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Research Article

A tale of an African ungulate in north-western Italy: population history, abundance, and ecology

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Abstract

Alien species are species that are introduced into an area where they are not naturally present. Some of them may exert negative ecological impacts, thus being defined as invasive. The aoudad or Barbary sheep *Ammotragus lervia* is a north-African ungulate commercialised and introduced for game hunting to Europe, South Africa, and America. As a generalist herbivore, the aoudad has a high capacity to adapt to new habitat conditions, possibly representing a threat to local biodiversity. We studied the aoudad population present in the Beigua Natural Regional Park in Liguria, north-western Italy. By using historical data and camera trapping data, we reconstructed the colonization process and current distribution, estimated minimum abundance, assessed population trends over the years, and investigated habitat selection and activity rhythms. Aoudads most likely escaped from a game reserve in Ponzone Municipality, Piedmont, and settled in the park at least since 2009. The minimum number alive doubled in 10 years, from 9 to 23, and the population shows an increasing trend. Aoudads showed a preference for steep, rocky and woody areas in the southern and warmer part of the Beigua massif, especially at intermediate elevations. Some observations have recently occurred in the northern part of the Park, potentially due to geographical expansion. Aoudads show mostly diurnal activity, unlike native ungulates such as roe deer *Capreolus capreolus* and wild boar *Sus scrofa* which were most active at dawn, dusk and during the night, possibly reflecting anti-predator behaviour towards wolf *Canis lupus*. Our results are in line with other studies, though births occurred across a wider period of time compared with native populations. As the potential ecological impacts of this alien species in the study area have never been investigated, it will be important to monitor the population and evaluate its ecological effects to provide the most appropriate management solutions.

Introduction

Invasive alien species play a crucial role in the loss of biodiversity worldwide (Convention on Biological Diversity, 2002). In the past, the term invasive was associated with alien species (i.e., species that are introduced in an area in which they are not naturally present) if these showed a high capacity to expand their geographic range (biogeographic criterion) and/or the exertion of negative effects on native species or habitats (impact criterion; Valery et al., 2008). Currently, the impact criterion is considered more relevant for defining whether or not a species is invasive (IUCN, 2000; Convention on Biological Diversity, 2002; Cassinello, 2018). In addition, the IUCN/CBD defines invasive species as "alien species whose introduction and/or spread threaten biological diversity" (https://www.cbd.int/invasive/terms.shtml).

Ungulates have been moved around the world for farming or game since prehistoric times (Diamond, 1997) and are among the taxa with the highest risk of becoming invasive, when introduced to regions where predators are not present and plant communities have evolved without large herbivores (Volery et al., 2020). Mouflon *Ovis aries*, wild boar *Sus scrofa*, and feral goat *Capra hircus* are examples of species that can strongly impact the ecosystems in which are introduced, possibly causing the decline and, at times, the extinction, of native species (Spear and Chown, 2009; Hart et al., 2020; Volery et al., 2020) either directly, through grazing, browsing, hybridization or indirectly, through competition or transmission of diseases (Volery et al., 2020).

The aoudad, or Barbary sheep *Ammotragus lervia*, is a mountain ungulate native to North Africa and extensively commercialised for game hunting between the late 19th and the early 20th century in Europe (Spain, Croatia, Italy, and Germany), South Africa, United States and Mexico (Gray, 1985; Cassinello, 2000, 2015; Mori et al., 2017; Cassinello et al., 2022). As a generalist herbivore, aoudad can easily adapt to new habitat conditions (Pinero and Luengo, 1992), and while most introduced populations have expanded their number and distribution, the species is threatened in its native range (Vulnerable IUCN, Cassinello et al., 2022). Currently, in Europe wild populations of aoudad can be found in Italy (Mori et al., 2017), Spain (Cassinello et al., 2022), Croatia (Prpić et al., 2020; Gančević, 2022) and France (Cugnasse and Tomeï, 2016), with low genetic diversity (Stipoljev et al., 2021). The first introduction of the aoudad in Italy dates back to 1920, when it was imported in some hunting reserves in the northern part of the country (Zammarano, 1930). Since then, free-ranging animals have been reported in Lombardy (Gagliardi et al., 2008; most likely extinct see Martinoli A. in Stipoljev et al., 2021), and Liguria (Pelliccioni Raganella et al., 2013; Mori et al., 2017; Pastorino et al., 2017). The first record of aoudad in Liguria was a picture of a subadult male in the Beigua Natural Regional Park in the southern slope

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of the Park, posted in June 2009 in a nature forum (Natura Mediterraneo, 2009), but only discovered in 2017 (Pastorino et al., 2017). The aoudads likely escaped from a hunting reserve in the Ponzone Municipality (Alessandria Province, Piedmont), where they were introduced for game purposes back in the 1980s Gagliardi et al., 2008; the reserve is located some 16 km NW from the Ligurian population core area. However, there is no definite and documented evidence of the relationship between individuals present in the protected area and the hunting reserve but, to the best of our knowledge, the species was not present anywhere else in Liguria or in Piedmont. Since the species was first detected, several opportunistic observations have been collected, also from hikers Pastorino et al. (2017). Moreover, a large-scale camera trap study aimed at monitoring the wolf *Canis lupus* in the entire Park, yielded a naïve occupancy of aoudad of 0.02 (2/100 sites, Fasano et al., 2013), in a restricted area in the southern slope of the Park, as apparently confirmed by block counts conducted with volunteers in 2017 (Pastorino et al., 2017).

