VOLUME 9 ISSUE 1 2023

ISSN 2454 – 3055

INTERNATIONAL JOURNAL OF ZOOLOGICAL INVESTIGATIONS

Forum for Biological and Environmental Sciences

Published by Saran Publications, India

International Journal of Zoological Investigations Vol. 9, No. 1, 446-463 (2023)

International Journal of Zoological Investigations
Contents available at Journals Home Page: www.ijzi.net
Editor-in-Chief: Prof. Ajai Kumar Srivastav
Published by: Saran Publications, Gorakhpur, India

ISSN: 2454-3055

Habitat Overlap and Resource Selection Between Native Blackbuck and Invasive Feral-horse at Point Calimere Wildlife Sanctuary, Southern India

Selvarasu Sathishkumar, Subhasish Arandhara and Nagarajan Baskaran*

Department of Zoology, A.V.C. College (Autonomous) (affiliated to Bharathidasan University, Tiruchirappalli, Tamil Nadu), Mayiladuthurai, Tamil Nadu, India

**Corresponding Author*

Received: 3rd February, 2023; **Accepted:** 26th February, 2023; **Published online:** 10th March, 2023

https://doi.org/10.33745/ijzi.2023.v09i01.050

Abstract: Conservation decisions must consider species' ecological resource requirements, invasive and anthropogenic impacts. Point Calimere Sanctuary has both native blackbucks and invasive feral horses coexisting, and a recent study showed that the latter may eventually displace the former. In this study habitat use, and resource selection were quantified at population level, by assessing resources availability at spatially replicated plots, during 2017-2019. For each species, habitat use was evaluated based on the Minimum Convex Polygon (MCP) and Kernel Density Estimates (KDE), the extent to which two species shared a habitat was estimated by Utilization Distribution Overlap Index (UDOI). In addition, seasonal Resource Selection Function (RSF) were estimated. Result showed Feral-horse used more habitat than blackbuck; grassland was used more than dry-evergreen in both dry and wet-seasons. It turned out that both species stayed clear of Prosopis cover during the dry-season, preferring instead to live in grasslands close to water sources and grass availability. The presence of feral-horse was also found to be a negative predictor of blackbuck. In contrast, during wet-season both species avoided the standing water proximity with significant overlap in habitat use, including habitat openness. The overlap in habitat uses and resource selection by feral-horse over blackbuck revealed the potential interference competition by invasive over native. Earlier studies have found negative effects on blackbucks from feral-horses and Prosopis, and these new findings add weight to those studies. To ensure the long-term survival of native ungulate species like the blackbuck elsewhere with similar conditions, it suggests measures for controlling these invasives.

Keywords: Blackbuck, Habitat Overlap, Point Calimere, Resource selection, Utilization Distribution Overlap Index

Citation: Selvarasu Sathishkumar, Subhasish Arandhara and Nagarajan Baskaran: Habitat overlap and resource selection between native blackbuck and invasive feral-horse at Point Calimere Wildlife Sanctuary, Southern India. Intern. J. Zool. Invest. 9(1): 446-463, 2023.

https://doi.org/10.33745/ijzi.2023.v09i01.050

Introduction

Animal communities are shaped by interactions between their components (Gause, 1934; Hutchinson, 1959). Competition between organisms of the same trophic level would result from the use of common resources with limited availability (de Boer and Prins, 1990). Animal

resource use patterns are highly influenced by their ability to deal with potential competitors (Namgail *et al*., 2009; Razgour *et al*., 2011; Vanak *et al*., 2013). An essential condition for competition to take place is that (1) the supply of a resource must be limited, and (2) that the effects of competition operate primarily at the individual level. As the effects of competition accumulate across individuals, however, they can eventually be translated to the population or metapopulation levels, leading to overall reductions in population growth rate of 1 or both species. Species should avoid competition through resource partitioning although resource overlap can occur (Hutchinson, 1959; MacArthur, 1972; Pianka, 1973; Schoener, 1974). As a result of competition, the inferior competitor may alter their behaviour and/or growth/survival and this can lead to population effects, at both local and global scales (Durant, 1998; Harris and Siefferman, 2013). This can have a direct impact on communities (Levi and Wilmers, 2012; Robertson *et al*., 2013).

Interspecific competition between wild herbivores has been often suspected to affect resource use, population trends, and/or species distribution, in both temperate and savannah ecosystems (Sinclair and Northon-Griffiths, 1982; Putman, 1996; Latham, 1999; Murray and Illius, 2000; Arsenault and Owen-Smith, 2002; Focardi *et al*., 2006; Namgail *et al*., 2009), but evidence of its effects on patterns of population dynamics remains scarce (Forsyth and Hickling, 1998).

Usually, exotic species are assumed to be introduced by humans, who act as the primary vectors of their spread (Valery *et al*., 2009). These species may determine a potential for competition in an area with taxa already present (Lovari *et al*., 2014), but the mechanisms of competition of a reintroduced ungulate on other large herbivores have been scarcely assessed (e.g., reduction of resource availability and numbers of the inferior competitor). It is also suggested that the use of quality food resources by herbivores is crucial to improve growth and survival, which, in turn, influences the population dynamics of wild herbivores (Clutton-Brock *et al*., 1984, 1986; Côté and Festa-Bianchet, 2001; Pettorelli *et al*., 2007). Thus, resource exploitation by a superior competitor should affect the viability of the inferior one. In such competitive situations, spatiotemporal partitioning of foraging habitats is recognized as the primary mechanism facilitating the coexistence of sympatric species (Prins and Olff, 1998). Coexisting species should differ in at least one or more dimensions of their ecological niches, such as resources, space or time. First, each species may specialize on distinct resources or respond in a different way to competitors. Second, they may use resources or avoid enemies at different times, or thirdly, in different spaces. Coexistence due to spatial niche partitioning can be facilitated in heterogeneous landscapes with a mosaic of habitat patches of various biotic and abiotic conditions, which provide appropriate resources for each species (Amarasekare, 2003; Wereszczuk and Zalewski, 2015).

Despite these mechanisms facilitating coexistence, often assumed to be the result of past competitive interactions between species, recent invasion of an ecosystem by an alien species poses a different kind of predicament because there may not have been sufficient evolutionary time for segregation in resource use to develop (Valery *et al*., 2009; Wiens *et al*., 2014). Therefore, understanding on habitat use patterns, diet and niche marks as an important suggestion toward elucidating the mechanisms behind competitions and or coexistence. The suitability of any location for a given species is determined by the available resources. Thus, understanding the selection of resources by animals is an essential component of conservation biology, wildlife management and applied ecology (Boyce and McDonald, 1999). The problem of habitat fragmentation and invasive species proliferation has led to a loss of continuous habitat, reduction in habitat patch sizes and an increase of patch isolation (Andren, 1994; Fahrig, 2003), which has become a global concern in the recent years. The concept of estimating resource selection patterns for a population can reveal what habitat features are

selected (or avoided) on the landscape. Resource selection functions are considered as a valuable tool for identifying important areas for a population so that the quantity and distribution of those areas across a population's range can be assessed. The resource-based approach may help to recognize and explain the spatial distribution patterns of animals, and to capture the functional and spatial interaction of animals with their environment (Dennis *et al*., 2003).

In Point Calimere Wildlife Sanctuary (PCWLS), the Indian Blackbuck (*Antelope cervicapra*) and Feral-horse (*Equus callabus*) are ecologically similar species and they co-occur spatiotemporally. Both the species dwell beside the perimeter of natural habitat and are active mostly from dusk to dawn. Blackbuck is native to the Indian subcontinent, it is a specialist grazer feeding on short grasses, is a medium sized antelope weighing around 40 kg. Feral-horse is an invasive species, a generalist grazer with broad, opportunistic diet, the species is larger than the blackbuck, and is found invasive globally. The later exhibits great adaptive plasticity and inhabit a wide range of habitats, studies report their effect on forested habitats where they have invaded and exhibit a significant threat to conservation and restoration of native ecosystems (Ali, 2005, Baskaran *et al*., 2020; Arandhara *et al*., 2020). In PCWLS, despite the evidence of co-occurrence and overlap in diet, studies mostly speculate feral-horse to procure resources more intensively than the blackbuck, few studies have gone beyond recording their occurrence and there is little information on space use patterns (Baskaran *et al*., 2016, 2020), diet selection (Baskaran *et al*., 2016), and magnitudes of overlap in tropic levels of space-diet even at population levels (Baskaran *et al*., 2019, 2020); also, studies determining resource selection of both species is scarce in the literature.

