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Cover: Leaves and fruits of *Terminalia arjuna* in water colour artwork on cold pressed water colour paper by Bhama Sridharan.

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ARTICLE

Social structure and ecological correlates of Indian Blackbuck *Antilope cervicapra* (Linnaeus, 1758) (Mammalia: Artiodactyla: Bovidae) sociality at Point Calimere Wildlife Sanctuary, India

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Abstract: Indian Blackbuck's social system is fluid and composed of distinct groups. Information on age-sex association, temporal stability, and socio-ecological correlates are scarce. For establishing a baseline information on these, we studied the Blackbuck population at Point Calimere Wildlife Sanctuary, southern India, aimed at understanding the (i) social structure, (ii) association patterns, temporal stability and (iii) socio-ecological correlates related to predation, season, and anthropogenic covariates. Focal herds were observed following scan sampling during 2017–2019. Female herds and territorial pseudo-harems spread tightly, while mixed herds were spread in different degrees. Bachelor herds were loose or scattered with small herds. Dyadic associations of female herds were stronger and more stable than mixed-sex herds and pseudo-harems, but males were in flux. Both grasslands and habitat openness were associated with higher levels of female sociality, indicating their importance in foraging, sociality, and predator vigilance, to which proliferating invasive *Prosopis juliflora* poses a detrimental effect. The presense of sympatric invasive species and lower level of anthropogenic activity was another significant covariate that influenced resource choice grouping, fission-fusion, and ultimately association dynamics. To help answer broader questions about the blackbuck's sociality, and its socio-ecological environment that drive its association patterns, we present here some baseline data on the species from a coastal forest. We suggest control of invasive species and more detailed societal studies to arrive at conservation and management clues through understanding evolutionary and ecological basis of sociability of the antelope species.

Keywords: Association, conservation, covariates, dyadic, herds, fission-fusion, invasive species, predation, temporal stability.

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Author contributions: The study was conceived and designed by NB. SA, SS, and SG all worked on the project in the field. SA performed analyses and led the writing. NB supervised the research; he also reviewed the manuscript's final version.

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INTRODUCTION

The ecology, behaviour, and population dynamics of a species can be better understood by looking at the society in which it exists (Whitehead 1997). A society is suggested to be composed of three interrelated components: (1) the social organization, (2) the mating system, and (3) the social structure, referring interactions and relationships among dyads of society (Kappeler & van Schaik 2002). Herds are fundamental to ungulate social structure. Social groups range from short-term associations (foraging groups) to long-term socially cohesive units (communal rearing groups) (Parrish et al. 1997; Krause et al. 2002). Social group variation may reflect a trade-off between fitness benefits and costs of decision to joining or leaving groups. These benefits and costs can be influenced by socio-ecological conditions and shared behavioural strategies, which cause variation in sociality. It may also be a response to predation (Hamilton 1971) and social foraging (Rieucau & Giraldeau 2011). Intrinsically, social groups may stratify based on age, relatedness, and sex (Pérez-Barbería et al. 2005).

Group membership in social mammals, which undergo frequent changes due to high fission-fusion dynamics, remains poorly understood (Couzin 2006; Smith et al. 2015; Ruczyński & Bartoń 2020). According to research on vertebrate sociality, factors like age (Michelena et al. 2008), relatedness (Wolf et al. 2011), sex (Pérez-Barbería et al. 2005), and predator pressure (Hamilton 1964, 1971) are key socio-ecological determinants that influence the strength and stability of an association (Janson 1986). The dynamic nature of fission-fusion societies provides an ideal framework for testing socioecological theory, which identifies ecological factors that drive variation in social behaviour. These can provide key insights into large-scale evolutionary processes. Temporal-spatial fluidity is thought to confer reproductive or survival benefits, allowing individuals to exploit their environment and reduce intraspecific competition (Webber & Vander Wal 2018). When groups are fluid, as in fusion-fission species (Kummer 1971), the mechanisms of association are not well understood. However, recent studies have shown their social structure is non-random and highly structured (Lusseau et al. 2003; Croft et al. 2005). When comparing the biological benefits and costs of group living in various habitats, the benefit-to-cost ratio may be greater in open habitats (e.g., grasslands) than in closed woody habitats (Fryxell et al. 2014)

Social structure related studies are rare on Indian antelopes, e.g., Four-horned Antelope (Baskaran et al. 2011; Meghwal et al. 2018); Blue Bull or Nilgai, and Chinkara (Bagchi et al. 2008; Dookia & Jakher 2013; Akbari et al. 2015). Earlier studies on Blackbuck sociality go in-depth on behavioral ecology, territoriality or lek mating system, e.g., the cost and benefits, and environmental factors influencing them (Mungall 1978; Isvaran & Jhala 2000; Isvaran 2003, 2005, 2007). Little is known about their social structure being shaped by age-sex association and temporal stability or determinants of the same. This gap offers an opportunity to examine social associations among herds in the antelope.

This foundational understanding is useful for predicting the persistence of Blackbuck societies, which is a crucial aspect of population biology (Leuchtenberger & Mouro 2008). Because it affects both gene flow and the spatial distribution pattern of the species, it can be used in conservation efforts (Whitehead 1997). Additionally, various limiting factors associated with antelope sociality in the study area would get revealed, allowing for subsequent recommendations to be made to neutralize or minimize their effects.

We studied the population of Blackbuck at Point Calimere Wildlife Sanctuary (PCWS), southern India, aimed at (i) establishing baseline information on social herd composition, size and spreading degree of the species; (ii) determining the patterns of association and temporal stability among and within age-sex classes of the social units; and (iii) investigate if habitat, predation, and anthropogenic factors influence the patterns of association in female dyads (where a dyad is a pair of individuals).

It is hoped that the recommendations made on the basis of the present study are also applicable to blackbuck populations elsewhere with similar conditions or other species with similar sociality. Besides, the new insights into animal societies and socio-ecological pressures, could in turn shed better light on the ecological and evolutionary mechanisms and the need for long-terms studies to comprehend them.

Study area

Point Calimere Wildlife Sanctuary is in Tamil Nadu (Figure 1) at the juncture of the Bay of Bengal and Palk Strait. Situated between 10.27° N, 79.83° E and 10.33° N, 79.84° E at a low elevation zone (4–9 m). The area extends over about 26.5 km^2. The reserve, established in 1967 has been noted as a Blackbuck area in scientific records since 1800s (Jerdon 1874). It receives an average of 1,366 mm of rain a year, and summer temperatures peak at 37^{o}C and dip to 21^{o}C. Daily humidity can be as low as 68% and as high as 82%. Humidity can reach 90% on foggy winter mornings (Jan–Feb) (using climatic data