Aoudad mainly inhabit semi-arid lands, where they select steep and rocky slopes, scrublands and mountain forests, across a wide altitudinal gradient (Šprem et al., 2022). Their activity rhythm typically follows a bimodal pattern (Šprem et al., 2022). As the species has been introduced into a variety of different habitats, evaluating and comparing habitat selection and activity rhythm in different contexts (Prpić et al., 2020), may provide insights into the potential for competition with native as well as with alien ungulates (Pascual-Rico et al., 2020; Fedele et al., 2022), and it provides useful information for management purposes.

We studied the population dynamics of the aoudad population that inhabits the Beigua Natural Regional Park, Liguria, between the provinces of Genoa and Savona, north-western Italy. The aims of this work were: (i) to reconstruct the history of this population, (ii) to describe the demographic population trend using camera-trap data, and (iii) to explore the habitat preferences of extant aoudads, as well as (iv) their activity patterns.

Materials and Methods

Study area

The Beigua Natural Regional Park (8715 ha) is located on the Beigua massif. The study was conducted between 2017 and 2020 over the entire southern slope of the Park (Fig. 1), at an elevation of 260 - 1100 m a.s.l. This area was selected based on information about aoudad presence, collected between 2009 and 2017 (Pastorino et al., 2017). The southern slope of the park is characterised by steep slopes, cliffs, and valleys carved by seasonal streams typical of a Mediterranean climate. Vegetation is mainly represented by Maquis shrubland at lower elevation, with mixed and coniferous woods, dominated by alien Austrian or black pine *Pinus nigra*, and secondary meadows at higher altitudes. A network of trails crosses the Park.

Data collection

In the first phase of the fieldwork, based on prior information (Pastorino et al., 2017), we focused on the species core-area (i.e., the area most used by aoudads, Fig. 1). Here, between 2017 and 2018, we systematically placed 10 infra-red camera-traps (Tab. S3) along an altitudinal gradient. Then, between 2018 and 2019, the entire study area was sampled (hereafter defined as systematic sampling, Fig. 1 and 2) by using 16 cameras: six cameras were deployed in the species core area, while five were used in each of two larger external sub-areas (Fig. 2), and they were moved in blocks every 30 days to increase the number of sampled sites (TEAM Network, 2011; Rovero and Zimmermann, 2016). Thus, 46 sites were sampled (6 in the core area and 20 for each external sub-area, Fig. 2); to assess potential seasonal difference in distribution, the sites were sampled twice: each sampling session lasted four months, the first from June to September 2018, and the second one from October 2018 to February 2019. The sampling sites in the external sub-areas were selected by creating a randomly placed regular grid, with squared cells of 500 m and then choosing a subset of grid nodes based on their accessibility (Rovero and Spitale, 2016) and elevation, to create elevational transects. In 2019 and 2020 we just sampled the core area due to cost limitations and camera traps were located in previously used sites for comparison purposes. Although the number of cameras changed each year we strove to maintain the same sampling sites of the previous years as much as possible within the species core area. In all the sampling phases cameras recorded 60 seconds long footage, then being inactive for 30 minutes in order to prevent battery drainage. Thus, given this 30 minutes minimum interval between subsequent videos, they were considered as independent events.

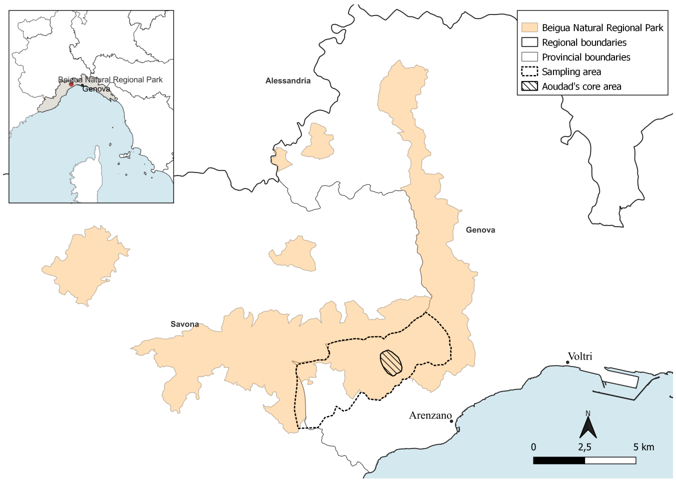

Figure 1 – Study area, Beigua Natural Regional Park in yellow. The dashed line depicts aoudad's core area sampled in 2017-2020, the dot line the sampling area of 2018-2019 (systematic camera-trapping, see Fig. 2).

