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Predation by Wolves (*Canis lupus pallipes*) on Blackbuck (*Antilope cervicapra*) in the Great Indian Bustard Sanctuary, Nannaj, Maharashtra, India

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ABSTRACT

Some aspects of predation on blackbuck (*Antilope cervicapra*) by wolf (*Canis lupus pallipes*) were studied in the Great Indian Bustard Sanctuary from 1991 to 1994. For each kill, data were collected on (a) sex and age, (b) habitat around kill sites, (c) biomass left unconsumed by wolves, (d) distance of kills from the den(s), Sanctuary boundary and the nearest thick vegetation cover. The wolves largely preyed on old and injured blackbuck and had a strong selection for males (U=42, P=0.01, Mann-Whitney U test). On an average, wolves made a kill every 3.65 days during winter (S.E.=0.58, n=19) and 2.1 days (S.E.=0.7, n=10) during summer. The consumption rate was found to be 1 kg/wolf/day and it was not correlated with the pack size (r_s=0.16, P=0.07). The wolves depended largely on blackbuck for food requirement during their non-breeding period and on livestock during denning or breeding period. The maximum number of kills were located within 4 m of distance from vegetative cover (34%, n=26). The distribution of kills differed significantly between habitats and the maximum number of kills were found in grasslands (37%), followed by scrubland (23%), plantations (21%) and grazing land (19%). The wolves killed blackbuck irrespective of the location of dens (D=0.246, P=0.462, Two-sample Kolmogorov-Smirnov test). Only two instances of food caching by wolves were recorded during the study period. Blackbuck used predator avoidance strategies such as encirclement of herds by large males with longest horns to threaten wolves, ground stumping, flashing tail while running, galloping as high as possible, blowing out air from the nostrils briskly and producing a grunting sound to alarm the remaining individuals of the group. On an average, predation by wolves removed 4% of the total biomass of blackbuck available to them in the Sanctuary and 3.5% when 10% of the biomass of kills was assumed to remain unutilised by them. They consumed 25 to 30 individuals of blackbuck annually in the Sanctuary.

Key Words: Indian Wolf, *Canis lupus pallipes*, Blackbuck, *Antilope cervicapra*, Predation, Hunting, Kill rate, Consumption Rate, Kill Utilisation, Biomass Consumption, Great Indian Bustard Sanctuary.

INTRODUCTION

The endangered Indian wolf (*Canis lupus pallipes* Sykes 1831) is the apex predator in grassland ecosystems, grazing lands and grassland-scrubland interfaces of Indian grassland plains in the Deccan following extinction of cheetah (*Acinonyx jubatus* Schreber, 1776). Predation on wild ungulates by wolves is one of the most widely studied aspects of their ecology in the world. The two long-term studies ever conducted on large mammalian predator-prey systems in the world happen to be of wolves and white-tailed deer (*Odoceileus virgianus* Zimmermorn 1780) in Superior National Forest, which started in 1946 and wolf-moose (*Alces alces* Linne 1758) investigations in Isle Royale, Michigan in the late 1950s (Mech 1970) that are still continuing. Wolves prey on a variety of wild and domestic ungulates available in their global distributional range. The major wild prey of wolf in India is blackbuck (*Antilope cervicapra* Linnaeus 1758) but it also consumes blacknaped hare (*Lepus nigricollis* Cuvier 1832) and rodents. However, the wolf regularly preys on domestic livestock all over its range in India. Blackbuck was abundant all over the Indian plains

especially in the Deccan that declined largely due to hunting during 1950s and 1960s. But after the enactment of the Wildlife (Protection) Act, 1972 there has been resurgence of blackbuck populations in certain areas (Rahmani 1991). This has benefited the wolf to some extent in the Deccan.

Wolves depend upon ungulates for food in the winter and supplement this with smaller mammals or alternate prey species during spring and fall in North America (Mech 1970, Pimlott 1967). In areas, where smaller mammals are not so abundant, ungulates usually account for more than 90 percent of the biomass consumed by wolves (Carbyn 1974, Fritts and Mech 1981, Holleman and Stephenson 1981). Studies of wolves and their food habits have provided conclusive evidence that they depend primarily on hoofed mammals for their sustenance (Gunson 1995).

There is however, no information on predation and food habits of wolves in India except from Velavadar National Park, few areas in the Deccan and Bhal region of Gujarat (Jhala 1993, Kumar and Rahmani 1995, Kumar, 1998, Kumar and Rahmani 2000, Jethva and Jhala 2004). The wolves are impulsive predators, which begin hunting only when they are triggered by hunger. They can consume food several times than their normal requirement when available in large amounts to them (Mech 1970).

The Indian wolf is unique with regard to food habits and the environment in which it lives in comparison to other geographical races of wolves. Unlike Indian wolf, its con-specifics in Israel have been reported to have more scavenging habits that are attracted to garbage dumps around human settlements (Mendelssohn 1983a and 1983b) and sheep and goat carcasses in Saudi Arabia (I.A. Nader 1992, pers. comm.).

In this study, we have attempted to describe the hunting methods of a pack of wolves named Nannaj Pack, prey selection, kill consumption, kill rates in non-breeding, and breeding and pup-rearing phases of the pack, kill utilisation, distribution of kills in different habitats, and predator avoidance or anti-predator behaviour of the prey. We have also attempted to give a brief account of the impact of wolf predation on blackbuck population.

