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Cover: Coromandal Sacred Langur *Semnopithecus priam* - made with acrylic paint. © P. Kritika.

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ARTICLE

Population demography of the Blackbuck *Antilope cervicapra* (Cetartiodactyla: Bovidae) at Point Calimere Wildlife Sanctuary, India

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Abstract: Demographic research utilizing vital rates and life tables is a standard aspect of planning protection and management strategies for wildlife populations. The Blackbuck *Antilope cervicapra* population at Point Calimere Wildlife Sanctuary, Tamil Nadu, has undergone fluctuations in recent decades. The cause remains elusive, and conservation efforts may be hampered by a lack of population data. This study aimed to estimate demographic parameters using population count and age-sex classification data collected for the years 2017–2020. The overall mean population estimate derived from line-transect distance sampling was 719, with annual estimates of 716, 727, 711, and 722 for the years 2017–2020 respectively. In total, 64% of Blackbucks counted were adults, 19% subadults, and 17% fawns. Mortality was highest for adult and subadult classes for the composite female class, and fawn mortality was 20%. The net reproductive rate (R_0) was as low as 3.28 offspring per generation contrasted with a rather longer mean generation time (G) as 4.75 years. Thus, the study observes a decrease in Blackbuck numbers postulated in earlier research to be driven principally by a conglomerate of factors, including reduction of usable space and interspecific resource competition. Our findings provide a baseline demography of the species and highlights the value of long-term demographic monitoring of age sex classes to understand the evolution of life histories.

Keywords: Age-structure, generation time, fecundity, life table, line transect, monitoring, mortality, reproductive rate, sex ratio.

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Author contributions: SA—data collection, analyses, and draft preparation. SS & SG—data collection, pruning, analyses, and draft preparation. NB—conceptualizing, supervising, data analyses, and final draft preparation

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INTRODUCTION

The Blackbuck *Antilope cervicapra* is a medium-sized sexually dimorphic antelope, with horns borne only by males, which are also more heavily built than females. The species is polygynous, highly social, and exhibits unique lek-mating behavior (Jhala & Isvaran 2016). Moreover, agro-industrial activities have radically altered its natural habitat over the last two centuries. This change is one of the major causes of the reduction and decline in populations within the range of the species. It is reported to be extinct and reintroduced in Bangladesh, Nepal, and Pakistan and introduced populations are found in Australia, Argentina, and USA (Mallon & Kingswood 2001). Presently, the IUCN Red List defines the species as 'Least Concern' (IUCN SSC Antelope Specialist Group 2017), while it is protected under Schedule I of the Indian Wildlife (Protection) Act, 1972.

Point Calimere Wildlife Sanctuary (PCWS) has been noted as a Blackbuck area since the 1800s (Jerdon 1874). After its establishment as a protected area in 1967, substantial efforts have been made to conserve and manage the Blackbuck which then numbered around 600. Until 1995, over 2,300 individuals were reported, after that the population appeared to be diminishing. In 2012 the population declined to 1560 individuals (Baskaran et al., 2016), with a further reduction to a threshold of 700–800 individuals evident during 2017–2020 (Baskaran et al. 2019; Arandhara et al. 2020).

Population declines in the area were due to unregulated hunting in general (Oza & Gaikwad 1973), natural predation by Golden Jackal *Canis aureus*, though only on fawns (Mr S. Sathishkumar, Forester, Vedaranyam Forest Range, April/2018 pers. comm.), however, declines may be suggestive of environmental and demographic stochasticity (Frankham et al. 2004). More recently, sympatric invasive competition and habitat contraction due to invasive *Prosopis juliflora* have been reported as case of decline in PCWS (Arandhara et al. 2020, 2021a).

Numerous research on the species have been undertaken at PCWS, e.g., population size, species interaction, and distribution (Daniel 1967; Nair 1976; Muralidharan 1985; Nedumaran 1987; Ali 2005; Baskaran et al. 2016; Arandhara et al. 2020, 2021b); behavioural ecology (Isvaran 2003, 2007); diet (Baskaran et al. 2016; Frank et al. 2021).

Lack of data on population change and demographics for any population might create an uncertainty about the underlying population process. This forms the basis of species management and conservation, providing information necessary for the evaluation of population trends (Sukumar 1989; Van Horne et al. 1997); life-history parameters (Sinclair 1977; Jhala 1991; Stearns 1992); sexual senescence (Promislow 1991); age-sex specific longevity (Smith 1989); relationships between demographic patterns and social systems (Armitage et al. 1996). Our objective in this study was to understand the demography of the Blackbuck by estimating the following parameters: (i) population size, (ii) age-sex composition, (iii) sex ratio, (iv) fecundity, (v) survival, (vi) mortality, (vii) population change, and (viii) life history parameters.

