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Prey selection, food habits and dietary overlap between leopard *Panthera pardus* (Mammalia: Carnivora) and re-introduced tiger *Panthera tigris* (Mammalia: Carnivora) in a semi-arid forest of Sariska Tiger Reserve, Western India

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Abstract

After the extermination of tigers in Sariska Tiger Reserve, Western India in 2004, three tigers were re-introduced in Sariska during 2008–2009. The present study examined the prey selection and dietary overlap between leopard and tiger after re-introduction of tiger in the study area. Scat analysis revealed the presence of nine prey species in leopard scat (n = 90 scats) and five prey species in tiger scats (n = 103 scats). Percentage frequency of occurrence of sambar (45.5%) was found to be the highest followed by chital (15.2%) > nilgai (8.9%) > cattle (7.1%) > common langur (6.3%) > peafowl (6.3%) > rodent (5.4%) > wild pig (2.7%) and hare (2.7%) in leopard diet. In the diet of tiger, sambar contributed maximum (41.7%) followed by chital (26.2%), cattle (19.4%), nilgai (10.7%) and common langur (1.9%). The present study revealed that both the predator utilized and preferred prey species in similar way, though there was difference in selection of prey species in terms of sex and age class as observed by kill records. The dietary overlap between leopard and tiger was found to be 94%. The results suggested considerable overlap between the two carnivores along diet axis.

Keywords: Distance sampling, leopard, niche breadth, scat analysis, tiger

Introduction

The survival of any predator is directly related to its habitat, presence of other competitor species and quality and quantity of its diet (Melville 2004). Prey selection of a predator determines spacing patterns, population growth rate and distribution of the species. The key factors that determine large carnivore habitats are prey abundance, less disturbance, water availability and forest continuity. The acquirement of food is a fundamental component for every predator's existence. Hence, prey selection is critical for understanding life history strategies of any carnivore (Miquelle et al. 1996).

A small population of tigers (10–12 individuals) got exterminated in Sariska due to poaching in 2004 (Sankar et al. 2005). Subsequently, reintroduction of tigers from Ranthambhore Tiger Reserve (Ranthambhore TR) to Sariska Tiger Reserve (Sariska TR) was envisaged by translocating

initial population of five tigers (two males and three females), with a supplementation of three tigers (one male and two females) in every two years for a period of six years (Sankar et al. 2005). An adult tiger and adult tigress were translocated from Ranthambhore to Sariska on 28th June and 4th of July, 2008 respectively. There after another tigress was reintroduced to Sariska from Ranthambhore on 25th February 2009. After the tiger extermination in Sariska, leopard took over the entire tiger habitat (Sariska National Park), which was the best habitat available in Sariska and became the top predator (Sankar et al. 2009). Afterwards, the re-introduced tigers again established their territory in the same area of Sariska National Park (Sankar et al. 2010). Several hypotheses have been proposed to explain the prey selection by competitor predators. The hypotheses pertain to ultimate causal factor such as energetic benefits and costs involved (Kruuk 1972; Schaller 1972;

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Griffiths 1975; Stephens & Krebs 1986) and seem to be affected by the change in development prey predator assemblages due to recent extinctions and simultaneous human predation on prey and predator species (Karanth & Sunquist 1995). However, both of these factors were observed to happen in the present study area (Sankar et al. 2005), it is expected that the prey-predator relations and the intra-guild competition between large predators in terms of food will get balanced after the reintroduction of tiger in the study area. In the present study, the prey selection of leopard and re-introduced tiger was studied and dietary overlap between these two top predators was examined between 2008 and 2009. The result was compared with the previous study (Sankar & Johnsingh 2002), when there were 12-16 tigers in the study area. In the present study, the prev selection of leopard was also compared with a previous study (Mondal et al. 2011), when there was no tiger in the study area.

