in the study herd might also be caused by

191 'familiarity' or 'friendship' (e.g., Palombit et al. 1997), which is expected to be

192 related to the time individuals live together. Thus, and to rule out any 'familiarity'

193 effects on association causes, we calculated the time the two individuals of a

194 given dyad have lived together in the study herd, and added this variable,

195 cohabitation time, as a random effect on our analyses.

196

197   We used parametric, two tailed statistical tests (basically standard least

198   squares models), and non-normal dependent variables were transformed

199   following Zar (1984): values were log-transformed and proportions transformed

200   into the arcsine of their square root. All R^2 shown are adjusted. To assess

201   suckling/weaning differences and female social ranks effects, we calculated

202   mean monthly distances for the individual dyads, and used the identity of dyads

203   as a random effect in Mixed Analyses of Variance to prevent pseudoreplication

204   (Hurlbert 1984). Dyads which had an individual in common were considered as

205   independent, because previous analyses of intra and inter-group variation

206   through one-way ANOVAs showed no significant differences for all the

207   response variables (e.g., average distance: $F_{1,1312}$=1.93, p=0.16; 0 distance

208   rate: $F_{1,1312}$=1.36, p=0.24). Non-significant results have been considered

209   sufficiently powerful when they have been obtained from high sample sizes and

210   yield high levels of probability of non-rejecting H_0 (see Johnsson 1996; cf.

211   Thomas & Juanes 1996). The statistical package used was JMP 6.0.3 (SAS

212   Institute Inc.).

213

214   RESULTS

215

216   <u>Association distances according to the type of dyad</u>

217

218   Firstly, we determined whether each type of dyad showed different average

219   distances. The Analyses of Variance showed that mother-calf dyads tend to rest

220   at the shortest distance, followed by male-male dyads; whereas no differences

221   were found between male-female and female-female dyads, which were

222   registered at the longest distances (see Table 1 and Fig. 1).

223

224   <u>Coefficient of Relationship, Age and Proximity</u>

225

226   We tested whether COR values and age difference between the two individuals

227   of a given dyad were related to individuals' association, measured as the

228   average distances maintained by individuals while resting as well as 0, 1, 2 and

229   3+ distance rates. Cohabitation time between the individuals of the dyads was

230   added in the model as a random effect to control for any 'familiarity' effect.

231   Mother-infant dyads were excluded from the analyses.

232

233   Sex composition of dyads significantly interacted with COR and age difference

234   on proximity, and post-hoc analyses showed that the effect of these factors

235   differed for male-female in relation to the rest of sex associations. According to

236   this, we repeated the analyses pooling male-male and female-female dyads.

237   Standard least squares models revealed that high COR values are associated

238   to short distances in male-male and female-female dyads (see Figure 2),

239   whereas male-female dyads closeness depends on age simillarity (see Table

240   2).

241

242   <u>Motherhood and Proximity</u>

243

244   Mother-calf dyads stay significantly closer to each other in comparison to other

245   dyad types ($F_{1,1312} = 73.28$, $p < 0.0001$; see also Table 1). Zero distance rate

246 was significantly higher in mother-calf dyads, too ($F_{1,1312}$ = 168.24, p < 0.0001).

247 No differences were found between dyads in 1 distance rate ($F_{1,1312}$ = 1.46, p =

248 0.23). Both 2 and 3+ distance rates were lower in mother-calf dyads than in the

249 other dyads ($F_{1,1312}$ = 8.39, p = 0.004, and $F_{1,1312}$ = 14.99, p = 0.0001,

250 respectively). No calf sex differences were appreciated.

251

252   Regarding mother-calf dyads during and after suckling period, it

253 appeared that weaned calves no longer show such close bond to their mothers,

254 as they stayed at a further mean distance ($F_{1,105.8}$ = 32.15, p < 0.0001, where

255 the individual dyads were entered as a random factor in the model).