STUDY AREA

The study site is located 20 km north of Solapur on Solapur-Barshi road, situated between 17°41′ N and 75°56′ E at 486 m elevation in the Great Indian Bustard (GIB) Sanctuary, which includes an extensive area of 8,496 km^2 falling in two districts of Maharashtra, namely Ahmadnagar and Solapur. It lies in the drought prone areas of the Deccan plateau that covers an area of 1,421,000 km^2 or 43% of the total land mass of the country (Rodgers and Panwar 1988). Due to the rain shadow created by the Western Ghats, the drought prone area of Solapur and its adjacent areas in the Deccan plateau receive an average rainfall of 750 mm which is distributed in 3-4 months (July to mid-October). The rainfall is erratic and droughts are common.

Climate of Solapur is semi-arid. The annual climate cycle includes: summer (February to mid-June), monsoon (mid-June to mid-October), and winter (mid-October to January) seasons. Monsoon starts in late June or early July. However, there are dry spells during late July and early August. A dry spell occurs when the rainfall in consecutive weeks is less than 15 mm. There is adequate rainfall in late August and September; more than half of which occurs in September. Rainfall ceases by mid-October. The temperature usually varies from 10°C (minimum) in December to 45°C (maximum) in May.

The substratum is comprised of half-decomposed basalt rock formations. The soil is derived from the basic igneous rock called basalt and is commonly called as black cotton soil. The terrain is gently undulating with mild slopes and flat topped hillocks with intermittent shallow valleys that form the major drainage channels.

Grasslands are distributed in disjunct, fragmented patches forming a mosaic of grazing and agricultural lands and human settlements. Most of the grasslands are present on cultivable slopes and tops of the hillocks. These grasslands are either government owned or private and constitute the 'commons' meant mainly for grazing.

In 1975 the Drought Prone Areas Programme (DPAP) financed by the World Bank was initiated in Solapur district. The DPAP is essentially an area development programme, aimed at integrating efforts in agriculture and allied sectors to mitigate the adverse effects of drought. It seeks to develop land, water, vegetation, livestock and the restoration of ecological balance. The establishment of grassland and plantation patches by the Forest Department under this scheme witnessed resurgence of wildlife, benefited by the effective protection and improvement of the habitat. These pastures and plantations serve as important source habitats for wolves (Figure 1a) providing them

Figure 1b. Wolves eviscerate blackbuck after killing and consume the viscera first.

Figure 1d. Among males, wolves usually kill the territorial bucks.

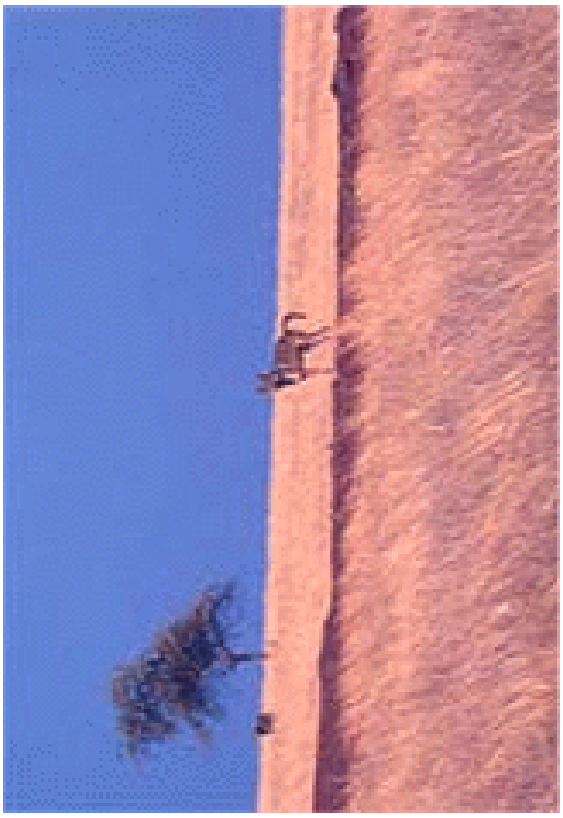

Figure 1a. Protected grassland patches and plantations as source habitats for wolves.

Figure 1c. The mode of feeding on kills by wolves is neat unlike dogs which feed haphazardly.

vital space for denning from where they disperse to other suitable habitats. In the early 1980's, few plantation plots were established under the District Rural Development Agency (DRDA).

The area around Nannaj can be broadly divided into: (a) protected land, (b) scrubland, (c) grazing land and (d) cropfields. The protected plots are under the control of the State Forest Department. All DPAP plots are surrounded by grazing or agricultural lands. The protected land can be sub-divided into plantation and grassland. Many new plots are coming up in the area under Social Forestry Plantation Schemes.

METHODS

In the study area, both wolf and pariah dogs prey on blackbuck. To investigate predation by wolves it was essential to identify and differentiate the kills made by these canids. Based on the following criteria, we differentiated the blackbuck kills made by wolves and dogs: (1) when there was no dog seen around the kill site for half an hour after it was located, it was presumed to be killed by wolves. The dogs did not leave their kills even when they were chased aggressively by wolves from the vicinity of kills. (2) The pattern of feeding by wolves and dogs was strikingly different. Dogs fed quite haphazardly, whereas the mode of feeding on kills by wolves was neat and organised, showing preference for particular organs or parts to be consumed first (Figure 1b and 1c). Wolves consumed all parts of their kills except for few bones and skull. With some experience, we could distinguish the kills of these canids. However, all those kills where it was difficult to ascertain if killed by wolves or dogs were discarded from analysis.