Study area

The study area is the Sariska Tiger Reserve (Sariska TR), Western India. The park lies between

Longitude: N27°05' to N27°45' and Latitude: E76°15' to E76°35' and is situated in the Aravalli Hill Range of semi arid part of Rajasthan (Rodgers & Panwar 1988). It became a wildlife sanctuary in 1955 and Tiger Reserve in 1982. The total area of the Tiger Reserve is 881 km² (Figure 1), of which 273.8 km² is a notified National Park. The altitude of Sariska varies from 540–777 m. Sariska terrain is undulating to hilly in nature and has numerous narrow valleys.

The climate of this tract is subtropical, characterized by a distinct summer, monsoon, post monsoon and winter. The vegetation of Sariska falls under Northern Tropical Dry Deciduous Forests and Northern Tropical Thorn Forest (Champion & Seth 1968). Apart from leopard and tiger, other carnivores present are striped hyena (Hyaena hyaena), jackal (Canis aureus), jungle cat (Felis chaus), desert cat (Felis silvestris), common mongoose (Herpestes edwardsi), small Indian mongoose (H. auropunctatus), ruddy mongoose (H. smithi) palm civet (Paradoxurus hermaphroditus), small Indian civet (Viverricula indica) and ratel (Mellivora capensis). Prey species of leopard and tiger in the area include chital (Axis axis), sambar

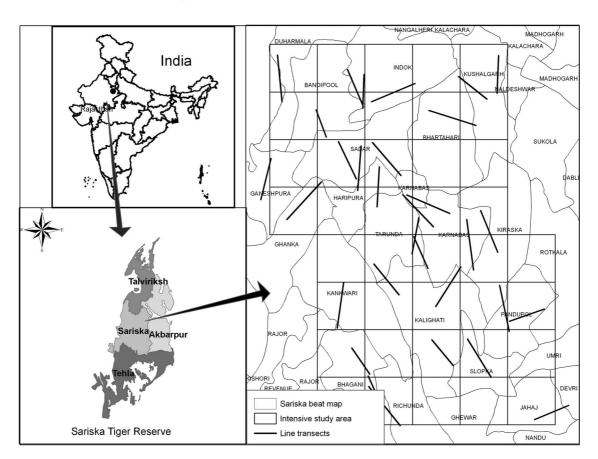


Figure 1. Geographic location of Sariska Tiger Reserve and location of line transects in the intensive study area.

(Rusa unicolor), nilgai (Boselaphus tragocamelus), common langur (Semnopithecus entellus), wild pig (Sus scrofa), rhesus macaque (Macaca mulatta), porcupine (Hystrix indica), rufous tailed hare (Lepus nigricollis ruficaudatus) and Indian peafowl (Pavo cristatus). The predominant domestic livestock found inside the reserve are buffaloes (Bubalis bubalis), brahminy cattle (Bos indicus) and goats (Capra hircus). There are 10 villages located inside the National Park area which are due for relocation since 1984. The human population is over 1700 in the villages of National Park along with a population 10,000 livestock including buffalo, cow, goat and sheep (Sankar et al. 2009). There are 21 villages located outside the National Park but within the Tiger Reserve. The human population in these villages is around 6000 and the livestock population is more than 20,000 (Sankar et al. 2009).

Materials and methods

Prey species density in the study area was estimated by line transect method under distance sampling technique (Burnham et al. 1980). This method has been widely applied to estimate densities of prey species in different forest in Indian subcontinent (Karanth & Sunquist 1995; Khan et al. 1996; Biswas & Sankar 2002; Sankar & Johnsingh 2002; Bagchi et al. 2003). The study area was divided into 40 grids of 4 km² covering 160 km² areas. A number of 32 line transects varying in length from 1.6 km to 2 km were laid covering the intensive sampling area of 160 km². The total transects length of 60.4 km were walked three times in early morning resulting in total effort of 181.2 km. On each sighting of prey species on line transects, total number of individuals, animal bearing and angular sighting distance were recorded. Program DISTANCE 5 (Laake et al. 2001) was used to estimate the density of prey species. The best model was selected on the basis of the lowest Akaike Information Criterion (AIC) (Burnham et al. 1980; Buckland et al. 1993). The half normal key function with cosine adjustment gave the best fit for all the prey species.