METHODS

Study area

Point Calimere Wildlife Sanctuary is in Tamil Nadu at the juncture of the Bay of Bengal and Palk Strait. It is situated between 10.27° N, 79.83° E & 10.33° N, 79.84° E, covering about 26.5 km^2. The sanctuary was established in 1967, but it has been identified as a Blackbuck area in scientific records since the 1800. The area receives an average annual rainfall of 1,366 mm, and summer temperature peaks at 37^{o}C and dips to 21^{o}C in winter. Humidity can reach up to 90% on foggy winter mornings (Jan–Feb). The sanctuary is covered by two major vegetation types: (i) tropical dry evergreen and (ii) grassland vegetation. The grassland habitat includes mainland sea beach grassland and salt marsh grassland, preferred by Blackbuck. *Prosopis juliflora* is the only invasive woody plant in the sanctuary. It was introduced in the late 1960 and is reported as harmful to native flora and fauna (Ali 2005; Baskaran et. al. 2019). The feral horse *Equus caballus* and the Chital *Axis axis* are both introduced mammals in the sanctuary and the former is considered invasive (Krishnan 1971; Baskaran 2016). Villagers are allowed to graze their domestic cattle and goats, but large groups are thought to disrupt the Blackbucks' social activity. Also, feral or stray dogs threaten the sanctuary's Blackbucks. Due to its coastal location, the sanctuary has the most human activity in the region, including fishing, firewood collection, and tourist visits (Arandhara et al. 2021b) (Figure 1).

Data collection

Data on age sex composition was recorded from the study area per month annually between 2017 and 2020. Overall, 11 adjacent foot transects (length: 2–4

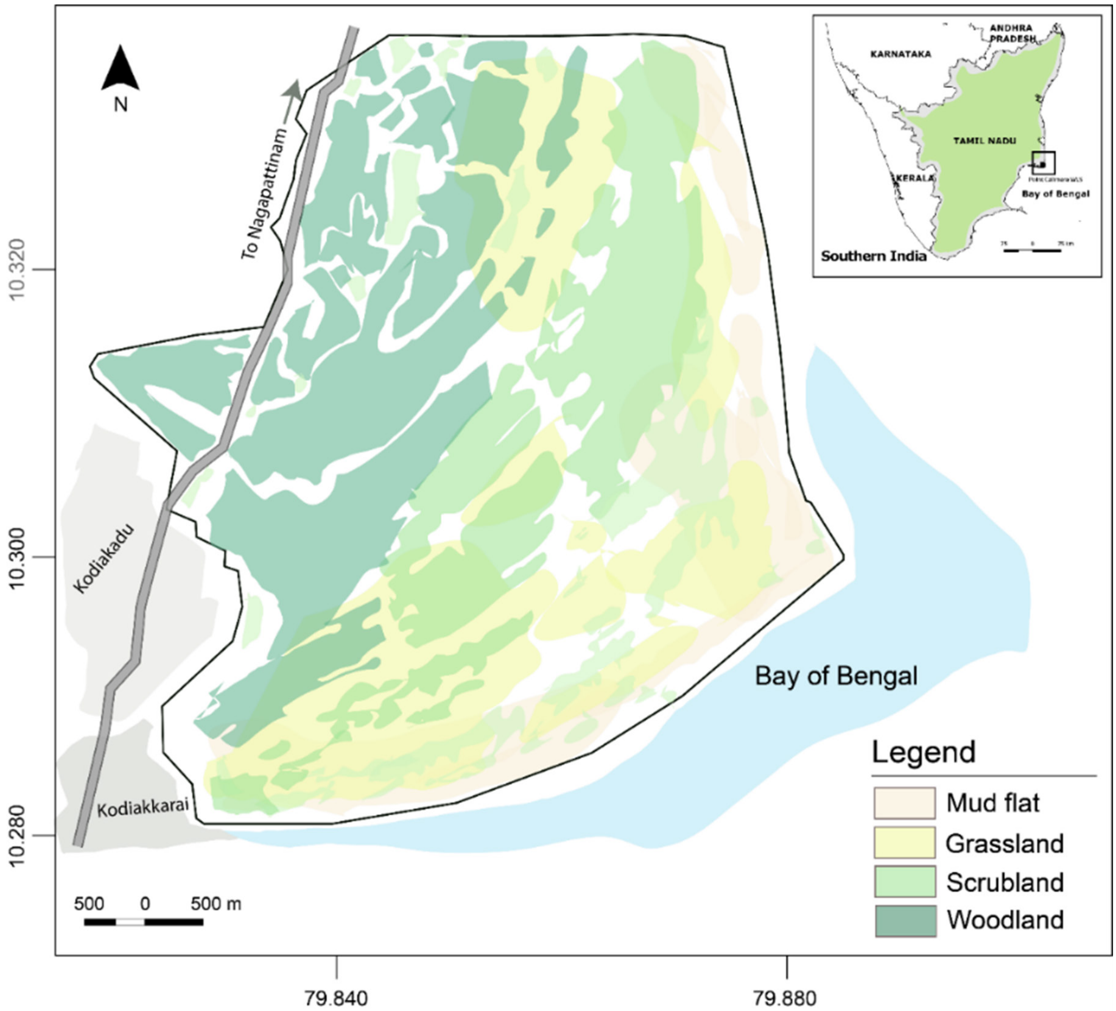

Figure 1. Study area (Point Calimere Wildlife Sanctuary).

km) and 0.5–1 km apart, covered almost the entire 26.5 km^2 extent of PCWS. The number of transect surveys within each month was >2, except a single survey during wet season months. Additionally, data on age sex composition was also collected from other surveys done by the authors (e.g., feeding observations, behavioral sampling). Surveys averaged 3–6 hours in duration, conducted during early morning hours when the Blackbucks are in open grassland and traversing their feeding activities at its peak. Sightings were noted by 1–2 observers, most commonly using binoculars or photographed by digital SLR camera.

