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Cover: Green Bee-eater with colour pencils and watercolor wash by Elakshi Mahika Molur.

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COMMUNICATION

Determinants of diet selection by Blackbuck *Antilope cervicapra* at Point Calimere, southern India: quality also matters

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Abstract: Unlike the wide-ranging habitat generalists that move seasonally across heterogenous habitats to optimize the energy intake, short-ranging habitat specialists fulfil the same by restricting to single habitat. Understanding how habitat-specialists do this is an interesting question and essential for their conservation. We studied the diet composition and evaluated the covariates belonging to climate, habitat and grass dynamics to assess the determinants of seasonal diet selection by Blackbuck *Antilope cervicapra*, an antelope endemic to the Indian subcontinent, at Point Calimere Wildlife Sanctuary, southern India. Diet composition studied following feeding trail observation (n = 102322) and the influence of covariates on the top five major diet species selected seasonally was tested using Regression with Empirical Variable Selection. The results showed that overall Blackbucks consumed 30 plant species—six browse and 27 grass species. While wet season diet was less diverse (22 species) with higher dependency on principal diet *Cyperus compressus* (>40%) and *Aeluropus lagopoides* (24%), the dry season diet was more diverse (30) species, with decreased dependency on principal diet. Among 13 covariates belonging to climate, habitat, and grass dynamics tested against selection of top five major diet plants by Blackbucks, grass dynamics covariates alone entered as the predictors both in wet and dry seasons. While cover and green leaves of the grass were the most common predictors in the top-five diets selection during wet season, in dry season besides cover and green leaves, grass texture (hard and soft), also entered as the most common predictors. The entry of grass cover, a quantitative related measure, and texture and green condition of the grass, quality related measures, as the drivers indicate that diet selection by Blackbuck is not just a matter of grass quantity, but also its quality.

Keywords: Diet selection, feeding site examination, grass dynamics, grassland, native species, quality of grass, soft texture grass, Ungulate.

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Author contributions: SS—Data collection, analyses, and draft preparation. SA—Data collection, pruning, analyses, and draft preparation. NB—Conceptualizing, supervising, data analyses, and final draft preparation.

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INTRODUCTION

In natural environment, ungulates exploit the heterogeneity of resources through selective grazing, choosing a diet of better quality than the average vegetation; on offer by preferring habitats that meet their foraging requirements (Prache et al. 1998). The habitat and the physical arrangement of various factors act as key ecological attributes influencing environmental conditions (Bell et al. 2012). The diverse topography along with remarkable variation in precipitation level in tropical environment results in spaciotemporal variations in resource quality and quantity (Baskaran et al. 2018). Habitat generalists, with wide-ranging nature, in heterogenous landscape use different habitats annually by moving among habitats in relation to season and resource availability. On the other hand, the habitat specialists, with restricted movement, fulfil their requirements within a given habitat round the year (Owen-Smith 2002). Understanding how habitat specialists cope-up within a habitat round the year and the factors that influence their resource-use pattern is an interesting area of research pertaining to long-term conservation. Diet selection and forage preference play a vital role in understanding the ecology of a species, as obtaining adequate quantity and quality of food for their survival and reproduction (Weterings et al. 2018).

Foraging decision and diet selection determine both; the nutrient intake by the animals and their impact on the vegetation. Thus, they are important for animal and vegetation management (Owen-Smith 1979; Prache et al. 1998). Earlier studies have reported that diet selection by ungulates is widely determined by many factors including forage quality, e.g., fiber, protein, micronutrients, secondary compounds (Forsyth et al. 2005; Renecker & Hudson 2007), plant phenology (Bee et al. 2010; Zweifel-Schielly et al. 2012) and forage availability/ quantity (Danell & Ericson 1986), time of day (Newman et al. 1995), interspecific competition (Dailey et al. 1984). Grasses, laden with fresh young leaves, are the prime forage of grazers during monsoon. Studies report that fresh leaves with soft texture, that are essentially more palatable due to lesser fiber and cellulose content and high protein content are preferred over dry and hard-textured grass (De Jong et al. 1995; Treydte et al. 2011; Kunwar et al. 2016). On the other hand, seasonal dry out or drought conditions, even periods of low water table, turn out to be a critical period for grazing, during which the forage species transform into leafless, dried and hard textured grass. This becomes a challenging situation for grazers to meet the minimal nutritional requirements. Hence, the quality and quantity of food that is available during the dry period must be the determining factor of ungulates diet selection. Thus, the determination of grass dynamics including phenology indicating the seasonality, is suggested as the primary need (Treydte et al. 2011; Kunwar et al. 2016). Further, the environment plays a major role in forage quantity and quality, which in turn are expected to greatly influence reproduction, as the process of reproduction is energetically demanding for ungulates (Sadleir 1969; Sinclair 1977; Bronson 1989; Schmidt-Nielsen 1997; Pekins et al. 1998; Sinclair et al. 2000).