Previous studies at PCWLS show spatial and dietary overlap between the two species at a coarse scale (Baskaran *et al*., 2016) and reveal a potential for competition in terms of species proximity at a finer scale (blackbuck avoiding feral-horse) and in acquisition of principal diet (blackbuck avoiding principal diet) (Baskaran *et al*., 2019; Arandhara *et al*., 2020). This study focused on population-level space use, diet, and resource selection using animal surveys and assessment of resource covariates. we take an integrative approach of (1) measuring habitat use overlap (second order selection); and to address the hypothesis that presence of feral-horse would determine the resource selection by blackbuck and vice versa and (2) to investigate the ecological relationships of the two sympatric through resource selection functions.

Materials and Methods

Study area:

The study has been carried out at PCWLS, a protected area covering ~27 km^2, located in the east-coast of southern India (Fig. 1). Here, the regional climate is characterized by two seasons: a wet season from September through December and a dry season from January through August. Its mean annual rainfall averages 1366 mm, and the annual temperature ranges from 23° to 37 °C. The dominant vegetation in the region is tropical semi-evergreen forest with patches of grassland distributed along the southeastern part of the park. The grasslands are highly susceptible to invasion of *Prosopis juliflora*, occasional invasive management by the forest department has produced a land cover mosaic of managed and unmanaged vegetation that includes the native open scrub vegetation, recently uprooted plots and plots with the invasive thickets. The sanctuary is devoid of perennial water bodies and during the wet season the sanctuary receives excess of water, that submerges grasslands that affects feeding and movement of blackbuck. Beyond the park area, there is very little or no woody vegetation. Salt production has been the main land use in the area including fishing as the common occupation of the inhabitants (Fig. 1).

Survey design:

Study subject surveys:

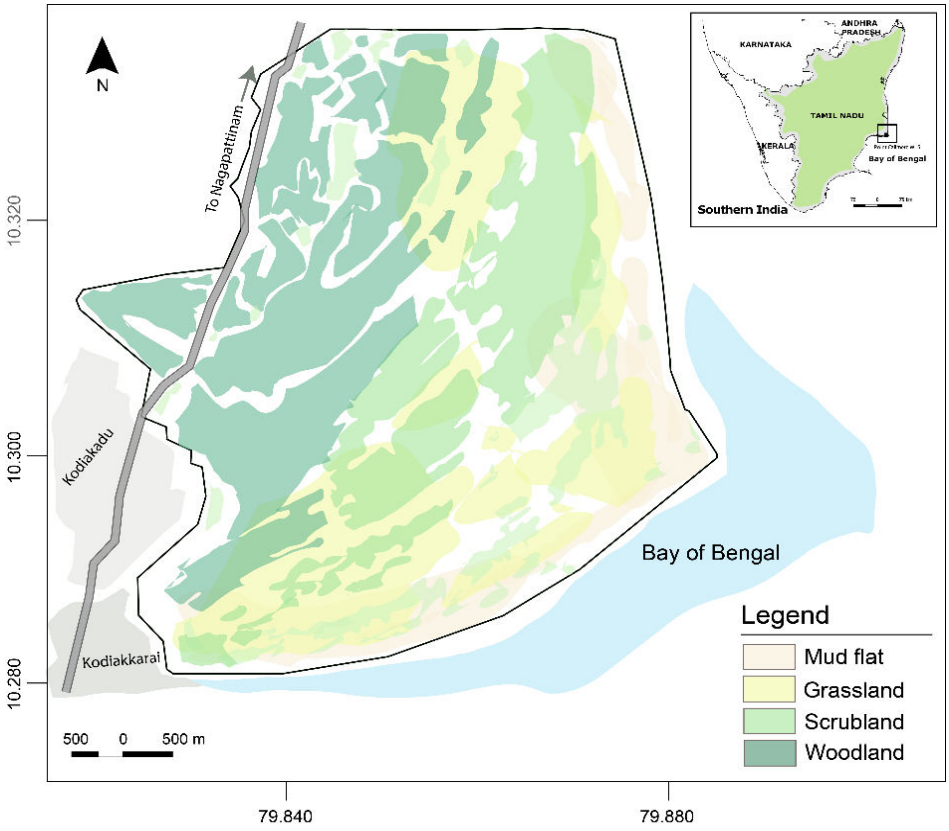

Fig. 1: Map showing the study area with an insert of Southern India.

From September 2017 to August 2019, seasonal blackbuck and feral-horse surveys were conducted. For quantifying space-habitat use and resource selection, the study follows the 'Design 1' approach, based on Thomas and Taylor (1990) i.e., inferences on space use and resource categories are made at the population level; individual animals are not identified; used, unused, or available resource units are made at recognised plots and spatially extrapolated for the entire study area. Location information on both the species were extracted following standardized surveys conducted at monthly interval and pooled for seasonal space use analyses. During a survey, at each direct sighting of the target species (blackbuck and feral-horse) we recorded the date, time, number of individuals, obtained the sighting location (geo coordinate) by a GPS device (using Garmin eTrex 30: position accuracy = approx 5 m), measure on distance to the animal using Rangerfinder (Hawk 600) and bearing (angle from north; using a Sunnto K20 see-through compass). Using the distance and bearing recorded for each animal sighting location, the individual detections were corrected for the exact locations using the Bearing Distance to Line tool and Feature Vertices to Points tool in ArcGIS 10.2. This resulted a new layer of offset x y coordinates that represented the actual location of each individual at the time of first detection. The offset/actual coordinates were used for the final analysis. This, monthly data were grouped into dry (February to August) and wet seasons (September to January), following Baskaran *et al*. (2020). The final geocoordinate database consisted of 5120 locations for blackbuck and 2450 locations for feral-horse with

a monthly average of 210 and 105, respectively. Using this dataset, the space use and blackbuck area overlapped by feral-horse was arrived.

Blackbuck mostly form herds with relatively close spatial cohesion (i.e., each member within 30 m of any other member). Once a herd is sighted, it was approached slowly to within disturbance threshold (approx. 50 m in open habitat of PCWLS) and record its location details. The three information was corrected for arriving at the actual coordinates on each of the animal sighted.

Ecological assessment:

Field surveys, remote sensing and geographic information system (GIS) based approaches were used to assess covariates related to climate, vegetation, anthropogenic, invasive pressure and effect of sympatric species. These information from spatially recognized plots and from line transects were used to classify animal locations into resource and or disturbance categories (details of the variables are given in Table 1). Satellite imagery (Landsat 8) at the extent of study area corresponding to the sampling seasons (dry and wet) were downloaded from USGS. These imageries were processed to classify the forest types using supervised classification based on ground truth locations at 30 m resolution. The images were processed at default resolution by the "Raster" package in R-program (v.3.6). Data from satellite imagery provided a broad-scale representation of the spatial distribution of different habitat types but lacked many of the fine-scale structures associated with habitat that affect resource use of the target species. Thus, to ensure better representation of vegetation attributes, field quantification of flora and other variables were sampled at 39, 1000 x 1000 m grid cells superimposed over the study area polygon. Within the cells, sampling comprised of trees (at 4, 30 x 30 m plots), shrubs (at 8, 5 x 5 m plots) and grasses/herbs (at 16, 1 x 1 m plots) were assessed, from the same plots. Other variables were measured and or cross-validated, belonging to climate, vegetation, anthropogenic, invasive pressure and effect of sympatric species (details of the covariates are given in Table 1). Each of the variables measured in field were processed using Nearest Neighbor Interpolation and ecological covariate raster layers were developed at the default 30 m resolution for modelling resource selection function.