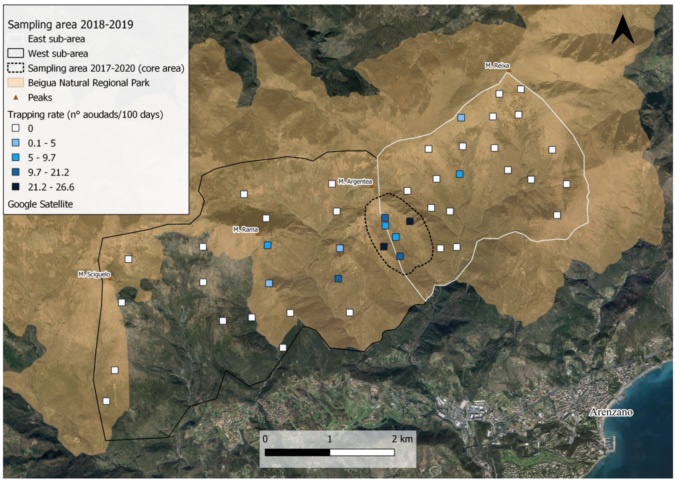

Figure 2 – Sampling areas and camera traps position in 2018-2019 sampling phase (shown by a dot line in Fig. 1), whose data were used to assess distribution, habitat selection and activity rhythm of aoudads.

Minimum population size and abundance trend

All data collected between 2017 and 2020, as well as previous data gathered since the discovery of this population via camera traps (Fasano et al., 2013) and also by block counts in 2017 (Pastorino et al., 2017), were used to describe the species distribution within the Park (including also opportunistic data, mainly collected by hikers), and to estimate the minimum population size for each year. Conversely, only data collected by camera traps in the core area from 2017 to 2020 were used to assess a relative abundance trend on a subset of sites repeatedly sampled over the years, in order to increase comparability. We calculated the minimum population size as the highest number of individuals of a certain age class and sex recorded together in the available videos in every annual interval, using pooled data regardless of the location of the camera trap because we considered this a suitable time interval to describe constantly changing wild populations (births, deaths, emigrations, immigration, etc.) in a sufficiently accurate way. Age and sex classes of adult animals were determined following Cassinello (1997). Some male aoudads had distinctive marks, such as horn scrapes, scars, and swollen areas of the body that made them recognizable (Fig. S2), thus the minimum number could be estimated by counting identifiable animals. New-borns can be easily recognized since they have no horn tips emerging, thus the minimum number for each year was estimated via the largest group simultaneously observed and by comparing dates of first observations: a different new-born was counted exclusively if it had been observed at least one month after the previous one, when horn tips emerge (Cassinello, 1997). This allowed to refine the estimate of adult females considering the 5.5 months of gestation time the minimum time-lapse between birth for the same female (Cassinello and Alados, 1996).

To assess the population trend, for each camera trap site within the core area, monitored in different years, we calculated a trapping rate per year accounting for group size, i.e. total number of recorded aoudads divided by total effective working days for each camera (Palmer et al., 2018; Ferretti et al., 2023). We fitted generalized mixed models using the *glmmTMB* package (Brooks et al., 2017) in R (R Core Team, 2020; RStudio Team, 2020), with the total number of aoudad recorded by each camera trap per year within the core area of the species as the response, accounting for different sampling effort by adding the logarithm of camera trap days as an offset (which essentially allows to model aoudad counts as a trapping rate), and the different sampling years (n=4, 2017-2020) as independent variable; camera site ID was fitted as a random intercept, since some sites were repeatedly sampled in different years. The *genpois* family distribution (generalized Poisson) was the best fit to the data, based on preliminary data exploration. Model residuals were checked for potential overdispersion using the *DHARMa* package (Hartig, 2020). To account for multiple comparison among years (Bretz et al., 2011), a post hoc test was performed to obtain pairwise comparison among each sampling session, using the *glht* function (with Tukey contrasts) of *multcomp* package (Hothorn et al., 2008). Next, we repeated the analyses separating aoudads older than 1 year from new-borns, to assess the trend in both age classes.