Blackbuck *Antilope cervicapra* an endemic species to Indian subcontinent; found in southern and central India, ranges in tropical and subtropical woodland, dry deciduous forests, open plain grasslands, riverbanks, semi-desert habitats, crop and pasture lands (Long 2003). The species is currently categorized under the least concerned category by the IUCN, but is listed under Schedule I species under the Indian Wildlife (Protection) Act 1972. Among the current populations in southern India, the Point Calimere Wildlife Sanctuary in Tamil Nadu harbors the largest population. Nevertheless, this population is also declining, from over 2,300 individuals in 1995 (Tamil Nadu Forest Department Census) to around 1,500 individuals in 2005 (Ali 2005) and 2010 (Jagdish 2011). A recent study using Multi Covariate Distance Sampling estimates the population at 750–900 individuals (Arandhara et al. 2020). Blackbucks are known to rely primarily on short grasses (<50 cm); with various research works reporting grasses as their major food resource under free-ranging conditions. A profound seasonality in its nutritional ecology is reported in regions where the species have access to high quantity and quality forage during the monsoon coinciding with periods of grass growth (Schaller 1967; Chattopadhyay & Bhattacharya 1986; Goyal et al. 1988; Henke et al. 1988; Pathak et al. 1992; Jhala 1997; Solanki & Naik 1998; Garg et al. 2002; Das et al. 2012; Jhala & Isvaran 2016; Baskaran et al. 2016, 2020; Frank et al. 2021). In contrast, browse species like *Prosopis juliflora* and *Acacia nilotica* can also form a significant portion of their diet (Ghosh et al. 1987; Ranjitsinh 1989; Jhala 1997). Further, studies based on gastrointestinal-digestive physiology classified the Blackbuck as intermediate feeder, which is reported to include considerable amounts of browse and other trees in its diet (Schaller 1967; Solanki & Naik 1998; Hummel et al. 2015).

The determinants of diet selection remain obscure and an understanding of whether it is quantity or quality or a combination of both influence diet selection and feeding behaviour of herbivores is crucial to manage the endemic species (Shrestha & Wegge 2006); and in devising conservation measures for their long-term survival (Belovsky 1997; Ahrestani & Sankaran 2016). Studies directed towards herbivore management suggest that; procuring reliable information on aspects of basic life history and ecology, key uncertainties rise from diet selection and nutrition (Newmaster et al. 2013). In this study, assessing the diet composition and evaluating weather, and habitat conditions, grass dynamics including phenology; we address the (i) seasonal diet selection and (ii) influence of climate, habitat and grass dynamics covariates on the individual selection of top five major/principal diet species by Blackbuck at Point Calimere, southern India. This study provides data on principal and preferred food plants and the factors influencing the principal diet species selection that are crucial for the management of Blackbuck population, the iconic species of the sanctuary concerned. We use regression with empirical variable selection (REVS) approach, which is shown to be more useful for ecological data than typical regression approaches (Goodenough 2012).

MATERIALS AND METHODS

Study area

The study was conducted between November 2017 and October 2018 at Point Calimere Wildlife Sanctuary (PCWS), (10.30N–79.85E and 10.35N–79.42E), which is home to the largest population of the Blackbuck in southern India. The area derives its name from the coast that takes 90^o at 'Point Calimere', where the Bay of Bengal and Palk Strait confluence, spreading over an area of 21.5 km^2 and is situated in Tamil Nadu, southern India (Figure 1). The sanctuary was established in 1967 for the conservation of Blackbucks. The area receives 1366 mm of annual rainfall with wet season running from October to January, and dry season running from February to September. The sanctuary has diverse habitats ranging from tropical dry-evergreen to grassland with patches of open-scrub and mudflats (Ali 2005). The grasslands situated in the southern region of the sanctuary are potential habitats for Blackbuck, along with the presence of other herbivores like chital *A. axis* & Black-napped Hare *Lepus nigricollis* and the introduced horse *Equus caballus* (Ramasubramaniyan 2012). There is no large carnivore, but jackal *Canis aureus*, often prey on Blackbuck fawns (Baskaran et al. 2016), and domestic dogs occasionally prey on adults and fawns (Selvarasu

