Running head: Aoudad expansion in southern Spain

Range expansion of an exotic ungulate (*Ammotragus lervia*) in southern Spain: ecological and conservation concerns

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Abstract

Evidence of aoudad *Ammotragus lervia* expansion in the southeastern quarter of the Iberian Peninsula is provided based on recent field surveys. Aoudads have become common in a limited region of the south east of Spain since its introduction as a game species in Sierra Espuña Natural Park in 1970. Its adaptability enabled it to colonise nearby areas in a short period. Apart from this source of expansion, the increasing number of aoudads in Spanish private game reserves provided other centers of dispersion. In addition, aoudads were introduced in La Palma Island (Canary Islands), becoming a serious threat to endemic flora. Of great conservation concern is the species potential as a competitor against native ungulates inhabiting the peninsula. Surveys conducted in southern Spain documented rapid colonization of new areas and established viable populations, consisting of adult males and females and the unequivocal presence of nursery groups, in the provinces of Alicante, Almería, Granada and Murcia. Also, aoudads have spread throughout the north and centre of La Palma. There are two main conservational concerns: the necessity of conducting detailed and reliable surveys in all potential regions where the species might expand, and the urgent need of changing current game policies in order to establish reliable controls on big game reserves to prevent animals from escaping.

Keywords: *Ammotragus*, Biological invasions, Conservation, Distribution, Management, Spain, Ungulates

Introduction

The introduction of exotic species has become a serious issue on conservation ecology (e.g. Lodge 1993; Ruesink et al. 1995), as it is one of the greatest threats to biodiversity (Diamond 1989; Wilcove et al. 1998). Nonindigenous fauna and flora may cause several deleterious effects on the host ecosystems, such as competition and displace of autochtonous or endemic species, and alterations in community structure, including

energy flow, biodiversity, and invasion-mediated extinction. Exotic species may also play an important role in evolution processes at contemporary timescales (Stockwell et al. 2003). Concerning exotic ungulates, their introductions have been dictated by sport hunting interests, particularly in western countries, disregarding the effects they may cause in the environment, such as potential threats to native ungulates and endemic flora.

The aoudad is a North African caprine successfully introduced in the USA and Spain, due to sport hunting interests (Gray 1985; Cassinello 1998). In its native distribution in northern Africa it is classified as Vulnerable (VU A2cd) by the IUCN (Hilton-Taylor 2000), due to habitat loss and poaching (Alados and Shackleton 1997); however, the introduced USA and Spanish populations are either stable or steadily increasing (Gray 1985; Cassinello 2000). The species became a common inhabitant in southeastern Spain since its introduction as a game animal in Sierra Espuña Natural Park, Murcia province, in 1970 (Cassinello 2000). Since then, and despite a mange epizootic in 1991 that reduced the population dramatically (González-Candela and León-Vizcaíno 1999), it has recovered rapidly (González-Candela et al. 2001) and continued to expand to nearby mountainous regions. In La Palma Island, some aoudads from Sierra Espuña were introduced in La Caldera de Taburiente National Park in 1972; soon afterwards it was evident it was a serious threat to endemic flora. Effective eradication has not been accomplished (see Ornistudio 1992). The aoudad is an appealing game species due to its impressive trophy and anatomical features; also its high reproductive rate and adaptation to Spanish habitats increase its game animal appeal (Cassinello 1998). Along with the population in Sierra Espuña, populations in game reserves are the main source for a recent dispersal, as in too many instances fences are not capable of impeding animals from escaping. Furthermore, the suitability

of the Mediterranean habitat in southern Spain increases its ability to disperse. The lack of monitoring by the regional environmental agencies has failed to document its range expansion.

Methods

The study areas

The Iberian study area is a Mediterranean ecosystem characteristic of the eastern third of the Cordillera Sub-Bética, which stretches across southeastern Spain (Figure 1a). In defining the vegetation types, we follow Rivas-Martínez's (1987) classification of Iberian vegetation according to altitudinal zones. Three areas can be distinguished. The southern one corresponds with the mountainous regions of northeastern Granada, northern Almería and northwestern Murcia, characterized by a dry climate (350-600 mm) and two rocky formations: limestones and dolomites, which support Meso-Mediterranean Oak Tree (*Quercus* spp.) Succession Series (*Paeonio-Quercetum rotundifoliae* S), and occur between 800-1400 metres above sea level; and a siliceous formation of slates and phyllites, ground for siliceous Meso-Supra-Mediterranean Oak Tree Succession Series (*Adenocarpo-Querceto rotundifoliae* S), located between 900-1900 m.a.s.l. The central area of the Cordillera Sub-Bética refers to the eastern mountains of Murcia and Alicante, characterized by a semiarid climate (240-330 mm), limestones and dolomites between 400-900 m.a.s.l., and the vegetation succession series *Rhamno lycioidis-Querceto cocciferae* S. Finally, there is an eastern area that corresponds with the mountainous regions of northwestern and northeastern Alicante, characterized by a dry-subhumid climate (300-650 mm), rocks formed by limestones and dolomites also occuring at 500-1500 m.a.s.l. and two typical Meso-Mediterranean vegetation successions: *Bupleuro rigidi-Quercetum rotundifoliae* S and *Rhamno-*

Quercetum rotundifoliae S. Throughout the whole area reforestations with *Pinus halepensis* and *P. pinaster* abound.