If Blackbucks were located on any of the visits, the number of individuals was counted, and their age and sex were assessed according to their coat color and body size, along with horn shape for males. Accordingly, animals were placed in one of three age categories: adult (animals of 2 years and older), subadult (animals between 1 and 2 years), and fawns (young one up to 1 year of age). The juvenile category was dropped due to inconsistency in identification of animals between 6 months and 1 year. The analysis was done for annual data, and therefore we assumed yearly recruitment of the fawns as the next subadult segment.

The age-sex classification was based on Mungall (1978), Ranjithsingh (1989), and Jhala (1991). We kept track on count of fawns by following each adult female, from which fawn mortality could be estimated as difference in number of fawns observed in a year and the subsequent year.

Demographic parameters

Population size

Line-transect distance sampling was used to estimate population size annually (Burnham & Anderson 1976; Marques et al. 2001). The study area was stratified systematically into eight grid cells, measuring 2 × 2 km. Spatially replicated line-transects (length ranging from 0.8–2 km each) were placed one each in the grid cells and surveyed on foot. For estimating density from line-transect data, we used the DISTANCE programme (Version: 7.0, Release: 3 for Windows OS).

Age-sex composition

Count data on sex and age groups were averaged from monthly surveys per year and relative proportion (%) of each age-sex class were obtained for each survey year.

Number of individuals age-sex wise

To derive number of individuals (n) of each age-sex class, annual estimates of population size (N) using distance sampling and % age-sex classes obtained in the previous step.

We estimated (n) by calculating the fraction of year wise % age-sex classes and annual population size estimate (N).

$$n_{AM}=\frac{\%AM}{100}\times N_{2017}$$

Here, n_{AM} is the number of individuals for adult male class in the population.

n is used further for estimation of fecundity rates, survival, and population growth rates based on a Leslie matrix.

Sex ratio

We considered operational sex ratio for adult category as the ratio of sexually active males to females, which itself is the subset of adults that are sexually active. Assuming a 1:1 sex ratio for fawns at recruitment into the adult population, the fawn category was considered equal as sex ratio at birth is equal. We used G^2-likelihood ratio test to check if the observed sex ratio differs from the expected ratio. The study area's 1967 sex ratio (1:1.9) was considered ideal for the population (Daniel 1967).

Fecundity

Fecundity, was estimated as the proportion of fawns produced per adult female, as the number of fawns (per individual of adult females alive at a given time step) censused at the next time step, given as:

$$\text{Fecundity} = \frac{\text{Fawns alive in current year}}{\text{Number of adult females in previous year}}$$

Fecundity estimate is used in estimating and predicting population growth rates (Cole 1954; Henny et al. 1970; Caswell 2001). Blackbucks are reported to produce an average of 1.5 fawns per reproductive female in 12 months (Mungall 1978; Ranjitsinh 1982). At Point Calimere, we observed two fawning peaks, one in early November and another in mid-March.

Survival

Survival rates were defined as the proportion of x-year old individuals that survive to be x+ 1 years old one year later, this definition applies to fawn and sub-adult ages. However, for adult age class which includes individuals ageing 3 and older, a composite class (collapsing the older age classes) is calculated by pooling the counts of subadult and adult age class following Akcakaya (1999) and Caswell (2001).

Mortality

We recorded sources of Blackbuck mortality in two contexts: as incidental observations made during field surveys, and death reports as per personal communications and through records being made after a catastrophic cyclone "Gajah" on the night of 15 November, 2018. The Blackbucks were washed up on the coastlines for roughly 60 km, all the way to the coast of Karaikal, Pondicherry. Using extensive coast surveys, forest department personnel, including the authors, were able to recover 28 carcasses.

The age sex specific mortality rates were estimated from dead carcass counts 'current life table' relative to the population size (Pielou 1977). During 2017–2020, the number of Blackbucks found dead in the study area included 38 females and 19 males, and 18 fawns. As personal communication with the forest department, only nine of the 18 reported dead fawns were able to be sexed. These deaths represented minimum numbers (Sukumar 1989). However, dead fawns are difficult to encounter in field conditions as they were easily preyed upon, moreover the rate of carcass decomposition was faster than in other age-sex classes. Thus, counts of dead fawns were estimated from censuses, as the difference between fawns observed in a census and the number of subadults in the next year census.

Population change (or growth)

We constructed a one-sex, deterministic, density-independent, and discrete time Leslie projection matrix for female age-sex, composed of survival and fecundity rates.

Using this model, annual finite rate of population change (λ) was arrived to project the Blackbuck population throughout the survey period (Akcakaya 1999; Caswell 2001). Additionally, stable age distribution (SAD: point at which the proportion of individuals in each class stays constant each generation, although the population keeps growing); reproductive value (R_v) as measure of the contribution of different kinds of individuals on future population growth assuming individuals of different age classes do not contribute equally to future population growth.