256

257 <u>Female Social Rank and Proximity</u>

258

259 In female-female dyads of known social ranks, we tested whether rank similarity

260 influences spatial association. No significant result was obtained; e.g., simple

261 regression with average distance: n = 516, R^2 = 0.04, $F_{1,156.2}$ = 0.91, p = 0.34. In

262 adult male-female dyads of known female social ranks, we tested whether

263 higher ranks are related to spatial association. No significant result was

264 obtained; e.g., simple regression with average distance: n = 96, R^2 = -0.36,

265 $F_{1,83.27}$ = 0.27, p = 0.60. Finally, in mother-infant dyads, we neither found

266 differences in spatial association patterns according to maternal rank and the

267 sex of the offspring (ANCOVA for average distance: calf sex as factor, $F_{1,13.59}$ =

268 0.002, p = 0.96; maternal rank as covariant, $F_{1,20.53}$ = 0.49, p = 0.49; interaction

269 term, $F_{1,20.53}$ = 0.15, p = 0.71); however, this last analysis should be taken with

270 caution, due to the small sample size and values obtained for effect size and

271 confidence intervals (see Thompson 2002; Nakagawa & Foster 2004). When

272 carrying out these analyses, the individual dyads identification was used as a

273 random factor to prevent pseudoreplication (Hurlbert 1984).

274

275   DISCUSSION

276

277 This study deals with factors determining individual spatial associations in a

278 captive population of aoudads, subject to a high degree of inbreeding. Despite

279 all the herdmates being genetically related, it emerges that individuals organize

280 in the space through familiarity and kin bonds, which suggests that individuals

281 are able to discriminate close relatives at a very small scale.

282

283   We have investigated individuals' spatial association while the study herd

284 was at rest because that was the only occasion when we were able to identify

285 all the individuals properly, and calculate distances maintained between them at

286 a given time. Our previous knowledge of the behaviour of the study population,

287 where focal samples were carried out periodically, indicates that individuals'

288 association does not vary essentially in other contexts (J. Cassinello, unpub.

289 data), such as feeding behaviour, when social groups were clearly identified

290 (Cassinello 2002), resembling the associations also identified in this study.

291

292   It is also interesting to note that, given that no resting place in the study

293 enclosure provided apparent advantages for the animals, and therefore no

294 costs would be associated to resting places, we might postulate that when costs

295 and benefits become weaker, the expected fitness benefits of bond associations

296 would temper and the associations observed would not reflect individuals bonds

297 as stronger as in other contexts, where costs and benefits are clearly involved,

298 such as foraging in the troughs. This might, perhaps, account for the low

299 variance explained in our results, which can also be a consequence of the low

300 range of COR values in the study population, only a 28% of the maximum range

301 (see, e.g., Lane 2007 on interpreting variance explained).

302

303 Our results show that spatial proximity between two given individuals in

304 the aoudad is determined by the coefficient of relationship, provided dyads are

305 of the same sex (male-male and female-female), and by the age difference in

306 male-female dyads. The higher their relatedness and age similarity, the smaller

307 the individuals' proximity. To our knowledge, this is the first evidence of fine-

308 scale kin recognition, based on a continuous measure of relatedness, in

309 ungulates. Indeed, most of the empirical studies dealing with kin recognition in

310 animals have distinguished a few discrete classes of relatedness (Herper 1991),

311 e.g., first order relatives (offspring, siblings), second order relatives

312 (aunts/uncles, half-siblings), and non-relatives (the rest of the population).

313 There are also a few studies on kin recognition dealing with first-cousins (e.g.,

314 Bateson 1982; Keane 1990). Recently, Ryan & Lacy (2003) carried out a fine

315 study in oldfield mice (*Peromyscus polionotus*) using a continuous measure of

316 kinship, as we have done here. These authors found that male mice are able to

317 bias their behaviour towards conspecifics according to very small differences in

318 their kinship (Ibid.).

319

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;

345   Gubernick 1981b). Once weaning has taken place, mother-calf attachment

346   loosens (Cassinello 1997b), and it is also reflected here, as weaned calves stay

347   at a further mean distance from their mothers than lactating ones. No calf sex

348   differences have been found, i.e., both sons and daughters show similar strong

349   maternal bonds in terms of spatial association. This measure of association

350   could be considered a form of maternal care with no apparent costs, which

351   happens not to be related either to maternal rank nor calf sex, contrary to the

352   sex-biased maternal investment observed in this species (Cassinello 1996).