Predators' diets have been found to be precisely studied by scat analysis as opposed to kills in forested habitats (Karanth & Sunquist 1995). Studies based on kills being biased towards large prey, the remains of which are more easily detected than those of small prey (Edgaonkar & Chellam 2002). Diet and food preference of leopard and tiger can be estimated from the scat analysis and as well as from the kills (Mukherjee et al. 1994; Biswas & Sankar 2002; Sankar & Johnsingh 2002; Bagchi et al. 2003; Mondal et al. 2011). Fresh leopard and tiger scats

were collected in all seasons whenever encountered during the study period. All the scats were washed, oven dried and subsequently preserved for future analysis. Micro-histological structures of hairs were used to identify the prey species (Johnsingh 1983; Mukherjee et al. 1994; Biswas & Sankar 2002; Sankar & Johnsingh 2002; Bagchi et al. 2003; Mondal et al. 2011). The biomass and number of individuals of the prey consumed by both the carnivores were estimated using Ackerman's equation (Ackerman et al. 1984) to get a more accurate estimate of prey consumption. The assumption for extrapolating of the above equation was that the leopard, tiger and cougar (Felis concolor) had similar utilization and digestibility (Karanth & Sunguist 1995). It was also presumed that the scats containing various prey items had similar decay rate and their detection was equally probable and would apply the same formula as mentioned above (Ackerman et al. 1984) to estimate the prey consumption by leopard and tiger.

Each scat yielded the remains of one or more species. It was necessary to know whether the number of scats analyzed reflect an accurate picture of the diet of the leopard and tiger. The following procedure was adopted to find out the adequacy of sample size. After all the scats were analyzed, an observationarea curve (Odum & Keunzler 1955) which is a curve for the percent frequency of occurrence of major prey species represented in the diet was calculated at an interval of every ten scats, after randomizing the order of the results obtained.

Prey selectivity by leopard and tiger was estimated for each prey species by comparing their availability and utilization data. The expected proportion of scats in the environment (i.e. availability) was calculated using the following equation (Karanth & Sunquist 1995): fi = [(di /dt) * λ i]/ Σ [(di/dt) * λ i], where fi= expected scat proportion in the environment, di= density of i th species, dt = sum of density of all species, $\lambda i = X/Y = \text{the average number of col-}$ lectible scats produced by leopard from an individual of i th prey species, X = average body weight of the species and Y = 1.980 + 0.035 X (Ackerman et al. 1984). Percentage biomass consumption and percentage individual consumption were also estimated using the parameters of percentage occurrence of the prey species in the scats, Ackerman's correction factor and average body weight of the prey species (Karanth & Sunquist 1995; Biswas & Sankar 2002; Mondal et al. 2011). The average body weight of prey species of leopard and tiger required for biomass estimation were taken from Karanth & Sunquist (1995), Sankar & Johnsingh (2002), Ramesh et al. (2008) and Mondal et al. (2011). The prey selection was also

determined by using Ivelev's index (Ivelev 1961), E = (u - a)/(u + a), where, 'u' was observed relative frequency occurrence of prey items in predator scats and 'a' was expected scat proportion in the environment. If a species was preyed relatively more frequently than it exists in the prey population then it was considered preferred, whereas if it was taken less frequently it was avoided.

To assess the dietary overlap between tiger and leopard, the Pianka's niche overlap index was used (Pianka 1973). Where: Pianka index = $(\sum pij^*pik)/\{\sum (pij)^2 * \sum (pik)^2\}$. Here, Pij = percentage of prey items i of predator j; Pik = percentage of prey items i of predator k. The index distributes between 0 and 1, the similarity is higher as the index is close to 1. The diet niche breadth of leopard and tiger were assessed using Levins measure (Levins 1968), standardized to a scale of 0–1 following Hurlbert (1978). Levin's Niche breadth B = $1/\sum pi^2$, where pi = Proportion of diet contributed by prey species i; Standardized Niche breadth Bs= (B-1)/(n-1), where n = Total number of prey species.