The Indian house crow (*Corvus splendens* Vieillot 1817), Indian jungle crow (*Corvus microrhynchos* Sykes 1832) and raptors such as parich kite (*Milvus migrens* Sykes 1832) helped to locate wolves on kills as they start hovering over the kills. Occasionally, stray dogs were observed moving around kills restlessly indicating presence of a kill(s) in the area. It was relatively easier to find out kills on such occasions.

G-test (Sokal and Rohlf 1981) was used for comparing distribution of kills in different habitat types. Since the areas of different habitat types were unequal, it was necessary to perform this test before making generalisations from the kill distribution data. A BASIC programme (PREFER) was used in conjunction with the G-test to find out the preference or avoidance of a particular habitat (Prasad and Gupta 1992).

Once the Nannaj pack was spotted on a kill, continuous attention was paid until it moved away from the kill. Data were collected on sex and age-class of the kill, weight of the biomass left unconsumed, location and distance of the kill from the protected area, distance of the kill from the den and distance to nearest vegetative cover from the kill. The topography and vegetation of the site were also recorded.

The weight of each kill remains and the number of wolves that were known to have fed on the kill with certainty were recorded cautiously to compute the mean consumption rate of wolves. It was not always possible to know exactly as how many wolves fed on the carcass particularly at longer distances. We could however, overcome this problem in 1993 when there were only four wolves in the pack and ultimately only the breeding male and female (Alpha pair) was left in the territory. It was possible to locate the pack of four and two wolves on blackbuck kills of wolves on 11 occasions consecutively, presuming that they did not make any other kill. Data on kills from 11 such kills was used for calculation of the average consumption by wolves and also food consumption per day per wolf.

Blackbuck population in the Sanctuary was estimated from 1991 to 1994 by conducting total counts in rainy season when most of the individuals dispersed to the surrounding area in summer return to the Sanctuary limits for higher availability of forage. Total counts were carried out for two consecutive days from 07:00 to 09:00 H and the average of the counts was considered as the total population of the antelope in the Sanctuary. The females were classified into two age-classes, namely adults and sub-adults whereas males were classified on the bases of coat colour, number of spirals in their horns and their length. Males with very short horns (spikes) were referred as yearling males (YM), males with short horns and without any spiral pattern having cream coloured pelage similar to female individuals as M4, males having long horns with one spiral (rarely two), light golden pelage, face slightly darker as M3, males with long horns having long spirals and rich brown pelage as M2, and black males having long horns and black pelage dorsally that appeared strikingly contrast to the white ventral side as M1.

The average weight of an adult male blackbuck has been reported as 39 kg, of female 28 kg, subadult male 28 kg, subadult female 20 kg, yearlings 16 kg and fawn 5.5 kg (Ranjitsinh 1989). Since the blackbuck become weak during summer and very weak during drought

periods, we considered the weight of an adult male blackbuck (M1 and M2 age-classes) to be 36 kg, of adult female 25 kg. Subadult male (M3) were considered 28 kg, sub-adult females, yearlings, sub-adult males (M4) 10 kg, and fawn 5.5 kg. For converting biomass of blackbuck consumed by wolves into individual numbers, we considered average weight (all sex and age categories) of blackbuck to be 21 kg. Linear regression (curve estimation) was used to know the effect of kill-interval on biomass consumption by wolves (Norušis 1994).

Pups refer to the individuals less than six months of age, yearlings as 1-2 years old and adults two and more than two years of age. However, it is extremely difficult to distinguish yearlings from adults in the field unless they are observed from very close quarters. Breeding or breeding and pup rearing period of wolves in this article refers to the months when they start preparing their dens, usually in the month of December, raise litters and continue remaining with their pups till July/August when they are seven to eight months old and start moving quite independently whereas non-breeding period refers to the period when wolves do not show denning, pup raising and pup rearing activities.

Mann-Whitney U Statistic (STATA 5.0 Version, 1997) was used to know difference in predation rates of wolves on male and female Blackbuck and Kruskal-Wallis one-way analysis of variance (SYSTAT 4.0 Version, 1988) was used for determining seasonal variation of blackbuck kills.

RESULTS

Hunting Strategy

The Indian wolf has distinctive long legs that are instantly noticeable on its slender body. It is adapted for cursorial mode of life and probably rank second among large carnivores after cats that are able to hunt sufficiently large prey that may be larger than their own body size. The endangered predator-prey system of the Sanctuary was very low in mammalian prey diversity comprising blackbuck as the major wild prey, blacknaped hare and some rodents as secondary or alternate prey. It is difficult for wolves to kill blackbuck since the latter are extremely swift. The wolves were found to employ the following hunting strategy:

(a) They avoided long pursuit of a healthy blackbuck because of low chances of success.
(b) Located a sick animal or an injured individual from a herd of blackbuck and chased it. In such cases, the chase always continued for long duration and mostly resulted in killing the animal.
(c) Coursing the grassland and scrubland areas where blackbuck fawns and blacknaped hare usually conceal. Any blackbuck fawn or hare that flushed from the vegetative cover was chased and usually captured by wolves within 100 to 150 meters distance.
(d) During rainy season, the black cotton soil has a high volume expansion with more moisture contents and it is difficult to walk in the patches with such soils. Wolves used to drive solitary individuals of blackbuck immediately after rain to such patches and chase them till they were captured.
(e) Occasionally, a resting individual or a territorial adult male blackbuck was ambushed by wolves by going through small bushes and shrubs. On some occasions, we saw wolves chasing a group of healthy blackbuck, probably without any intention of killing them.