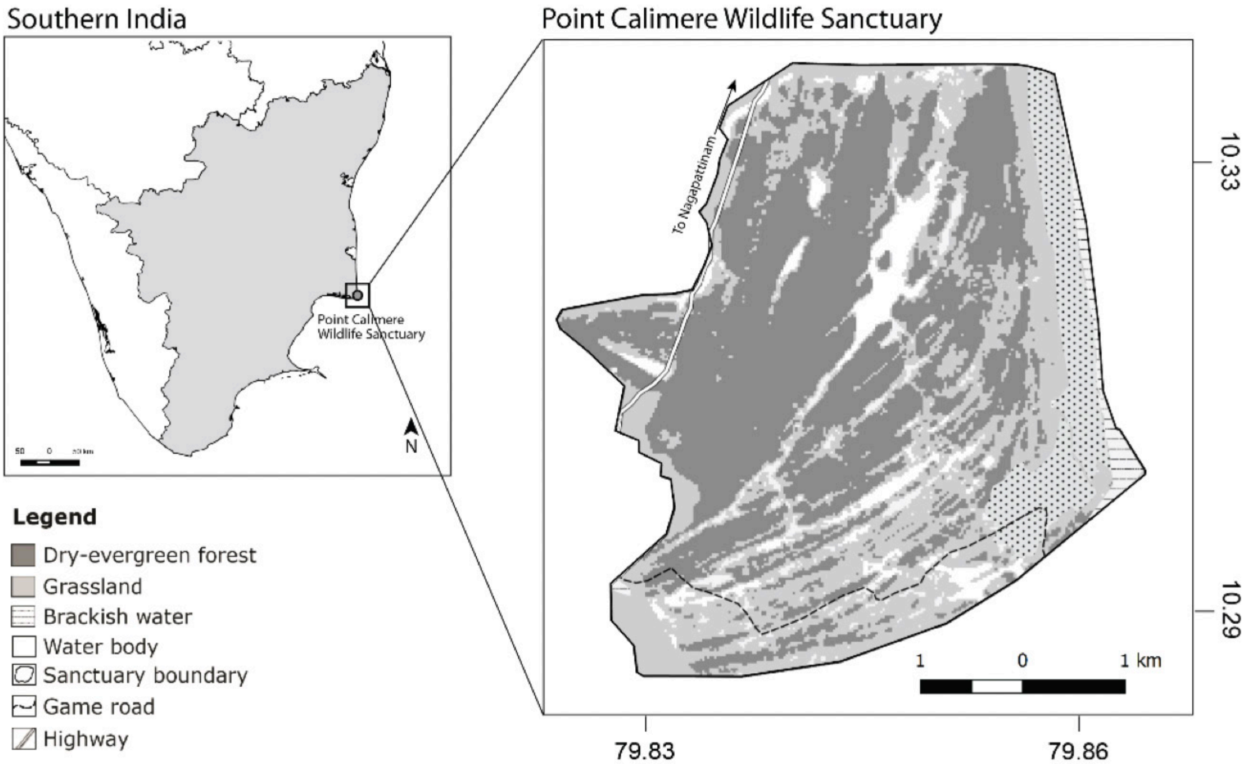

Figure 1. Point Calimere Wildlife Sanctuary, southern India.

Sathishkumar pers. obser. 05 April 2018). Its natural habitat experiences anthropogenic pressure in the form of cattle grazing (Baskaran et al. 2016) and proliferation of *Prosopis juliflora*, an alien invasive species (Ali 2005).

Feeding site examination

The diet composition or food habits of ungulates is often studied by direct observation while feeding or noting down the locations where the animals grazed/ browsed. Subsequently, the site is inspected to record the species consumed (Wallamo et al. 1973). The first of these methods is called grazing minutes or seconds (Hahn 1945; Buecher 1950), and the latter is feeding site examination by direct observation (Lovaas 1958). Since the study species is primarily a grazer (Prater 1965), we adopted the method of feeding site examination. Thirty quadrats of 1m^2 each were laid at six feeding sites examined per month and the feeding sites were chosen from areas where the study species were found in their peak feeding time at 0600–1000 h and 1500–1800 h. A feeding site examination refers to the observation of study species feeding for an hour and subsequent recording of the plant species devoured in the observed area. At each feeding site, 5–7 quadrats measuring 1 m^2 were placed at uniform intervals along a feeding site as suggested elsewhere (Lovaas 1958; Baskaran 2016) and the frequency of various plant species eaten were recorded based on fresh feeding signs such as exudation of sap, crushed tissue and fresh clippings (Shrestha & Wegge 2006; Baskaran et al. 2016). Overall, 270 1-m^2 quadrats consisting of 1,02,322 fresh feeding signs were recorded, with feeding signs during the wet season accounting for marginally higher (n = 52,938 or 52%) from 121 quadrats (mean 438 feeding signs/quadrat) compared to the dry season (n = 49,384 feeding signs or 48%, from 149 quadrats - mean of 331 feeding signs/ quadrat). The duration of observation during the wet season was 119 h (mean of 7.4 feeding signs/min) and 143 h during the dry season (mean of 5.8 feeding signs/min). In addition, 13 covariates that are likely to influence the diet selection belonging to climate (n = 3), habitat (n = 3) and grass dynamics (n = 7), as listed in Table 1, were assessed at the respective feeding sites, following standard procedures, as given in Table 1. All covariates pertaining to grass dynamics were obtained using quadrats of one 1 m^2 as suggested by Baskaran et al. (2010).

Statistical analysis

The compiled data were checked for homogeneity of variance and normality prior to detailed analysis. The Kolmogorov-Smirnov (KS) test on major five food plants in both the season showed that the distribution of *A. lagopoides* (KS: 0.165; *p* = >0.05), *D. aegyptium* (KS: 0.402; *p* = >0.05), *C. compressus* (KS: 0.234; *p* = >0.05), *C. barbata* (KS: 0.422; *p* = >0.05), *C. polystachyos* (KS: 0.487; *p* = >0.05), and *B. barbata* (KS: 0.483; *p* = >0.05) was neither normal, nor could be transformed to normal with four different transformations. Therefore, the difference in the selection of this species between seasons were tested using non-parametric Mann-Whitney U-test. All statistical tests were run using SPSS program (v.23). To comprehensively provide baseline data on how the five major diet species were selected in relation to each covariate, we split each covariate level into two categories as low and high and tabulated the consumption rate of five major diet species respectively. For example, in case of the covariate on ambient temperature, the replicates with temperature range ≤30^0 C were categorized as low level and those of >30^0 C level, as high level and the observed difference in consumption of major five diet between the two levels were tested using Mann-Whitney U-test. The seven covariates belonging to grass dynamics were tested with the selection of each major diet, in three different combinations, viz.: (i) effect of a grass dynamics covariate, for example grass height of a given major diet species on its own selection, similarly, (ii) the collective effect of the same covariate i.e., grass height belonging to (ii) the other four major diets species and (iii) also the rest 17 minor diet species during wet season and 25 species during dry season on the selection of a given major diet.

Influence of covariate on principal diet selection (Multivariate analysis - REVS)

To identify the covariates influencing the selection of individual principal diet species by the Blackbuck, regression with empirical variable selection (hereafter REVS) was employed using LEAPS package in R Library, in R Software Version 3.3.3 (R Core Team 2019; Ihaka & Gentleman 1993). This method employs all subsets in regression to quantify empirical support for every covariate. To quantify and assign empirical support to the simultaneous effects of each covariate belonging to climate, habitat and grass dynamics, the REVS analysis branch and bound all subsets regression technique. Further, the REVS analysis can handle collinearity (Goodenough et al. 2012), therefore we did not test our data for collinearity. These criteria allowed the REVS approach to be the better approach than multiple stepwise regression. Initially, we incorporate the data

Table 1. Details of covariates belonging to environmental, habitat, and grass dynamics assessed to identify their influence on diet selection by Blackbuck at Point Calimere.