The Canary study area was in La Palma Island, located in the northwest of the Canary Archipelago (Figure 1b), in an area of 728 km^2. The area is centered in La Caldera de Taburiente National Park, formerly a volcano, which is the main feature of the island orography. Located in the northern half of the island, it occupies 30 km^2 and ranges in altitude from 300 to 2430 metres above sea level. The vegetation that predominates is a mountainous shrub formation dominated by *Adenocarpus viscosus*, and scattered cedar trees (*Juniperus cedrus*), as well as pine trees *Pinus canariensis* in lower altitudes. A great number of endemic plants are present, some of them already recorded in aoudad diet (Rodríguez-Piñero and Rodríguez-Luengo 1992).

The study animals

Conforming to a regional game policy, 36 aoudads were introduced in Sierra Espuña Natural Park from zoos in Casablanca and Frankfurt between 1970 and 1972. This stock was held in enclosures, after which 34 individuals were released, and dispersed up to 80 km (Bigalke 1986); by 1973 there were 79 arruis, the population increasing at an average annual rate of 30% a year to 1982, when numbers were approximately 750 (Gray 1985). Despite hunting initiated in 1977, by 1991 the population number reached about 2000 individuals, and started to disperse to the surrounding mountains (ARMAN-Murcia 1991). A mange epidemic in 1991 drastically reduced the aoudad population (González-Candela and León-Vizcaíno 1999), probably a maximum of 200 individuals survived in 1992 (R. Sánchez, pers. comm.). However the population slowly recovered and again reached high numbers. Approximately 500-1000 aoudads inhabited the Park by 1999 (González-Candela et al. 2001). Concerning the Canary Islands, 16 individuals

from Sierra Espuña were introduced in 1972 close to the Caldera de Taburiente National Park in La Palma (Rodríguez-Piñero and Rodríguez-Luengo 1992). They expanded successfully and now inhabit the most remote and mountainous regions. The population increased without effective management (Ornistudio 1992).

In recent years the species steadily increased in private game reserves. These are a new potential source for expansion. We conducted surveys in the province of Alicante because we were informed there was a newly established free-roaming aoudad population.

The surveys

Surveys were conducted unevenly during three years (from 1999 to 2001), mainly during August, September and October. We focused our efforts in the southeastern quadrant of the Iberian Peninsula, surveying the provinces of Alicante, Almería, Granada, Jaén and Murcia (see Figures 1 and 2), where the species is known to have become established in several mountainous regions (Cassinello 2000). We also conducted some surveys in La Palma (Canary Islands). Information was collected by direct field observations and by interviewing shepherds, hunters, forest rangers, fire managers, and naturalists, as well as biologists and park managers from regional environmental agencies. Most of the information gathered by other people was verified by visiting areas where aoudads were reported. We recorded every observation in a UTM 10x10 cartographic map.

Due to the diverse sources of information used and the lack of previous age-sex class criteria (see Cassinello 1997), only a rough estimate of adult males, adult females, and juveniles was possible in some cases. Thus, we distinguished up to four age-sex classes in only 36 of the 165 observations: nursery groups (consisting of adult females

and juveniles), mixed groups (adult males and females), male or bachelor groups, and solitary males. During La Palma island surveys, sex and age were not recorded.

Statistics

Analysis of Variance was used to test differences between average group size and different independent variables. Average group size was tested for normality (homoscedasticity and randomness), and transformed into its logarithm for conformity (Zar 1984).

Results

Our survey results are summarized in Tables 1 to 4. They provided information on aoudad presence in southeastern Iberian Peninsula and La Palma Island (Canary Islands); the Iberian population is located in the eastern borders of the Spanish Cordillera Sub-Bética (see Figure 1a). In Figure 2 the provinces surveyed and the proposed current distribution of the species is shown, along with probable expansion areas due to sporadic movements of solitary males. Three main populations can be distinguished: Murcia, Alicante and La Palma. The number of observations varied between provinces, being highest in La Palma (75) and lowest in Jaén (1); most of the information obtained was collected during the last 4 years (see Tables 1 to 4).

Our surveys show an expansion originating in Sierra Espuña, Murcia (Figure 2), mainly towards nearby southern and western mountainous regions, reaching the provinces of Almería, Granada and Jaén. Furthermore, there is a new wild population in Alicante province, originated from a private game reserve located in Sierra de Peñarroya (Figure 2), probably due to escaping individuals from enclosures with broken fences in 1990 (anom. comm.). The founder population consisted of 49 females and 10

males (anom. comm.). We also know of five more individuals that escaped in 1999 from another reserve in Sierra de Aitana (anom. comm.) (Figure 2). Finally, our recent visit to La Palma island confirmed that public attempts to reduce aoudad population have been unsuccessful and that the species has expanded from La Caldera de Taburiente National Park, and now occurs in the two northern thirds of the island (Figure 1b).

The seasonal composition of age-sex classes is shown in Figure 3. Only nursery groups were documented during the entire year, whereas there was one sighting of a male group during the summer; solitary males were seen in every season except winter, and mixed groups were recorded in autumn and winter. The data were not analysed statistically because survey methods were not identical.