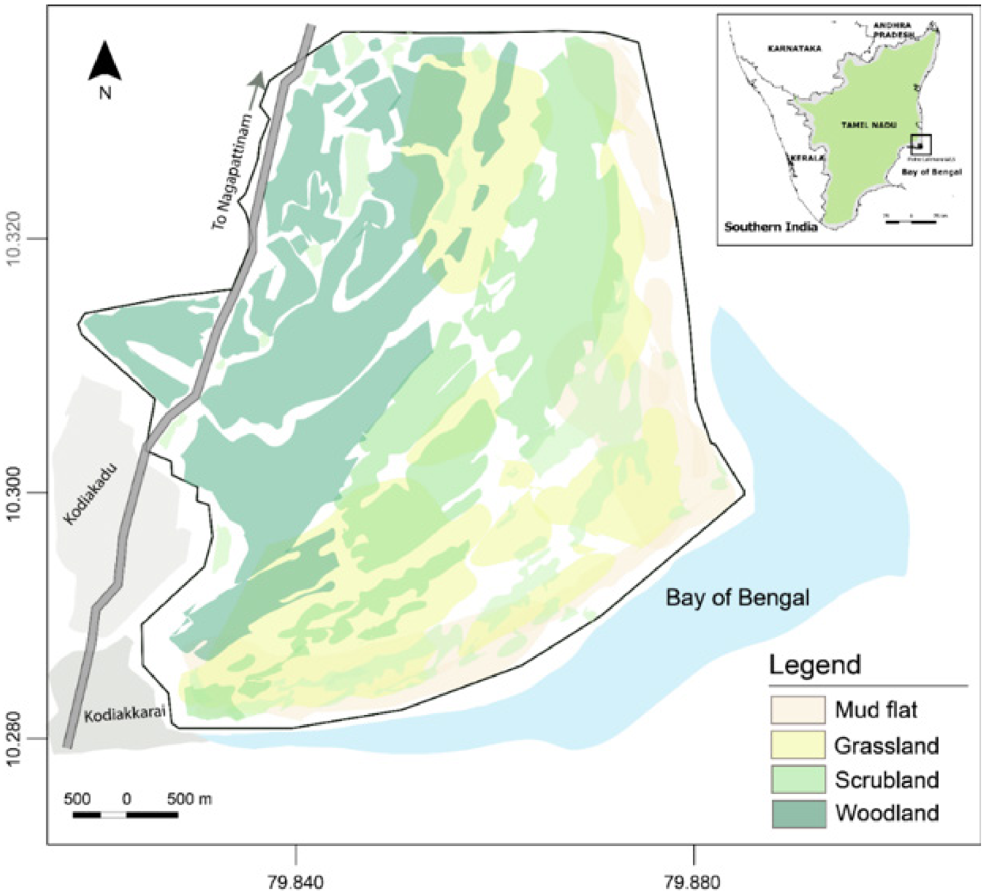

Figure 1. Study area (Point Calimere Wildlife Sanctuary).

from Kodikkarai Light house 2 km apart). This area lacks a perennial water supply, but rains replenish natural and man-made water sources.

The sanctuary's core is tropical dry evergreen, but Blackbuck avoid its thick wood and graze near natural and man-made water holes. The grassland habitat of PCWS includes mainland sea beach grassland and salt marsh grassland, home to Blackbuck and the feral horse. *Prosopis juliflora* is the only invasive woody plant in the sanctuary. It was introduced in the late 1960s and is reported as harmful to native flora and fauna (Ali 2005; Baskaran et al. 2019). The feral Horse *Equus caballus* and the Chital *Axis axis* are both introduced mammals in the sanctuary and the former is considered invasive, sympatric with the Blackbuck (Krishnan 1971; Baskaran et al. 2016). Villagers are allowed to graze their domestic cattle and goats. Cattles in foraging groups as large as 50 individuals and a mean group size of eight individuals were observed during the sampling and the large groups are thought to disrupt the Blackbucks' social activity. There are also reports that feral/stray dogs threaten the Blackbucks in the sanctuary. Due to its coastal location, the sanctuary has the most human activity in the region, including fishing, firewood collection, and tourist visits (Arandhara et al. 2021).

Study species

The Indian Blackbuck *Antilope cervicapra* is endemic to the Indian subcontinent, historical numbers approximated four million and the species inhabited wherever conditions were favorable (Jerdon 1874; Groves 1972). Presently, they are classified as 'Least Concern' on the IUCN Red List and are protected under Schedule I Category in Indian Wildlife (Protection) Act (1972). The species inhabit in scrub and grassland, and may also penetrate more open parts of predominantly deciduous forests (Prater & Barruel 1971). It is known to be a social species living in with fission-fusion dynamics (Isvaran 2007). The species is territorial, and males are known to exhibit characteristic lek mating strategy. Their social herds are composed of female herds of different age groups, mixed age-sex herds, bachelor herds and pseudo-harem herds that are tended by territorial males.

METHODS

Defining Social groups and Sampling

Herds were defined as the collection of individuals within a 50 m radius who were engaging in the same or similar behavioural activities (Clutton-Brock & Isvaran 2007; Isvaran 2007). Herds were separated by an average of 350 m in space, and within each herd, individuals were categorized according to their age-sex structure. The distance between two herds or from the observer and the angle between the herds were measured by using rangefinder. A trigonometric cosine calculation was done to arrive at the distance between the two herds, which was then averaged. For each herd, the average distance between members was measured, and herd size was calculated using total counts, a method recommended for open-area socially aggregating species (Sutherland 1996; Jethva & Jhala 2004; Isvaran 2007).

The herds were classified into: female-herd, mixed-herd, territorial pseudo-harem, and bachelor-herd (based on Mungall 1978; Jhala 1991). These were then categorized according to their spreading degree. In a 'tight herd'**,** separation between herd members was greater than one body length and less than five body lengths, and a mean neighbor distance was <5 m. In a 'loose herd' the separation was greater than five body lengths apart with <10 m mean neighbor distance. In 'scattered groups' the individuals were spread apart by >10 m and <50 m distance.

Group size

When estimating grouping tendencies, studies on animal sociality suggest that the typical group size, i.e., the group size in which an animal participates on average, is a more useful measure than the mean group size (Leuthold 1979; Clutton-Brock et al. 1982; Jarman 1982). Group size was measured as typical group size experienced by individuals (based on Jarman 1974; see Reiczigel et al. 2008).

Typical group size = $(\Sigma N_g(i)^2) / (\Sigma N_g(i))$, where N_g is the size of each group.

Scan sampling

After three–four weeks of habituating the animals to the presence of observers during December 2017–January 2018, data were obtained by scanning a focal herd for 30 minutes at a distance of 50–150 m, ensuring non-interference with natural behaviours (Altmann 1974). Herds were recognized according to the number of individuals with similar age-sex classes and socializing at proximate locations. One herd observed in the morning from approximately 0600 h to 1200 h, was observed in the afternoon from 1330 h to 1830 h the alternate day and vice versa. During a scan progressing in one direction, behavioural records on an individual and its proximate conspecific, i.e., the nearest neighbor, were recorded, including other variables, mentioned in later section.

In total, 34 focal herds were observed, covering 816 hours of observation (n = 136 days) during January 2018 to June 2019. Data were collected through Animal Observer app (Caillaud 2012) on an Apple® iPad-5th gen (customized for behavioural observations for the Blackbuck). The collected data in the form of sftp (Secure File Transfer Protocol) was exported to a computer and converted in to SocProg (Whitehead 1999) usable format using the animal observer toolbox in R program (R Core team 2019).