	Covariate	Description
Climate		
1	Ambient temperature (°C)	Measured using a generic digital thermometer-cum-hygrometer device (model: HT01) at each observation at the feeding site.
2	Humidity (Relative %)	As described above.
3	Weather	Recorded visually as cloudy or sunny weather at the start of each feeding site examination.
Habitat (m)		
4	Distance to water	Measured as the distance from a given quadrate to the water source using a rangefinder or obtained from land-use land-cover map.
5	Distance to shade	Measured as the distance from a given quadrat to the nearest canopy cover area using a rangefinder.
6	Distance to road	Measured as the distance from a given quadrat location to the nearest road or obtained from land-use land-cover map.
Grass dynamics (%)		
7	Grass height (cm)	Grass height was measured using a measuring scale, from the ground level to the highest leaf blade bend, at five points (one each at four corners and one at the center) of the quadrate.
8	Grass cover	Assessed visually assuming 100% for the entire quadrat and estimating the proportion of area within a quadrat covered by each grass.
9	Soft texture	Examined crushing the leaves by hands, if leaf's structure could be squashed into a ball- proportion of such leaves for a given grass species in quadrat was rated in % rating.
10	Hard texture	Examined crushing the leaves by hands, if leaf's structure could not be squashed into a ball- proportion of such leaves for a given grass in quadrat was rated in % rating.
11	Green leaves	Assessed visually quantifying the proportion of leaves in a given species with green grass, assuming 100% for all the leaves of the same species.
12	Dry leaves	Assessed visually quantifying the proportion of leaves in a given species with dry grass, assuming 100% for all the leaves of the same species.
13	Reproductive phase	Evaluated visually quantifying the proportion of a given grass with flowers fruits and seed in % rating.

into R Program following the code of Goodenough et al. (2012) and obtained the best regression model ranked by AIC and subject it to interpretation and incorporate into the results (Goodenough et al. 2012). The seven grass dynamics covariates were fed into REVS in respect to (i) a given major diet species, (ii) other four major diet species (arriving a mean from the four species) and (iii) the minor species (arriving a mean from them); in 21 columns (7 covariates x 3 different set of species, as listed above = 21). Therefore, the effect of a set of given covariates (for example grass height) belonging to a given major diet, the rest four major diet species and all other 17 minor diet species during wet season or 25 minor diet species during dry season, was tested against the selection of given major diet. In addition, six covariates belonging to climate and habitat were also included into the REVS equation. The analysis was carried out for each major five diet species season-wise separately.

RESULTS

Diet selection

During the two years of study, Blackbucks consumed 30 plant species, which include six browse and 24 grass species (Supplementary Table 1). However, the number of species and their proportion in the diet varied seasonally (Table 2). For example, during wet season Blackbucks were dependent on just 22 food plant species, with *C. compressus* (>40%) and *A. legopoides* (<25%) contributing more than two thirds of the wet season diet. Contrarily, during the dry season, their dependency on individual species decreased, more specifically on *C. compressus* (11%), with the exception of *A. legopoides* (29%) but relied on more varieties (n = 30). Two major species, viz., *A. legopoides* (>35%) and *C. compressus* (>20%) formed more than two-fourth of the available fodder species of Blackbuck in the environment during the wet season. However, the Blackbucks relied on later species double the quantity that of former species. During dry season, the later species availability reduced considerably (<10%) and similarly the *C. polystachyos*, resulting a marginal increase in the availability of *A. legopoides* (>40%; Figure 2).

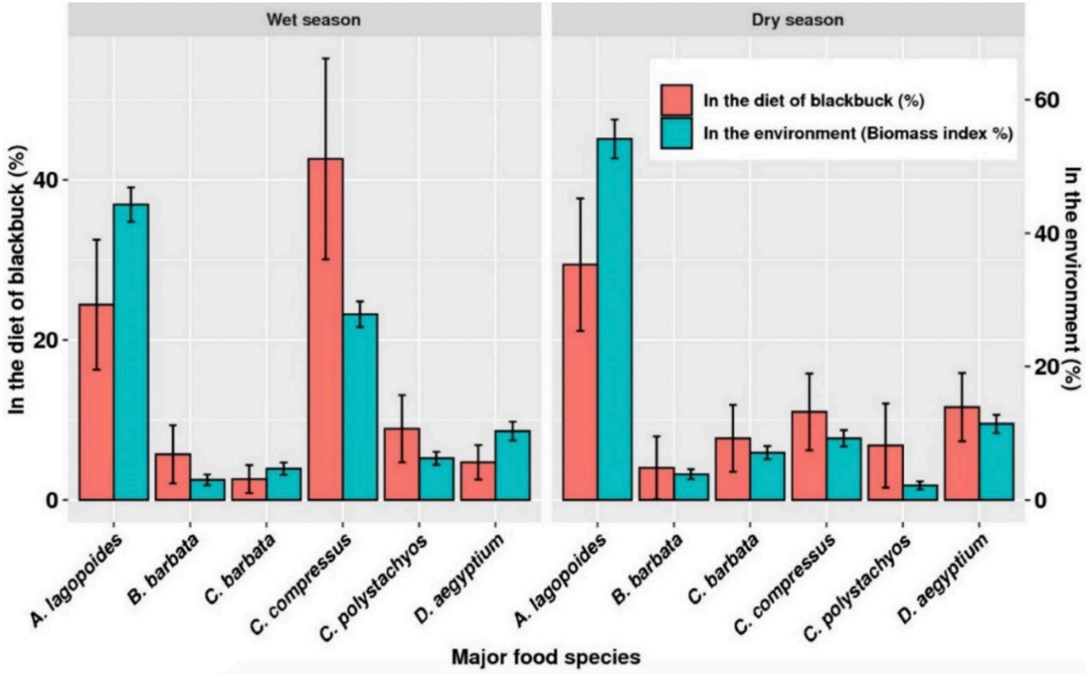

Figure 2. Seasonal selection of five major diet species by Blackbucks and their availability in environment at Point Calimere Wildlife Sanctuary, southern India.