Data analysis:

Survey effort: A total of 792 hours were spent seeking for blackbuck and feral-horse during 2017-2019. In total, count on 332 blackbuck herds and 145 feral-horse herds were recorded. Survey effort was not different across the habitat types (woodland= 233 h; scrubland= 255h and grassland= 304h; K-W X^2= 5, p=0.18)

Habitat use: An animal's space use was based on utilization distribution (UD) of animal locations, i.e., probability density function describing the relative use of space by an animal, within a defined area. UD of blackbuck and feral-horse were calculated at monthly basis using (1) 100% minimum convex polygon (MCP), to arrive at the maximum distribution area; (2) 50% kernel density estimates to delineate core areas of saturated use. For the 50% kernel distribution, least squares cross validation (LSCV) algorithm was used as the smoothing parameter. These estimates were averaged over seasonal and annual scales for arriving at the extent(s) of interspecific habitat use. Classified habitat type maps at 30 m resolution were used to delineate the animals' habitat utilization at the scales of animal space use (based on selection of various habitat patches within the space use polygon), as given by Johnson (1980). 100% distribution area, and 50% core area contours were overlaid to clip the habitat type maps and estimate the area of habitat classes for the space use extents. Evaluation of habitat type within an area of interspecific space use was processed in ArcGIS 10.2 (ESRI). For each of the habitat classes within the 100%, and 50% distribution contours, and UDOI was calculated to arrive at the percentage and probability of space use overlap.

Habitat overlap: Utilization distribution overlap

Table 1: Details covariates and the methods their assessment

Covariate	Sampling unit (Sample size)	Justification[a] and Method[b]
Climate		
Temperature	At every sighting of target species (757)	[a]Blackbuck adapted for moderate to high ambient temperatures, as they possess an enormous capacity to regulate body temperature (Jhala *et al*., 1992). Thus, temperature is not expected to influence the distribution. [b]Measured using generic digital thermometer-cum-hygrometer device (model: HT01) in degree Celsius at each observation along line-transect.
Humidity (%)	At every sighting of target species (757)	[a]Due to a high humidity in the morning hours, when surveys were carried out, the blackbuck are suggested to be more detectable in the open areas with forage availability (Jhala *et al*., 1992). [b]Measured same as above, but in percentage unit.
Habitat		
Woodland (%) Scrubland (%) Grassland (%)	30×30 m resolution	[a]Blackbuck being a social species of open grasslands and semi-arid areas with short grass, grasslands would influence positively, as they provide food (Prater, 1948) and early detectability of predators to escape (Isvaran 2007), while habitat with trees or shrubs influence negatively, as they hinder their free movement (Raman *et al*., 1996). [b]Obtained from LANDSAT 8 imagery acquired in 2018 from USGS and subjected to supervised classification using ENVI 4.8 and ArcMap 10.1.
Elevation (m)	At each grid cell: 2×2 km (26)	[a]Low altitude area that provides conducive temperature gradient (moderate to high) and ideal short-grass habitats to blackbucks, expected to support higher density than high altitude areas. [b]Obtained at five locations/grid cell, one each at four corners and one at the centre, using a GPS device and from these arrived at mean elevation/grid cell.
Habitat openness (m^2)	At every sighting of target species (757)	[a]Since open habitat provide early detectability to escape from predators better than woodlands, blackbucks prefer open grasslands over the woodlands (Ranjitsinh 1989; Jhala 1997; Isvaran, 2005). [b]Area of open habitat was arrived at each of sighting location measuring habitat openness visible on four major directions (north, south, east and west), using a rangefinder.
Habitat heterogeneity index	At each transect (26)	[a]Since blackbuck herd sizes correlate negatively with habitats heterogeneity (Isvaran, 2007), density also expected to decrease. [b] Habitat heterogeneity index was calculated as the number of habitat segments obtained in a transect cut by points falling in open habitat or points with closed-thicket, divided by the total number of segments (total segments = open habitat + closed thicket) (Isvaran, 2007).
Distance to water (m)	At each 250 m interval of line-transect (104)	[a] Although, blackbucks can live without water for long time due to their ability to conserve and depend on preformed water in their forage (Jhala *et al*., 1992), given the choice of surface water, grid-cells with water can support higher density than those without. [b]Obtained from land use map and temporary water provision locations by forest department for each 250 m segment of line-transect using ArcMap 10.

Distance to shade (m)		[a]Given the tremendous capacity of blackbucks to regulate heat (Jhala *et al*., 1992), shade may not be a driving factor of their distribution. [b]Measured using rangefinder at each 250m interval of line-transect.
Vegetation		
Tree density / 900m^2 Tree diversity Tree richness Tree cover/ 900m^2	Four quadrats (30 × 30 m^2)/grid-cell (104)	[a] Same reason as given above for woodlands. [b] Tree species density (number of individuals/unity area), diversity (Shannon), richness (number of species) and tree cover (multiplying crown length and crown width of each tree) were arrived for each grid-cell using the tree species (>20cm GBH) data collected from the four quadrats laid (one each at four corners) at each grid-cell.
Shrub density /25 m^2 Shrub diversity Shrub richness Shrub cover (%)	Eight quadrats (5 × 5 m2)/grid-cell (208)	[a] Same reason as given above for woodlands. [b]Shrub density (number/unit area), diversity (Shannon), richness (number of species) and shrub cover (% area occupied within a given quadrat visually) were arrived from shrub (>5 GBH) count data (excluding *Prosopis*) from 8 quadrats laid in each grid-cell by placing two each/tree plot diagonally opposite corners.
Grass cover/m^2 Grass biomass index/m^2	Eight quadrats (1 × 1 m^2)/grid-cell (208)	[a]Blackbuck being a grazer on shortgrass (Jhala 1997; Baskaran *et al*., 2016), gird-cell with more shortgrass cover and biomass expected to support higher density than those with lower cover and biomass. [b]Grass cover (% area occupied by grass/m^2 visually) and grass biomass index (multiplying mean grass height – measured at five locations/m^2 and grass cover % following Isvaran (2007) measured from 8 quadrats laid by placing two each/tree plot diagonally opposite corners.
Invasive pressure		
Prosopis density/25 m^2 Prosopis cover/25 m^2	Eight quadrats (5 × 5 m^2)/grid-cell (208)	[a] Same reason as given above for woodlands. [b] *Prosopis* density (number of individuals/unit area) and cover (multiplying crown length and crown width of each individual) were arrived from *Prosopis* (>5 GBH) count data from 8 shrub quadrats.
Anthropogenic pressure		
Distance to road (m)	At each 250 m interval of line-transect (104)	[a]Road, vehicle and people, as anthropogenic disturbance, the decrease in distance to road, and vehicle and increase in number of people and vehicle would decrease blackbuck abundance, as shown by four-horned antelope (Krishna *et al*., 2016).
Distance to vehicle (m)	At every vehicle frequency record (38)	[b]Distance to road obtained from land use map at each 250 m segment of line-transect using ArcMap 10 program. Distance to vehicle (measured using range finder), frequency of people and vehicle (counted using binocular) were recorded at every sighting of target species.
People frequency		Count on number of people
Sympatric species		
Feral horse density/km^2 Blackbuck density/km^2		Density of animals estimated through line transect distance sampling surveys

index (UDOI) were computed to calculate the extent of spatial overlap in blackbuck area by feral-horse. UDOI is a probabilistic component, a symmetrical measure of joint distribution or shared space use based on the product of UD(s) of both the species (Fieberg and Kochanny, 2005). UDOI is based on the assumptions by Hurlbert (1978) and described by Fieberg and Kochanny (2005). UDOI values range from zero (no overlap) to 1 (uniformly distributed and have 100% overlap). The UDOI values were scaled into percentages for interpretation. The overlap indices were computed in adehabitatHR package for R (Calenge 2011).