Association analysis

Associations were defined based on "gambit of the group" approach, that assumes clustered animals in a herd are in association (Whitehead & Dufault 1999). Physical interactions are difficult to observe in antelopes like Blackbuck and their relatives because they are not "contact animals" but rather "distance animals," maintaining a certain "proximate distance" between each other except during mating, nursing fawns, and males fighting (Hediger 1941; Walther et al. 1983). In such taxa, relationships suggested to be expressed through associations rather than interactions (Whitehead 1999). Further, we considered abstractions of relationships among pairs of individuals to age-sex classes of individual, due to inability to discriminate visually all individuals from a herd reliably during different field days as (i) the animals were unmarked, (ii) there is a chance that an individual can move to a different herd (Perry 1996; Whitehead 2009). To determine patterns of association, age-sex categories were considered when engaged in proximate activities (forming a dyad) within a herd (Owen et al. 2002; Rogers et al. 2004; Möller et al. 2006).

Association data were converted to a binary matrix (0: non-association; 1: association) between two individuals' age sex classes. Simple ratio association index (SRI) was used as the association metric for dyads among age-sex classes of Blackbuck (Cairns & Schwager 1987; Ginsberg & Young 1992). This index was chosen for its accuracy, as it does not double count or average sightings, and is best for small data sets (Ginsberg & Young 1992). The SRI metric is defined as the proportion of time two individuals (or dyad) spent in association (ranges from 0–1) (Cairns & Schwager 1987; Ginsbergand & Young 1992), calculated as,

$$SRI = X/(X+Y_{AB}+Y_A+Y_B)$$

where X is the number of observations during which individual A and B were observed together, Y_{AB} is the number of observation periods during which A and B were observed separate, Y_A is the number of observation periods during which only A was observed, and Y_B the number of observations in which only B was observed. Days were used to define the sampling period, and 30 minute scan sampling for a herd was used to define associations. The simple ratio association matrix was computed to test whether there were statistically significant associations within and among the classes by using a Mantel t-test. The calculation of the association index (AI) and subsequent analyses were carried out in SOCPROG 2.4 (Whitehead 2009) run in the MATLAB computing environment.

Test for preferred and avoided associations

Preferred or avoided associations between sampling periods were examined using permutation tests (Manly 1995; Bejder et al. 1998). This permutation technique was used as significance test for relationship between associations that occur more frequently against the null hypotheses that animals associate randomly or expected by chance (Manly 1995; Bejder et al. 1998). Associations were permuted at 10,000 permutations (at the 0.05 significance level), based on comparisons between observed and random associations. 1:0 matrix was subjected at 1,000 flips, while keeping the herd size and the number of times an individual was seen constant, until the p-value is stabilized within sampling intervals, this is reported to remove possible demographic effects (Whitehead 1999; Whitehead 2008a,b). The observed number of animals was also tested against group size as expected by random association, which was determined using the same permutation method as described above. Preferred associations are identified as animals that were regularly seen in groups (>0.975 of the population) or avoided (<0.025 of the population) than expected by random association.

Temporal stability of association

To address temporal stability of associations of age-sex classes at population and herd level, standardized lagged association rates (SLAR) was used, this metric estimates the probability that two currently associated individuals or age sex will continue to associate after a specified time lag (τ). SLAR estimates were compared to the standardized null association rates (SNAR) to determine whether preferred associations were stable in the population over time. SNAR represents the values associated with SLAR, if animals are randomly associated (Whitehead 2008).

For species where individuals cannot be identified in groups, standardizing the lagged and null association rates is recommended to account for variation in individual and associates within sampling periods (Whitehead 1995; 2008). The temporal association patterns (SLAR) shown by the herds were then fitted into four default social stability models. Interpreted as (i) constant companions (CC): individuals stay acquainted throughout the study period; (ii) casual acquaintances (CA): individuals associate for time, disassociate, and may reassociate; (iii) constant companions and casual acquaintances (CC + CA): the lagged association rate falls but stabilizes above the null association rate. A situation in which units have a permanent core membership but there are also “floaters” who move between units; iv) two levels of casual acquaintances (2CA). This represents the short-term movement of strongly associated individuals among social groups, and the long-term disassociation of these bonds because of movement between social units, shifts in preferred companions, mortality, emigration, or a combination of these. The quasi likelihood Akaike Information Criterion (QAIC) was computed in SocPROG to determine which of these models best fit the data (Whitehead 2007).

Ecological correlates

While scan sampling a herd, apart from noting dyadic associations, ecological variables such as habitat type: grassland, open-scrub; habitat openness: >0.2/<0.2 km^2; sympatric species: feral-horse and cattle (presence/absence); predators: jackal and domestic dogs (presence/absence); anthropogenic-activity (presence/absence); and season (dry-season/wet-season) were noted down. Association index was calculated for each dyad under either category of the ecological variables stratified at population levels. Manly & Bejder permutation significance test was run to arrive at the preferred associations between a covariate category (e.g. habitat type: grassland or open scrub) for within female sex class. To test which covariates significantly influenced associations, we carried out a multiple regression quadratic assignment procedure (MRQAP) test using the “double- semi-partialing” technique for each covariate (predictor variable) and calculated standardized partial correlation coefficients (Whitehead & James 2015), this procedure builds on the Mantel test to examine for a relationship between a dependent matrix and an independent matrix while controlling for multiple independent matrices, all of which are dyadic variables (Dekker et al. 2007).

Further, to understand the effects of multiple covariates on dyadic associations, we run a GLMM using a set of six a priori models based on biology of Blackbuck (Table 9). Each dyad was considered a random effect while the covariates (habitat type, habitat openness, sympatric species, predator, anthropogenic activity, and season) were considered fixed. Models were fit using 'lme4' (Bates et al. 2016) and 'MuMIn' (Barton 2015) packages in R-program. We also constructed the null model (with the intercept only) and used information-theoretic approach for model selection following Burnham & Anderson (2002). Δ (Delta) Akaike information criteria (corrected for small sample size, AICc) values were computed to give the difference in AICc scores between the best model and other models. Model weights (Akaike-weight, Wi) were computed to identify comparative explanatory power of models.

RESULTS

Group composition

The survey yielded 31 herds, each herd varying between 6–38 individuals, totaling 516 individuals, in which 331 females (196 adults, 135 subadults), 95 males (39 adults, 56 subadults) and 90 fawns were observed (Table 1). Most herds were composed by female adults, subadults and fawns, whereas the bachelor herd comprised of few male adults and subadults only. Female herd and territorial pseudo-harem were observed predominantly in the tight spreading degree, with lower mean neighbor distance. Bachelor herd were either loose or in scattered aggregation with the smallest group size, individuals apart at the highest distance between individuals (Table 1). No bachelor herd were found in tightly aggregated groups, while no female-herd and pseudo-harem tend to be in scattered dispersion except when disturbed but, reunited when disturbance ceased. Significant difference was observed in the group size between the Bachelor-herd vs. the following herds: Female-herd (Man Whitney-U = 23, p = 0.025); Mixed-herd (U = 76, p = 0.013); Territorial Pseudo-harem (U = 57, p = 0.032).

Patterns of association

Variation in the association indices was observed within and between the age-sex classes with the highest association values (mean and maximum) usually within the same female age class, this is due to the high-level female-female associations (Table 2), exhibiting female's preferred associates within her cohort group and fawns especially in herds with females age sex. Males of the either age class associated less often with females of the either age and fawns had no or little associations with males. In bachelor herds, there is evidence of adult males associated with other adult males indicated that they are maximum associate of the same age-class. Similarly, subadult males were maximum associates with other subadult males.