Average group size was 7±1.0 individuals, and an analysis including as independent factors the three main populations and seasonality showed no interaction between both factors. There were larger group sizes in summer than during spring and winter (see Table 5 and Figure 4). This is due to nursery groups, which are more commonly observed in summer (see Figure 3). As a whole, though, mixed groups account for the largest number of individuals, as shown by an analysis between nursery and mixed groups ($F(1,27)=14.32$, $P=0.001$; see Figure 5).

Discussion

This study was an attempt to highlight our concern of the deleterious impacts that a rapid increase of this exotic ungulate can have on endemic flora, as reported in the aoudad population from La Palma, Canary Islands (Rodríguez-Piñero and Rodríguez-Luengo 1992), and native fauna, as reported on diet overlap with mule deer *Odocoileus hemionus* and desert bighorn *Ovis canadensis nelsoni* in the USA (see Simpson et al.

1978; Bird and Upham 1980; Krysl et al. 1980).

Our surveys provided location, groups size, age-sex class identification, and an attempt to identify the origins of these populations (such as releases in natural parks or game reserves). Although surveys were not systematic, a general view of aoudads' presence in the different provinces could be inferred from personal communications from regional park managers and forest rangers. Our major objective was to determine the current status of aoudad distribution in Spain.

The distribution clearly indicates that in the Iberian Peninsula aoudads are expanding from their original release in Sierra Espuña (Murcia), mainly in a westward direction through the provinces of Granada and Almería. The presence of numerous solitary animals and small groups indicated a colonization tendency in these areas, as the presence of bachelor groups and solitary males are the advance party or first stage in aoudad population dispersal and colonization (Barrett 1980; Dickinson and Simpson 1980). However, colonization should be well documented as, for instance, the sighting of a relatively large group of aoudads in Jaén would not necessary imply the species is already established in this province. Concerning aoudad population in La Palma Island, previous unpublished data reported low numbers, around 200 individuals at most (Ornistudio 1992; Cabrera-Rodríguez 2000); however, our own surveys suggest that current population estimates are higher than previously reported.

Differences in group composition according to the season are as expected, although the scarcity of reports of bachelor or male groups suggest extreme difficulties in detecting them. As no specific age-sex classes were reported (see Cassinello 1997), we cannot yet identify the main parturition season and therefore mating season, as gestation is known to last about 5.5 months (Cassinello and Alados 1996).

Our results show a fast dispersal process by this African caprinae in the Iberian

Peninsula. Two main issues have to be discussed here: effects on native biota and private game reserves management.

Effects on native biota

Studies on aoudad diet composition have already shown that the species is a serious risk for the survival of endemic flora in La Palma Island (see Rodríguez-Piñero and Rodríguez-Luengo 1992); yet, no diet studies have been conducted in the Iberian range of the species, where endemic flora abounds (see, e.g., Laguna et al. 1998). The aoudad has a strong potential to displace native ungulates due to its formidable abilities as a competitor: the aoudad is a generalist herbivore, whose diet may include shrubs, forbs and grasses, depending on seasonal availability, being capable of resting on a few resources during harsh winters (Ogren 1965). Simpson et al. (1978) estimated that aoudads in Palo Duro Canyon, Texas, may disperse about 7.25 km a year. Such a dispersion rate would enable it to spread quickly and widely.

There is no evidence of direct competition between aoudads and other ungulate species. However, according to Simpson et al. (1978), aoudads are a threat to desert bighorns in American sites where both species overlap; and a similar situation may occur between aoudad and mule deer in New Mexico (Bird and Upham 1980) and Texas (Krysl et al. 1980). These authors focused their studies on potential competition based on diet overlap between aoudads and autochthonous ungulates. Diet overlap may not necessarily indicate competition is occurring, as spatial segregation and resource use may differ between the species (e.g. Ramanzin et al. 2002); nevertheless, under certain circumstances, such as resource shortage, a competition event may easily arise. In Spain, potential risks to Spanish ibex *Capra pyrenaica hispanica* and red deer *Cervus elaphus* are evident, as apparently aoudads have already reached mountainous regions

inhabited by these autochthonous species (Serrano et al. 2002a).

Private game reserves management

Aoudad's interest as a game species is remarkable since its introduction in game reserves in USA in mid-20th century (Ogren 1965; Christian 1980). In Spain, there is an increasing number of private hunting reserves stocked with this species (Ortuño and De la Peña 1979; Serrano et al. 2002b). Unfortunately, as commented above, introductions in the past have not considered the potential threats to the environment (Barrett and Beasom 1980; Fandos and Reig 1992; Cassinello 2000). Aoudads have escaped from two private reserves in Alicante, which is a concern as far as managing exotic species. Current Spanish legislation on hunting reserves do not contemplate exotic or allochtonous species (concerning big game: aoudad and mouflon *Ovis ammon musimon*) (see, e.g., Montoya-Oliver 1989); and given the high risk they represent to autochthonous fauna and flora, legislation should be changed accordingly. Thus, there should be a strict and periodic monitoring of fenced reserves, in order to prevent accidental escapes from deteriorated fences. We encourage further studies on aoudad effects on the Spanish montane environments and highlight its devastating potential as a competitor. Preserves that breed aoudad should follow rigorous management procedures, and be regulated by national and/or regional population control legislation.