We chose to use this model, assuming that (1) the current population size is not likely to produce a measurable feedback on the vital rates of the population, thus used exponential density dependence (density-independent model), also as the carrying capacity is unknown, we assumed that the Blackbuck density is relatively low (Otway et al. 2003); (2) the population is closed; i.e., there is no immigration or emigration; (3) model only represents the female component of the population and thus presumes that there is no lack of males who can inhibit reproductive potential; (4) all individuals in a given age-stage are subject to identical mortality, growth, and fecundity schedules.

Life history parameters

Life history parameters were arrived from indirect estimation of life-table on females based on mortality adjusted for known rate of population change (Caughley 1967; Sinclair 1977; Jhala 1991; Krebs 2010).

The carcasses obtained at sub-adult and adult segments were age sex identified, assuming no bias in ages at death. However, fawn mortality counts were estimated from censuses (mentioned earlier).

Fecundity schedules were obtained from the literature (Mungall 1978; Ranjitsingh 1982; Jhala 1991). Age-specific probability of surviving (lx), probability of dying (dx), mortality rates (qx), and fecundity rates (mx) were calculated following Sinclair (1977). The population change rate ($r = \ln(\lambda)$) estimated from the Leslie matrix for the study period was used for the cohort corrected for changing population size. Using this life table, we estimated net reproductive rate (R_o—as the mean number of female offspring produced per female over her lifetime); mean generation time (T_c—as the mean age of reproduction); and intrinsic rate of natural increase (r_m).

RESULTS

Population size

Annual population size estimation based on line-transect distance sampling yielded a mean estimate of 719 individuals for the period 2017–2020, with annual estimates of 716 ± 146.7 individuals for 2017, 727± 162.9 for 2018, 711± 145.5 for 2019, and 722± 168.9 for the year 2020 (S-Table 1).

Age-sex composition

The age-sex composition of Blackbuck individuals sampled during 2017–2020 showed that a mean of 64% were adults in the population (AM = 24%; AF = 40%), 19% were subadults (SAM = 4.5%; SAF = 14.5%) and 17.5% were fawns (Table 1; Figure 2). Among the four years sampled, there was no significant difference within the age sex classes, viz., (AM: Kruskal-Wallis test, $X^2 = 3.74$, $p = 2.9$; AF: $X^2 = 2.0$, $p = 0.54$; SAM: $X^2 = 3.7$, $p = 0.28$) but difference was evident in SAF ($X^2 = 8.7$, $p = 0.017$) and FA: $X^2 = 7.4$, $p = 0.5$. During the study, there was no significant trend in either of the age-sex classes (AM: $z = 0.54$, $p = 0.47$; AF: $z = 0.11$, $p = 0.99$; SAM: $z = -0.70$, $p = 0.37$; SAF: $z = -0.25$, $p = 0.93$; FA: $z = 0.1$, $p = 0.87$).

Sex ratio

The adult sex ratio did not deviate significantly for the year(s) 2017, 2018, 2020 and for the combined years the ratio was in favor of the females, not departing

Table 1: Year wise % age-sex composition of blackbuck at Point Calimere WS.

Year	AM (n)	AF (n)	SAM (n)	SAF (n)	FA (n)	Population size (N)
2017	22 (154)	41 (293)	6 (42)	13 (94)	18 (132)	716
2018	22 (158)	40 (292)	4 (30)	14 (93)	21 (153)	727
2019	29 (207)	36 (259)	4 (30)	18 (54)	16 (161)	711
2020	24 (176)	44 (319)	4 (28)	13 (91)	15 (108)	722
Mean ±SE	24.25 ± 1.19	40.25 ± 0.74	4.5 ± 0.43	14.5 ± 1.46	17.5 ± 1.22	719

AM—adult male | AF—adult female | SAM—subadult male | SAF—subadult female | FA—fawn | **n**—number of individuals derived from fraction of year wise % age-sex composition recorded through monthly direct observation and yearly population size estimate (**N**) obtained by line transect distance sampling. (**n** is used for estimation of fecundity rates, survival, and population growth rates based on Leslie matrix).

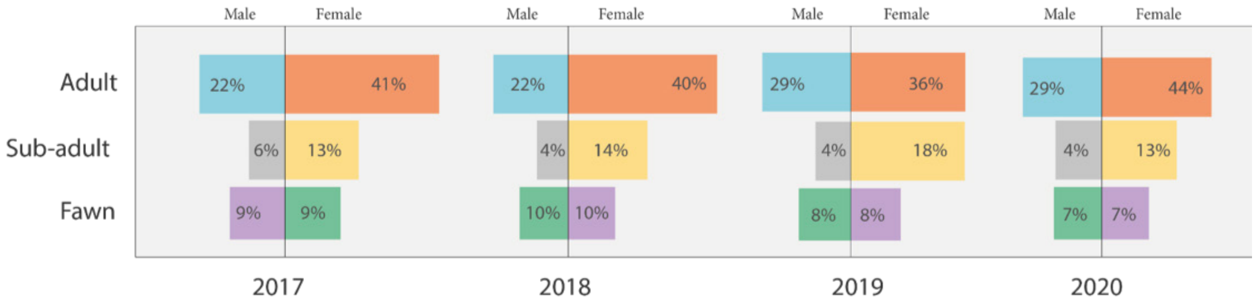

Figure 2. Age class pyramid depicting percentage age-sex composition among the years surveyed. (Values represent percentage composition).