Some blackbuck get injured while escaping from the nooses of the snares laid by irate farmers for Blackbuck that frequent crop fields during nights. The animals that get entangled in the snares injure their tarsi severely and are unable to run. They became an easy prey to hunting wolves. The members of Nannaj pack were observed hunting such injured blackbuck twice during the day light hours. Wolves were particularly attentive for females with neonates probably with an intention of capturing the crop relatively easily. The hunting wolves after capturing a blackbuck, eviscerated it and showed feeding preference for a particular part to be consumed first. The visceral parts were consumed first followed by rump area and then neck region and limbs and lastly the head region. The digestive tract was dragged few meters from the kill and usually abandoned. The wolf pack used to urinate repeatedly around kills after consuming them and the pack members always returned to the kill sites and chewed the remaining bones. The wolf pack was frequently spotted on kills between 06:00-07:00 H, rarely after 07:30 H when people started moving in the area. The pack members that left the kill in the last were usually the young wolves.

Table 1. Sex and age composition of blackbuck killed by wolves in the GIB Sanctuary, Nannaj, Maharashtra, July 1991 to August 1994.

Year	Adult		Sub-adult			Fawn	Pack Size
	Males	Females	Males	Females	Unsexed		
1991*	10	–	1	2	2	6	7
1992	17	7	5	3	2	3	12
1993	8	4	–	–	1	4	2
1994**	7	2	2	1	1	1	8
Total	42	13	8	6	6	14	

* = kills from July to December, ** = kills from January to August.

Prey Selection

The sex and age composition of blackbuck killed by wolves in the GIB Sanctuary has been given in Table 1. Adult males of blackbuck were killed more often by wolves than adult and sub-adult females. We found that among all individuals of blackbuck of known sex and age (except fawns) that were killed by wolves, about 61% (n=42) comprised adult bucks (Table 1).

Out of 11 observations of different age groups of blackbuck chased by wolves, the latter singled out a sick or an injured animal (n=7). The chase never continued for long when wolves knew their limits perhaps by judging the speed of the animal(s) being chased.

The pack members used to keep a strict watch on movement of blackbuck herds with fawns. When a herd grazing in a grassland moved ahead leaving behind some of the fawns in the grass, they were usually chased by wolves (n=18). Wolves killed 14 fawns on 18 occasions out of which ten were probably one or less than one day old (neonates) and were overcome and captured by them within a short distance of 100 to 150 m during the chase. The remaining four were chased for long distance and the outcome remained unknown. All the fawns were killed in open grasslands during the peak fawning season of blackbuck, i.e., January to April. On all occasions, either a solitary or two wolves chased fawns.

They also showed a strong selection for bucks (Figure 1d) (also see predation patterns), especially the territorial individuals, probably because of their reluctance to leave territories.

The pack members kept visiting the kill sites and sniff around them until the kills were almost completely consumed by them. In July 1992, we found that four individuals of the Nannaj Pack comprising 12 wolves coming to a kill for four consecutive days. Sometimes the pack was spotted on kill sites where almost nothing except few bones was left unconsumed.

Kill and Consumption Rates

Based on our data on 11 consecutive kills, average consumption rate of wolves was 3.68 kg $wolf^{-1}$ $kill^{-1}$ (S.E.=0.17). On an average, wolves made a kill every 3.65 days (S.E.=0.58, n=19) during winter (November to December) whereas the kill-interval was 2.1 days (S.E.=0.7, n=10) during summer (May to June), which coincided with their pup-rearing period. The everyday consumption rate of the pack was 1 kg $wolf^{-1}$.

Consumption rate of wolf was not correlated with pack size (r_s=0.16, P=0.07). Although the average food consumption was computed, but there was a wide variation in pack size as well as biomass consumption of wolves.

The effect of kill-interval on biomass consumption per wolf was estimated by linear regression. The slope estimate was found to be 0.321 (S.E.=0.061) and 5.30 as the ratio of slope to its standard error. The regression analysis revealed that average biomass consumption per wolf increased about 0.321 kg for every one-percentage increase in the kill-interval. Besides carnivory, which was generally exhibited by wolves, they were also observed to feed on fruits such as grapes (*Vitis vinifera* Linnaeus) and ber (*Zizyphus* Linn.). The latter was very common in their winter scats.

Predation Patterns

During 1991-1992, a total of 99 kills were located in the territory of the Nannaj pack. The maximum were

blackbuck (46.5%), followed by goat (37.4%) and sheep (16.2%) Therefore, livestock contributed about 54% of the total kills. Whereas during 1993-1994, 76 kills were recorded in total out of which, blackbuck contributed 36.8%, goat 52.6% and sheep 10.5%. The following are the major findings of analysis of the predation on blackbuck by wolves:

Predation pressure on blackbuck by wolves was significantly higher (U=461, P=0.01, Mann-Whitney U test) than on livestock during their non-breeding period (Figures 2 and 3). In other words, during the non-breeding period, wolves were found to depend largely on the primary prey species (i.e., blackbuck), but during the breeding period, livestock contributed mainly to their dietary spectrum (Figure 1a and 1b). Wolves were found to have a strong selection for male blackbuck (U=42, P=0.01, Mann-Whitney U test) despite the higher availability of female individuals in the population.