Final considerations

Our study should be considered as a first step in an attempt of a more ambitious study on aoudad distribution in Spain. Given the potentiality for the species to expand from private game reserves, a detailed registration of these reserves is urgently needed. In addition, where the species is suspected to occur sympatrically with native ungulates

(such as Spanish ibex and red deer), behavioural and diet studies should help in determining competition. Furthermore, ecological studies of Spanish aoudad may help in preserving threatened African aoudad populations, as paradoxically the species is suffering from a strong decline in its natural habitat (Alados and Shackleton 1997).

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Figure 1. Location of the Spanish Cordillera Sub-Bética (in grey) and aoudad population distributions in (a) southeastern Iberian Peninsula and (b) La Palma Island in the Canary Islands (in black). Note the arrow indicating a relatively isolated western aoudad population.

Figure 2. Closer view of the distribution of aoudad populations in southeastern Spain, distinguishing the provinces concerned. Grey areas indicate where sporadic adult male sightings occurred and which may represent probable expansion movements. Stars represent three source release sites: from left to right, Sierra Espuña, Sierra de Peñarroya and Sierra de Aitana.

Figure 3. Number of seasonal sightings of four aoudad age-sex classes.

Figure 4. Aoudad average group size (+SE) during the four seasons. Sample size is included.

Figure 5. Aoudad average group size (+SE) for two age-sex classes.

Table 1. Aoudad sightings in Alicante province

Location/sierra (Sª)	UTM	Date	No. individuals	Group type	No. males	No. females	No. subadults
Vall de Alcala	30SYH408971	4/2/94	2	.	.	.	.
Sª del Menejador	30SYH136825	2/2/98	8	.	.	.	.
Sª Serrella	30SYH335877	5/3/98	1	Solitary male	1	0	0
Maigmo	30SYH069649	22/10/98	15	Mixed	.	.	.
Sª Aitana	30SYH405821	1/2/99	7	.	.	.	.
Sª Aitana	30SYH381787	5/3/99	4	.	.	.	.
Sª de la Foradada	30SYH367989	11/4/99	4	Nursery	0	3	1
Hedrera	30SYH343827	2/5/99	5	Nursery	0	3	2
Puig Campana	30SYH425769	19/5/99	3	.	.	.	.
Embalse Tibi	30SYH112637	10/7/99	2	.	.	.	.
Ctra Tibi-Ibi	30SYH144675	10/7/99	5	.	.	.	.
Ctra Castalla-Biar	30SXH958775	12/7/99	11	Nursery	.	.	.
Balcon de Alicante	30SYH069637	15/7/99	5	Nursery	.	.	.
Ctra Jijona-Tibi	30SYH136706	28/7/99	5	.	.	.	.
Sª Penyaroja	30SYH143736	1/8/99	2	Males	2	0	0
Sª Penyaroja	30SYH146731	1/8/99	3	.	.	.	.
Sª Penyaroja	30SYH138713	16/8/99	25	.	.	.	.
Sª de la Grana	30SYH273726	28/8/99	15	Nursery	.	.	.
Sª del Aguilar	30SYH353759	30/8/99	11	Nursery	.	.	.
Sª dels Plans	30SYH225779	1/9/99	2	.	.	.	.
Sª Onil	30SXH986782	10/9/99	3	Nursery	.	.	.
Sª Onil	30SXH967776	7/12/99	11	Mixed	.	.	.
Sª Penyaroja	30SYH138713	12/9/00	10	.	.	.	.
Sª Penyaroja	30SYH144675	13/9/00	16	Nursery	0	4	6
Sª Alfaro	30SYH410971	12/3/01	5	.	.	.	.
Sª Alfaro	30SYH410971	10/4/01	3	Nursery	.	2	1

Table 2. Aoudad sightings in Almería, Granada and Jaén provinces

Province	Location/sierra (Sª)	UTM	Date	No. individuals	Group type	No. males	No. females	No. subadults
Almería	Sª Larga	30SWG865795	12/6/90	7	.	.	.	.
Almería	Sª Oria	30SWG567504	12/11/92	29	Mixed	.	.	.
Almería	Sª del Oso	30SWG835875	11/11/93	4	Nursery	0	3	1
Almería	La Solana	30SWG664179	24/9/97	1	Solitary male	1	0	0
Almería	Sª Larga	30SWG862795	12/6/99	50	.	.	.	.
Almería	Sª Estancias	30SWG625402	15/12/99	4	.	.	.	.
Almería	Sª Gigante	30SWG875765	5/9/00	3	.	.	.	.
Almería	Pto Maria	30SWG752724	2/11/00	1	Solitary male	1	0	0
Almería	Cueva Botia-Sª Maria	30SWG695683	15/8/01	9	.	.	.	.
Granada	Sª Seca	30SWH295012	5/9/90	1	Solitary male	1	0	0
Granada	Campo de Bugéjar	30SWG635938	3/10/93	2	.	.	.	.
Granada	Ctjo Perentil	30SWG595674	2/6/96	1	Solitary male	1	0	0
Granada	Sª Seca	30SWH295012	5/7/96	1	Solitary male	1	0	0
Granada	Cerro Juan Lopez	30SWG515645	12/4/97	4	.	.	.	.
Granada	Bco Mereva	30SWG515665	24/11/99	30	Mixed	.	.	.
Granada	Guillimona	30SWH505066	3/6/00	10	.	.	.	.
Granada	Sª Zarza	30SWG655988	4/3/01	2	.	.	.	.
Granada	Bco Junco	30SWG498655	3/4/01	3	.	.	.	.
Granada	Encarba-Chiscar	30SWG552669	28/4/01	4	.	.	.	.
Granada	Argerin	30SWG525655	15/5/01	2	.	.	.	.
Granada	Encarba	30SWG545665	23/8/01	3	Nursery	0	1	2
Granada	Dehesa Orce	30SWG596654	3/10/01	2	Nursery	0	1	1
Jaén	Collado-Pinar Saucar	30SWH360242	3/9/99	20	Mixed	.	.	.