Resource selection: Previous PCWLS studies on blackbuck and feral horses have shown the influence of habitat type, diet, habitat openness, invasive species, and other factors on the distribution of these species' populations (Arandhara *et al*., 2020). This study uses resource selection functions (RSF), an approach that gives the probability that a particular resource (ecological covariates) will be used by an animal species. RSF models were developed considering the combination of climate, vegetation, anthropogenic, invasive pressure and effect of sympatric species variables, that were assumed to be a priori in understanding resource selection by both grazers. The covariate rasters were stacked and the raster values at default resolution were extracted for each use (animal locations) and available locations (sampled locations, plots). RSF were estimated for each species seasonally and at 100% distribution area, that represent selection for the maximum area a species can transverse. Non-exponential logistic RSF were evaluated, as studies suggest this approach to provide better fit to the data than the commonly used exponential RSF (Lele and Keim, 2006). RSF analyses were computed using the Package 'ResourceSelection' that deals with 'Use-Availability' data (Lele *et al*., 2019) in R program (R Development Core Team, 2005). To evaluate candidate models representing alternative hypotheses about the influence of environmental conditions and interspecific interactions on each species' patterns of resource use, we used AIC values to rank models considering low parsimony (Burnham and Anderson, 2002). To determine the direction, range, and effect of the covariates, we considered regression coefficients and evaluated the 95% confidence intervals.

Results

Habitat overlap: Overall distribution area, (100% MCP) in terms of habitat use, blackbuck utilized lesser extent of three major habitat types viz. woodland, scrubland and grassland than that of feral-horse (Table 2). No significant difference was observed in the extent of habitat use between the seasons ($F = 15.5$, $df = 21$, $p < 0.13$) (Fig. 2A).

UDOI at 100 % distribution area revealed a considerable overlap in the blackbuck area by feral-horse. The distribution area shared in grassland by both species (UDOI 100% = 91.5 % ± 7.43SE ranging from 87-95%), was higher than in the woodland (UDOI 100% = 66.5% ± 9.54SE, ranging from 58-66%) than in scrubland (UDOI 100%= 62.8% ± 8.22 SE, ranging from 60-66%). We found significant difference in overlap estimates between the habitat types ($F = 14$, $df = 21$, $p < 0.023$) and seasons ($F = 9.9$, $df = 21$, $p < 0.018$).

Core distribution area (50% KDE) used by blackbuck (woodland=3.8 km^2 ± 0.84SE, scrubland= 2.8 km^2 ± 0.75SE, grassland= 4.6 km^2 ± 0.91SE) was lesser than the extent used by feral-horse (woodland=5.9 km^2 ± 0.61SE, scrubland= 4.3 km^2 ± 1.09SE, grassland= 6.0 km^2 ± 0.67SE). Habitat wise UDOI 50% indices representing the grassland was 70.7% ± 4.34SE ranging between 65-76 %, while in the scrubland it was 65.3 % ± 4.34SE ranging between 54-75% and in woodland the extent of overlap was 64.8 % ± 5.94SE ranging from 60-72%. A significant difference in habitat overlap between the habitat types were observed ($F = 5.9$, $df = 21$, $p < 0.02$) and between the seasons ($F = 5.9$, $df = 21$, $p < 0.02$) (Table 2; Fig. 2B).

Resource selection functions: Considering II-order resource selection function and extent of total

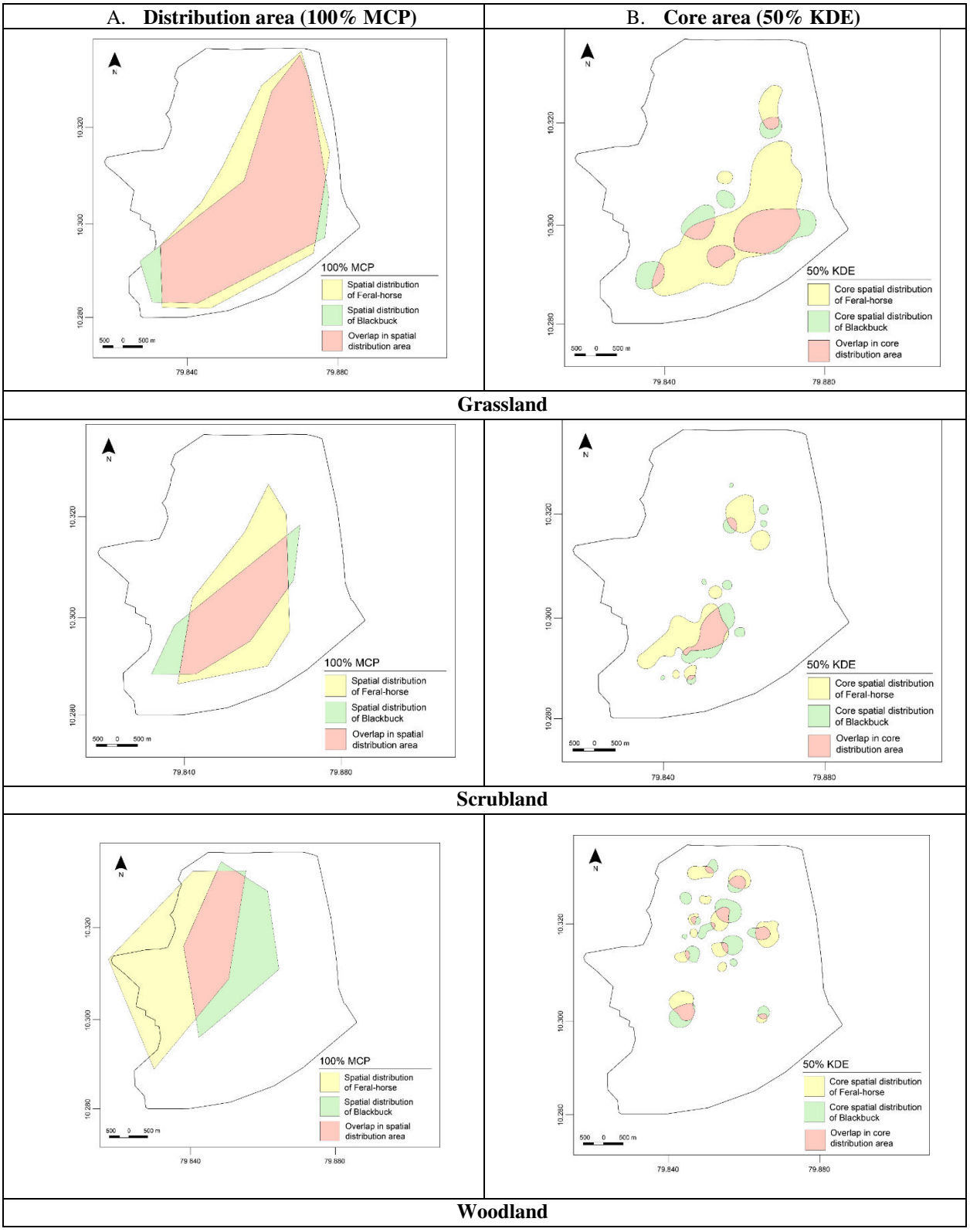

Fig. 2: Habitat overlap in distribution area and core area of blackbuck by feral-horse in different habitat.

Table 2: Overlap in habitat use between blackbuck and feral-horse at Point Calimere, southern India