Habitat selection

To assess habitat selection we used data collected during systematic sampling carried out from June 2018 to February 2019, analysing how the trapping rate recorded by each camera trap (see above) was affected by environmental factors. We fitted generalized mixed models using the *glmmTMB* package (Brooks et al., 2017): the total number of aoudads recorded by each camera trap was fitted as the response variable, accounting for different sampling efforts by adding the logarithm of camera trap days as an offset. Each camera trap site was sampled twice, in different seasons (spring/summer and autumn/winter), thus the sampling session was added as explanatory variable and camera site ID as a random term. The *genpois* family distribution (generalized Poisson) was the best fit to the data, based on preliminary data exploration. Spatial correlation among camera trap sites was assessed using the Mantel test for each sampling season and both day and night data, with nonsignificant results. Environmental variables (explanatory variables) were extracted using QGIS software version 3.8 (Quantum GIS Development Team, 2020). For each camera trap site, elevation (m a.s.l.), distance from the nearest trail (m), and distance from the nearest stream (m) were obtained. Moreover, other environmental features were extracted from buffers of different sizes: 50, 100, 200, and 400 m. Variables included mean slope (°), roughness, aspect (Northness and Eastness, in radians), and cover (%) of: coniferous forest, deciduous forest, meadows and bushes. We then fitted a full model for each buffer of different radius and compared models via AICc values. The model with the 400 m buffer had the lowest AICc value and was therefore selected for further analyses. We checked for collinearity among predictors, and since slope and roughness were highly correlated, only the former was used after the AICc comparison. All independent variables were standardized. Several models (n=16) were fitted with different combinations of covariates, testing a quadratic effect of elevation and interactions between variables. Models were then ranked according to AICc values and since the best 3 models had a ΔAICc<2, they were averaged through *MuMIn* package functions (Burnham et al., 2011) to obtain final estimates. Model residuals were checked for potential overdispersion using the *DHARMa* package (Hartig, 2020).

Activity rhythm

To determine the daily activity of aoudads we used data collected during the systematic sampling (2018-2019); the time when animals were recorded in independent events was analysed using the packages *plotrix* (Lemon, 2006) and *chron* (James and Hornik, 2022), following Rovero and Spitale (2016). The analysis was based on the same data used to assess habitat selection, as explained above. Basically, the aoudad activity pattern was assessed for both sampling sessions by plotting a clock diagram (radial plot) based on hourly counts of events; the effects of daytime and season were also evaluated within the habitat selection analysis.

Mean values reported in the paper are always associated with standard error (SE) estimates.

Results

Our results confirm the species presence in the southern slope of the Park, even though increasing the presence sites toward east and west (Fig. 2), compared with previous data (Fig. 3). In 2019, moreover, some individuals (including also a female with a subadult) were opportunistically observed in the northern slope of the Park, but never seen again (Fig. 3).

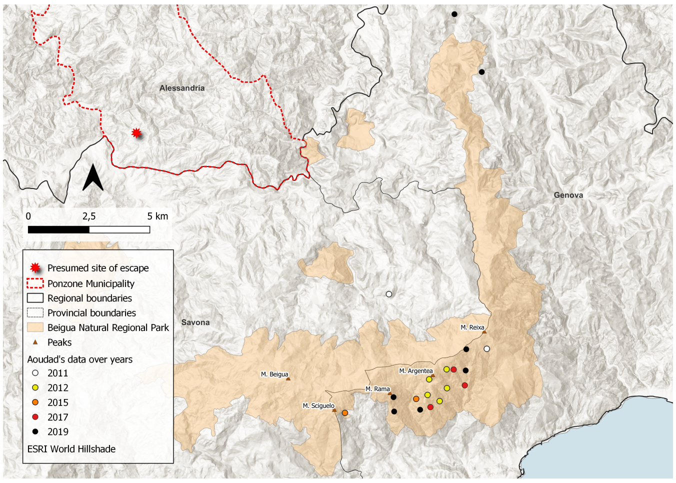

Figure 3 – Presence data of aoudads in the Beigua area over the years. To improve clarity, not all data are shown in the core area; points represent areas in which aoudad presence was progressively discovered (observations in the northern site of 2011 and the westernmost one of 2015 have never occurred again). The first observation of 2009 lacks of coordinates, but it was most probably in the southern slope.

Minimum population size and abundance trend

Overall, the camera-traps data used to estimate minimum population size were collected during 14.652 working days from 2012 to 2020 (including 8614 days in 2011-2013, Fasano et al., 2013, and 369 in 2017, Pastorino et al., 2017), resulting in 423 videos of aoudad, which recorded 869 individuals in total (Tab. 1). The subset of data used to calculate the population trend from 2017 to 2020 (Tab. 2) comprised 21 annual data from 11 sites (3358 working days), for a total of 298 aoudad events, recording 646 individuals (561 older than 1 year and 85 kids).

Both the minimum number of individuals and the rate of aoudads detected by camera traps within the core areas increased over the years (Tab. 1 and 2, Fig. 4). In 2012 the minimum population size was 9, increasing to 20 in the subsequent estimate in 2017. In the following years the minimum population estimate has slightly increased, reaching 23 individuals in 2020. The rate of camera-trapped aoudads significantly increased between 2017 and 2020 both for individuals older than 1 year and kids less than 1 year old. Post-hoc Tukey contrasts applied to the fitted models showed significant pairwise differences in the trapping rate of individuals older than one year: the 2017/18 estimate was lower than the estimate in 2019 (difference=0.80, SE=0.30, z-value=2.64, p=0.041) and in 2020 (difference=1.28, SE=0.30, z-value=4.24, p<0.001), and the estimate in 2018/19 was lower than that of 2020 (difference=0.98, SE=0.25, z-value=3.90, p<0.001). Kid trapping rates were significantly different only between 2017/18 and 2020 (difference=1.44, SE=0.48, z-value=2.97, p=0.016). Both the model with aggregated age classes (i.e. total number of aoudads) and the model without kids showed significant differences among years, as detected by Tukey post-hoc test. On the contrary, group size did not show a significant trend over the last four years of sampling (Tab. 1).