Table 2. Seasonal variation in diet selection by Blackbuck at Point Calimere.

Diet species	Composition (%) Mean ± SE		Mann-Whitney U	p
	Wet season (n = 52938)	Dry season (n = 49,384)		
Aeluropus lagopoides	24.4 ± 8.12	29.4 ± 8.28	8699.5	0.617
Bulbostylis barbata	5.7 ± 3.63	4.0 ± 3.93	8629.0	0.306
Chloris barbata	2.6 ± 1.75	7.7 ± 4.18	7376.0	0.001
Cyperus compressus	42.6 ± 12.55	11.0 ± 4.79	4324.0	0.000
Cyperus polystachyos	8.9 ± 4.20	6.8 ± 5.26	8107.0	0.024
Dactyloctenium aegyptium	4.7 ± 2.15	11.6 ± 4.26	7106.5	0.000
Other species	11.13 ± 7.12	29.51 ± 9.05	6416.5	0.000

Influence of covariates on diet selection

REVS analysis on the influence of 13 covariates belonging to climate, habitat and grass dynamics factors on the selection of the five major diet species during wet season showed that in all the five major diet species selection, only grass dynamics factors entered as the key predictors. Further among the grass dynamics covariates, cover of the same species in all the five major species, and green leaves in four out of five major species and soft-textured grass of minor diet species in three out of five species appeared as the predictors during wet season. Overall, during wet season, 26 covariates entered as the significant predictors, explaining a mean variation of 65% for the top five species selection, minimum with three covariates explaining 44% of the variations in *D. aegyptium* selection and maximum seven covariates explaining 86% of the variations in *C. compressus* (Table 3).

During dry season, like the wet season, though grass dynamics covariates alone entered as the key predictors, the grass cover and green leaves were influencing in the selection of all the five major diet species, the hard texture of the other four major species and 21 minor diet species influenced significantly in four out of five species. Note that the same covariate (hard-texture) influenced only in one species during wet season. Unlike the wet season, during dry season more covariates (33) influenced a higher % of the selection (mean 75%) of five major diet species, a minimum with five covariates explaining 59% of the variations in *A. lagopoides* selection and a maximum 89% of the variations in *C. polystachyos,* but by five covariates (Table 4).

DISCUSSION

Our study based on a large sample size (1,02,322) and duration (2 years) produces a comprehensive data on dietary composition including its seasonality and

Table 3. Regression with empirical variable selection (REVS) to assess the effect of climatic, habitat and grass dynamics covariates on the selection of principal diet by Blackbuck during wet season at Point Calimere Wildlife Sanctuary.

Dependent factors	Predictor (covariate)	Coefficient ± SE	t	Pr (>|t|)	f	p	AIC	Adjusted R^2
Aeluropus lagopoides	(Intercept)	-204.7 ± 83.85	-2.44	0.015	28.4	0.000	1693	0.61
	Grass cover of *A. lagopoides*	2.6 ± 0.31	8.36	0.000				
	Grass height of *A. lagopoides*	0.3 ± 0.07	4.68	0.000				
	Dry leaves of 17 minor species	0.5 ± 0.29	1.63	0.000				
	Soft texture of *A. lagopoides*	1.5 ± 0.68	2.17	0.013				
	Green leaves of 17 minor species	-0.2 ± 0.08	-2.52	0.000				
	Grass cover of rest top four major species	-0.6 ± 0.22	-2.49	0.013				
Bulbostylis barbata	(Intercept)	17.9 ± 43.87	0.40	0.683	94.3	0.000	1513	0.82
	Grass cover of *B. barbata*	2.9 ± 0.27	-7.16	0.000				
	Hard texture of rest top major species	4.7 ± 1.12	4.15	0.000				
	Green leaves of *B. barbata*	3.8 ± 0.73	5.17	0.000				
	Hard texture of 17 minor species	1.6 ± 0.32	5.19	0.000				
	Grass height of rest top four major species	-0.4 ± 0.17	2.30	0.022				
	Soft texture of 17 minor species	-0.4 ± 0.18	2.06	0.040				
Cyperus compressus	(Intercept)	2.2 ± 9.01	0.25	0.802	129	0.000	1667	0.86
	Grass cover of *C. compressus*	1.9 ± 0.66	2.93	0.003				
	Green leaves of *C. compressus*	9.7 ± 4.88	-1.99	0.048				
	Soft texture of *C. compressus*	11.6 ± 4.81	2.41	0.017				
	Soft texture of 17 minor species	-0.6 ± 0.19	-3.56	0.000				
	Green leaves of 17 minor species	-0.8 ± 0.26	2.97	0.003				
	Dry leaves of 17 minor species	1.8 ± 0.7	2.36	0.019				
	Dry leaves of rest top four major species	11.9 ± 5.46	-2.19	0.029				
Cyperus polystachyos	(Intercept)	-2.6 ± 3.47	-0.73	0.462	107	0.000	1532	0.54
	Grass cover of *C. polystachyos*	2.4 ± 0.56	4.23	0.000				
	Green leaves of *C. polystachyos*	0.6 ± 0.17	3.4	0.000				
	Grass cover of rest top four major species	-0.9 ± 0.31	2.89	0.004				
	Green leaves of rest top four major species	-0.5 ± 0.22	2.38	0.018				
Dactyloctenium aegyptium	(Intercept)	0.8 ± 6.70	0.11	0.09	11.8	0.000	1584	0.44
	Grass cover of *D. aegyptium*	0.5 ± 0.30	1.65	0.011				
	Green leaves of *D. aegyptium*	0.6 ± 0.14	4.13	0.000				
	Soft texture of 17 minor species	-0.2 ± 0.13	2.08	0.039				