Habitat	Season	Year	Distribution Area (km²)			Core Area (km²)		
			Blackbuck	Feral-Horse	Overlap (%) ± SE	Blackbuck	Feral-Horse	Overlap (%) ± SE
			Mean (km²) ± SE	Mean (km²) ± SE		Mean (km²) ± SE	Mean (km²) ± SE	
Woodland	Dry season	2017-2018	5.3 ± 1.86	7.2 ± 1.65	73.2 ± 16.55	3.1 ± 0.89	5.1 ± 0.67	60.0 ± 4.22
		2018-2019	4.8 ± 1.23	8.7 ± 3.16	55.1 ± 6.23	4.3 ± 0.63	5.9 ± 0.75	72.5 ± 6.92
	Wet season	2017-2018	5.8 ± 4.86	7.3 ± 1.81	78.6 ± 9.24	3.9 ± 0.76	6.3 ± 0.34	61.2 ± 6.30
		2018-2019	5.7 ± 2.31	9.7 ± 6.10	59.0 ± 6.21	4.1 ± 1.08	6.3 ± 0.68	65.4 ± 6.32
		Mean	**5.4 ± 2.60**	**8.2 ± 3.21**	**66.5 ± 9.54**	**3.8 ± 0.84**	**5.9 ± 0.61**	**64.8 ± 5.94**
Scrubland	Dry season	2017-2018	6.3 ± 1.87	10.4 ± 2.14	60.4 ± 10.47	3.1 ± 0.97	4.1 ± 0.87	75.6 ± 7.03
		2018-2019	5.6 ± 2.34	9.5 ± 2.14	58.9 ± 7.54	2.0 ± 0.75	3.6 ± 0.76	55.8 ± 7.02
	Wet season	2017-2018	5.8 ± 3.22	8.6 ± 1.80	66.6 ± 7.41	3.1 ± 0.65	4.1 ± 1.69	75.7 ± 5.02
		2018-2019	5.3 ± 3.87	8.1 ± 3.11	65.1 ± 7.35	2.9 ± 0.64	5.4 ± 1.05	54.1 ± 4.03
		Mean	**5.7 ± 2.81**	**9.2 ± 2.35**	**62.8 ± 8.22**	**2.8 ± 0.75**	**4.3 ± 1.09**	**65.3 ± 4.34**
Grassland	Dry season	2017-2018	17.3 ± 6.72	19.1 ± 8.61	90.5 ± 8.32	4.7 ± 0.89	5.8 ± 0.73	59.4 ± 8.10
		2018-2019	12.5 ± 4.69	13.1 ± 6.27	95.4 ± 9.29	4.7 ± 1.03	5.8 ± 0.41	82.3 ± 5.02
	Wet season	2017-2018	15.3 ± 5.61	17.1 ± 6.36	89.4 ± 5.63	4.6 ± 0.73	5.7 ± 0.22	79.0 ± 5.94
		2018-2019	13.2 ± 6.40	14.6 ± 7.37	90.4 ± 6.44	4.6 ± 0.99	6.6 ± 1.32	62.0 ± 2.29
		Mean	**14.6 ± 5.91**	**16.0 ± 7.14**	**91.5 ± 7.43**	**4.6 ± 0.91**	**6.0 ± 0.67**	**70.7 ± 4.34**

Table 3: Resource selection function models of blackbuck and feral-horse at Point Calimere, southern India

Model						K	-2 log L	AIC	Δ AIC
Blackbuck (n=646)									
Dry season	Habitat openness	Forest type	Prosopis cover	Grass biomass		6	1052	1080	0
	Habitat heterogeneity	Forest type	Distance to water	Feral horse density	Vegetation density	10	1071	1081.8	1.8
	Null Model					0	3477	3381	2301
Wet Season	Forest type	Distance to water	Habitat openness	Prosopis cover		6	2805	2201	0
	Distance to water	Habitat openness	Prosopis cover	Distance to road	Distance to water	5	3012	2203	2
	Null Model					0	3075	2387	186
Feral-horse (n=453)									
Dry season	Forest type	Distance to water	Habitat openness	Grass biomass		6	804	798	0
	Grass biomass	*Prosopis* cover	Habitat heterogeneity	Habitat openness		4	809	802	4
	Null Model					0	1126	1086	288
Wet Season	Distance to water	Grass biomass	Habitat openness	Forest type		7	841	1966	0
	Vegetation cover	Habitat openness	Forest type	Grass biomass		8	845	1972	6
	Null Model					0	2353	2345	1547

distribution area surveyed during the dry season, the most supported resource selection model for blackbuck included the covariates viz. habitat openness (β=7.2, CI=5.67—8.18), forest type (Woodland: β= -3.32, CI=-5.27—-2.78; Scrubland: β=-2.72, CI=-2.02—-3.19; Grassland: β=2.11, CI=1.89 — 2.96), *Prosopis* cover (β=-3.09, CI= -3.67 — -2.51) and grass biomass (β= 4.03, CI= 3.13 — 4.99), followed by the next supported model with habitat heterogeneity (β= -2.8, CI=-3.5—-2.12), forest type, distance to water (β= -4.82, CI=-5.33 — -3.99), Vegetation cover (Tree cover: β= 3.33, CI= 2.19 — 4.58; Shrub cover: β= -2.25, CI=-2.77 — -1.97; Grass cover: β= 4.25, CI=3.55—5.84), vegetation density (Shrub density: β= -3.71, CI=- 4.13 — -2.45; Tree density: β= -3.2, CI= -3.85 — -2.69).

Selection through wet season included the covariates as Forest type with grassland (β= 2.45, CI= 1.61—6.22) showing positive, including Habitat openness (β= 4.6, CI= 2.95—7.37); Distance to water (β= 5.1, CI= 2.42—7.87). While a negative selection was indicated by woodland (β= -2.25, CI= -7.13—-1.38) and scrubland (β= -1.93, CI =-4.78—-1.17); similar negative trend was shown by *Prosopis* cover (β= -2.33, CI=-4.56—-2.01).

The best model for feral-horse during the dry season included the covariates viz. forest type (Woodland: β=4.17, CI=3.79—4.65; Scrubland: β= -1.56, CI=-0.93—-2.1; Grassland: β= 5.29, CI=4.08—5.74), distance to water (β= -7.85, CI=-6.35—-8.23), habitat openness (β= 9.6, CI=7.41—10.87), grass biomass (β= 8.16, CI=7.35–9.32). The subsequent model showed to include grass biomass, *Prosopis* cover (β= -3.56, CI= -4.25—-2.09), habitat heterogeneity (β= -1.9, CI=-2.31—-1) and habitat openness were the significant

Table 4: Univariate parameter estimates β from the resource selection function models for blackbuck and feral-horse

	Dry season				Wet season			
Covariate	**β**	**SE**	95% CI **UL**	95% CI **LL**	**β**	**SE**	95% CI **UL**	95% CI **LL**
Blackbuck								
Woodland (%)	-3.32	0.864	-5.27	-2.78	-2.25	0.635	-7.13	-1.38
Scrubland (%)	-2.72	0.592	-3.19	-0.82	-1.93	0.377	-4.78	-1.17
Grassland (%)	2.11	0.304	1.89	2.96	2.45	0.513	1.61	6.22
Habitat openness (km^2)	7.2	0.452	5.67	8.18	4.6	1.735	2.95	7.37
Habitat heterogeneity	-2.8	0.920	-3.5	-2.12	-1.98	0.73	-4.13	-1.26
Distance to water (m)	-4.82	1.108	-5.33	-3.99	5.1	2.13	2.42	7.87
Distance to shade (m)	5.36	1.025	4.3	5.76	-1.7	0.93	-3.87	-1.03
Shrub density	-3.71	0.084	-4.13	-2.45	-6.37	3.56	-9.55	-1.49
Tree density	-3.2	0.134	-3.85	-2.69	-5.19	2.38	-9.1	-3.35
Tree diversity	-1.18	0.302	-2.09	-0.93	-3.76	1.46	-6.17	-1.44
Shrub diversity	-3.41	0.214	-4.04	-2.83	-1.89	0.78	-5.66	-1.97
Tree cover	3.33	0.509	2.19	4.58	6.56	2.19	1.95	8.55
Shrub cover	-2.25	0.311	-2.77	-1.97	-5.32	1.93	-8.16	-1.81
Grass cover	4.25	0.612	3.55	5.84	3.16	0.826	1.28	5.54
Grass biomass index/m^2	4.03	0.512	3.13	4.99	7.44	1.63	5.66	9.12
Prosopis density/25 m^2	-2.56	0.032	-3.72	-1.45	-4.2	0.782	-6.52	-2.16
Prosopis cover/25 m^2	-3.09	0.097	-3.67	-2.51	-2.33	0.51	-4.56	-2.01
Distance to road (m)	-1.01	0.032	-1.72	-0.58	-2.67	0.32	-4.45	-1.75
People frequency	-0.76	0.019	-1.29	-0.32	-2.95	1.53	-5.53	-0.32
Feral horse density	-2.34	0.104	-2.77	-1.52	-2.34	0.104	-2.77	-1.52