Table 3. Aoudad sightings in Murcia province

Location/sierra (Sª)	UTM	Date	No. individuals	Group type	No. males	No. females	No. subadults
Sª Ponce	30SXG125955	2/4/82	20	.	.	.	.
Sª Cabras	30SXH015065	3/4/84	5	Nursery	0	3	2
Sª Cambron	30SXH145000	12/9/89	4	.	.	.	.
Sª Tercia	30SXG215785	2/3/90	5	Nursery	0	3	2
Sª Torrecilla	30SWG965725	15/3/90	4	.	.	.	.
Sª Carrascoy	30SXG505875	6/1/91	4	.	.	.	.
Sª Puerto	30SXG573935	12/3/91	4	.	.	.	.
Sª Carrascoy	30SXG535915	3/5/91	7	.	.	.	.
Sª Gigante	30SWG885795	15/1/93	7	.	.	.	.
Sª Carrascoy	30SXG505878	19/6/93	10	.	.	.	.
Sª de la Puerta	30SXH055225	11/12/93	2	.	.	.	.
Sª del Molino	30SXH195324	14/1/94	2	.	.	.	.
Sª del Puerto	30SXH214405	14/1/94	3	Nursery	0	2	1
Sª de la Muela de Alhama	30SXG384926	27/1/94	6	.	.	.	.
Sª de la Muela de Alhama	30SXG395924	10/2/94	8	.	.	.	.
Sª Tercia	30SXG185785	3/4/94	7	.	.	.	.
Sª Torrecilla	30SXG015695	8/4/94	6	.	.	.	.
Sª Carrascoy	30SXG500675	7/2/95	7	.	.	.	.
Sª Gigante	30SWG884796	21/4/96	5	Nursery	0	3	2
Sª del Oro	30SXH345315	12/1/98	5	Mixed	2	2	1
Sª Espuña	30SXG265945	15/1/98	4	.	.	.	.
Sª del Oro	30SXH305285	15/2/98	5	Nursery	0	3	2
Sª Espuña	30SXG265915	3/3/98	4	.	.	.	.
Sª Espuña	30SXG225915	4/3/98	7	.	.	.	.
Sª de la Muela	30SXH395205	1/5/98	6	Nursery	0	4	2
Sª Gigante	30SWG890800	8/5/98	3	Nursery	0	2	1
Sª Almirez	30SWG935895	4/7/98	6	.	.	.	.
Sª Quipar	30SXH045115	6/8/98	4	.	.	.	.
Sª Espuña	30SXG285945	4/10/98	8	.	.	.	.
Sª del Oro	30SXH315305	3/3/99	3	.	.	.	.
Sª Carrascoy	30SXG506875	10/3/99	3	.	.	.	.
Sª Lavia	30SXH075035	3/4/99	8	Nursery	0	6	2
Sª Puerto	30SXG595955	2/5/99	7	.	.	.	.
Sª Espuña	30SXG235965	3/5/99	7	.	.	.	.
Sª Tercia	30SXG215800	5/5/99	6	.	.	.	.
Sª Torrecilla	30SXG045695	17/5/99	7	Nursery	0	5	2
Sª Espuña	30SXG205915	12/9/99	13	Mixed	.	.	.
Sª Pinosa	30SWG755965	15/9/99	5	Mixed	2	1	2
Sª de Ricote	30SXH385245	2/4/00	4	.	.	.	.
Sª Gigante	30SWG885795	5/3/01	40	.	.	.	.
Sª Pericay	30SWG905815	5/3/01	4	.	.	.	.