353

354   Our results also show that male-male dyads are characterized by a

355   higher spatial association than female-female and male-female ones. This might

356   resemble the bachelor groups than can be seen in the wild, probably made up

357   of related adult males in search of new territories, while leaving apart their

358   parental herds (Dickinson & Simpson 1980). There are a series of costs

359   associated with dispersal, such as moving to unfavourable habitats or

360   increasing predators encounters (Greenwood 1980; Waser & Jones 1983;

361   Pusey & Packer 1987). Thus, if dispersing groups are made up of related

362   individuals, reciprocal cooperation may be favoured (see Trivers 1971; Axelrod

363   & Hamilton 1981), which would confer inclusive fitness advantages to the

364   members of the group. It would be interesting to test this in the field, comparing

365   the behaviour of dispersing aoudad groups of dissimilar kinship.

366

367   The hierarchical status of the adult females does not relate to spatial

368   association in the aoudad. Although these analyses were made using a small

369   sample size, it is not surprising that resting behaviour was not ruled by social

370 ranks. A high social status confer priority access to limited or critical resources

371 (e.g., Appleby 1980; Drews 1993), however, to our view, the study enclosure

372 did not have any particularly protected or more comfortable resting sites, which

373 would be appealing to the animals and, thus, prone to be controlled by high-

374 ranking individuals. Finally, as mature males (older than 3 years) show a higher

375 social status than any adult female (Cassinello 1995), we tested whether adult

376 male-female association is relaxed according to female rank. No relationship

377 was found, evidencing that high social status in females does not confer closer

378 spatial association with adult males in the aoudad.

379

380   ACKNOWLEDGEMENTS

381

388

389   LITERATURE CITED

390

391 Alados, C. L. & Vericad, J. R. 1993. Aoudad. *Ammotragus lervia* from Western-

392   Sahara. International Studbook. Bol. Inst. Est. Almer. Ciencias **11/12**, 65-97.

393 Alexander, G. 1977. Role of auditory and visual cues in mutual recognition

394   between ewes and lambs in Merino sheep. Appl. Anim. Ethol. **3**, 65-81.

395 Appleby, M. C. 1980. Social rank and food access in red deer stags. Behaviour

396   **74**, 294–309.

397 Archie, E. A., Moss, C. J. & Alberts, S. C. 2006. The ties that bind: Genetic

398   relatedness predicts the fission and fusion of social groups in wild African

399   elephants. Proc. R. Soc. Lond. B **273**, 513-522.

400 Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. Science **211**,

401   1390-1396.

402 Ballou, J. 1983. Calculating Inbreeding Coefficients From Pedigrees. In:

403   Genetics and Conservation: A Reference for Managing Wild Animal and

404   Plant Populations (Schonewald-Cox, C. M., Chambers, S. M., MacBryde, B.

405   & Thomas, L., eds). Benjamin/Cummins Publishing Co., London, pp. 509-

406   520.

407 Barnard, C. J. & Burk, T. 1979. Dominance hierarchies and the evolution of

408   'individual recognition'. J. theor. Biol. **81**, 65-73.

409 Barrett, R. H. 1980. History of the Hearst Ranch Barbary Sheep Herd. In:

410   Symposium on Ecology and Management of Barbary Sheep (Simpson, C. D.,

411   ed). Texas Tech University Press, Lubbock, pp. 46-50.

412 Bateson, P. 1982. Preferences for cousins in Japanese quail. Nature **295**, 236-

413   237.

414 Bengtsson, B. O. 1978. Avoiding inbreeding: at what cost? J. theor. Biol. **73**,

415   439-444.

416 Caprinae Specialist Group 1996. *Ammotragus lervia*. In: IUCN 2006. 2006

417   IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded

418   on 28 June 2007.

419   Cassinello, J. 1995. Factors modifying female social ranks in *Ammotragus*.

420   Appl. Anim. Behav. Sci. **45**, 175-180.

421   Cassinello, J. 1996. High ranking females bias their investment in favour of

422   male calves in captive *Ammotragus lervia*. Behav. Ecol. Sociobiol. **38**, 417-

423   424.

424   Cassinello, J. 1997a. High levels of inbreeding in captive *Ammotragus lervia*

425   (Bovidae, Artiodactyla): Effects on phenotypic variables. Can. J. Zool. **75**,

426   1707-1713.

427   Cassinello, J. 1997b. Mother-offspring conflict in the Saharan arrui,

428   *Ammotragus lervia sahariensis*: Relation to weaning and mother's sexual

429   activity. Ethology **103**, 127-137.