For the community levels (herds), within age sex class associations were higher, based on Mantel test, the mean association indices varied significantly between and within age-sex class of Blackbuck, in case of overall population level: t = 8.84, p = 0.001; female herd: t = 2.918; p = 0.0035 and Mixed herd: t = 2.918; p = 0.0035. No significant difference was observed in case of the bachelor and pseudo-harem herds (Mean and max level of associations for each herd given in S-table 1–4).

Preferred and avoided associations

Analysis of the association patterns using permutation tests confirmed that the standard deviation of mean association index for the observed data was significantly higher than the randomly permuted data in the following age-sex classes, adult female-adult female (overall population: p <0.01; female herd: p <0.01; pseudo harem: p = 0.05); adult female-subadult female

Table 1. Summary of group (herd) age-sex composition, neighbor distance and spreading degree of Blackbuck herds.

Herd (no. of herds)	Typical group size	Adults		Subadults		Fawn	Mean neighbor distance (m)	No. of herds with spreading degree		
		M	F	M	F			Tight	Loose	Scattered
Population level (31)	16.3 ± 2.37	39	196	56	135	90	10.65 ± 2.12	13	14	4
Female-herd (9)	18.6 ± 3.47	-	75	-	56	37	7.1 ± 1.57	5	4	-
Mixed-herd (7)	22.1 ± 3.46	5	63	25	36	26	11.6 ± 2.11	2	3	2
Territorial Pseudo-harem (9)	15.5 ± 2.06	9	58	4	43	27	6.7 ± 0.98	6	3	-
Bachelor-herd (6)	9.2 ± 1.06	30	-	22	-	-	97.2 ± 14.59	-	4	2

Table 2. Mean and max level of associations within and between age sex classes for overall population.

Classed by Age-sex	**AF**	**SAF**	**FA**	**AM**	**SAM**
Mean (SD)					
AF	0.19 (0.11)	0.12 (0.08)	0.08 (0.07)	0.01 (0.01)	0.01 (0.01)
SAF	0.12 (0.08)	0.05 (0.04)	0.05 (0.05)	0.01 (0.01)	0.01 (0.01)
FA	0.08 (0.07)	0.05 (0.05)	0.03 (0.03)	0.01 (0.01)	0.01 (0.01)
AM	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.09 (0.05)	0.05 (0.01)
SAM	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.05 (0.01)	0.06 (0.05)
Within associations	0.16 (0.14)				
Between associations	0.06 (0.04)				
Max (SD)					
AF	0.49 (0.27)	0.35 (0.19)	0.24 (0.19)	0.11 (0.10)	0.03 (0.01)
SAF	0.35 (0.19)	0.21 (0.14)	0.18 (0.15)	0.03 (0.02)	0.04 (0.04)
FA	0.24 (0.19)	0.16 (0.15)	0.08 (0.08)	0.03 (0.01)	0.02 (0.02)
AM	0.11 (0.10)	0.03 (0.02)	0.03 (0.01)	0.18 (0.11)	0.08 (0.06)
SAM	0.03 (0.01)	0.04 (0.04)	0.02 (0.02)	0.08 (0.06)	0.15 (0.11)
Within associations	0.42 (0.33)				
Between associations	0.37 (0.19)				
Mantel test	**t = 8.849 (p = 0.001)**				
Matrix correlation	**0.255**				

AF—Adult-female | SAF—Subadult female | FA—Fawn | AM—Adult male | SAM—Subadult male. Values represent mean of simple ratio index, larger value indicated higher level of association.

(overall population: p = 0.02; female herd: p = 0.08); adult female-fawn (overall population: p = 0.01; female herd: p = 0.01; mixed herd = 0.03); subadult female-fawn (overall population: p <0.01; female herds: p = 0.01). Thus, the null hypothesis of no long-term preferred associations could be rejected showing evidence for long-term preferential association among adult and subadult females, but not among females and males (Table 3; S-table 5–8).

At overall population, 49 dyads associated significantly more or less than expected at random over the total duration of the study, out the total, 35 and 14 dyads exhibited preferred and avoided associations respectively, female-female dyads had the most number (21) showing preferred associations and male-male dyads showed the most (five) number of significant avoidances. Similarly, at herd levels: (female herd = preferred: 35, avoided: 12; mixed-herd = preferred: three, avoided: one; pseudo-harem = preferred: 15; avoided: three; bachelor-herd = preferred: 0; avoided: 0). Bachelor-herd indicated that males were at random association (Table 4).

Temporal stability of association

Lagged association rates computed for female-female associations for overall population and female herd were best described by constant companion + casual acquaintances model (CC + CA), in case of mixed herd and pseudo harem, they were modelled as two levels of casual acquaintances (2CA). For all the herds with female age class and at overall population level, female-all associations were formed as constant companion + casual acquaintances model (CC + CA). Male -male and male- all associations exhibited casual acquaintances model at overall population and other herd types except bachelor herd modelled by two levels of casual acquaintances (2CA) (Table 5; Figure 2).

Ecological correlates of Blackbuck sociality

Permutation tests used to examine the influence of covariates on the association between the female sex classes. Significantly higher SD of the observed associations compared to random indicated preferred and avoided associations among these individuals under the influence of grassland habitat type (p = 0.003); more open habitat openness (p = 0.001); absence of feral-horses (p = 0.004); and the absence of anthropogenic activity (p = 0.034). Further, MRQAP tests revealed a similar significant correlation of associations with grassland habitat (r = 0.66; p = 0.001), more open habitat

Table 3. Tests for preferred association for overall population.

Age sex class	Mean association		SD of association		p-value (SD)
	Observed	Random	Observed	Random	
All individuals	0.07	0.07	0.14	0.14	p-value= <0.01
AF-AF	0.19	0.19	0.21	0.2	p-value= <0.01
AF-AM	0.01	0.02	0.05	0.08	0.97
AF-SAF	0.12	0.12	0.15	0.15	0.02
AF-SAM	0.01	0	0.03	0.03	0.95
AF-FA	0.08	0.08	0.15	0.14	0.01
AM-SAF	0.01	0	0.03	0.04	0.99
AM-FA	0.01	0	0.04	0.04	0.91
AM-SAM	0.25	0	0.17	0.17	0.9
SAM-SAF	0.01	0	0.03	0.03	0.83
SAM-FA	0.01	0	0.02	0.02	1
SAF-FA	0.05	0.05	0.09	0.09	p-value= <0.01
AM-AM	0.32	0	0.26	0.27	0.9

If the standard deviation of the mean association indices for the observed data was significantly higher than the random data, then the null hypothesis that there is no preferential association is rejected.