Table 4. Aoudad sightings in La Palma island

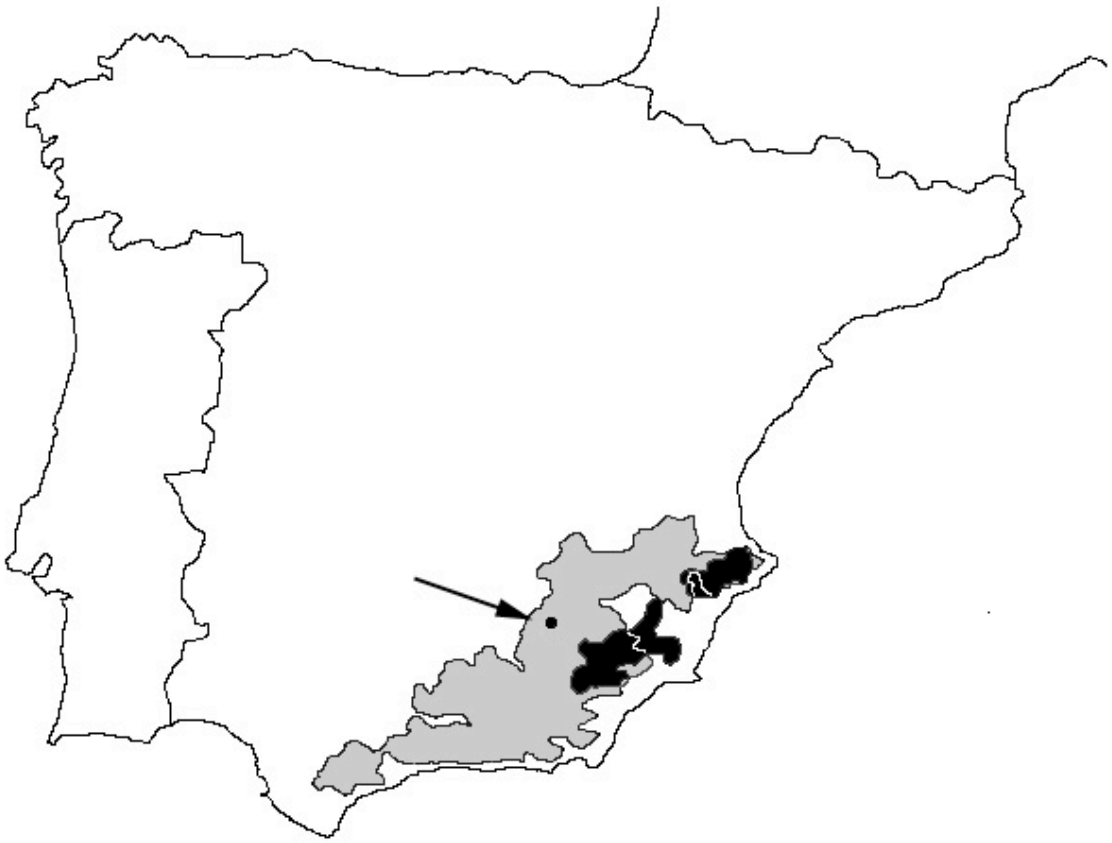
Location	UTM	Date	No. individuals	Location	UTM	Date	No. individuals
Cumbre Nueva	28RBS225688	1/3/00	1	Arroyo Almendro	28RBS193806	6/4/01	7
Cumbrecita	28RBS212768	8/1/01	2	Senda Bco Angustias	28RBS185805	10/4/01	3
Cantos	28RBS195835	19/1/01	10	Subida Tenerra	28RB169799	23/4/01	4
Cantos	28RBS197833	19/1/01	4	Cantos	28RBS191831	25/4/01	14
Bco Agua	28RBS187827	20/1/01	3	Cantos	28RBS192836	25/4/01	9
Bco Agua	28RBS189828	20/1/01	7	Cantos	28RBS194834	25/4/01	4
Risco Liso	28RBS178813	24/1/01	9	Pico Sabina	28RBS201832	25/4/01	3
Crater Duraznero	28RBS233634	4/2/01	2	Pico Sabina	28RBS203835	25/4/01	3
Fte Gatos	28RBS188782	13/2/01	6	Pico Sabina	28RBS201831	30/4/01	11
Hoyo de los Pinos	28RBS204788	13/2/01	5	Las Laderas	28RBS775215	1/5/01	12
Tenerra	28RBS171804	15/2/01	8	Bejenao	28RBS776188	2/5/01	1
Picos Tonei	28RBS193803	17/2/01	5	Hoyo Verde	28RBS193831	3/5/01	2
Idafe	28RBS195795	17/2/01	5	Cantos	28RBS193838	3/5/01	20
Idafe	28RBS196799	17/2/01	7	Cantos	28RBS196838	3/5/01	2
Río Almendro	28RBS198806	17/2/01	4	Pico de la Nieve	28RBS242813	3/5/01	6
Subida Galería Alfonso	28RBS198817	19/2/01	2	Bco Taburiente	28RBS202818	5/5/01	6
Bco Taburiente	28RBS207825	19/2/01	3	Fuente del Fabal	28RBS178806	10/5/01	11
Bco Agua	28RBS186828	20/2/01	10	Bco Agua	28RBS186823	10/5/01	10
Estrabito	28RBS168815	23/2/01	4	Galería Aridane	28RBS788213	14/5/01	7
Galería Aridane	28RBS217793	26/2/01	3	Bco Taburiente	28RBS194823	15/5/01	7
Galería Hoyo de los Pinos	28RBS218804	26/2/01	5	Bco Taburiente	28RBS195813	15/5/01	8
Fte Guanches	28RBS213828	27/2/01	9	Galería Guanche	28RBS215827	21/5/01	10
Fte Guanches	28RBS214826	27/2/01	4	Galería la Paya	28RBS218803	21/5/01	7
Subida Galería Alfonso	28RBS195812	28/2/01	2	Bco Taburiente	28RBS194822	22/5/01	9
Cantos	28RBS195829	28/2/01	2	Bco Taburiente	28RBS198818	24/5/01	4
Loma de Pablo	28RBS238824	7/3/01	3	Galería la Paya	28RBS218808	27/5/01	2
Bco Taburiente	28RBS196812	11/3/01	4	Bco Taburiente	28RBS195813	8/6/01	20
Lomo Zocamos	28RBS205815	11/3/01	6	Cantos	28RBS192838	14/6/01	14
Cantos	28RBS198837	22/3/01	7	Cantos	28RBS195834	14/6/01	21
Fuente Mayantiguo	28RBS202836	22/3/01	3	Senda Verduras Alfonso	28RBS208822	21/6/01	7
Lomo Zocamos	28RBS209819	22/3/01	6	Cantos	28RBS193839	24/6/01	14
Veleta de la Arena	28RBS218803	22/3/01	4	Senda Hoyo Verde	28RBS189836	26/6/01	7
Cantos	28RBS192832	23/3/01	11	Cantos	28RBS196837	28/6/01	12
Galería Aridane	28RBS214785	23/3/01	3	Ctra Mirador Andenes	28RBS185854	15/9/01	2
Lomo Cumplido	28RBS215821	23/3/01	2	Verduras Alfonso	28RBS215831	15/9/01	17
Roque del Hus	28RBS183813	27/3/01	12	Playa Taburiente	28RBS194823	17/9/01	4
Hoyo Verde	28RBS187837	27/3/01	3	Bejenao	28RBS772183	18/9/01	5
Fuente Ataud	28RBS192841	27/3/01	10	Cantos	28RBS195829	22/9/01	3