430   Cassinello, J. 1998. *Ammotragus lervia*: a review on systematics, biology,

431   ecology and distribution. Ann. Zool. Fen. **35**, 149-162.

432   Cassinello, J. 2000. *Ammotragus* free-ranging population in the south east of

433   Spain: a necessary first account. Biodivers. Conserv. **9**, 887-900.

434   Cassinello, J. 2001. Offspring grazing and suckling rates in a sexually dimorphic

435   ungulate with biased maternal investment (*Ammotragus lervia*). Ethology

436   **107**, 173-182.

437   Cassinello, J. 2002. Food access in captive *Ammotragus*: The role played by

438   hierarchy and mother-infant interactions. Zoo Biol. **21**, 597-605.

439   Cassinello, J. 2005. Inbreeding depression on reproductive performance and

440   survival in captive gazelles of great conservation value. Biol. Conserv. **122**,

441   453-464.

442 Cassinello, J., Acevedo, P. & Hortal, J. 2006. Prospects for population

443   expansion of the exotic aoudad (*Ammotragus lervia*; Bovidae) in the Iberian

444   Peninsula: clues from habitat suitability modelling. Divers. Distr. **12**, 666–678.

445 Cassinello, J., Serrano, E., Calabuig, G. & Pérez, J.M. 2004. Range expansion

446   of an exotic ungulate (*Ammotragus lervia*) in southern Spain: ecological and

447   conservation concerns. Biodivers. Conserv. **13**, 851-866.

448 Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. Red Deer. University

449   of Chicago Press, Chicago.

450 Colgan, P. W. 1983. Comparative Social Recognition. John Wiley and Sons,

451   New York.

452 Crnokrak, P. & Barrett, S.C.H. 2002. Perspective: purging the genetic load: a

453   review of the experimental evidence. Evolution Int. J. Org. Evolution **56**,

454   2347–2358.

455 Dickinson, T. G. & Simpson, C. D. 1980. Home range, Movements, and

456   Topographic Selection of Barbary Sheep in the Guadalupe Mountains, New

457   Mexico. In: Symposium on Ecology and Management of Barbary Sheep

458   (Simpson, C. D., ed). Texas Tech University Press, Lubbock, pp. 78-86.

459 Drews, C. 1993. The concept and definition of dominance in animal behavior.

460   Behaviour **125**, 283-313.

461 Duarte, L. C., Bouteiller, C., Fontanillas, P., Petit, E. & Perrin, N. 2003.

462   Inbreeding in the greater white-toothed shrew, *Crocidura russula*. Evolution

463   **57**, 638-645.

464 Espmark, Y. 1971. Individual recognition by voice in reindeer mother-young

465   relationship. Field observations and playback experiments. Behaviour **40**,

466   295-301.

467 Falconer, D. S. & Mackay, T. F. C. 1996. Introduction to Quantitative Genetics,

468   4th edn. Longmann & Co., London.

469 Fletcher, D. J. C. & Michener, C. D. (Eds.) 1987. Kin Recognition in Animals.

470   John Wiley & Sons, Inc., New York.

471 Gheusi, G., Bluthe, R. M., Goodall, G. & Dantzer, R. 1994. Social and individual

472   recognition in rodents: methodological aspects and neurobiological bases.

473   Behav. Proc. **33**, 59-87.

474 Green, W. C. H., Griswold, J. G. & Rothstein, A. 1989. Post-weaning

475   associations among bison mothers and daughters. Anim. Behav. **38**, 847-

476   858.

477 Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and

478   mammals. Anim. Behav. **28**, 1140-1162.

479 Griffin, A. S. & West, S. A. 2002. Kin selection: fact and fiction. Trends Ecol.

480   Evol. **17**, 15-21.

481 Gubernick, D. J. 1981a. Mechanisms of maternal 'labelling' in goats. Anim.

482   Behav. **29**, 305-306.

483 Gubernick, D. J. 1981b. Parental and Infant Attachment in Mammals. In:

484   Parental Care in Mammals (Gubernick, D. J. & Klopfer, P. H., eds). Plenum,

485   New York, pp. 243-289.

486 Halpin, Z. T. 1991. Kin Recognition Cues in Vertebrates. In: Kin Recognition

487   (Hepper, P. G., ed). Cambridge University Press, Cambridge, pp. 220-258.