Feral horse								
Woodland (%)	-4.17	0.741	-8.79	-2.55	-2.48	0.74	-4.65	-1.79
Scrubland (%)	-1.56	0.234	-2.1	-0.93	-3.42	1.09	-5.76	-1.31
Grassland (%)	5.29	0.145	4.08	5.74	4.78	2.34	2.83	6.3
Habitat openness (km^2)	9.6	0.032	7.41	10.87	7.4	0.56	2.36	8.92
Habitat heterogeneity	-1.9	0.188	-2.31	-1	-2.11	0.78	-4.31	-1.06
Distance to water (m)	-7.85	0.672	-8.23	-6.35	6.05	1.02	2.06	9.75
Distance to shade (m)	1.2	0.569	0.75	1.93	2.06	0.34	0.88	3.27
Shrub density	-0.78	0.019	-0.89	-0.54	-0.32	0.054	-3.63	-0.14
Tree density	1.92	0.102	1.22	2.17	3.12	0.76	2.05	4.88
Tree diversity	2.34	0.187	1.98	2.67	4.21	1.1	1.98	5.12
Shrub diversity	-2.49	0.966	-3.17	-1.75	-4.08	0.73	-5.11	-2.15
Tree cover	2.03	0.106	1.23	2.87	7.25	1.18	4.55	10.26
Shrub cover	-0.73	0.218	-1.28	-0.5	-3.08	1.2	-6.36	-2.98
Grass cover	7.27	0.836	5.06	8.82	1.43	0.26	0.09	3.18
Grass biomass index/m^2	8.16	0.043	7.35	9.32	3.95	0.043	1.09	5.77
Prosopis density/25 m^2	-0.18	0.168	-0.29	-0.1	-2.26	0.73	-4.4	-1.7
Prosopis cover/25 m^2	-3.56	0.587	-4.25	-2.09	-5.94	1.27	-7.62	-3.8
Distance to road (m)	2.19	0.548	1.21	3.09	1.73	0.91	1.09	4.54
People frequency	1.66	0.096	1.03	2.17	3.11	1.59	0.96	4.34
Blackbuck density	0.88	0.037	0.38	3.26	2.15	0.64	1.43	5.31

covariates contributing to the next most supported model.

During the wet season, feral-horse resource selection was determined by distance to water showing a positive selection (β= 6.05, CI= 2.06—9.75); Grass biomass (β=3.95, CI= 1.09—5.77); Habitat openness (β= 7.4, CI= 2.36—8.92); Forest type with scrubland (β=-3.42, CI=-5.76—-1.31) and woodland (β=-2.48, CI= -4.65—-1.79) entered as negative and while grassland (β= 4.78, CI=2.83—6.3) were positive. In the next supported model, vegetation cover with grass cover (β= 1.43, CI= 0.09—3.18) and tree cover (β= 7.25, CI= 4.55—10.26) entered as positive, while shrub density (β= -0.32, CI= -3.63—-0.14) indicated a negative trend. Habitat openness, Forest type with grassland showed positive selection along with grass biomass (Tables 3, 4).

Discussion

Habitat overlap:

The negative impacts of invasive feral-horse on the native blackbuck at PCWLS have been highlighted by earlier studies (Ali, 2005; Baskaran *et al*., 2016; Arandhara *et al*., 2020). In particular, to assess potential segregation between species distributions at the population level, the information on space use, habitat use, and level of spatial overlap addressed by this study revealed sympatric blackbuck and feral-horse to exhibit a high degree of interspecific spatial overlap in PCWLS, with shared areas used heavily and similarly by both species.

We hypothesize that there might be segregation at habitat level, which ultimately facilitate coexistence between blackbuck and feral-horse at PCWLS. The findings showed a significant overlap between the feral-horse and blackbuck in habitat use and these support the earlier study (Baskaran *et al*., 2016). The overlap in core area estimates further suggest that feral-horse would further respond to increased sharing of grassland habitat with blackbuck by expanding its movements to include core areas as well. For both the species, we found that grassland was the major forest type, where the species was

distributed. However, both the species were located occasionally in dry evergreen forests or along edges, but use of the same by blackbuck was relatively less.

This spatial relation between the two species might as well give a hint of the detrimental consequences faced by the grassland-centric social antelope like the blackbuck, as the ability to cover beyond its territorial range is likely limited by social and foraging constraints. The home range of antelopes is likely to be smaller, as it socializes in groups and thus requires less space for socializing and feeding compared to the larger-body feral-horse with presumably greater energetic requirements, and thus its movement for foraging activities is presumably more. In our study area, the home ranges of blackbuck, delineated by the MCP, on an average, extend approximately 0.91±0.41 km^2. On the other hand, the mean annual home-range size of the feral-horse is nearly thrice as large as the blackbuck, MCP = 2.64 ± 0.77 (Arandhara *et al*., 2020). This variation in the home range sizes and similarity in space-use patterns between the two species is perhaps best explained by differences in sociality, with the blackbuck, a ruminant grazer, showing territorial behaviour and resource use as well, while feral-horse, a non-ruminant bulk feeder, has a dietary overlap suggested by an earlier study (Baskaran *et al*., 2016).

Again, at a finer scale of individual distances when considered, there was a negative association between both the species. In relation to distance from feral-horse, the blackbuck had significantly lower density estimates, while in proximity to feral-horse (β = 12.1: f = 11: p <0.01; R^2 = 0.16) (Baskaran *et al*., 2020). It is suggested that interactions between sympatric taxa shape the structure of ecological communities on the demography, distribution, and behaviour of species (Holt and Polis, 1997; Berger and Gese, 2007). It is also coherent with Gause's (1934) observation that coexisting species should differ in at least one or more dimensions of their ecological niches, such as resources, space or time. The trend of blackbuck keeping away from the feral-horse, as showed by Multiple Covariate Distance Sampling (MCDS), in an earlier study from this area clearly indicates avoidance of spatial coexistence (Arandhara *et al*., 2020). These findings suggest that the feral-horse competitively displaces the smaller-sized blackbuck in resource-constricted locations, and thus the blackbuck keeps away to avoid interference competition, suggesting that invasive feral-horse is a major threat to blackbuck in space use in the sanctuary.

Resource selection:

Our results provide an empirical assessment and have implications for understanding the ecological covariates that determine resource selection of blackbuck and feral-horse and provide insights on seasonal differences in resource selection highlighting resource similarities between the two species and on the potential effects of the invasive feral-horse and *Prosopis* on the native blackbuck. Considering the "first order, Design 1" resource selection function at population level, during the dry season; habitat openness, forest type, grass biomass was revealed as the most influential predictors of resource use probability and with a positive relationship. Blackbuck largely inhabited towards open habitat distributed in grassland as the major habitat type and the species avoided *Prosopis* cover. Blackbuck are known to be open grassland species and the positive relationship with grass biomass was also evident as the species depend on short-grass coincides with increasing fresh grass biomass (Prater, 1948; Baskaran *et al*., 2016; Arandhara *et al*., 2020). Further to be vigilant from predators and traverse their activities while maintaining their social characteristic, open habitat becomes necessary attribute towards their life history. In contrast, selection for *Prosopis* cover, habitat heterogeneity turned out to be negative indicated that blackbuck select for *Prosopis* free and homogenous habitat, i.e., open grassland. *Prosopis* cover and woody habitat as well creates impenetrable thorn thickets and offer very limited ground cover and low graze for herbivores (Cochard and Edwards,

2011). Further, in the subsequent model along with the habitat covariates, highlight the presence of feral-horse as a negatively influencing factor in resource selection by blackbuck. The covariate distance to water indicates the importance of water on resource selection, especially during the dry season with low-quality diet and reduced water availability, the blackbuck responds by passing concentrated alkaline urine and dry faeces, escalates its drinking frequency, and thus most individuals may restrict themselves close to water sources, as that of observed around the surface water areas throughout the year in arid and semi-arid zones (Rahmani and Shankaran, 1991; Jhala and Isvaran, 2016).

The wet season is important for the large herbivores in PCWLS, and the top wet season model includes forest type with grassland habitat showing positive support, grassland appears to be critical resource for large herbivores during the wet season. The first flush of grass and sedges, which occurs after the rains in October, lasting till December, is utilized extensively by the animals. However, due to the characteristic undulating grassland terrain of PCWLS, major parts of grassland get lodged in water. Due to this effect, we obtain an interesting trend of blackbuck avoiding water proximity and elevated grazing locations are selected in wet season avoiding the submerged locations where grasses lost its grazable characteristic, also as a behavioural adaptation to defend the fawns getting into water (Arandhara *et al*., 2020). Further, in the wet season model, negative effect was shown by *Prosopis* cover and distance to road, indicating that the animals were distributed proximate to roads that are elevated above water, while habitat openness indicated a positive effect as supposed to be.