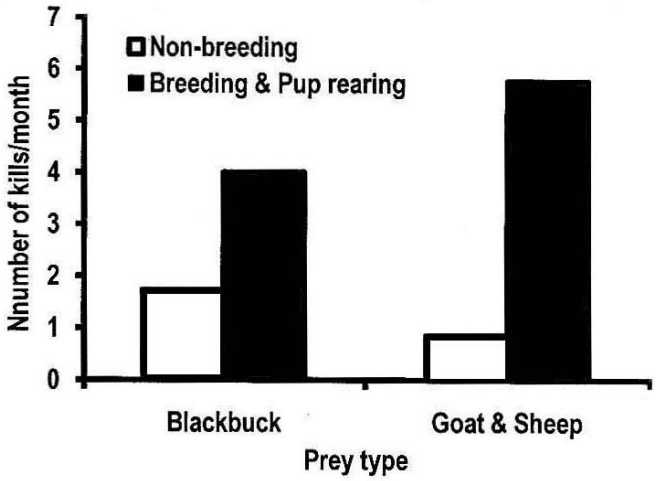

Figure 2. Wolf predation on blackbuck and livestock (goat and sheep) during 1991-1992.

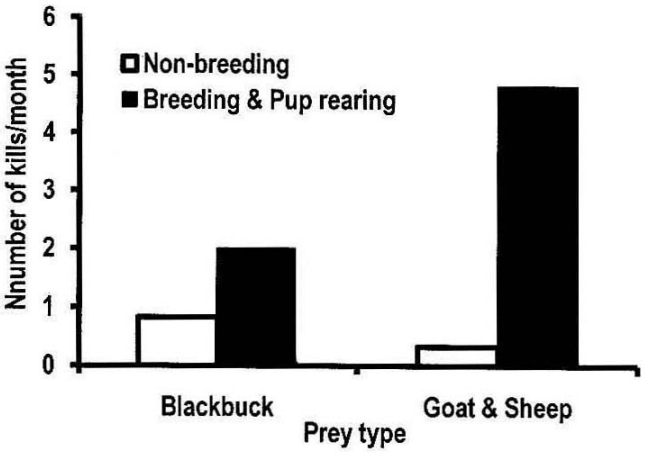

Figure 3. Wolf predation on blackbuck and livestock (goat and sheep) during 1993-1994.

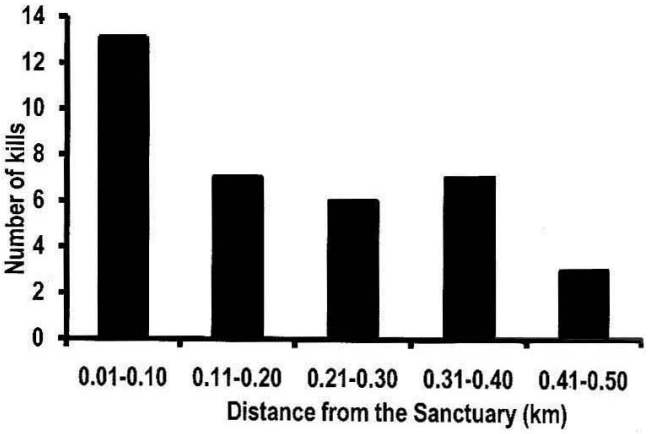

Figure 4. Distribution of kills in relation to distance from the Sanctuary in km during 1991-1994.

Distribution of Kills in Relation to Sanctuary Limits

During daylight hours, the wolves were seen most of the times within the Sanctuary. More than half of the kills (52%) were located in grassland and plantation patches of the Sanctuary. The remaining 36 kills (48%) were found in the grazing lands. The maximum distance where a blackbuck kill was located from the Sanctuary was 0.5 km. Among the remaining 36 wolf kills of blackbuck (48%) found in the grazing land, the maximum (36%, n=13) were located at a distance of 0.01-0.10, 19% at 0.11-0.20, 17% at 0.21-0.30, 19% at 0.31-0.40 and only 8% at 0.41-0.50 km from the Sanctuary (Figure 4).

Kill Utilization

The maximum amount of the kill remains recorded among all observed kills was of an adult doe that weighed 16.5 kg. The number of wolves recorded feeding on the kill was two. The minimum amount of unutilized biomass of a kill was 0.5 kg for an yearling male, 3 kg for an adult male, 1.7 kg for a fully grown adult female and 1 kg for an yearling female. The probable numbers of wolves known to have fed on the

above kills were three, eight, nine and six, respectively. For the remaining kills, the biomass left unconsumed other than the rumen contents included horns, skull, pelvis and the backbone. On three occasions, limbs were also left unconsumed by wolves.

There was a clear pattern of feeding on kills by wolves than stray dogs. The dogs left most of the kills unutilised whereas the mode of feeding by wolves was neat. For some of the blackbuck kills (n=5) it was not possible to distinguish them from those killed by dogs.

Vegetation around Kills

The maximum numbers of blackbuck kills (29%) were located within 1-4 m distance from the nearest vegetative cover. The minimum number of the kills (5%) were at a distance of about 1 m from vegetation (Table 2). All these blackbuck were probably ambushed by the wolves. Of the remaining kills, 11% were within 5-8, 8% within 9-12, 15% within 13-15 and 13% within 16-20 m distance from the nearest vegetative clump. It was not possible to make out the exact location of about 19% wolf-killed blackbuck. The fawns were hunted in open grasslands.