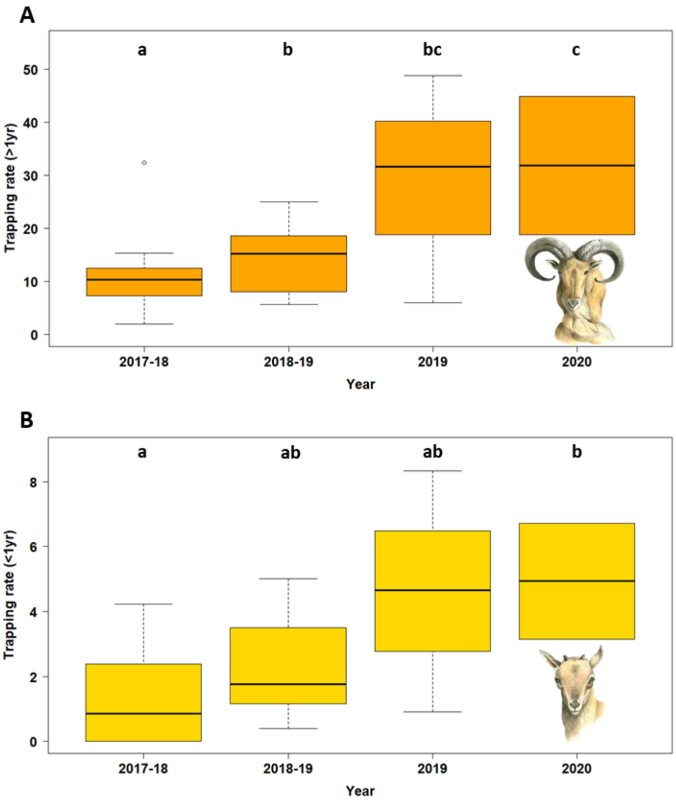

Figure 4 – Boxplots of the aoudad trapping rates (raw data, n° aoudads / 100 days) calculated from camera traps sites within the species' core area in different years for A) adults and B) new-borns. When panels have different letters, their values are statistically different at the 0.05 level by post-hoc Tukey test..

Habitat selection

Habitat selection was evaluated on a dataset of 113 events, recording 240 aoudads in total, collected over 3503 working days from 45 replicated sites (45 during the first sampling session, 41 during the second one, due to theft and malfunctioning of cameras). Overall, aoudads were recorded in 12 of 45 sites distributed along the southern slope of the Park (naïve occupancy = 0.27, with no difference between seasons): the species was detected most frequently in the core area, but also by some cameras toward east and west (Fig. 2). Slope had a strong positive effect on the number of camera-trapped aoudads, mostly recorded in steep areas (>30°); also daytime had a clear effect with higher numbers of aoudads camera-trapped during the day than during night (Fig. 5 and 6; Tab. 3). The other variables had confidence intervals (CI) overlapping zero, and their effect was negligible (Tab. 3). Nevertheless, the quadratic effect of elevation, as well as the effect of coniferous forest cover, were strong: the probability of aoudad presence reached a maximum at intermediate elevation and showed wide variance at higher sites (Fig. 5); number of aoudads also seemed to increase where the 400 m buffer comprised cover of coniferous forest higher than 50 % (Fig. 5). Conversely, distance from the closest stream and trail did not have a strong effect on the number of aoudads (Tab. 3). Coniferous forest appeared in only one of the 3 best models, while distance from paths and water in two of them; slope, daytime and elevation were included in all 3 best models (Tab. S1). Models including season were not ranked among the best by AICc comparison, and indeed there was no difference in number of recorded aoudads between the two seasons (Tab. 4 and *Activity rhythm*).

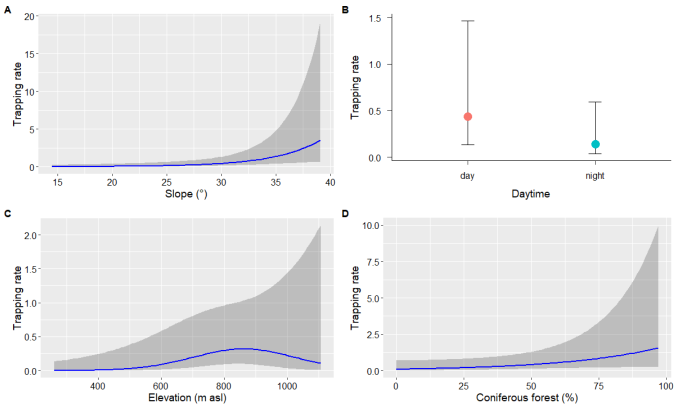

Figure 5 – Marginal effects of different explanatory variables on trapping rate of aoudads recorded by camera traps during the 2018-2019 systematic sampling (400 m buffer): A) Slope B) Difference between day and night C) Elevation D) Cover of coniferous forest. Confidence intervals are shown..