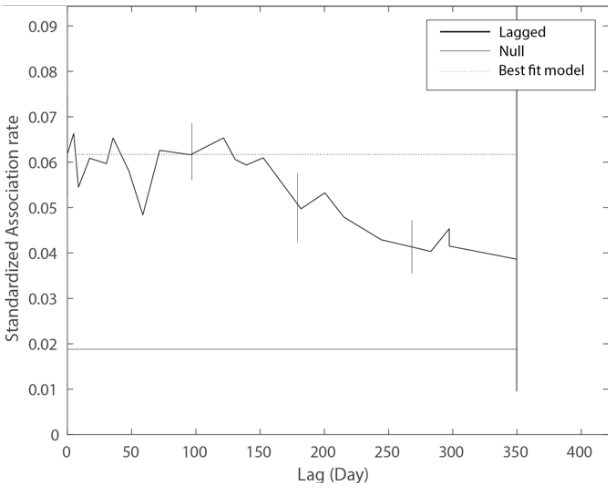

Figure 2. Standardized Lagged Association Rate for individuals recorded for female-female herd. The best-fit model: Casual Acquaintances + Constant Companions (CA + CC) [$0.06+0.02-0.065\tau$], null association rate is included for reference.

openness (r = 0.87; p = 0.001), absence of feral-horses (r = 0.89; p = 0.001), absence of cattle (r = 0.34; p = 0.041), and anthropogenic activity (r = 0.56; p = 0.051) (Table 6).

The best model (model 4) explaining variation in dyadic association included the interaction effects of habitat type * habitat openness + sympatric species * anthropogenic activity + predator * sympatric species. This model accounted for 57% of the AICc weight and indicated a significant relationship between the association strength and the explanatory predictors (The a priori models given in Table 7).

The effect of habitat type [grassland], interaction between habitat type * habitat openness, and anthropogenic [absence] shows positive significance in explaining the association strength. While, habitat type [dry-evergreen], predator [presence], sympatric species [presence], and interaction between sympatric species * anthropogenic activity shows a negative trend (Table 8a,b,c).

DISCUSSION

To help answer broader questions about antelope sociality and the theoretical link between ecological covariates that drive association patterns, we present here some baseline data on the social structure of Blackbuck from a coastal forest. Here we first describe the summaries related to group composition, neighbor distance and spreading degree; then explore the social associations among the age-sex classes of different herd types, know their temporal stability of associations and determine the ecological correlates of sociality.

Group composition

Blackbuck group sizes varied greatly within the study population. Of the 31 herds surveyed, the typical group size ranged around 16.3 individuals at the population level, which is consistent with previous findings in the study area (Jhala & Isvaran 2016). For the most part,

Table 4. Number of dyads associating significantly different from random for the herds studied.

Herd	Preferred associations (p >0.975)	Avoided associations (p <0.025)
Overall population	**35**	**14**
Female-female	21	4
Female-fawn	7	1
Female-male	1	1
Male-male	6	5
Male-fawn	0	3
Female-herd	**35**	**12**
Female-female	27	8
Female-fawn	8	4
Mixed-herd	**3**	**1**
Female-female	2	0
Female-fawn	1	0
Female-male	0	0
Male-male	0	1
Male-fawn	0	0
Territorial pseudo-harem	**15**	**3**
Female-female	8	1
Female-fawn	4	2
Female-male	1	0
Male-male	2	0
Male-fawn	0	0
Bachelor-herd	**0**	**0**
Male-male	0	0

Table 5. Models of temporal stability of Blackbuck herds.

Herd	**Model**	**Best fit**	**ΔQAIC**
Overall population			
Female-female	CC+CA	$0.06+0.02^{-0.065\tau}$	0
Female-all	CC+CA	$0.04+0.02^{-0.065\tau}$	0
Male-male	CA	$0.04^{-0.0002\tau}$	2
Male-all	2CA	$0.03^{-0.24\tau}+0.05^{-0.0002\tau}$	0
Female-herd			
Female-female	CC+CA	$0.05+0.07^{-0.52\tau}$	0
Female-all	CC+CA	$0.04+0.06^{-0.53\tau}$	1
Mixed-herd			
Female-female	2CA	$0.12^{-0.59\tau}+0.06^{-0.001\tau}$	2
Female-all	CC+CA	$0.05+0.18^{-1.11\tau}$	0
Male-male	CA	$0.62^{-0.03\tau}$	0
Male-all	CA	$0.96^{-0.07\tau}$	0
Pseudo-harem			
Female-female	2CA	$0.68^{-0.64\tau}+0.45^{-0.001\tau}$	0
Female-all	CC+CA	$0.56+0.28^{-0.36\tau}$	1
Male-male	CA	$0.51^{-0.0001\tau}$	2
Male-all	CA	$0.05^{-0.0006\tau}$	2
Bachelor-herd			
Male-male	2CA	$-0.03^{-1.2178\tau}+0.08^{-0.0008\tau}$	1

Interpreted as (i) constant companions (CC)—individuals stay acquainted throughout the study period | (ii) casual acquaintances (CA)—individuals associate for some time, disassociate, and may reassociate | (iii) constant companions and casual acquaintances (CC+CA).

larger herds were found in the sanctuary's southeastern portion, generally around the larger grassland extent, where the species can gain a higher level of social and foraging opportunities. Smaller herds were found in patchy grassland interspersed between dry evergreen trees and shrubs throughout the sampling period. Female herds and territorial pseudo-harems were primarily found in a degree of tight spreading, with female herds ranging up to 31 m in mean neighbor distance. While pseudo-harems were even compact at up to 26 m. This can be viewed in light of the habitat availability in which the herds are dispersed and social activity they experience.

Despite maintaining individual distances, the majority of female herds are dispersed closely in open grasslands, scattered through a network of patchy trees and shrubs. Individuals closely clustered together reap social benefits, as explained by cohesion, which is dependent on the motivation of individuals to remain together while maintaining inter-individual distance (Hediger 1955; McBride 1963). Further, greater attraction between individuals of the same sex would make single-sex herds more cohesive and less prone to split than mixed-sex herds whatever the level of activity within the herds (Michelena et al. 2008).

In pseudo-harems, females temporarily stay with a territorial male, their size might be expected to be as the same as that of pure female groups. In a territory, when a herd enters such a territorial mosaic, each buck tries to herd females in his territory, and he cuts out a section of the big herd, the tight spreading is mainly due to the male that ensures the females are within the territory by exhausting himself in an outburst of herding and chasing actions, it is considered to assist with group cohesiveness (Mungall 1978).

Mixed herds were found in all three of the spreading degrees. Fewer herds exhibited tight clustering, while some herds had individuals as far apart as 40 m from one another. In vast expanses of the grassland habitat, wider extent available space facilitated the individuals with the option of spreading out more while still having neighbors (Couzin & Krause 2003).

Table 6. Female preferred or random associations at different covariate categories.