Results

In the intensive study area (Sariska National Park), estimation of cluster size, group encounter rate and density of different prey species of leopard and tiger was given in the Table I. In program DISTANCE 5, the selected model was half normal with cosine adjustment 2, 3 (P = 0.69783, Chi-square = 0.1507 and degree of freedom = 1). The density of peafowl was found to be the highest (121.4/km²) followed by goat (54.1/km²), chital (44.3/km²), cattle (36.5/km²), sambar (25.2/km²), common langur (22.1/km²), nilgai (18.9/km²), wild pig (14.9/km²), hare (3.6/km²).

Nine prey species were identified in 90 leopard scats and five prey species in 103 tiger scats. Frequency of occurrence and percentage occurrence of prey species of both leopard and tiger are given in Table II. Sambar contributed maximum (45.5%) in leopard's diet followed by chital (15.2%), nilgai (8.9%), cattle (7.1%), common langur (6.3%), peafowl (6.3%), rodent (5.4%), hare (2.7%) and wild pig (2.7%). In tiger's diet, sambar contributed maximum (41.7%) followed by chital (26.2%), cattle (19.4%), nilgai (10.7%) and common langur (1.9%).

To know the required sample size to analyze the food habits of leopard and tiger in the study area, successively ten scats were randomly drawn from the total sample size, which gave the cumulative frequency of occurrence of each species (Figures 2 and 3). The proportion of different prey species in scats got stabilized once a sample 70 scats were analyzed of leopard and 80 scats of tiger. Hence, it is suggested that a minimum of 70–80 scats should be analyzed to understand the food habits of leopard and tiger in the study area. In addition, no new prey species were found after analyzing 70 leopard scats and 80 tiger scats, as shown by diet stabilization curve (Figures 4 and 5).

Estimation of relative biomass contribution of different prey species in the diet of leopard and tiger, using the equation developed by Ackerman et al. (1984) gave an assessment of prey use by both the predators in the study area. Biomass contribution of each prey species in the diet of leopard and tiger is given in Table II. Comparison of observed utilization and expected availability was done using Ivlev's index (Ivlev 1961) to know the prey selection by leopard and tiger in the study area. Sambar (P < 0.05) and Chital (P < 0.05) were preyed upon by both leopard and tiger in excess of their availability, suggesting

Table I. Density, cluster size and group encounter rate of different prey species in the intensive study a	area (National Park)
in 2008.	

Species	No. of sightings	Cluster Size		Group Encounter Rate		Density/km ²		Biomass/km ²
		Mean	SE	ER	SE	D	SE	
Chital	64	6.40	0.67	0.37	0.06	44.30	9.26	1993.50
Sambar	71	3.14	0.24	0.44	0.07	25.23	4.83	3153.75
Nilgai	73	2.47	0.21	0.41	0.05	18.91	3.24	3403.80
Wild pig	27	5.44	1.00	0.15	0.03	14.95	4.31	568.10
Peafowl	223	5.35	0.42	1.24	0.10	121.43	15.02	412.86
Cow	38	9.44	1.46	0.21	0.05	36.51	11.51	6571.80
Goat	23	23.13	2.11	0.12	0.03	54.10	16.19	865.60
Hare	27	1.25	0.08	0.15	0.03	3.45	0.92	12.42
Common langur	21	10.33	1.29	0.11	0.02	22.06	6.39	176.48

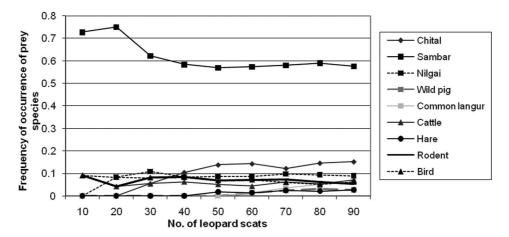


Figure 2. Frequency of occurrence of prey species in leopard diet with increasing number of scats in Sariska Tiger Reserve, Rajasthan, India.