The top models explaining resource selection for feral-horse during dry season and wet season resulted covariates with varied effects both in intensity and precision, but direction were similar as the covariates for blackbuck; viz. forest type with woodland and scrubland entered as negative including *Prosopis* cover and habitat heterogeneity; while grassland; habitat openness and grass biomass showed positive relationship indicating the importance of grassland habitat to the feral-horse as well with associated covariates such as habitat openness and grass biomass. Linked to habitat use by both the species, a considerable overlap in grassland habitat by feral-horse in blackbuck habitat use during the two seasons indicated the importance of habitat openness in life history of both the species. Likewise, negative trend of distance to water during dry season indicated its water dependence for each of the species and avoidance during the wet season.

Another study using Multiple Covariate Distance Sampling presents an evidence of niche partitioning based on distribution of principal diet that would alleviate strong competition. Arandhara *et al*. (2020) reported a positive trend in detectability of feral-horse in the presence of principal diet and a significant increase in its density in the presence of principal diet (post-stratification analysis) also supports the above observations. A notable opposite pattern was observed in the case of blackbuck, in which there was an insignificant but negative trend in its density, where the principal diet was abundant, suggesting of its distribution in locations where it is scarce. This finding along with the trend of blackbucks keeping away from the feral-horse indicates that the latter is competitively displacing the smaller-sized blackbuck towards sub-optimal resource-constricted locations, as feral-horse also depends on the same grass species as its principal diet (Baskaran *et al*., 2016), resulting in a kind of a resource partitioning. Competition builds up when one species efficiently reduces the use of shared food resources of another species (Illius and Gordon, 1987; Murray and Illius, 1996; Prins and Olff, 1998; Long, 2003). If resource partitioning via competition is occurring, and because blackbucks keeping away from the feral-horse at least in the wet season as suggested, competition theory predicts that in the absence of the invasive

species, the distribution of blackbuck would include locations with abundant principal diet. There are no studies available in PCWLS where blackbuck distribution and diets have been examined in the absence of the feral-horse. In contrast to feral-horse effecting blackbuck resource selection, we found no evidence in the feral-horse models that the spatial distribution of blackbuck influences the resource use by feral-horse.

By this study, we provide an insight into the mechanisms and likely consequences of competitive interactions between native blackbuck and invasive feral-horse through field surveys evaluating the habitat use and resource selection relationships. Considerable level of overlap in use of habitat, and resource selection between the two species indicated a high potential for competition, especially in prime grassland habitat. Further similarities in resource selection and avoidance reveal the likely evidence for establishing the existence of interspecific competition as indicated by overlap in resource use between potential competitors and resource use of feral-horse affecting the resource use (availability) of the blackbuck.

The scenario seen in PCWLS in absence of major predators turns out to be interesting due to the presence of the invasive feral-horse, likely to affect the fitness of the native blackbuck generally linked to shrinkage of usable space and diet. The suspected interspecific competition in a long-run and shrinkage of usable vegetation may be used to justify management interventions to curtail or prevent population growth via some form of culling of the invasives, importantly the feral-horse and *Prosopis juliflora* species (Shackleton *et al*., 2003; Pyšek *et al*., 2012).

Conclusion

The introduction of new species to natural habitats is of concern and to consider managing their populations is as essential as the native ones. Results from our study indicated a strong potential for both overlap and evidence towards interference competition between the native blackbucks and introduced feral-horse as well, and that availability and use of habitat and resource are likely to be the most emphasizing factors revealing the interaction/relationship between these species. These findings support the conclusions of Ali (2005); Baskaran *et al*. (2016) and Arandhara *et al.* (2020). in that the existence of feral-horse as a potential competitor throws light upon conservation on the native blackbuck. The patterns of blackbuck keeping away from feral-horse in spite of showing a major overlap in the habitat use and especially, when it is made evident that the blackbucks are pushed away from locations harboring principal diet species by an earlier study are suggestive of an essential component of competition.

The management and conservation of grassland habitat, which is a chief focus of habitat improvement strategies for blackbuck in the study areas, makes the protection of grassland habitat even more important because any loss of habitat will likely pose further constrain due to overlap of limited resources, thereby increasing competitive pressure and leading to additional negative impacts on the native blackbucks. Our additional observation from our extended studies addressing the impact of *Prosopis* provide an insight of how the exotic might appear to be detrimental to blackbucks and associated habitat in the study sites. Thus, the findings of the present study could help understand the resource-use, distribution and interaction of the invasives with native species and will help guide the management on decisions to refine the management process to control the invasives including feral-horse and *Prosopis* for the long-term survival of the native blackbuck at Point Calimere and other species of ungulates elsewhere in similar conditions.

We suggest the following management measures:

Managing open grasslands: Managing grasslands without much invasion by woody plants is needed to maintain a high-density population of the blackbuck. The invasion of exotic weed *Prosopis juliflora* is already modifying the open grasslands

into woodlands (Ali, 2005), which leads to reduced habitat openness, a prime predictor of blackbuck density and biomass of short grass. Therefore, exotic weed management, especially of *Prosopis*, should be given higher priority. The managers concerned are aware of the situation and are taking measures to uproot these exotic weeds, but it is happening gradually. We suggest synchronized massive effort to uproot the invasive, to reduce the probability of its further dispersal in the sanctuary, and hence, to conserve the native biodiversity and succeed in reverting the indigenous ecological processes.

Elimination invasive feral-horse: It is very credible that the feral-horse, an invasive species to the ecosystem, is a real competitor to the blackbuck in the study area, which is ecologically a stressed environment with low soil fertility, and high salinity along with competition from the domestic cattle. Thus, it is important to take measures to compassionately check the population of the feral-horse using contraception or capture and translocate or domesticate its females.

Acknowledgements

This work was supported by the Science and Engineering Research Board [Grant File. No. EMR/2016/001536], Department of Science and Technology, New Delhi, Government of India. We express our sincere thanks to the Tamil Nadu Forest Department, especially its former Chief Wildlife Wardens, Mr. P.C. Thyagi, I.F.S. and Sanjay Kumar Srivastava, I.F.S., and the Wildlife Warden Point Calimere, Nagapattinam for granting permission to conduct the study and support to it. We are also thankful to the Management and Principal of A.V.C. College for their constant support to this project.

References

Ali R. (2005) Field studies for the conservation and management of point Calimere Complex. Foundation for ecological research, advocacy and learning. A Report for the Tamil Nadu Forest Department, 40.

Amarasekare P. (2003) Competitive coexistence in spatially structured environments: a synthesis. Ecol Letters 6(12):1109-1122.

Andren H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71: 355-366.

Arsenault R and Owen-Smith N. (2002) Facilitation versus competition in grazing herbivore assemblages. Oikos 97(3): 313-318.

Baskaran N, Arandhara S and Sathishkumar S. (2020) Monitoring report submitted to Department of Science and Technology, SERB, India. Jan, 2020, Unpublished, p. 10.

Baskaran N, Arandhara S, Sathishkumar S and Gupta S. (2019) Assessing the changes in land use and land cover by invasive species and its influence on native flora & ungulates in selected protected areas of Tamil Nadu, India using GIS and remote sensing. Technical report submitted to SERB, Government of India.

Baskaran N, Ramkumaran K and Karthikeyan G. (2016) Spatial and dietary overlap between blackbuck (*Antilope cervicapra*) and feral horse (*Equus caballus*) at Point Calimere Wildlife Sanctuary, Southern India: Competition between native versus introduced species. Mammalian Biol. 81(3): 295-302.

Berger KM and Gese EM. (2007) Does interference competition with wolves limit the distribution and abundance of coyotes? J Animal Ecol. 76(6): 1075-1085.

Boyce MS and McDonald LL. (1999) Relating populations to habitats using resource selection functions. Trends Ecol Evol. 14(7): 268-272.

Calenge C. (2011) Home range estimation in R: the adehabitat HR package. Office national de la classe et de la faune sauvage: Saint Benoist, Auffargis, France.

Clutton-Brock TH, Albon SD and Guinness FE. (1984) Maternal dominance, breeding success and birth sex ratios in red deer. Nature 308(5957): 358-360.