Age sex class	Female-all others					
	Mean assoc.		SD assoc.		p	MRQAP r (p)
	Obs.	Rand.	Obs.	Rand.		
habitat type						
grassland	0.222	0.221	0.375	0.37	0.003	0.66 (<0.001)
open scrub	0.171	0.174	0.219	0.221	0.583	0.48 (0.07)
habitat openness						
less	0.195	0.195	0.23	0.231	0.784	0.19(0.64)
more	0.276	0.275	0.294	0.291	0.001	0.87(<0.001)
feral-horse						
Presence	0.1	0.1	0.138	0.14	0.181	0.11 (0.41)
Absence	0.152	0.151	0.177	0.175	0.004	0.89 (<0.001)
cattle						
Presence	0.194	0.197	0.242	0.242	0.33	0.28(0.054)
Absence	0.169	0.166	0.217	0.217	0.06	0.34(0.041)
predators						
Presence	0.08	0.08	0.117	0.118	0.67	0.27(0.67)
Absence	0.359	0.352	0.416	0.417	0.17	0.39(0.3)
anthropogenic-activity						
Presence	0.261	0.266	0.27	0.271	0.45	0.43(0.086)
Absence	0.364	0.361	0.389	0.388	0.034	0.56(0.051)
season						
dry-season	0.195	0.198	0.204	0.204	0.58	0.37(0.07)
wet-season	0.258	0.254	0.295	291	0.003	0.67(0.061)

Mixed herds have been reported to show an ever-changing mix of individuals. There are "casual herds of variable size and composition forming, breaking up, and reforming at frequent intervals", characteristic of "fission-fusion" society (Conradt & Roper 2005).

Bachelor herd was either loose or in scattered aggregation with the smallest group size, separated at the greatest distance of over 40 m. No bachelor herds were found in tightly aggregated groups, and no female herds or pseudo-harems were found in scattered dispersion except when disturbed but regrouped when the disturbance ceased. Formation of herds are very unstable, However, dyadic relationships among age sex classes were stable. When females interact, they usually avoid contact (Walther et al. 1983).

Table 7. Details of 6 "a priori" models to explain Blackbuck female association strengths.

Covariate-model ID	1	2	3	4	5	6
Habitat type	x		x		x	x
habitat openness	x	x	x		x	
Sympatric species	x		x			x
Predator	x	x	x			x
Anthropogenic activity	x		x		x	
Season	x	x	x	x		x
Habitat type * habitat openness			x	x		
Sympatric species * anthropogenic activity			x	x	x	
Predator * sympatric species			x	x	x	

Female associations

Although female herds are unstable associations, the strength of associations between members of the female sex was greater than that of associations among members of different sexes, indicating that female Blackbucks exhibit sex-based homophily, in which individuals preferentially group with conspecifics of the same sex (Hirsch et al. 2012; Brambilla et al. 2022).

This is consistent with previous findings that adult female-female spatial associations are generally stronger than male-male and female-male spatial associations in different age classes (Carter et al. 2013; Mejía-Salazar 2017). Females who share a home range are said to be more likely to be in the same herd as females who don't. Females may form herd based on their current physiological state, such as those who are nearing the end of their pregnancies or those who are nursing young. Female social bonds may improve reproductive success (Wittemyer et al. 2005). As a result of these social bonds, individuals have easier access to food (Silk 2007), experience less harassment (Cameron et al. 2009), and have lower levels of glucocorticoids (Cameron et al. 2009; Silk et al. 2012). In Blackbucks, the females leave the herd to give birth, and the calf lies out before rejoining the herd for varied amounts of time before rejoining (Mungall 1991). Calves may create crests in the herd, and females of similar age and sub-adults are known to form close bonds. Adult females' spatial associations are expected to strengthen as a result of these actions (Walther et al. 1983).

Male associations

In this study, the strength of associations among males were weak as compared to females. A territorial male endeavor to exclude all other territorial males and attempts to herd all females that enter his territory, where he has exclusive mating rights. He may allow bachelor herds to enter his territory, but when females are present, he will typically drive them away. In a few species, they may be kept entirely outside the territory (Walther et al. 1983).

Non-territorial adult and sub-adult males form bachelor herds. Territorial males often keep sub-adult males from mingling with the herd's females, but bachelor males are often allowed entry into the territories. Individuals in bachelor herds are free to join, but because their home ranges coincide, the herds often see each other again (Mungall 1978).

Temporal stability

Using the LAR, we were able to measure for the first time in the blackbuck species the stability of relationships between and within certain age-sex classes. For all the herds with female age class and at overall population level, female-female and female-all associations were formed as constant companion + casual acquaintances model (CC + CA). They were more likely to associate with casual acquaintances who disassociated and re-associated over time, which is typical of the fission-fusion society they lived in. But there are some associations that remain constant over time. There is strong evidence from previous studies that females are more likely to associate with each other based on their reproductive status and previous social familiarity (Herzing & Brunnick 1997). Primates have shown that female reproductive success depends on the successful raising of young, and females will use social relationships to achieve their reproductive goals (Sterck et al. 1997). Benefits to female grouping may be ecological in nature, such as increased predator

Table 8a. GLMM models used to characterize relationship between dyadic association and covariates.

Model ID	logLik	AICc	ΔAICc	Weight
Model 4	**-383.04**	**773.984**	**0**	**0.57456**
Model 3	**-383.8**	**776.416**	**1.9608**	**0.15808**
Model 1	-385.32	778.62	4.6208	0.02736
Model 6	-389.88	786.828	12.8364	0.00076

Table 8b. GLMM output showing significant covariates (fixed effect) and dyads (random effect) affecting association of female Blackbuck at PCWS.

Predictors	Estimates	CI	p
(Intercept)	**1.51**	**1.46 – 1.55**	**0.003**
Habitat type [Grassland]	0.06	0.01 – 0.23	**0.002**
Habitat type [Dry-evergreen]	-0.09	-0.13 – -0.05	**0.005**
Habitat type*habitat openness	0.03	0.02 – 0.18	**0.054**
Predator [Presence]	-0.45	-0.33 – -0.19	**<0.001**
Sympatric species [Presence]	-0.18	-0.29 – -0.16	**<0.001**
Anthropogenic [High]	-0.02	-0.08 – -0.05	**0.046**
Predator*Sympatric species	0.03	0.01 – 0.14	0.12
Sympatric species*Anthropogenic activity	-0.07	-0.16 – 0.04	**0.033**
Random Effects			
σ^2	265		
τ_{00} Dyad	<0.01		
N	1432		
Observations	11154		
Marginal R^2	0.652		

σ^2 = represents the mean random effect variance of the model | **τ_{00}** = the random intercept variance, or between subject variance | N = number of observations.

Table 8c. GLMM output showing influence of random effect covariate (dyads) contributing towards association.

Covariate	Term	Variance	SD
Dyad	(Intercept)	0.83	0.66
Residual		7.9	4.58

protection and food distribution (Sterck et al. 1997), or social, including calf care and social learning (Miles & Herzing 2003; Bender et al. 2008; Gibson & Mann 2008). Results indicate that familiarity and reproduction are strong influences in female sociality. Adaptive value of sociality is described for female Bottlenose Dolphins in a unique approach by Frère et al. (2010), showing that sociality influences the fitness trait in a wild population, consistent with the results of many social analyses (like this study) that show strong associations between females. Thus, genetic and social effects on fitness are intertwined, both important in determining female success (Frère et al. 2010). Although mixed-sex herds and pseudo-harems were structured similarly to female herds, they were weaker and less stable over time than the female herds.

Male-male and male-all associations exhibited the casual acquaintances model in the overall population as well as in other male-present herds, according to the findings. There were two levels of casual acquaintances (2CA) in most bachelor herds, indicating that they were in a state of constant flux on a daily basis. There are likely more factors shaping the temporal association patterns between individuals and classes. More precise data on the age of individuals will help to make such definitions more precise.