Table 5. Two-factor ANOVA of aoudad group size

	DF	F-VALUE	P-VALUE
SEASON	3	3.644	0.014
POPULATION	2	0.258	0.773
SEASON * POPULATION	6	1.735	0.117
Residual	150		

Analysis of variance carried out for the dependent variable aoudad group size. The fixed factors are season (spring, summer, autumn and winter) and population (Alicante, Murcia and La Palma). A Fisher's PLSD post-hoc test showed that during summer group sizes are larger than in spring and winter (P=0.01).

a)



b)

FIGURE 1

FIGURE 2

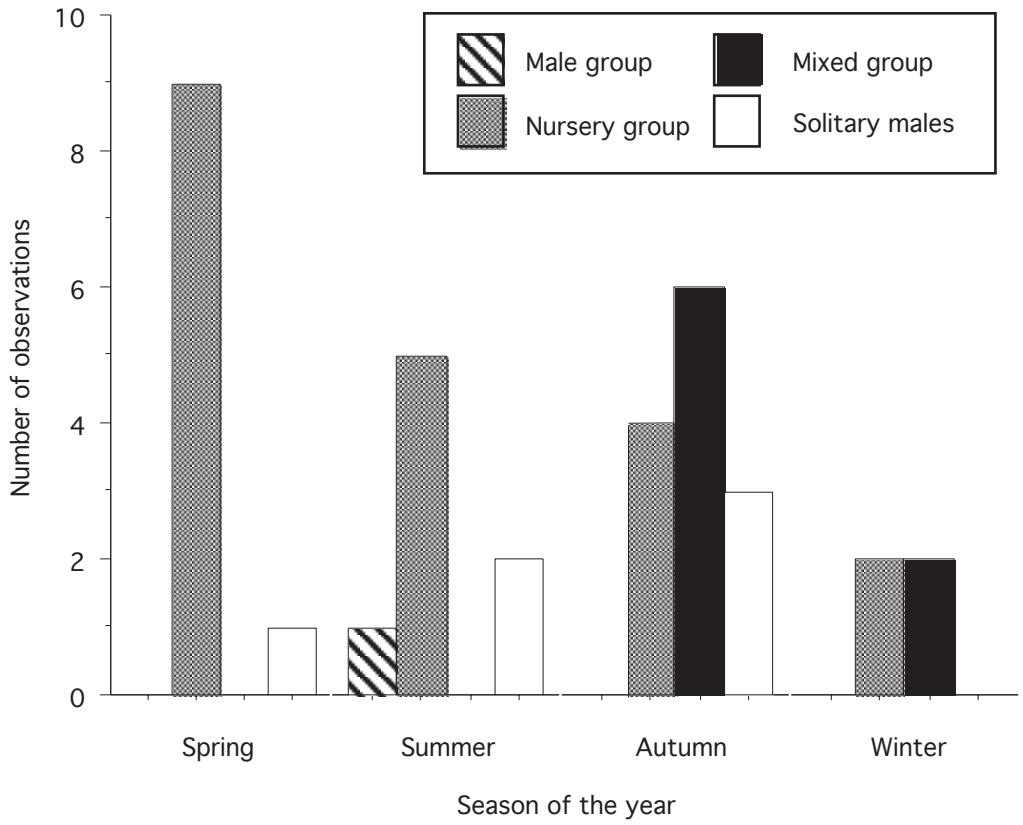

10
8
6
4
2
0
Number of observations
Male group
Mixed group
Nursery group
Solitary males
Spring
Summer
Autumn
Winter
Season of the year