488 Hamilton, W. D. 1963. The evolution of altruistic behaviour. Am. Nat. **97**, 354-

489   356.

490 Harvey, P. H. & Ralls, K. 1986. Do animals avoid incest? Nature **320**, 575-576.

491 Hepper, P. G. 1991. Kin Recognition. Cambridge University Press, Cambridge.

492 Hoogland, J. L. 1992. Levels of inbreeding among prairie dogs. Am. Nat. **139**,

493   591-602.

494 Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field

495   experiments. Ecol. Monogr. **54**, 187–211.

496 Johnsson, J. I. 1996. Statistics and biological sense: a reply to Thomas &

497   Juanes. Anim. Behav. **52**, 860.

498 Keane, B. 1990. The effect of relatedness on reproductive success and mate

499   choice in the white-footed mouse, *Peromyscus leucopus*. Anim. Behav. **39**,

500   264-273.

501 Kendrick, K. M. 1991. How the sheep's brain controls the visual recognition of

502   animals and humans. J. Anim. Sci. **69**, 5008-5016.

503 Kendrick, K. M. & Baldwin, B. A. 1987. Cells in temporal cortex of conscious

504   sheep can respond preferentially to the sight of faces. Science **236**, 448-450.

505 Lane, D. M. 2007. Cautions in interpreting variance explained. In: HyperStat

506   Online Statistics Textbook. http://davidmlane.com/hyperstat/index.html.

507 Lent, P. C. 1974. Mother-Infant Relationships in Ungulates. In: The Behaviour of

508   Ungulates and its Relation to Management, Vol. 1. (Geist, V. & Walther, F.,

509   eds). I.U.C.N, Morges, Switzerland, pp. 14-55.

510 Lickliter, R. 1984. Mother-infant spatial relationships in domestic goats. Appl.

511   Anim. Behav. Sci. **13**, 93-100.

512 Lindsay, D. R. & Fletcher, I. C. 1968. Sensory involvement in the recognition of

513   lambs by their dam. Anim. Behav. **16**, 415-417.

514 Mateo, J. M. 2003. Kin recognition in ground squirrels and other rodents. J.

515   Mammal. **84**, 1163-1181.

516   Nakagawa, S. & Foster, T. M. 2004. The case against retrospective statistical

517   power analyses with an introduction to power analysis. Acta Ethol. **7**, 103-

518   108.

519   Palombit, R. A., Seyfarth, R. M. & Cheney, D. L. 1997. The adaptive value of

520   'friendships' to female baboons: Experimental and observational evidence.

521   Anim. Behav. **54**, 599-614.

522   Pfeffer, P. 1967. Le Mouflon de Corse (*Ovis ammon musimon* Schreber 1782);

523   position systématique, écologie et éthologie comparées. Mammalia **31**

524   (Suppl.), 1-262.

525   Poindron, P. & Carrick, M. J. 1976. Hearing recognition of the lamb by its

526   mother. Anim. Behav. **24**, 600-602.

527   Porter, R. H., Lévy, F., Poindron, P., Litterio, M., Schaal, B. & Beyer, C. 1991.

528   Individual olfactory signatures as major determinants of early maternal

529   discrimination in sheep. Develop. Psychobiol. **24**, 151-158.

530   Pusey, A. & Wolf, M. 1996. Inbreeding avoidance in animals. Trends Ecol. Evol.

531   **11**, 201–206.

532   Pusey, A. E. & Packer, C. 1987. The evolution of sex-biased dispersal in lions.

533   Behaviour **101**, 275-310.

534   Ralls, K., Lundrigan, B. & Kranz, K. 1987. Mother-young relationships in captive

535   ungulates: spatial and temporal patterns. Zoo Biol. **6**, 11-20.

536   Rutberg, A. T. 1983. Factors influencing dominance status in American bison

537   cows (*Bison bison*). Z. Tierpsychol. **63**, 206-212.

538   Ryan, K. K. & Lacy, R. C. 2003. Monogamous male mice bias behaviour

539   towards females according to very small differences in kinship. Anim. Behav.

540   **65**, 379-384.

541 Scott, J. P. 1962. Hostility and Aggression in Animals. In: Roots of Behaviour

542   (Bliss, E. L., ed). Harper, New York, pp. 167-178.