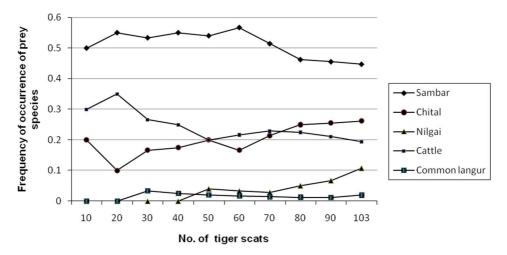


Figure 3. Frequency of occurrence of prey species in tiger diet with increasing number of scats in Sariska Tiger Reserve, Rajasthan, India.

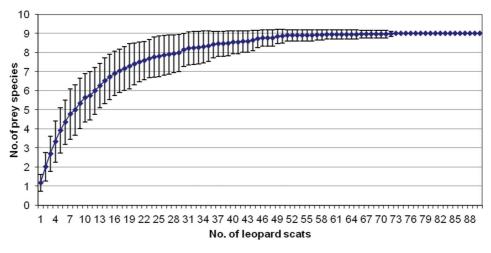


Figure 4. Diet stabilization curve of leopard in Sariska Tiger Reserve, Rajasthan, India.

positive selection or preference, while nilgai (P < 0.05) and cattle (P < 0.05) were preyed upon less than their availability, suggesting negative selection or rejection. The common langur was preyed upon

more than its availability (P > 0.05) by leopard but avoided by tiger (Figure 6). The index of prey selection by leopard at individual species level was in the following order: sambar > common langur>

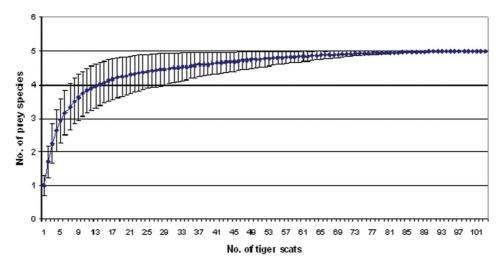


Figure 5. Diet stabilization curve of tiger in Sariska Tiger Reserve, Rajasthan, India.

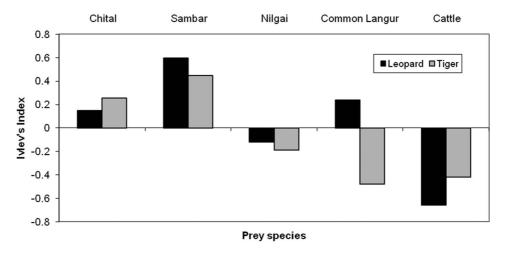


Figure 6. Prey selection of leopard and tiger in the study area of Sariska Tiger Reserve, Rajasthan, India.

Table II. Frequency of occurrence, percentage of occurrence and percentage biomass consumed of different prey species by leopard and tiger as shown by scat analysis.

Species	Frequency o	Percentage occurrence		(%) Biomass consumed		
	Leopard N = 90	Tiger N = 103	Leopard	Tiger	Leopard	Tiger
Chital	17	27	15.2	26.2	10.1	15.2
Sambar	51	43	45.5	41.7	54.2	43.2
Nilgai	10	11	8.9	10.7	14.1	14.7
Wild pig	3	_	2.7	_	1.7	_
Common langur	7	2	6.3	1.9	2.9	0.8
Cattle	8	20	7.1	19.4	11.1	26.2
Hare	3	_	2.7	_	1.1	_
Porcupine	6	_	5.4	_	2.5	_
Peafowl	7	_	6.3	_	2.5	_

chital > nilgai > cattle (Figure 6) and that of tiger was sambar > chital > nilgai > cattle > common langur (Figure 6).