associated covariates influence on the selection of major diet species by Blackbuck at Point Calimere, southern India. Overall Blackbucks diet consists of 30 plants, with richness of diet species being more during dry (n = 30) compared to wet season (n = 22). The diet species richness recorded in the present study is double that of Baskaran et al. (2016) (n = 14), which was restricted to only seven months (January -June and December). During the wet season, both grass availability and quality (crude protein and digestibility) are generally higher and thus ungulates find more nutritive and palatable grasses everywhere. In contrast, during dry season owing to unfavorable conditions particularly with severe dryness, both above-ground productivity or biomass and palatability of grass drop (Murray 1995; Jhala, 1997; Pradhan et al. 2008; Jhala & Iswaran 2016), leading to herbivores dependence on a wide spectrum of plants unlike wet season. These findings go in support of earlier studies on other herbivores in India (Four-horned Antelope: Kunwar et al. 2016; Asian Elephant: Baskaran et al. 2010). The inadequate quantity and quality during dry season, especially the principal diet,

Table 4. Regression with empirical variable selection (REVS) to assess the effect of climatic, habitat and grass dynamics covariates on the selection of principal diet by Blackbuck during dry season at Point Calimere Wildlife Sanctuary.

Dependent factors	Predictor (covariate)	Coefficient ± SE	t	Pr (>|t|)	f	p	AIC	Adjusted R^2
Aeluropus lagopoides	(Intercept)	-87.0 ± 24.01	-3.63	0.000	22.9	0.000	1868	0.59
	Grass cover of *A. lagopoides*	1.1 ± 0.16	7.23	0.000				
	Soft texture of rest top four major species	-1.9 ± 0.26	7.42	0.000				
	Grass cover of rest top four major species	-0.5 ± 0.19	3.08	0.000				
	Green leaves of *A. lagopoides*	0.7 ± 0.29	2.38	0.020				
	Dry leaves of 25 minor species	0.5 ± 0.15	3.26	0.000				
Chloris barbata	(Intercept)	-38.1 ± 16.80	-2.26	0.020	29.3	0.000	1594	0.64
	Grass cover of *C. barbata*	2.4 ± 0.32	7.54	0.000				
	Soft texture of *C. barbata*	1.4 ± 0.37	3.83	0.000				
	Green leaves of *C. barbata*	1.3 ± 0.30	4.40	0.000				
	Soft texture of rest top four major species	-1.4 ± 0.32	-4.55	0.000				
	Hard texture of 25 minor species	1.5 ± 0.37	-4.10	0.000				
	Grass cover of 25 minor species	-0.3 ± 0.13	2.97	0.000				
	Grass cover of rest top four major species	-0.4 ± 0.02	2.10	0.040				
Cyperus compressus	(Intercept)	4.2 ± 4.93	0.85	0.390	59.6	0.000	1522	0.82
	Grass cover of *C. compressus*	1.6 ± 0.31	5.04	0.000				
	Soft texture of *C. compressus*	2.6 ± 0.37	6.82	0.000				
	Green leaves of *C. compressus*	0.7 ± 0.14	5.23	0.000				
	Green leaves of rest top four major species	-2.1 ± 0.35	-6.03	0.000				
	Dry leaves of rest top four major species	0.3 ± 0.14	2.14	0.030				
	Grass cover of rest top four major species	-0.8 ± 0.23	-3.47	0.000				
	Hard texture of 25 minor species	0.2 ± 0.09	-2.19	0.030				
	Hard texture of rest top four major species	0.2 ± 0.09	2.11	0.040				
	Green leaves of 25 minor species	-0.3 ± 0.09	-3.05	0.000				
Cyperus polystachyos	(Intercept)	-1.4 ± 1.64	-0.86	0.390	216	0.000	1369	0.89
	Grass cover of *C. polystachyos*	60.3 ± 8.27	-7.29	0.000				
	Green leaves of rest top four major species	-1.2 ± 0.13	-8.96	0.000				
	Green leaves of *C. polystachyos*	32.8 ± 4.39	7.48	0.000				
	Green leaves of 25 minor species	-63.5 ± 8.49	-7.48	0.000				
	Hard texture of 25 minor species	93.7 ± 12.67	7.40	0.000				
Dactyloctenium aegyptium	(Intercept)	32.1 ± 20.0	1.60	0.110	65.8	0.000	1505	0.79
	Grass cover of *D. aegyptium*	1.4 ± 0.16	9.08	0.000				
	Hard texture of 25 minor species	0.1 ± 0.05	-2.52	0.010				
	Hard texture of rest top four major species	0.3 ± 0.10	3.39	0.000				
	Grass cover of rest top four major species	-0.4 ± 0.20	-2.02	0.040				
	Green leaves of *D. aegyptium*	0.2 ± 0.12	2.27	0.020				
	Dry leaves of 25 minor species	0.7 ± 0.16	4.79	0.000				
	Soft texture of rest top four major species	-1.1 ± 0.16	2.63	0.010				

resulting a lower contribution of individual diet species to the diet, perhaps force herbivore to rely on a more diverse spectrum of food plants.