Ecological correlates

Significant correlations were found in dyadic associations between the covariates sampled, as revealed by per MRQAP test and GLMM. According to this finding, females have different social options depending on how their society is structured in relation to the covariates, elaborated below:

Influence of habitat and predation

We obtain non-random associations at grassland habitat as shown by higher SD of observations, a significant MRQAP correlation and positive relationship between association strength of dyads. This pattern of association is supported by "resource, habitat and predation hypothesis" (Crook 1965; Jarman 1974; Clutton-Brock 1989; Davies 1991) which suggests that female grouping is related to resource available habitats and occur where competition for high-quality food is low, food availability is patchy, and presence predation risk either favors larger herds or does not influence group size. Males comprise a negligible proportion of the herds, so female-to-female associations are shaped primarily by their presence.

Another disturbance in PCWS is due to proliferation of *Prosopis juliflora*, which has been seen growing exponentially changing the grassland into thickets (Arandhara et al. 2021), it is difficult for social species like the Blackbuck that lives in large herds to socialize or flee at early detection of a predator in a habitat with impenetrable bushes. These transitions may lead to spatially clumped resource distributions and, consequently, disturb the species societies. In PCWS, *Prosopis* has been reported to show detrimental effect on Blackbuck (Ali 2005; Arandhara et al. 2021) and elsewhere in India (Ranjitsinh 1989).

Predators are reported to influence social dynamics, according to the "predation pressure hypothesis," female home range and herding are influenced by predation pressure and that Blackbuck form larger herds in PCWS, where there are no large predators other than jackals (Baskaran 2016, 2019). In our GLMM results we obtain a negative influence. Although predation was considered as a factor in this study, there were no large predators in the area except for jackal and the feral dog, which mostly pose a threat to neonate and young fawns. Feral dogs, which prey on Blackbucks, are reported to carry diseases that affect the wild ungulate population (Butler et al. 2004; Ali 2005; Jyoti & Rai 2021). According to our observations, jackals in open grasslands of PCWS maintain 200 m (mean) and beyond from the herds of Blackbucks. This pattern is also supported by the results as there is no significant random association when predators appear, when Blackbucks socialize.

Influence of sympatric invasives

Management of feral-horse at point Calimere has been a subject of recommendation for several years (Ali 2005; Baskaran et al. 2016, 2020; Arandhara et al. 2020). This study shows random association with negative effect of female Blackbuck dyads when sympatric feral-horse, coexist in proximity over time and space. Further, the result shows a similar pattern of significant dyadic preference in the absence of cattle herds. Even in open habitats, Blackbucks were observed to be distributed away from cattle herds with a minimum distance of about 150 m. It is essential for Blackbucks to restrict their movements to areas near water sources during the dry season, as a result of decreased water content in forage; whereby the restriction of movement due to presence of cattle might also add further constrain in limiting the food and water. Furthermore, because grass biomass is estimated to be higher near fresh water sources, cattle presence may pose a displacing threat to Blackbuck societies, which is a specialist grazer. There are reports that feral-horses, which are larger and more aggressive than other medium sized antelopes, influence Blackbuck's foraging habits by keeping the latter away from the primary food source (Arandhara et al. 2020). Further, studies have attributed low female associations with high feeding competition and feral-horse out-competes native ungulates for water (Miller 1983; Ostermann-Kelm et al. 2008; Perry et al. 2015; Gooch et al. 2017); overlaps in diet and spatiotemporally with the blackbuck (Baskaran et al. 2016). This finding provided corroborating evidence that feral-horses and cattle impose negative effect on social integrity of the blackbuck species at Point Calimere.

Influence of anthropogenic activity

Animals observed in and around anthropogenic areas at PCWS show nonrandom sociality, also exhibited by a significant MRQAP test and negative relationship between dyadic association. Increasing levels of anthropogenic activities are evident in the beaches adjacent to the study area, in the form of fishing, boating, and other shore activities, these activities have minimal disturbance to the wildlife. Inside the sanctuary, the species frequently come across tourist vehicles and recreational visitors, Blackbuck being a diurnal species, the visitors time (0900–1700 h) coincides with peak activity hours of Blackbuck, influencing the grouping, fission-fusion, and association dynamics of the Blackbuck herds. Anthropogenic concentrations of food can alter mammals' foraging behaviour (Ali 2005; Baskaran et al. 2019) and deliberate provisioning can cause change in animals' social interactions (Wrangham 1974).

Influence of season

Even though the results of MRQAP and GLMM do not show significance in season determining association strength, permutation test results show a non-random female association during the wet season. Mating season for blackbuck at PCWS lasts from mid-August through late October, as females enter estrus coinciding before the onset of early downpours and predictably increase in foraging resources for the next months. During this cyclic peak adult males being more aggressive tend harems in their territories, we were able to identify 30% (during September–October) territorial pseudo-harems and 23% non-territorial 'floaters' seeking opportunity to tend female herds by increased frequency of fights for dominance, as reported earlier studies (Mungall 1978; Walther et al. 1983). Non-random associations are evident in this wet season as females become cohesive, when in pseudo-harem herds. Weaker association strengths are likely caused by frequent chasing when females flee and young adults reported to severely harass females during the lek breeding (Anderson & Wallmo 1984; Prothero 2002; Isvaran 2003), these situations incline a female herd towards seeking older adult males' attention in order to keep harassing males away.

As expected in environments with well-defined seasonality as in PCWS, fawning peak correlates with growth of grasses, low in fiber, high in nutrients and significantly high biomass (Sathishkumar et al. 2023). Once fawns are born during the onset of dry season, mothers remain isolated with their offspring, away from other individuals, the peak of lactation coincides with the peak of food availability. Isolation lasts till (May–June) when mothers and fawns join larger herds.

CONCLUSION AND RECOMMENDATIONS

Among Blackbuck group units, the female herds and territorial pseudo-harems spread tightly, while the bachelor herds were loose or scattered with small groups. Female-herd based dyadic associations were stronger and more stable than mixed-sex herds and pseudo-harems, but males were in flux. Ecological correlates viz. grasslands and habitat openness were associated with higher levels of female sociality, indicating their importance in foraging, sociality, and predator vigilance, which is negatively affected by rapidly growing alien invasive *Prosopis juliflora*. Therefore, management of grasslands is essential to avoid invasion of alien woody plant. Invasion of *Prosopis*, which is modifying the natural habitats, suggests for management intervention on priority. One of the other significant covariates that threaten Blackbuck societies, especially in allocating feeding resources while socializing, is the presence of feral-horses and cattle. Invasive herbivores are predicted to outcompete natives, so they should be controlled. The feral-horse in the sanctuary, which competes with the native Blackbuck for resources and poses a serious threat, drives the Blackbuck away from suitable habitats. Thus, it is essential to humanely control the population of feral horses as the native population of Blackbuck is already showing a declining trend. To better manage a polygamous social species, it is important to understand its social preferences and their effects on females' lifetime reproductive success. Future research should examine the ecological costs and benefits of female social relationships, kin selection, male competition, behaviour-specific associations, covariate-specific association, and socio-spatial variation of populations.

This would help assess social organisation in this taxon and provide management clues by better understanding the evolutionary and ecological basis for antelope conservation and management.

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S-Table 1. Mean (a) and max (b) level of associations within and between age sex classes for female herds.