Table 2. Distance of blackbuck and livestock kills from the nearest vegetation cover.

Prey Type	Distance from nearest vegetation cover					
	<1m	1-4m	5-8m	9-12m	13-16m	17-20m
Blackbuck	4	22	8	6	11	10
Livestock	4	50	16	9	1	–

Seasonal Variation in Occurrence of Kills

There was no significant difference in frequency of occurrence of kills (Kruskal-Wallis one-way analysis of variance test, H=0.090, P=0.956) during different seasons of the year.

Distribution of Kills in Different Habitats

There was a significant (G=98.9, P=0.05) difference in distribution of kills among different habitat types (Table 3). The grassland and plantation habitats were preferred by wolves in relation to their availability. In scrubland habitat, wolf-killed blackbuck were found in relation to availability of the habitat. The grazing land was avoided by wolves since the number of kills found in this habitat was less than expected (Table 4). Out of the total 75 kills of blackbuck, 37% (n=28) were found in grassland, 23% (n=17) in scrubland, 21% (n=16) in plantations and 19% (n=14) in grazing land.

The distance of locations of kills of blackbuck from the Sanctuary limits during denning and pup rearing cycle of wolves was similar to the distance of kills during their non-denning period (Two-sample Kolmogorov-Smirnov test, D=0.2463, P=0.462). Also, the distance of locations of kills from the dens did not differ significantly (Mann-Whitney U test, U=366.50, P=0.30) during denning and pup rearing and non-denning periods of wolves.

Food Caching

Food caching was observed in the Nannaj pack only twice during the study period. A single wolf that remained stationed at the kill after the other pack members

Table 3. G-statistic for the log-likelihood ratio goodness-of-fit test for distribution of blackbuck kills in different habitats.

Habitat	Relative area in ha	Observed kills	Expected kills	ln (observed/ expected)	Observed × ln (observed/ expected)	G = 2Σ observed × ln (observed/expected)
Grassland	0.085	28	6.38	1.48	41.44	G = 98.9
Grazing land	0.711	14	53.33	−1.34	−18.76	
Scrubland	0.133	17	9.98	0.53	9.01	
Plantation	0.070	16	5.25	1.11	17.76	
		Σx = 75		Σobserved × ln (observed/expected) = 49.45		

χ^2 = 7.81, d.f. = 3, P = 0.05.

Table 4. Simultaneous Bonferroni confidence intervals for occurrence of blackbuck kills in different habitats.

Habitat	Relative area (ha)	Expected kills	Observed kills	Expected proportional kills	95% Bonferroni confidence intervals
Grassland	0.185	6.375	28	0.085	$0.234 \le p \le 0.513^{***}$
Grazing land	0.711	53.325	14	0.711	$0.074 \le p \le 0.299^{*}$
Scrubland	0.133	9.995	17	0.133	$0.106 \le p \le 0.348^{**}$
Plantation	0.071	5.250	16	0.071	$0.095 \le p \le 0.332^{***}$

* : The number of kills found were less than expected, ** : The number of kills found were in proportion to availability of the habitat, *** : The number of kills found were more than expected.

had left was observed in the morning (07:00 H) to conceal food remains within a heap of dried grass lying few metres from the kill. The wolf did not make any effort to dig a hole or bury its food cache. The wolf rather hurriedly covered the food with grass and rushed to join other members of the pack that had already moved from the kill. Upon examining the site, it was found to be a part of hind leg of a female blackbuck, which weighed about 0.75 kg. The remaining kill had totally been consumed by the pack of seven.

On another occasion, a yearling wolf was carrying a portion of a leg of an animal and dropped it in a trench having thick vegetative cover. The wolf did not attempt to cover or bury the cache. There was no other wolf seen around that area for two hours. Subsequently, upon investigation the food cache was found to be a part of the hind leg of cattle, which kept lying in the same ditch for several days without being attended by any of the pack members.

Anti-predator Behaviour and Predator Avoidance

When chased by wolves blackbuck fawns used to course zigzag in grassland patches instead of running straight. Observations on wolf hunts directed at blackbuck were extremely low. The sequence of hunting which resulted in killing of blackbuck was observed only twice during the study period, but unsuccessful chases were noticed several times (n=13). The following were the predator avoidance strategies of blackbuck during unsuccessful hunts of wolves:

(1) When the wolves approached a large herd of blackbuck, the adult males came to the front of the herd facing the approaching wolves. Such reaction of the prey frightened wolves to enter the herd. On an occasion when two wolves tried to enter a blackbuck herd, one was aggressively hit by a buck with horns.
(2) The common defensive strategy employed by blackbuck to avoid their encounter with wolves was to flee rapidly.
(3) Ground stumping, flashing tail and galloping as high as possible in the air. Blowing out air from the nostrils briskly and producing a grunting sound to alarm the remaining individuals of the group.
(4) As reported earlier, the fawns coursed zigzag and were occasionally successful in avoiding predation by wolves.

Biomass of Blackbuck and its Consumption

It is extremely difficult to exactly assess the impact of wolf predation on blackbuck population since the predator-prey ratio is highly flexible, spatially as well as temporally in the Sanctuary. The population of blackbuck fluctuate seasonally as well as annually in the Sanctuary especially during drought periods, which were experienced frequently in the study area.