Table 2. Year wise sex ratio for adult and sub-adult categories of Blackbuck.

Year	AM: AF	G^2 (p)	SAM: SAF	G^2 (p)
2017	1:1.9	3E-04 (0.97)	1:2.2	0.79 (0.31)
2018	1:1.8	0.1 (0.77)	1:3.5	**6.2 (0.01)**
2019	1:1.2	**19.6 (9E-06)**	1:4.2	**3.05 (0.02)**
2020	1:1.8	0.25 (0.61)	1:3.3	**6.4 (9E-03)**
Combined	1:1.9	3E-04 (0.97)	1:3.0	**0.88 (0.03)**

G^2 -test based on expected 1:1.9 ratio derived from the same study area during 1967 (Daniel, 1967). AM—adult male | AF—adult female | SAM—sub-adult male | SAF—sub-adult female | FA—fawn. Bold letters indicate significant values.

Table 3. Age-sex specific mortality rate (field observations) of Blackbuck during 2017–2020.

Age-sex category	Mean no. of individuals in the population, Q_x	No of deaths reported	No. of deaths in the age-sex class per year, D_x	Age-sex specific mortality rate (Q_x/D_x)
*FAF	69	28	2.3	10.1
SAF	83	9	2.3	2.7
AF	291	29	7.3	2.5
*FAM	69	28	2.3	10.1
SAM	33	6	1.5	4.6
AM	174	13	3.3	1.9

* FAF: represents fawn female and FAM represents: fawn male. Fawn were difficult to sex and thus assumed, as sex ratio at birth is equal. AM—adult male | AF—adult female | SAM—sub-adult male | SAF —sub-adult female.

significantly from the expected 1:1.9 ratio. However, for the year 2019 we found a significant deviation. Similarly, for the subadult categories, in 2017 there was no significant deviation from the expected ratio. While for 2018, 2019, and 2020 and ratio for the combined years were highly female biased, thus alternately deviates from the expected ratio. Table 2 provide sex ratio estimates for the years sampled.

Fecundity and survival

Natality rates could not be determined as it is challenging due to the behavior of newborn fawns, which involve lying down and concealing themselves in bushes alongside their mothers. It takes the newborn fawns and their mothers a few weeks to month to start following the rest of the herds. However, age-specific differences in fecundity were evident from the age sex composition. The fecundity and survival rates were estimated for constructing Leslie matrix, fecundity was highest in 2018 ($F = 0.45$) and overall mean for the years sampled was ($F = 0.44$), fecundity did not vary significantly among the years ($X^2 = 8.8$, $p = 0.9$). The survival rates were 0.75 for composite adult female class, 0.57 for female fawns and 0.37 for sub-adult females (Year wise and mean fecundity rate tabulated in S-Table 2; fecundity and survival rates given in Leslie matrix in S-Table 3).

Mortality

Age sex specific mortality from dead carcass counts on females was 2.7% per annum for the SAF and 2.5 for the AF category. Similarly, 4.6 % and 1.9 % were attributed to male classes, SAM and AM respectively. For each of the fawn category, using census data and carcass, mortality rate of 20% was estimated (FAF = 10%; FAM = 10%) (Table 3).

Population change (or growth)

From the female-based Leslie matrix model, the finite rate of population change (λ) was 0.97 representing a declining trend of population during the survey years. It was converted into instantaneous growth rate, ($r = -0.025$) required for age frequency correction in the subsequent life tables based on mortality. Stable age distribution (SAD) for the age classes were FAF = 0.16, SAF = 0.19, and AF = 0.62, and reproductive values (R_v) were FAF = 1, SAF = 1.08, and AF = 2.90. (Vital rates and life history parameters given in Table 4). Leslie matrix given in S-Table 3.

Table 4. Stable age distribution, reproductive values and growth rates derived from Leslie matrix and life history measures (Net reproductive rate, mean generation time, intrinsic rate of increase) derived from life table based on female mortality for the Blackbuck population.

Growth parameters	FAF	SAF	AF
Stable age distribution	0.16	0.19	0.62
Reproductive value	1	1.08	2.90
Finite growth rate, λ	0.97		
Instantaneous growth rate, r	-0.025		
Net reproductive rate, R_0	3.28		
Mean generation time, G	4.75		
Intrinsic rate of increase, r^m	0.24		

AF—adult female | SAF—sub-adult female | FAF—female fawn.

Based on reproductive rates estimated in our study through life tables (S-Table 4), the net reproductive rate (R_0) was estimated to be 3.28 per generation (Table 4) defined as the mean number of female offspring produced per female over her lifetime, contrasted with a rather low value of mean generation time (G) was 4.75 years. The intrinsic (or instantaneous) rate of population increase r^m was 0.24.