The higher consumption of *C. compressus* during wet season, despite higher availability of *A. lagopoides* in the environment indicate that Blackbucks are selective feeder. Further, the *C. compressus* is found mostly in high moisture area and its leaves are fleshy and succulent than *A. lagopoides.* Studies on nutrient composition of grass species show that *C. compressus* constitutes more moisture content (83%) and less crude protein (7.8%) than *A. lagopoides* (moisture 60% and crude protein 9.07%) (Mohsenzadeh et al. 2006; Moinuddin et al. 2012 ; Nurjanah et al. 2016). The fleshy and succulent quality leaves of *C. compressus* perhaps increases the digestibility, palatability and would also meets the water requirements. In addition, it could also be related to the level of secondary component found in the diet species, as herbivores are known to avoid plants with higher secondary metabolites (Owen-Smith 2002; Weterings et al. 2018).

Influence of covariates on principal diet section

The present study with empirical data on 13 covariates belonging to climate (n = 3), habitat (n = 3) and grass dynamics (n = 7) tested against the selection five major diet species as the dependent factor using REVS. The results revealed that grass cover and green leaves of grass are the most appeared significant predictors in the selection all five major food plants both during wet and dry season. This followed by soft-texture of grass in four out five major species both during wet and dry seasons, dry leaves in two out of five species during wet and three out of five during dry season and hard texture of grass in one out of five during wet season and four out of five during dry season and grass height in two out of five species during wet season. Among the six significant predictors, the grass cover and height covariates are associated to quantity and the rest four predictors viz. green leaves, dry leaves, soft-texture and hard-texture of grass are the covariates associate with digestibility and palatability, which indicate quality.

Soft-textured green grass owing to lower fiber and cellulose content and higher protein content is more appetizing and easily digestible than dried and hard-textured grass, which is higher in fiber, cellulose, and low in protein (Sukumar 1989; Sivaganesan 1991; Jhala 1997; Klaus-Hügi et al. 1999; Jhala & Iswaran 2016). Therefore, green leaves and soft-texture act as indicators of higher palatability and nutrient level compared to dry-leaves and hard-texture. Thus, the higher level of former two covariates (i.e., green leaves and soft-texture) in each major diet positively influenced its selection, while their higher level in other four major diets or minor species (17 and 20 during wet and dry season, respectively), negatively influenced the selection of a given major diet. Further, plant species during reproductive phase contains more secondary metabolites (Hartmann 2004) and high fiber, and cellulose and low protein content (Sukumar 1989; Jhala 1997). Thus, the negative influence of hard-textured dry grass could be to avoid secondary metabolite and higher fiber, and cellulose, and low protein as reported elsewhere in Blackbuck (Jhala 1997; Jhala & Iswaran 2016) on other antelope (Bongo *Tragelaphus eurycerus* Klaus-Hügi et al. 1999), ungulates (Owen-Smith 2002), and Asian Elephants (Sukumar 1989; Sivaganesan 1991). Our findings go in support of earlier studies on Blackbuck that reports that Blackbucks in Velavadar National Park, northern India, depended on high quantity and quality (crude protein 11%) food during monsoon and early winter (7%) coinciding with period of grass growth. But after seeding, the grasses lose nutritive quality rapidly during late winter and in summer seasons, when Blackbucks experience nutritional bottlenecks as their diet become less digestible and with low protein content (Jhala & Iswaran 2016). The selection of soft-textured green grass by Blackbuck reported in this study is a quantitative assessment. Similar observations were also made on other antelopes (Four-horned Antelope: Kunwar et al. 2016, Oli et al. 2018; Thomson's Gazelle: Talbot &Talbot 1962; Sable Antelope: Le Roux 2010, Duncan 1975), ungulates (Lowland Tapir: Prado 2013; Sheep & Goat: Bartolome et al. 1995; Impala & Blue wildebeest: Treydte et al. 2011), and Roe deer (De Jong et al. 1995). Further, the grass height although entered as one of the predictors, its influence only during the wet season, where grass growth is not limited, and only in two out of the five major diet species, which indicate the species can withstand or dependence on shortgrass. This finding goes in support of the earlier findings that Blackbuck is a selective feeder and adapted to feed on shortgrass (Prater 1965), which is predominantly available in open habitats (Baskaran et al. 2020).

Further, as reported by Jhala & Iswaran (2016), during summer though the protein content of the Blackbucks' diet drops significantly (>4%), well below the maintenance requirement for ruminants, which is between 5.5–9 % (Robbins 1983), with negative protein balance (as they lose more protein via feces than they can obtain from the forage during summer) and a significant drop in dry mater digestibility (from a high of 76.5% during the monsoon to a low of 32% during summers), their ability to catabolize proteins with reduced forage-intake and movement during summer ensure them to survive on seasonally low-quality diets and live as a primary grazer. Such adaptation could be a trade-off strategy perhaps Blackbuck uses to fulfill it requirements within a single habitat, mostly of open shortgrass land, unlike wide-ranging species that overcome by moving to other optimal habitats. Overall, as covariates associated to both quantity and quality entered as the predictors of the principal diet selection, the study points out in addition to quantity, quality also matters in the selection of major diet species by Blackbuck.

Conclusion and management recommendation

Overall, the study quantitatively assessing the covariates belonging to climate, habitat and grass dynamics and comparing them with the seasonal diet composition of Blackbuck demonstrated that the principal diet selection is determined not only by just the quantity, but also quality in the form of soft-texture green grass due to higher palatability, digestibility and nutrients. The findings indicate the selective feeding on palatable short-grass by Blackbucks. Thus, the need for maintaining the grasslands habitats to support a viable population of Blackbuck and wild ungulates. The Blackbuck being the flagship species of the sanctuary, managing grassland habitat free of invasive species like feral-horse, an effective competitor of Blackbuck (Baskaran et al. 2016, 2020; Arandhara et al. 2020) and *Prosopis juliflora*, an alien invasive affecting grassland habitat (Baskaran et al. 2020; Arandhara et al. 2021), would benefit the conservation of Blackbuck population. Further, we suggest, the need for future focus on the influence of nutritional composition in diet species selection by Blackbuck.