During the study period, maximum numbers of blackbuck were counted in 1991 and 1994 (Table 5). The total biomass of blackbuck available to wolves from 1991 to 1994 was 56,058.5 kg (mean=14,014.6). Of the available biomass of blackbuck, wolves could consume only 3% in 1991, 7% in 1992, 3% in 1993 and 2% in 1994 (Table 6).

If 10% of a kill is not utilized on an average, about 54.28 kg of biomass can be subtracted from the mean annual biomass (i.e., 542.75 kg) considered to be consumed by wolves from 1991 to 1994. From the mean biomass of blackbuck (i.e., 14,014.6 kg) available to wolves from 1991 to 1994, they removed only 4% and 3.5% when 10% biomass of kills was considered as

Table 5. Population structure of blackbuck based on total counts in the Great Indian Bustard Sanctuary, Nannaj, Maharashtra, from 1991 to 1994.

Year	Total	Males					Total Males	Females		Total Females	Fawns
		M1	M2	M3	M4	YM		Adult	Sub-adult		
1991	708	30	25	18	17	30	120	431	134	565	23
1992	584	25	18	18	16	26	103	399	65	464	17
1993	577	15	21	22	18	19	95	414	43	457	25
1994*	650	18	25	23	21	27	114	439	65	504	32

* Forest Department Census data; for abbreviations, see methods.

Table 6. Biomass of blackbuck available and its consumption by Nannaj pack in the GIB Sanctuary, Nannaj, Maharashtra.

Year	Available biomass of blackbuck (kg)*	Biomass taken by wolves (kg)	Av. Weight of blackbuck kill S.D.	No. of kills
1991	15,195.5	461.00 (3.03)	21.95 ± 14.50	21
1992	13,190.5	942.50 (7.15)	25.47 ± 11.80	37
1993	13,199.5	420.00 (3.18)	24.71 ± 13.02	17
1994	14,473.0	347.50 (2.40)**	24.82 ± 12.79	14
Total	56,058.5	2,171.00		89
Mean	14,014.6	542.75		22.25

* Estimated from the total counts data of blackbuck population given in Table 5. The values in parentheses represent percent biomass of blackbuck consumed by wolves.
** Data from January to September

kill remains and subtracted from the mean annual biomass consumed by wolves. Thus the total number of blackbuck that were preyed upon by wolves annually is quite low. It appears from the data that consumption of blackbuck by wolves may not affect its population. Percentage consumption of biomass of blackbuck due to predation by wolves revealed it to be below optimal level, which may not have substantial negative impact on population of blackbuck.

DISCUSSION

Hunting Strategy

The wolf is one of the carnivores in which olfaction, vision and hearing are very strong and well developed. It can hear the howling of other wolves at a distance over 6.5 km. Wolves depend on their strong smelling power in the forested areas, and sight in the "open" habitat (Mech 1970). They depend on sight as a tool in hunting in the open areas (grassland and grazing lands) whereas olfaction is used while hunting in the "closed" habitat types (plantations). Hunting also depends on the terrain and circumstances, for instance, chasing the prey upon judging its running speed, ambushing an individual in a wooded patch.

Prey Selection

Wolves are capable of hunting and killing prey species much bigger than their own body size. But they supplement their diet occasionally with lagomorphs and small rodents. The pack hunters like wolf and the Cape hunting dog (*Lyacon pictus* Temminck 1820) are amply dependent on large ungulates such as moose,

deer, sheep (*Ovis* Linnaeus 1758), and antelopes such as gazelle (*Gazella* Blainville 1816) and blackbuck that are found in their respective habitats (Estes and Goddard 1967, Kruuk and Turner 1967, van Lawick and van Lawick-Goodall 1971, Mech 1970, Jhala 1993, Kumar and Rahmani 1997, Kumar et al. 1997). The higher numbers of males among wolf-killed blackbuck support other wolf studies conducted in North America by Stenlund (1955), Pimlott et al. (1969) and Mech et al. (1971). Wolves mainly kill adult male blckbucks because they are reluctant to leave their territories and partly due to the fact that they become very weak during mating season and fall prey to wolves easily. A study on lekking behaviour of blackbuck conducted at Velavadar National Park, Gujarat by Isvaran and Jhala (2000) has revealed that the central males with territories located inside the designated centre have been reported to spend more time (77.55%) on the lek and less time in day foraging than peripheral and bachelor males during the rutting peak. It appears that the central bucks especially those holding better territories may be reluctant to leave them and become victims of wolf predation easily. Also, they become weak because of spending less time in foraging during rutting season becoming thereby easy prey to wolves. We found that most of the male bucks (62%, n=31) out of the total (n=50, Table 1) that were killed by the Nannaj pack were recorded during October to December and February to April coinciding with their rutting season. All these behavioural attributes of adult bucks may be contributing to their higher predation by wolves.