FIGURE 3

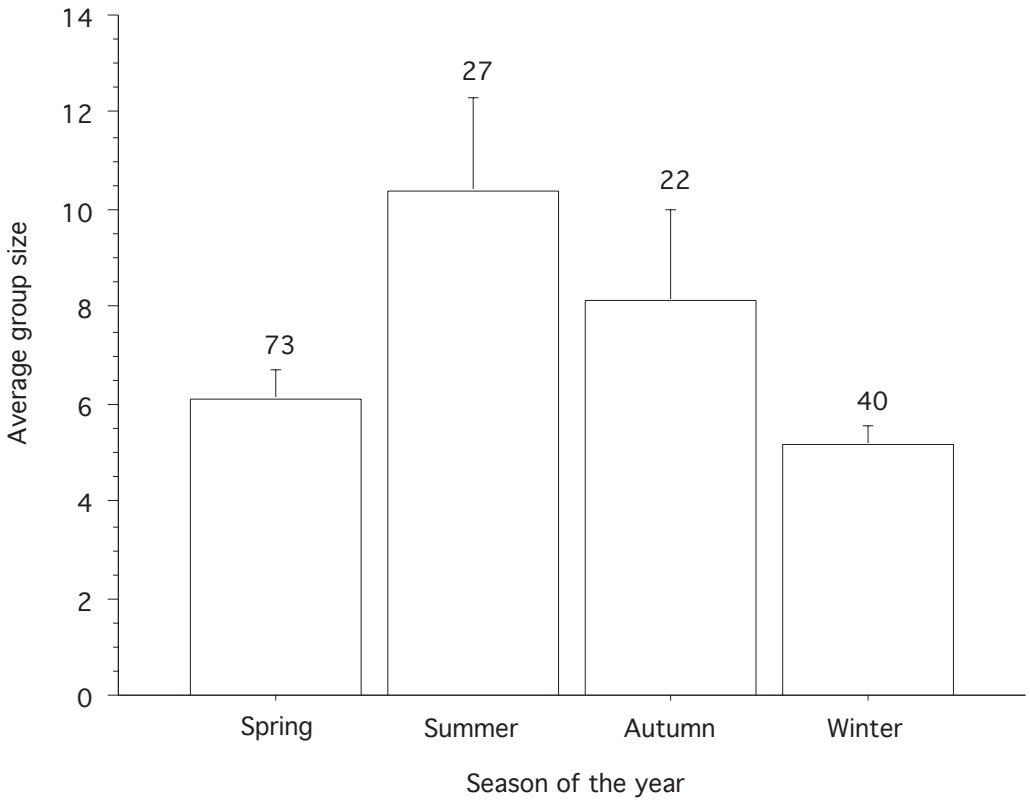

14
12
10
8
6
4
2
0
Average group size
27
22
73
40
Spring
Summer
Autumn
Winter
Season of the year

FIGURE 4

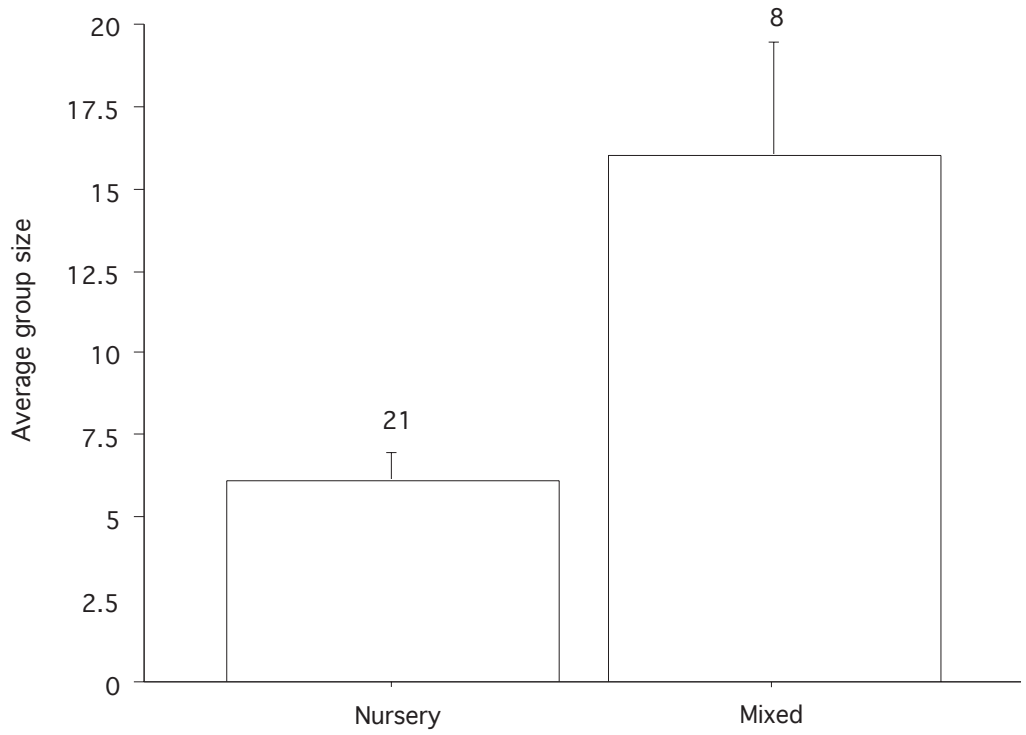


FIGURE 5