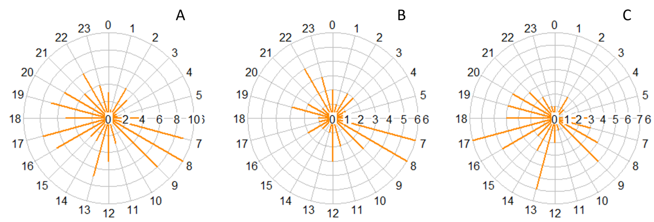

Figure 6 – Clock diagram of time of video recordings in 2018-2019: A) cumulative data from the entire 2018-2019 sampling season; B) first sampling season (spring-summer); C) second sampling season (autumn-winter). Numbers on the circumference indicate hours, numbers on the horizontal line the total of independent videos.

Activity rhythm

The most frequent observations were recorded in early morning or late afternoon, but there were many events at other times of the day (Fig. 6). Aoudads were mostly camera-trapped during daytime (mean number by camera trap: day=2.21±0.65 individuals, n=86; night=0.67±0.28 individuals, n=86, Tab. 4). Conversely, there was no seasonal difference: spring/summer=1.54 ± 0.57, n=90; autumn/winter=1.37 ± 0.41, n=82. These results were confirmed by models. The proportion of aoudad observed during day or night was not influenced by season (χ^2=0.004, df=1, p-value=0.95), with a similar higher proportion of diurnal observation (75.45 vs 75.89 %, Tab. 4).

Discussion

Hunting is one of the oldest reasons why species, especially mammals (mostly *Artiodactyla* and *Lagomorpha*) and birds (mostly *Galliformes* and *Anseriformes*), were introduced to areas where they never occurred (Lever, 2005; Charles and Dukes, 2007; Genovesi et al., 2012; Monaco et al., 2016). Aoudads in the Beigua Regional Natural Park are no exception, as they probably escaped from an hunting reserve and formed a population that, while limited in size, has doubled in 10 years, although it is probably confined to a restricted area in the southern slope of the park. In 2019, however, some individuals (including also a fe-

Table 1 – Abundance estimates of aoudad and camera-trapping effort in different years; data from 2012 and 2017 are taken from Fasano et al. (2013) and Pastorino et al. (2017).

		Sampling year					
		2012/13	**2017 (spring)**	**2017/18**	**2018/19**	**2019**	**2020**
Age class & sex	Adult male	3	3	6-7	6-7	8	8
	Adult female	2	5-6	6	4	5	5
	New-borns	2	1	4-5	3	3	2
	Subadult (1-3 yrs)	2	3-4	4	4	5	8
Abundance	Minimum estimate	9#	13#	20	17	21	23
Camera-traps variables	Working days	8614	369	1235*	3503	517*	414*
	N° sites	100	5	10	45	3	2
	Presence sites	2	1	10	12	3	2
	N° events	24	14	107	113	103	62
	N° aoudads	33	32	228	240	203	133
	Group size (mean±SE)	1.38± 0.13	2.29± 0.40	2.13±0.16	2.12±0.13	1.97±0.16	2.15±0.23

Estimates obtained by comparison of camera-traps and direct observations data (Pastorino et al., 2017).
* Some cameras had missing data on working days, thus minimum estimates are likely biased low.

Table 2 – Data used to assess the trend in relative abundance of aoudads (trapping rate: n° aoudads / 100 days), derived from camera traps deployed within the species core area in the Beigua park. The same sites were monitored across the years.

	2017-18	**2018-19**	**2019**	**2020**	**Total**
Camera-trap sites	10	6	3	2	**21**
Working-days	1082	1345	517	414	**3358**
Mean working days	108	224	172	207	/
SE working days	9.61	21.98	44.18	16.0	/
N° events	56	100	68	74	**298**
Total n° aoudads	132	216	141	157	**646**
Aoudads >1yr	119	184	122	136	**561**
New-borns (<1yr)	13	32	19	21	**85**
Trapping rate (total)	12.2	16.06	27.27	37.92	/
Aoudads >1yr	11.0	13.68	23.60	32.85	/
New-borns (<1yr)	1.2	2.38	3.68	5.07	/

male with a subadult) were observed in the northern slope of the Park, suggesting a possible increase in distribution.

Although the average group size in different years was almost constant, the model accounting for both capture rate and group size suggests a growing population trend, thus driven by an increased capture rate. It should be noted that mean group size was 5.5 individuals for native populations of aoudads in Tunisia (Ben Mimoun et al., 2016), while the Ligurian population has currently a lower value, slightly above 2.