Kill and Consumption Rates

Since scavenging habits were of rare occurrence in the Indian wolf in the GIB Sanctuary indicating thereby that the pack may also be dependent for its food requirements on other food sources such as domestic livestock (Kumar and Rahmani 2000). However, some kills made by wolves far off from the most frequently utilised core area of the Sanctuary may have remained undetected by us particularly when the pack contained only two individuals in 1993. We may explain this in the background of some investigations, which have revealed that kill rates of small packs are higher than large packs (Thurber and Peterson 1993, Hayes and Russell 1998, Hayes et al. 2000, Kaczensky et al. 2005) making it evident that there is a strong influence of pack size on kill rates (Thurber and Peterson 1993, Dale et al. 1994). Also, there is greater variability in daily food consumption per wolf for small wolf packs (Thurber and Perterson 1993). The single wolves or pairs probably could kill deer just as easily as could packs (Mech et al. 1971). Besides variation in pack size, the kill and consumption rates of wolves also differ all over their global distribution range due to several factors such as variation in their own body size, prey types and variation in their body size, duration of snow cover and depth and different scavenging rates of kills occurring in different areas for different wolf pack sizes. Scavenging of wolf kills, which is known to affect their kill rates is negligible in our study site contrary to the recent study on the same aspect by ravens in the Yukon (Kaczensky et al. 2005), which suggests it to be considerable than previously assumed. The kill and consumption rates of our study pack are not comparable to those of North American wolves because of great variability in their prey types, size of prey and pack size. However, these attributes in this study are almost similar to that reported for wolves in Velavadar National Park, Gujarat (Jhala 1993).

Predation Patterns

Prey species may also become victims of wolf predation due to a variety of factors such as parasites, viral infection or injury. Usually the young crop of the prey population or its old individuals are often vulnerable to wolves. Some individuals become very weak during drought period, which fall prey to wolves easily.

We presume that wolves depend largely on blackbuck during their non-breeding period because they may afford to spend more time in searching vulnerable prey and hunting whereas during breeding and pup rearing period they may seek quick access to prey to feed pups, which they probably do by switching over to livestock that may relatively be easy to hunt. The adult males may be killed more often than female blackbuck because of their bimodal rutting during which they spend less time in foraging and more on the leks. They are at higher risk of predation during the rutting season and may easily be killed by wolves as well as stray dogs.

Food Caching

Food caching in carnivores involves hiding food from con-specifics. It has been reported in leopard (Ewer 1985, Seidensticker 1976), tiger (Johnsingh 1983), North American wolves (Murie 1944, Cowan 1947, Harrington 1981, Mech 1988, Mech et al. 1998, Mech

and Adams 1999), captive coyotes (Harrington 1982), red fox (*Vulpes vulpes* Linnaeus 1758) (Macdonald 1976) and African wild dog (Malcolm 1980).

Rare occurrence of food caching could be due to maximum consumption of the kills. Whenever a kill was left partially consumed, the pack kept returning to the same several times until it was consumed completely. The wolves frequented one kill lying close to the road for four days consecutively. Mech et al. (1971) have also observed timber wolves to remain close to their kills for a period of 1-7 days, depending on how recently they had eaten other prey.

The same behaviour of caching food by wolves has also been recorded at Rollapadu Wildlife Sanctuary in Andhra Pradesh (R. Manakadan, pers. comm.). Food caching when performed at an individual level appears to be a selfish behaviour in species such as the wolf, which is a highly social carnivore and contradicts the degree of cooperation for their sociality in terms of group hunting and cooperative rearing of pups.

Kruuk (1976) has reported food caching in adult as well as sub-adult striped hyaenas (*Hyaena vulgaris* Desmarest 1820). They push down the object to be stored into the vegetation with the snout making no attempt to cover it up. The similar behaviour of caching food has been observed in brown hyaena (*Hyaena brunnea* Thunberg 1820) whereas in spotted hyaenas (*Crocuta crocuta* Erxleben 1777) the occurrence is rare and different as they simply dropped food in water (Kruuk 1976). This behaviour is more primitive than food-caching by canids. The latter dig a pit or a hole and cover the food with earth or vegetation (Kruuk 1964, Mech 1970). Wolves have also been observed caching food around large kills, burying whole hares, regurgitating into holes and caching it and covering halves of calves (L.D. Mech, pers. comm.).

Impact of Wolf Predation on Blackbuck

Wolves are known to risk their existence while attempting to kill large prey species (Murie 1944, Rausch 1967, Mech 1970, Peterson 1977, Pasitschniak-Arts et al. 1988). The large prey species of wolves comprise moose, white-tailed deer, musk-ox (*Ovibos moschatus* Zimmerman 1780) and bison (*Bison bison* Linne 1758).

It has been found that wolf predation is generally selective, removing young, old and otherwise inferior animals from prey populations (Mech 1970). However, whether predation regulates or limits prey populations is very difficult to measure in natural ecosystems because of complexity of several factors often associated with the process. Often the investigations involving assessment of the impact of predation on prey populations are speculative having several assumptions and are aimed for management of predator-prey systems.

The number of blackbucks consumed by the Nannaj pack in the GIB Sanctuary appears low. Our data indicate that the pack removes about 25-30 individuals annually from a population of 600 to 650 blackbucks present in the Sanctuary. On an average, predation by Nannaj pack (average pack size=7.25) removed 4% of the total biomass of blackbucks available to it in the Sanctuary and 3.5% when 10% of the biomass of kills remained unutilised by the pack members. They consumed 25 to 30 individuals of blackbuck annually in the Sanctuary. Since the wolves were not radio-collared, it is likely that they may be killing more blackbuck outside the Sanctuary, which remain undetected. Consequently our estimate of biomass removed by the pack annually may remain poorly underestimated than the actual amount. The numbers of blackbuck killed annually by wolves in the GIB Sanctuary is low and is unlikely to have a regulatory control over blackbuck population. But if there are more number of kills by the pack that we may have missed wolf predation may exercise regulatory effect on blackbuck population. Intensive monitoring of different wolf packs for predation by using radio-telemetry may help in determining fine details of these aspects of their ecology.

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