DISCUSSION

Population size

Point Calimere had over 2,300 individuals by 1995, but by 2017–2020 the population had dropped to 700–720 individuals presently as shown by this study. Point Calimere has a larger Blackbuck population than the other three remnant populations of Tamil Nadu: (1) Guindy National Park, Chennai, with 60 individuals (Annual census 2018, 2019 using line-transect distance sampling), (2) Sathyamangalam Tiger Reserve (Moyar Valley) with 600 individuals, and (3) Vallanadu Blackbuck Sanctuary, Tuticorin, with an average of with an average of 148 individuals (using line-transect distance sampling; Baskaran et al. 2020). In Velavadar, Gujrat about 400 Blackbucks were present when the preserve was established in 1969. After a decade, in 1976, the population peaked at around 2,500, and since then it has steadily declined to its current low of around 1,400 (Jhala & Isvaran 2016). In Karnataka, Blackbuck populations are still thriving only in a handful of remote locations. There are approximately 2,000 in the Ranebennur Blackbuck Sanctuary, 500 in the Jayamangali Blackbuck Conservation Reserve, and 800 in the Bidar area alone (Mohammed & Modse 2016). Odisha's Blackbuck population is concentrated in the Ganjam District in southern Odisha, with an estimated 43 Blackbucks per km^2 as of 2021 using a line transect distance sampling strategy (Patnaik 2021).

Age-sex composition

Our results show differences in sub-adult females were visible across the four years we looked at, but there were no statistically significant differences between the other age-sex groups. Although the proportion of fawns and subadult females decreased significantly over the course of the study, no significant trend emerged among other age-sex groups overall. Low recruitment rates into the population, as indicated by long-term trends or consistently low proportions at the young age classes, would lead to a decline in population size and persistence probability (Eberhardt & Breiwick 2012).

Sex ratio

The sex ratio at Point Calimere was 1:1.9, decades ago (Daniel 1967). The current study shows that this ratio has not changed significantly from the expected in the year(s) surveyed. This is the case until 2019, when we discover a significant deviation in adult category. Similar to the adult categories, there was no significant deviation from the expected ratio for the sub-adult categories in 2017. But from 2018–2020 and combined year ratios were much heavily skewed toward females.

Similarly in other areas as reported, Sathyamangalam Tiger Reserve shows female biased sex ratio, but the ratio is equal at Guindy indicating it did not fit into the expected level and shows deviation from the polygynous ratio (Baskaran et al. 2020).

In Blackbuck, males tend to be solitary; sub-adults tend to leave their mothers shortly after being weaned (Mungal 1978). Antelopes, due to their increased exposure to predators when exhibiting territoriality including intrasexual combat for mates, males are likely to have a higher mortality rate than females, as expected in polygynous mating system (Estes 2012). Males also emerge to range more widely than females. Also, sub-adult males, subordinate to adult males are treated agonistically until they disperse, mate competition provides the best explanation for male dispersal. Subsequently, a few adult males move into areas where the females are living and begin protecting territories (Walther et al. 1983). Adult males have a negligible effect on population shifts in any given population or site, population swings and long-term steadiness both result from shifts in the proportion of females in a population (Nunney 1991, 1993).

In mammals, females tend to outnumber males in the adult population (Emmel 1976). Any disparity from a gender balance of 50:50 points to male migration or mortality rates being higher than female ones. The males' tendency to disperse and the polygynous mating system in the Indian Blackbuck are both factors in the species' increasingly female-biased sex ratio and patterns. Results show a female preponderance in the species' sex ratio, and similar patterns were reported in studies of polygynous large herbivores (Graf & Nichols 1966; Schaller 1967; Dinerstein 1980; Johnsingh 1983; Karanth & Sunquist 1992; Khan et al. 1995; Sankar & Acharya 2004). Further, variation in sex ratio is both a cause and a consequence of sex- specific reproductive strategies, and these inter-relationships is reported to shape species-typical types of social organization, opportunities for different forms of paternal care.

Fecundity, survival and mortality

Despite the high female mortality caused by the Gajah cyclone at the end of 2018, we discovered that fecundity rates weren't lower in 2019 and is comparable to the other years surveyed. Since newborn fawns do not immediately join social groups, instead lie alone for the first few months of their lives (Mungall 1991), natality rates could not be determined (Jhala 1991). The demographic breakdown of the age groups and sexes, however, made age-dependent differences in fecundity obvious. Due to the interplay between fecundity and survival rates, fecundity alone may not be indicative of the direction or magnitude of changes in population size (Brongo et al. 2005). This suggests that estimates of both survival and fertility may be needed to better understand population dynamics (Sorensen & Powell 1998). Our findings showed that adult females had the highest survival rate, followed by female fawns, and then subadult females.

Mortality rate estimates for adult and subadult classes showed a higher mortality for the composite female class, however male subadult class showed much higher as a single age sex group. For the fawn category, using census data and carcass, mortality rate of 20% was estimated attributing 10% for each of the sex classes. The high rate of decomposition and the speed with which predators consume fawn remains make the possibility of a mortality incidences among fawns extremely hard to record relative to the older age classes (Indra et al. 2022).