543 Simpson, C. D. (ed.) 1980. Symposium on ecology and management of Barbary

544   sheep. Texas Tech University Press, Lubbock.

545 Simpson, C. D., Krysl, L. J., Hampy, D. B. & Gray, G. G. 1978. The Barbary

546   sheep: a threat to desert bighorn survival. Desert Bighorn Council Trans. **22**,

547   26-31.

548 Thomas, L. & Juanes, F. 1996. The importance of statistical power analysis: an

549   example from animal behaviour. Anim. Behav. **52**, 856–859.

550 Thompson, B. 2002. What future quantitative social science research could look

551   like: confidence intervals for effect sizes. Educ. Researcher **31**, 25-32.

552 Thompson, K. V. 1993. Aggressive behaviour and dominance hierarchies in

553   female sable antelope, *Hippotragus niger*: implications for captive

554   management. Zoo Biol. **12**, 189-202.

555 Trivers, R. 1971. The evolution of reciprocal altruism. Q. Rev. Biol. **46**, 35-57.

556 Waser, P. M., Austad, S. N. & Keane, B. 1986. When should animals tolerate

557   inbreeding? Am. Nat. **128**, 529-537.

558 Waser, P. M. & Jones, W. J. 1983. Natal philopatry among solitary mammals.

559   Q. Rev. Biol. **58**, 355-390.

560 Weinrich, M. T. 1991. Stable social associations among humpback whales

561   (*Megaptera novaeangliae*) in the Southern Gulf of Maine. Can. J. Zool. **69**,

562   3012-3018.

563 Whitehead, H. & Dufault, S. 1999. Techniques for analyzing vertebrate social

564   structure using identified individuals: review and recommendations. Adv.

565   Stud. Behav. **28**, 33-74.

566 Wolski, T. R., Houpt, K. A. & Aronson, R. 1980. The role of the senses in mare-

567   foal recognition. Appl. Anim. Ethol. **6**, 121-138.

568 Wright, S. 1922. Coefficients of inbreeding and relationship. Am. Nat. **56**, 330-

569   338.

570 Zar, J. H. 1984. Biostatistical Analysis, 2nd edn. Prentice-Hall, Inc., Englewood

571   Cliffs, New Jersey.

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

582   Table 2. Summary of standard least squares models for the average distance

583   and four distance rates maintained by herdmates (dyads), according to two

584   independent variables, their Coefficients of Relationship (COR) values and age

585   difference in the study aoudad population. Herdmates' cohabitation time in the