Trapping rate applied to large-bodied, non-migratory herbivores have proved an effective index of abundance (Carbone et al., 2001; O'Brien et al., 2003; Rowcliffe et al., 2008; Tobler et al., 2008; Rovero and Marshall, 2009; Palmer et al., 2018; Ferretti et al., 2023). Unfortunately, we could not validate our trapping rate estimates with density estimates obtained by independent methods (as suggested by Palmer et al., 2018; Ferretti et al., 2023), due to lack of funding and personnel.

Table 3 – Effects of covariates on total number of aoudads recorded by camera-traps in 2018-19. Estimates (standardized values) were obtained by conditional average of the 3 best models selected by AICc comparison. In bold variables with CI not overlapping zero.

	Estimate	**SE**	**CI 2.5 %**	**CI 97.5 %**
Intercept	-5.09	0.68	-6.42	-3.75
Slope	**1.43**	**0.51**	**0.44**	**2.43**
Daytime: night	**-1.17**	**0.36**	**-1.87**	**-0.47**
Distance from closest path	-0.10	0.34	-0.76	0.56
Distance from closest stream	0.45	0.28	-0.09	0.99
Elevation	8.52	9.03	-9.19	26.22
Elevation^2	-13.87	7.09	-27.76	0.02
Coniferous forest	0.99	0.55	-0.09	2.08

Table 4 – Total number and proportion of camera-trapped aoudads during 2018-2019 systematic sampling, depending on season and daytime.

Season	**Day (%)**	**Night (%)**	**Total (%)**
Spring/Summer	105 (42.3)	31 (12.5)	136 (54.8)
Autumn/Winter	85 (34.3)	27 (10.9)	112 (45.2)
Total (%)	190 (76.6)	58 (23.4)	248 (100)

Currently, the population size of aoudad in Beigua Park is at least 20-25 individuals. Although the estimated population size is small, it is interesting to note that in other areas, large and stable populations have developed from a small number of aoudads: e.g. in Murcia (Spain), the population increased from 36 aoudads in 1970 to 2000 animals in 1991 (Cassinello, 1998); in Texas, 31 aoudads were released in Palo Duro Canyon in 1957 (DeArment, 1971), and in 1970 the population reached 2500 animals (Simpson et al., 1978); in Croatia, the current population of 140 animals originated from five individuals illegally released (Lazarus et al., 2019). The numerical expansion of our study population could be limited by several potential limiting factors, including predators such as wolf (Gančević, 2022) and, especially for kids, golden eagle *Aquila chrysaetos* (Nardelli, 2017), fox *Vulpes vulpes* and wild boar; the role of poaching cannot be ruled out, and low genetic diversity due to founder effect and isolation (Stipoljev et al., 2021) may also limit population size. The population seems to be well structured, including animals of all sex and age classes, and twin births were documented. New-borns have been observed across several months during the study period: births occurred not only in spring, as usual for this species, but also in late summer (as reported in the US Gray and Simpson, 1982, and in captivity Abáigar et al., 2012), probably because the aoudads are not as photoperiodic as native ungulates in temperate zones, but the breeding season is conditioned by the weather, in particular rainfall, as for ungulates in tropical areas (Ogutu et al., 2014). The much higher rainfall and consequent water (and food) availability in this area compared with the native range probably explains the wider timeframe of births (late February-August). Based on birth date, mating should probably occur between September and March.

The habitat selection and activity rhythm of aoudad in Mediterranean regions have been investigated in some European countries such as Spain (Cassinello, 2000; Acevedo et al., 2007; Pascual-Rico et al., 2020) and Croatia (Prpić et al., 2020; Šprem et al., 2022), but also in native populations (Ben Mimoun et al., 2016). Our results are in line with previous findings: at large scale, aoudads selected the southern and warmer part of Beigua Park, while at finer scale they selected the steepest rocky slopes at intermediate altitudes, where bare rocks are alternated with woodland, shrub areas and small clearings. The species' agility allows the aoudad to take advantage of inaccessible and rugged terrain, where it can elude terrestrial predators (Cassinello et al., 2022), avoid human disturbance, wean the offspring, and seek shade during the warmest months (Johnston, 1980). The dominant vegetation in the study area is coniferous woodland, mostly of alien pines: the southern slope of the park has relatively young forests in which the undergrowth is developed and provides food and shade for a generalist herbivore such as the aoudad. The scarcity of observations collected at the lower and summit elevations of the study area may be due to the different types of vegetation: at lower elevation the dominant vegetation is dense Mediterranean shrub, which could limit both the movements of this large herbivore and the camera-traps activation range; on the contrary, at higher elevation secondary meadows are dominant and are sometimes used for feeding, but they lack sheltered areas from the sun and do not provide the necessary protection from predators due to less steep slopes, especially on the mountains wide watershed. The distance from streams had no consistent effect on detection, probably due to the aoudads' ability to obtain water just from feeding (Cassinello et al., 2022) and widespread occurrence of small streams in the area, even though seasonally. Despite this, a camera trap deployed for years by a small pond within the core area collected several videos of bathing aoudads of all ages, in different seasons (*Supplemental materials*); this is consistent with other studies on the species (Etchart, 2021).