Blackbuck population breed seasonally at Point Calimere, and the timing of breeding coincides with that of the population in Guindy National Park during September and October, both the areas showed a fawning peak between January and March, and a gap between April and August (Sathishkumar, forester at PCWS pers. comm. April/2018). They also breed seasonally in the Sathyamangalam Tiger Reserve, but there they have a birth peak in November. This disparity could be caused by rainfall patterns having two peaks during May and October in Sathyamangalam, which results in different plant growth patterns and an altered timing in the availability of food (Baskaran et al. 2020). Birth at captive population at Vandalur Zoo, Chennai, showed a peak between January and March, and a gap between April and August (pers. comm: Vandaloor Zoo Vet. Dr Boon Alvin 8/12/2018). Blackbuck at Valanadu Wildlife Sanctuary, Tootukodi, had a birth peak between October–December, which was the same as found at Sathyamangalam (Baskaran et al. 2020). Records of fawn seen at Point Calimere even indicated that some were born throughout the year (as per pers. comm: Mr S. Sathishkumar, Forester, Vedaranyam Forest Range, April/2018), but cull data indicated that the majority were seasonal (Baskaran et al. 2020). Similarly, in Velavadar, Blackbuck population is reported to exhibit two calving peaks: one after the monsoon (September) and one before the nutritionally stressed summer (March–April) (Jhala & Isvaran 2016).

In most large herbivores, the survival of fawns is generally low and varies over time in response to a wide range of proximal factors (Gaillard et al. 2000). While predation on and starvation of neonate fawns are reported to be major sources of mortality, at Point Calimere, feeding conditions are good with peak forage availability during the peak breeding and fawning time (Baskaran et al. 2020). This can probably explain proximate cause of mortality is not starvation. The Golden Jackal, the only known predator at Point Calimere, has been seen stalking fawns as they move with their mothers, usually they hide in halophytic bush *Sueda monioca* and given a chance, they attack on isolated mothers and their young (as per pers. comm: Mr S. Sathishkumar, Forester, Vedaranyam Forest Range, April/2018).

Population change (or growth)

Analysis using life tables assumes a closed population and this assumption is valid with group living and territorial animals (such as Blackbuck) (Skalski 2010).

With a finite rate of population change (λ) at 0.97, the female-based Leslie matrix model indicates a downward trend in population during the survey years. The negative instantaneous growth rate (r = -0.025) between the 2017 and 2020 periods was brought about primarily through reduced adult survival and fawn recruitment suggested the population was declining.

These analyses have created a representation of Blackbuck demography that depicts a population that contains 62% adult females and approximately 16–19% fawn female and subadults. It can be noted that our observed female age class distribution is not very dissimilar to the stable age distribution that we have predicted from our Lessie matrix, and hence, we can conclude that the population has been growing at a relatively constant and lower rate for some time, even the population has been affected by the 2018 Gajah Cyclone. Further, it is important to keep in mind that there may be more adults than fawns because adults typically stay in this age class for several years, whereas younger age classes typically only stay in their respective age classes for one or two years. Typically, when a growing population has a higher value of adult-stable age or stage distribution, its age structure changes (Gaillard et al. 1998, 2000) leading to an increase in the average age of adult females and so in the next few years, it is likely to obtain a greater adult mortality (Festa-Bianchet et al. 2003).

Similarly, age specific reproductive value (r_v) estimated for the population shows female fawns and sub-adult exhibiting r_v around 1, while the adults showed r_v around 3. This is a standard measure of the expected contribution of an individual in each state to the future population (Fisher 1930). Reproductive value initially increases with age, because each pre-reproductive year that an individual survives increases the probability that it will survive to reproductive age. r_v usually peaks near the age of first reproduction as the individual has its entire reproductive span yet to come.

The best parameter to describe and evaluate the growth of a population of a species to environmental conditions is the intrinsic rate of natural increase (r^m), which we obtained for the Blackbuck population as 0.24, using life tables. This value was close to, and somewhat less than zero, suggesting a population decline (Skalski 2006). A limited number of studies have highlighted population growth in terms of life table parameters, and there is a paucity of information on r_m-values for Blackbuck and other antelopes in India. A major barrier to using life tables is the large sample size required, also in many instances, individuals must be followed from birth to death, which can be challenging (Kajin et al. 2008).

Based on reproductive rates estimated in our study through life tables, the net reproductive rate (R_0) was estimated as low as 3.28 offspring per generation for a population, this value can be compared with another declining population of Blackbuck at Velavadar Wildlife Sanctuary, where Jhala (1991) found a similar trend with 3.2 offspring per generation. Further R_0 contrasted with a rather longer mean generation time (G) as 4.7 years (5.3 years: in Jhala 1991). Ungulates even if they are subjected to none or least predation reveal an increase in generation time and a population decline, because the low survival is not compensated by reproduction or recruitment rates and it is suggested that with moderate hunting pressure, particularly in the absence of large predators, ungulate populations display a colonizing demographic regime, characterized by high recruitment, a young female age structure, few senescent individuals, and shortened generation times (Crampe et al. 2006; Nilsen et al. 2009). At Point Calimere alternate pattern emerges, emphasizing the existence of factors such as effect of invasives, competition or other intrinsic socio-ecological determinants likely to reduce the population of Blackbuck (Baskaran et al. 2016, 2020; Arandhara et al. 2020, 2021). Earlier, Baskaran et al. (2016) reported possible effects of decline of this native species in the presence of invasive species like the feral horse in the community, for a long run and Arandhara et al. (2021a). marks the effect of invasive *P. juliflora* on the distribution ecology of Blackbuck in the sanctuary. Consistent with our results, Sophiya (2020) and Arandhara (pers. obs. March/2021) pointed out that limiting the number of vehicles and visitors to the park, as well as establishing specific visiting hours and zones, would benefit mating behavior, reproduction, and ultimately the viability of the Blackbuck population.