586   enclosure was added as a random effect. Male-female dyads were

587   differentiated from male-male and female-female dyads. Sample size is n =

588   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

589

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

590

591

592   FIGURE LEGENDS
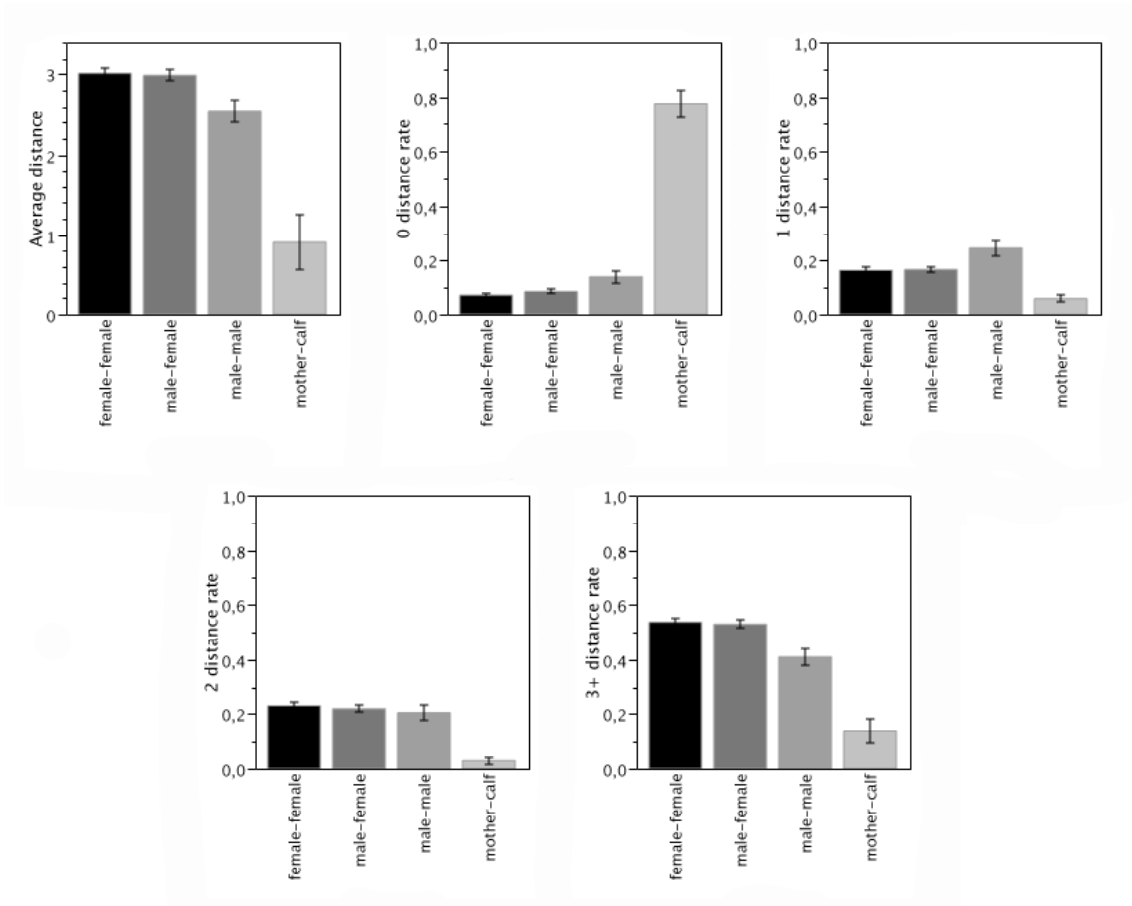
593

594   Figure 1. Average (±SE) distance (in body-lengths) and average (±SE)

595   distances rates maintained by the different dyad types included in the analyses.

596

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

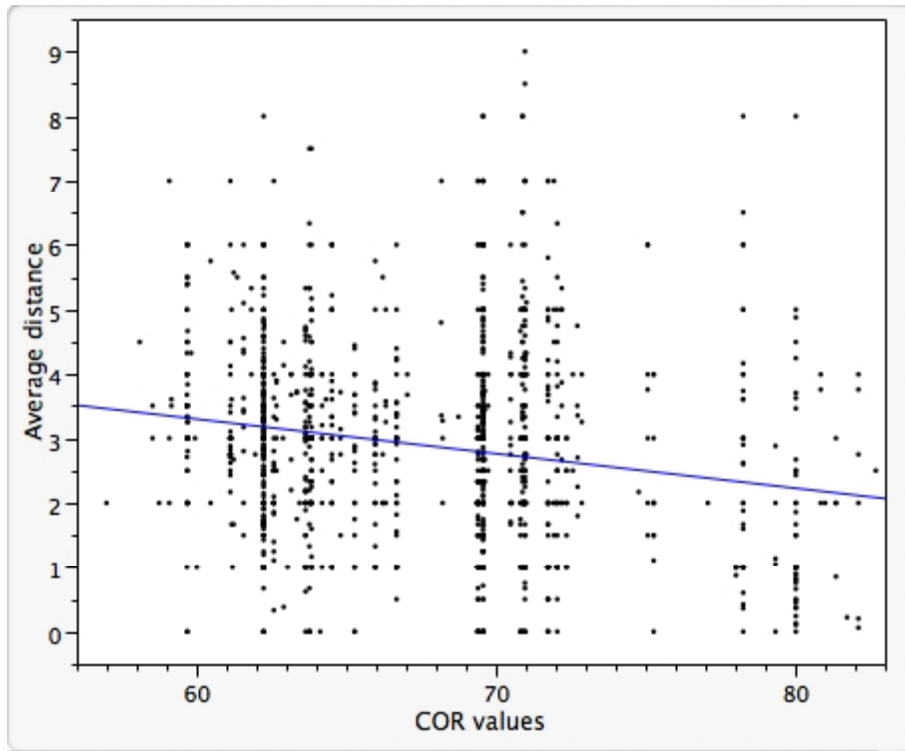598   male and female-female dyads.

599

600

601

602   FIGURE 1

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605

606   FIGURE 2