Unlike other ungulates present in the study area, e.g., the nocturnal wild boar (Bieber and Ruf, 2005) and the crepuscular roe deer, aoudad is active mainly in the daytime. This activity rhythm has already been observed in aoudads (Prpić et al., 2020) and other ungulates (Darmon et al., 2014; Centore et al., 2018), for which photoperiod regulates endogenous processes (Walton et al., 2011). It is interesting to note the difference in the number of animals observed during day or night, with larger groups being generally composed of females with offspring (nursery), probably limiting night-time movements in favour of daytime ones, for anti-predator reasons (Prpić et al., 2020). The season does not seem to affect animal observations, possibly due to food and water availability and the large number of shelter areas on the territory (rocky inlets, shrubs, forest patches), limiting the area used by the animals. It would be interesting to account for sex-specific patterns in the analyses, in order to explore sexual segregation as suggested by previous studies (Habibi, 1987; Ben Mimoun et al., 2016; Pastorino et al., 2017).

Recent studies integrating the concepts of risk assessment and risk management for potentially invasive species (Booy et al., 2017, 2020; Volery et al., 2020) suggest that the aoudad is not an extremely dangerous alien species in terms of spread (low dispersal), impact on biodiversity and human well-being, but could be a threat to some Mediterranean habitats (Bertolino et al., 2020), even though this does not seem to occur in mainland Spain, where there is no empirical evidence of any negative impact on native fauna or flora (Cassinello, 2015, 2018) and the diet is comparable with that of autochthonous ungulates (Perea et al., 2014, 2015; Fernandéz-Olalla et al., 2016; Velamazán et al., 2017). In our study area also feral goats are present, probably exerting a similar effect on vegetation. Conversely, strong negative impacts of aoudads were detected on islands' vegetation, where ungulates were naturally absent (e.g. La Palma, Canary islands , (Garzón-Machado et al., 2012). Studies on aoudad's interaction with other ungulates, such as bighorn, mouflon, mule deer *Odocoileus hemionus*, and Iberian wild goat *Capra pyrenaica*, showed diet and habitat overlap, even if this does not necessarily translates into competition (Simpson and Gray, 1983; Acevedo et al., 2007; Sicilia et al., 2011; Miranda et al., 2012). In fact, Cassinello (2018) highlights how Iberian wild goat, the closest native ungulate in Spain, have expanded in areas already occupied by aoudads, in some cases even apparently displacing the alien species. The aoudad was considered a generalist herbivore (Bounaceur et al., 2022), combining grazing and browsing, but recent studies on feeding habits in several countries found a selection for forbs and grasses, suggesting it is primarily a grazer (Miranda et al., 2012; Ben Mimoun et al., 2015; Bounaceur et al., 2016; Lazarus et al., 2019; Bachiri et al., 2021), with an effect of woody plants similar to native species (Velamazán et al., 2017), thus it could be beneficial for the conservation of open areas in Mediterranean habitat (Cassinello, 2018), where grazing has generally positive effects for biodiversity conservation (Sartorello et al., 2020).

In 2014 the European Union adopted a regulation on the prevention and management of the introduction and spread of invasive alien species (EU Regulation 1143/2014). Whether the alien aoudad should be defined invasive, i.e. a species exerting negative effects on ecosystems (Jeschke et al., 2014) or not, requires solid scientific evidence of its ecological impacts. The aim of our work was to determine the minimum population size, numerical trend, use of space and time in an introduced population; although it was not the objective of the study, we did not notice a clear impact of this population on the ecosystem or on wild populations. Aoudad is a threatened species in its native range of distribution, and it has been suggested that the introduced populations could act as reservoirs, if no harmful effects are detected in the ecosystems (Garzón-Machado et al., 2012; Velamazán et al., 2017; Cassinello, 2018; Pascual-Rico et al., 2020). It is worth pointing out that these animals are located within a protected area whose main task remains the conservation and protection of the local natural species and habitats. Prevention is an absolute priority and avoiding the establishment and spread of new species greatly reduces the risk that they will become invasive (Genovesi and Shine, 2004; Finnoff et al., 2007). It is therefore of fundamental importance to support and encourage monitoring activities, assess the ecological effects of this alien species and consequently evaluate the most appropriate management solution. In this respect, species of conservation interest for the park should be monitored and protected from the presence of alien species. Dietary studies of aoudad in the park should be conducted, together with an analysis of the competition between this and other species of ungulates.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Model averaging of the 3 best models, out of 16 compared by AICc. All models had working days as an offset and camera trap site as random intercept.

Figure S2 Examples of morphological features that allowed individual identification of adult males.

Table S3 Camera traps models used.