Clutton-Brock TH, Albon SD and Guinness FE. (1986) Great expectations: dominance, breeding success and offspring sex ratios in red deer. Animal Behaviour 34(2): 460-471.

Cochard R and Edwards PJ. (2011) Structure and biomass along an *Acacia zanzibarica* woodland–savanna gradient in a former ranching area in coastal Tanzania. J Veg Sci. 22(3): 475-489.

Côté SD and Festa-Bianchet M. (2001) Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127(2): 230-238.

De Boer WD and Prins HH. (1990) Large herbivores that strive mightily but eat and drink as friends. Oecologia 82(2): 264-274.

Dennis RL, Shreeve TG and Van Dyck H. (2003) Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102: 417-426.

Durant SM. (1998) Competition refuges and coexistence: an example from Serengeti carnivores. J Animal Ecol. 67(3): 370-386.

Fahrig L. (2003) Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, and systematics*, pp.487-515.

Fieberg J and Kochanny CO. (2005) Quantifying home-range overlap: The importance of the utilization distribution. J Wildlife Managem. 69(4): 1346-1359.

Focardi S, Aragno P, Montanaro P and Riga F. (2006) Inter-specific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer C*apreolus capreolus italicus*. Ecography 29(3): 407-417.

Forsyth DM and Hickling GJ. (1998) Increasing Himalayan tahr and decreasing chamois densities in the eastern Southern Alps, New Zealand: evidence for interspecific competition. Oecologia 113(3): 377-382.

Gause GF. (1934) Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. Science 79(2036): 16-17.

Hamel MA, Andréfouët S and Pressey RL. (2013) Compromises between international habitat conservation guidelines and small-scale fisheries in Pacific Island countries. Conservation Letters 6(1): 46-57.

Harris MR and Siefferman L. (2014) Interspecific competition influences fitness benefits of assortative mating for territorial aggression in eastern bluebirds (*Sialia sialis*). PLoS One 9(2): e88668.

Holt RD and Polis GA. (1997) A theoretical framework for intraguild predation. American Naturalist 149(4): 745-764.

Hurlbert SH. (1978) The measurement of niche overlap and some relatives. Ecology 59(1): 67-77.

Hutchinson GE. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93(870): 145-159.

Illius AW and Gordon IJ. (1987) The allometry of food intake in grazing ruminants. J Animal Ecol. 56: 989-999.

Isvaran K. (2005) Female grouping best predicts lekking in blackbuck (*Antilope cervicapra*). Behavioral Ecol Sociobiol. 57(3): 283-294.

Isvaran K. (2007) Intraspecific variation in group size in the blackbuck antelope: the roles of habitat structure and forage at different spatial scales. Oecologia 154(2): 435-444.

Jhala YV. (1997) Seasonal effects on the nutritional ecology of blackbuck Antelope cervicapra. J Appl Ecol. 34:1348-1358.

Jhala YV, Giles JRH and Bhagwat AM. (1992) Water in the ecophysiology of blackbuck. J Arid Environ. 22(3): 261-269.

Jhala YV and Isvaran K. (2016) Behavioural ecology of a grassland antelope, the blackbuck *Antilope cervicapra*: linking habitat, ecology and behaviour. In: The ecology of large herbivores in South and Southeast Asia, (eds.) Ahrestani F.S. and Sankaran M., Springer Nature Publication, Dordrecht, pp. 151-176.

Johnson DH. (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61(1): 65-71.

Krishna YC, Kumar A and Isvaran K. (2016) Wild ungulate decision-Making and the role of tiny refuges in human-dominated landscapes. PLoS One 11(3): e0151748.

Latham J. (1999) Interspecific interactions of ungulates in European forests: an overview. Forest Ecol Managem.b120(1-3): 13-21.

Lele SR and Keim JL. (2006) Weighted distributions and estimation of resource selection probability functions. Ecology 87(12): 3021-3028.

Lele SR, Keim JL, Solymos P, Solymos MP and Imports MASS. (2019) Package 'ResourceSelection'. Google Scholar.

Levi T and Wilmers C. (2012) Wolves–coyotes–foxes: a cascade among carnivores. Ecology 93(4): 921-929.

Long JL. (2003) Introduced mammals of the world: their history, distribution, and influence. CSIRO Publishing.

Long N. (2003) Development sociology: actor perspectives. Routledge.

Lovari S, Ferretti F, Corazza M, Minder I, Troiani N, Ferrari C and Saddi A. (2014) Unexpected consequences of reintroductions: competition between reintroduced red deer and A pennine chamois. Animal Conserv. 17(4): 359-370.

MacArthur RH, Diamond JM and Karr JR. (1972) Density compensation in island faunas. Ecology 53(2): 330-342.

Murray MG and Illius AW. (1996) Multispecies grazing in the Serengeti. In: The ecology and management of grazing systems, (eds.) Hodgson J. and Illius A.W., CAB International, Wallingford, pp.247-272.

Murray MG and Illius AW. (2000) Vegetation modification and resource competition in grazing ungulates. Oikos 89(3): 501-508.

Namgail T, Mishra C, De Jong CB Van Wieren SE and Prins HH. (2009) Effects of herbivore species richness on the niche dynamics and distribution of blue sheep in the Trans-Himalaya. Diversity Distributions 15(6): 940-947.

Newbery DM, Prins HHT and Brown ND. (1998) Dynamics of Tropical Communities: 37th Symposium of the British Ecological Society. Cambridge University Press.

Owen-Smith N. (1982) Factors influencing the consumption of plant products by large herbivores. In: Ecology of tropical savannas, Springer, Berlin, Heidelberg, pp. 359-404.

Pettorelli N, Pelletier F, Hardenberg AV, Festa-Bianchet M and Côté SD. (2007) Early onset of vegetation growth vs. rapid green-up: Impacts on juvenile mountain ungulates. Ecology 88(2): 381-390.

Pianka ER. (1973) The structure of lizard communities. Annual Rev Ecol Systematics 4: 53-74.

Prater SH. (1948) The book of indian animals. Bombay Natural History Society, Bombay.

Putman RJ. (1996) Ungulates in temperate forest ecosystems: perspectives and recommendations for future research. Forest Ecol Managem. 88(1-2): 205-214.

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U and Vilà M. (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Glob Chang Biol. 18(5): 1725-1737.

Rahmani AR and Sankaran R. (1991) Blackbuck and Chinkara in the Thar Desert: a changing scenario. J Arid Environ. 21(3): 379-391.

Ranjitsinh MK. (1989) Indian blackbuck. Natraj Publishers.

Razgour O, Korine C and SaltzD. (2011) Does interspecific competition drive patterns of habitat use in desert bat communities? Oecologia 167(2): 493-502.

Robertson SJ, Zhou JY, Geddes K, Rubino SJ, Cho JH, Girardin SE and Philpott DJ. (2013) Nod1 and Nod2 signaling does not alter the composition of intestinal bacterial communities at homeostasis. Gut Microbes 4(3): 222-231.

Schoener TW. (1974) Competition and the form of habitat shift. Theoretical Population Biol. 6(3): 265-307.

Shackleton RT, Le Maitre DC, Van Wilgen BW and Richardson DM. (2015) The impact of invasive alien *Prosopis* species (mesquite) on native plants in different environments in South Africa. S Afr J Bot. 97: 25- 31.

Sinclair ARE and Norton-Griffiths M. (1982) Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. Oecologia 53(3): 364-369.

Thomas DL and Taylor EJ. (1990) Study designs and tests for comparing resource use and availability. J Wildlife Managem. 54(2): 322-330.

Valéry L, Fritz H, Lefeuvre JC and Simberloff D. (2009) Invasive species can also be native. Trends Ecol Evol. 24(11): 585.

Vanak AT, Fortin D, Thaker M, Ogden M, Owen C, Greatwood S and Slotow R. (2013) Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology 94(11): 2619-2631.

Wereszczuk A and Zalewski A. (2015) Spatial niche segregation of sympatric stone marten and pine marten–avoidance of competition or selection of optimal habitat?. PLoS One 10(10): e0139852.

Wiens JD, Anthony RG and Forsman ED. (2014) Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. Wildlife Monographs 185(1): 1-50.