Conclusion and management recommendations

Our research adds to the basic understanding of these demographic attributes for large herbivores, establishing a baseline of data on the species, shedding light on life-history implications that can be expected for large herbivores in similar environments where similar conditions prevail.

To better manage a polygamous social species, like the Blackbuck, it's important to understand the social preferences, survival and lifetime reproductive success. The following management recommendation is made:

(i) Management of grasslands is essential to avoid invasion of alien woody plant. Invasion of *Prosopis* which is modifying the natural habitats, which suggest giving it higher priority. (ii) Blackbuck is a diurnal species, and the visitors time coincides with peak activity hours of Blackbuck, influencing the social dynamics of the

Blackbuck herds. Anthropogenic concentrations can alter mammals' foraging behavior (Ali 2005; Baskaran et. al. 2019). (iii) The feral-horse in the sanctuary, which competes with the native Blackbuck for resources and poses a serious threat, drives the Blackbuck away from suitable habitats. Thus, it is essential to humanely control its population so that it may not exclude the native species eventually.

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Supplementary Table 1. Density estimate of Blackbuck at Point Calimere Wildlife Sanctuary, Tamil Nadu, using line transect direct sighting method and distance sampling analysis for 2017–2020.

Parameters	2017	2018	2019	2020
No. of transects	8	8	8	8
Effort (l/km)	160	174	165	169
Number of group detection (n)	199	365	354	277
Key function model	Half Normal	Uniform	Half Normal	Half Normal
Key adjustment	Simple Polynomial	Cosine	Simple Polynomial	Simple Polynomial
Detection probability	0.31 ± 0.066	0.36 ± 0.087	0.29 ± 0.045	0.35 ± 0.157
Effective strip width (m)	205 ± 12.8	205 ± 12.8	205 ± 12.8	205 ± 12.8
Encounter rate of group/km (n/l)	1.44	1.52	1.35	1.74
Mean group size	2.9 ± 0.59	3.8 ± 0.66	4.2 ± 0.36	3.6 ± 0.47
Group density/km^2	8.0 ± 0.77	7.8 ± 0.62	8.5 ± 0.84	7.7 ± 0.93
Individual density/km^2	**27.6 ± 5.5**	**29.3± 4.3**	**28.7± 3.8**	**31± 8.4**
Population size for PCWLS	**716 ± 146.7**	**727± 162.9**	**711± 145.5**	**722± 168.9**

Supplementary Table 2. Year wise and mean fecundity rate of Blackbuck at Point Calimere Sanctuary, southern India.

Year	Fecundity	Mean fecundity	SE
2017	0.44		
2018	0.45	0.44	0.002
2019	0.44		

Supplementary Table 3. Leslie matrix for estimating population growth parameters of Blackbuck at Point Calimere Sanctuary, southern India.

Age-sex category	FAF	SAF	AF
FAF	0	0	0.44
SAF	0.58	0	0
AF	0	0.37	0.75

AF—adult female | SAF—sub-adult female | FAF—female fawn.

Supplementary Table 4. Mortality based life table analysis for female Blackbuck at Point Calimere Sanctuary, southern India.

Age(x)	f_x	f_x^1	f_x^2	$d_x e^{rx}$	l_x	m_x	$l_x(m_x)$	$l_x(m_x)x$
0	0	0	28	28	1.00	0.00	0.00	0.00
1	9	237	230	224	0.97	0.25	0.24	0.24
2	3	79	77	73	0.71	0.75	0.53	1.07
3	2	53	51	47	0.63	0.75	0.47	1.41
4	3	79	77	69	0.57	0.75	0.43	1.72
5	1	26	26	23	0.50	0.75	0.37	1.86
6	2	53	51	44	0.47	0.75	0.35	2.11
7	3	79	77	64	0.42	0.75	0.31	2.20
8	5	132	128	104	0.35	0.75	0.26	2.08
9	3	79	77	61	0.23	0.75	0.17	1.53
10	6	158	153	119	0.16	0.75	0.12	1.18
11	1.0	26.3	25.0	18.9	0.0	0.8	0.0	0.2
12	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0
13	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0

fx—no. of dead carcass recorded | fx^1—hypothetical cohort of 1000 carcass of the age classes other than fawns | fx^2—hypothetical cohort including potential fawns and other age classes summing up to 1000 | dx e^{rx}—corrected age frequencies, here, coefficient (e^{rx}) corrects the age frequencies for bias caused by population growth (or decline) r—Lnλ | l_x— survivorship | m_x—fecundity schedules (Sinclair 1977; Krebs 2017).

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