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Supplementary Table 1. Season-wise percentage contribution of various food plants to the diet of Blackbuck and in the environment at Point Calimere Wildlife Sanctuary.

	Food plant species (Grass/Browse)	Wet season		Dry season	
		% cover ± SE in environment	% consumption ± SE in the diet of Blackbuck	% cover ± SE in environment	% consumption ± SE in the diet of Blackbuck
1	*Acacia nilotica* (B)	0.0 ± 0.00	0.3 ± 1.19	0.6 ± 0.32	0.1 ± 0.01
2	*Aeluropus lagopoides* (G)	36.9 ± 2.15	**24.4 ± 8.12** *Second*	45.1 ± 2.42	**29.4 ± 8.28** *First*
3	*Aristida adscensionis* (G)	0.8 ± 0.66	0.0 ± 0.00	1.7 ± 0.74	0.5 ± 0.16
4	*Brachiaria ramosa* (G)	2.5 ± 0.67	0.0 ± 0.00	0.2 ± 0.13	0.1 ± 0.04
5	*Bulbostylis barbata* (G)	2.5 ± 0.67	**5.7 ± 3.63** *Fourth*	3.2 ± 0.62	4.0 ± 3.93
6	*Canthium parviflorum* (B)	0.3 ± 0.17	0.4 ± 1.19	0.4 ± 0.20	0.2 ± 0.40
7	*Cenchrus ciliaris* (G)	0.3 ± 0.17	1.6 ± 1.68	0.6 ± 0.25	1.4 ± 2.51
8	*Chloris barbata* (G)	3.9 ± 0.78	2.6 ± 1.75	5.9 ± 0.82	**7.7 ± 4.18** *Fourth*
9	*Chrysopogon aciculatus* (G)	2.0 ± 0.32	0.6 ± 2.01	0.5 ± 0.22	0.5 ± 1.15
10	*Commelina benghalensis* (B)	0.2 ± 0.13	1.2 ± 2.20	0.1 ± 0.12	0.6 ± 1.89
11	*Cyanotis axillaris* (B)	0.6 ± 0.20	0.0 ± 0.00	0.6 ± 0.16	1.2 ± 1.48
12	*Cynodon dactylon* (G)	0.0 ± 0.00	0.0 ± 0.00	0.2 ± 0.11	0.2 ± 0.33
13	*Cyperus compressus* (G)	23.2 ± 1.60	**42.6 ± 12.55** *First*	7.7 ± 1.03	**11.0 ± 4.79** *Third*
14	*Cyperus polystachyos* (G)	5.2 ± 0.80	**8.9 ± 4.20** *Third*	1.8 ± 0.50	**6.8 ± 5.26** *Fifth*
15	*Cyrtococum trigonum* (G)	0.0 ± 0.00	3.3 ± 3.11	0.3 ± 0.15	0.4 ± 0.73
16	*Dactyloctenium aegyptium* (G)	8.6 ± 1.19	**4.7 ± 2.15** *Fifth*	9.5 ± 1.13	**11.6 ± 4.26** *Second*
17	*Desmodium triflorum* (B)	6.3 ± 0.52	0.3 ± 0.67	4.7 ± 0.70	5.2 ± 3.75
18	*Dichanthium annulatum* (G)	0.2 ± 0.15	0.0 ± 0.16	1.5 ± 0.44	1.7 ± 2.19
19	*Digitaria longiflora* (G)	0.1 ± 0.07	0.2 ± 0.58	0.6 ± 0.18	0.5 ± 0.60
20	*Eriochloa procera* (G)	0.1 ± 0.05	1.2 ± 1.27	0.7 ± 0.22	0.7 ± 0.76
21	*Fimbristylis cymosa* (G)	5.7 ± 0.60	0.1 ± 0.32	8.1 ± 1.02	5.8 ± 3.33
22	*Fimbristylis ovata* (G)	0.3 ± 0.20	0.0 ± 0.00	0.4 ± 0.20	1.8 ± 2.78
23	*Hemarthria compressa* (G)	0.0 ± 0.00	0.0 ± 0.00	0.1 ± 0.04	0.0 ± 0.00
24	*Heteropogon contortus* (G)	0.0 ± 0.00	0.8 ± 1.64	0.2 ± 0.08	0.0 ± 0.12
25	*Kyllinga nemoralis* (G)	1.2 ± 0.35	0.2 ± 0.56	3.6 ± 0.62	6.2 ± 3.67
26	*Paspalum paspaloides* (G)	0.0 ± 0.03	0.8 ± 1.41	0.1 ± 0.05	0.3 ± 0.62
27	*Pedalium murex* (B)	0.0 ± 0.04	0.8 ± 1.42	0.1 ± 0.06	0.2 ± 0.63
28	*Perotis indica* (G)	1.4 ± 0.28	0.0 ± 0.00	2.9 ± 0.35	1.6 ± 1.58
29	*Trachys muricata* (G)	0.0 ± 0.00	0.2 ± 0.58	0.1 ± 0.06	0.1 ± 0.30
30	*Urochloa maxima* (G)	0.2 ± 0.14	0.0 ± 0.00	0.2 ± 0.08	0.4 ± 0.74

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