Classed by Age-sex	**AF**	**SAF**	**FA**
Mean			
AF	0.21 (0.11)	0.13 (0.08)	0.05 (0.05)
SAF	0.13 (0.06)	0.03 (0.03)	0.03 (0.03)
FA	0.05 (0.05)	0.03 (0.03)	0.00 (0.00)
Within associations	0.10 (0.12)		
Between associations	0.08 (0.06)		
Max			
AF	0.55 (0.28)	0.60 (0.22)	0.38 (0.22)
SAF	0.67 (0.18)	0.94 (0.14)	0.15 (0.15)
FA	0.21 (0.17)	0.19 (0.16)	0.00 (0.00)
Within associations	0.28 (0.30)		
Between associations	0.37 (0.22)		
Mantel test	t = 2.918; p = 0.0035		
Matrix correlation	0.1051		

S-Table 2. Mean (a) and max (b) level of associations within and between age sex classes for Bachelor herds.

Classed by Age-sex	**AM**	**SAM**
Mean		
AM	0.43 (0.09)	0.38 (0.16)
SAM	0.38 (0.12)	0.55 (0.09)
Within associations	0.48 (0.11)	
Between associations	0.38 (0.14)	
Max		
AM	0.88 (0.17)	0.60 (0.22)
SAM	0.67 (0.18)	0.94 (0.14)
Within associations	0.90 (0.16)	
Between associations	0.63 (0.20)	
Mantel test	t = 1.645; p = 0.100	
Matrix correlation	0.1609	

S-Table 3. Mean (a) and max (b) level of associations within and between age sex classes for Mixed herds.

Classed by Age-sex	**AF**	**SAF**	**FA**	**SAM**
Mean				
AF	0.41 (0.11)	0.32 (0.11)	0.32 (0.07)	0.05 (0.05)
SAF	0.32 (0.08)	0.26 (0.05)	0.22 (0.05)	0.03 (0.04)
FA	0.32 (0.07)	0.22 (0.06)	0.22 (0.03)	0.03 (0.05)
SAM	0.05 (0.06)	0.03 (0.05)	0.03 (0.05)	0.00 (0.00)
Within associations	0.30 (0.14)			
Between associations	0.25 (0.09)			
Max				
AF	0.69 (0.22)	0.58 (0.20)	0.59 (0.20)	0.09 (0.09)
SAF	0.65 (0.16)	0.52 (0.18)	0.40 (0.11)	0.06 (0.08)
FA	0.64 (0.16)	0.41 (0.14)	0.34 (0.06)	0.07 (0.09)
SAM	0.14 (0.11)	0.09 (0.13)	0.09 (0.13)	0.06 (0.08)
Within associations	0.52 (0.27)			
Between associations	0.60 (0.22)			
Mantel test	t = 3.268; p = 0.0011			
Matrix correlation	0.2269			

S-Table 4. Mean (a) and max (b) level of associations within and between age sex classes for Territorial pseudo-harem herds.

Classed by Age-sex	**AF**	**SAF**	**FA**	**AM**	**SAM**
Mean					
AF	0.25 (0.09)	0.21 (0.14)	0.21 (0.17)	0.39 (0.00)	0.09 (0.10)
SAF	0.21 (0.07)	0.24 (0.05)	0.18 (0.07)	0.33 (0.00)	0.19 (0.09)
FA	0.21 (0.11)	0.18 (0.10)	0.12 (0.07)	0.36 (0.00)	0.07 (0.06)
AM	0.39 (0.00)	0.33 (0.00)	0.36 (0.00)	0.09 (0.10)	0.25 (0.00)
SAM	0.09 (0.01)	0.19 (0.03)	0.07 (0.02)	0.25 (0.00)	0.67 (0.00)
Within associations	0.25 (0.15)				
Between associations	0.19 (0.11)				
Max					
AF	0.68 (0.21)	0.38 (0.25)	0.40 (0.31)	0.85 (0.00)	0.30 (0.00)
SAF	0.50 (0.18)	0.43 (0.11)	0.34 (0.11)	0.65 (0.00)	0.22 (0.10)
FA	0.55 (0.28)	0.36 (0.12)	0.20 (0.13)	0.75 (0.00)	0.08 (0.09)
AM	0.85 (0.00)	0.65 (0.00)	0.75 (0.00)	0.36 (0.12)	0.30 (0.00)
SAM	0.28 (0.04)	0.35 (0.07)	0.16 (0.08)	0.30 (0.00)	0.67 (0.00)
Within associations	0.52 (0.25)				
Between associations	0.50 (0.25)				
Mantel test	t = 1.687; p = 0.0915				
Matrix correlation	0.1105				

S-Table 5. Tests for preferred association for female herd.

Age sex class	**Mean association**		**SD of association**		**p-value (SD)**
	Observed	**Random**	**Observed**	**Random**	
All individuals	0.09	0.09	0.15	0.13	0.00
AF-AF	0.19	0.19	0.21	0.20	0.00
AF-SAF	0.13	0.13	0.15	0.14	0.08
AF-FA	0.05	0.05	0.09	0.09	0.01
SAF-FA	0.03	0.03	0.08	0.06	0.01

S-Table 7. Tests for preferred association for mixed herd.

Age sex class	**Mean association**		**SD of association**		**p-value (SD)**
	Observed	**Random**	**Observed**	**Random**	
All individuals	0.27	0.27	0.21	0.21	0.84
AF-AF	0.41	0.41	0.21	0.22	0.92
AF-SAF	0.32	0.32	0.21	0.21	0.64
AF-SAM	0.05	0.00	0.08	0.00	1.00
AF-FA	0.32	0.32	0.19	0.18	0.31
SAM-SAF	0.03	0.00	0.06	0.00	1.00
SAM-FA	0.03	0.00	0.07	0.00	1.00
SAF-FA	0.22	0.22	0.13	0.15	0.95

S-Table 6. Tests for preferred association for bachelor herd.

Age sex class	**Mean association**		**SD of association**		**p-value (SD)**
	Observed	**Random**	**Observed**	**Random**	
All individuals	0.42	0.42	0.28	0.28	0.83
AM-AM	0.43	0.00	0.29	0.00	0.91
AM-SAM	0.38	0.00	0.26	0.00	0.99

S-Table 8. Tests for preferred association for pseudo harem herd.

Age sex class	**Mean association**		**SD of association**		**p-value (SD)**
	Observed	**Random**	**Observed**	**Random**	
All individuals	0.20	0.20	0.21	0.20	0.07
AF-AF	0.25	0.24	0.25	0.23	0.05
AF-AM	0.39	0.00	0.33	0.00	1.00
AF-SAF	0.21	0.21	0.19	0.19	0.81
AF-SAM	0.09	0.00	0.10	0.00	1.00
AF-FA	0.21	0.22	0.24	0.25	0.39
AM-SAF	0.33	0.00	0.22	0.00	1.00
AM-FA	0.36	0.00	0.29	0.00	1.00
AM-SAM	0.25	0.00	0.07	0.00	1.00
SAM-SAF	0.17	0.18	0.10	0.09	0.05
SAM-FA	0.07	0.07	0.05	0.05	0.05
SAF-FA	0.18	0.18	0.14	0.14	0.16
SAM-SAM	0.67	0.00	0.33	0.00	1.00

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