The dietary overlap between leopard and tiger was calculated to be 94% (Pianka index). The Levin's niche breadth for the diet of leopard in the study area

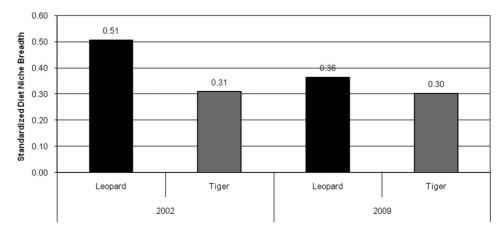


Figure 7. Standardized diet niche breadth of leopard and tiger in the study area in 2002 and 2009.

was 3.91 and that of tiger was 3.41. The standardized diet niche breadths of leopard and tiger in the study area were 0.36 and 0.30 respectively (Figure 7).

Discussion

Leopards hunt by stalking, utilizing their prey opportunistically and mostly at night (Nowell & Jackson 1996; Arivazhagan et al. 2007). The prey of leopards varies in different geographical areas. In Kruger National Park, South Africa, leopards were found to kill mainly medium-sized prey such as Impala (Aepyceros melampus), though a wide variety of small animals including hyraxes (Procavia capensis), civets (Civettictis civetta) and mongooses (Herpestes sp.) also formed part of their diet (Bailey 1993). In Tai Natinal Park, Ivory Coast, leopards prey upon 30 species of animals (Hoppe-Dominik 1984). Small prey also constituted a significant proportion of leopard diet in Tsavo, Kenya (Hamilton 1976). Muckenhirn and Eisenberg (1973) reported that in Sri Lanka leopards preyed mainly on chital and wild pig, while also feeding on sambar, common langur, black-naped hare, porcupine and calves of domestic buffalo. In India, Schaller (1967), Johnsingh (1983), Karanth & Sunquist (1995, 2000) studied leopard food habits; the major prey reported were chital, sambar, barking deer, goral and livestock. In Bandipur, Johnsingh (1983) found that 66% of leopard kills were chital. Chellam (1993) found that in Gir, 40% of leopards scats consisted of chital and 25% common langur. In the tropical forest of Nagarhole, Karanth & Sunquist (2000) found that chital constituted the major prey base of leopards. In the present study it was found that leopard and tiger were utilizing prey species in similar manner. Comparing with previous study, it was found that, leopard largely used to prey upon rodents when there was an established population of 12-16 tigers in Sariska TR (Sankar & Johnsingh 2002). During the present study, both leopard and tiger largely preved on sambar and chital (Table I). The contribution of rodent in leopard's diet was 44.2% in 1990, when the study area was largely occupied by tigers (Sankar & Johnsingh 2002), but after the local extermination of tiger from the study area (2007-08), Mondal et al. (2011) found no contribution of rodent in leopard's diet. Later, after the re-introduction of tiger in the study area (in 2009), the contribution of rodent in leopard's diet raised to 5.4% (Table III). In 1990, chital contributed maximum in tiger diet (57.2%) followed by sambar (18.1%) and in leopard diet, rodent contributed maximum (44.2%) followed by chital (20.2%), sambar (19.4%) and nilgai (7%). But after the local extermination of tiger from the study area, the diet of leopard changed significantly. The contribution of sambar and nilgai in leopard's diet increased to 40.3% and 11.5% respectively in 2007-08, when there was no tiger in the study area (Mondal et al. 2011) (Table III). It was evident that, leopard shifted their diet from lesser prey species

Table III. Percentage occurrence of different prey species of leopard and tiger scats between 1990 and 2009 in Sariska Tiger Reserve, Rajasthan, India.

	199	0	2008	2009		
	Leopard	Tiger	Leopard	Leopard	Tiger	
Chital	20.2	57.2	22.4	15.2	26.2	
Sambar	19.4	18.1	40.3	45.5	41.7	
Nilgai	7.0	2.2	11.5	8.9	10.7	
Common langur	6.2	17.4	10.4	6.3	1.9	
Rodent	44.2	4.3	0	5.4	_	
Peafowl	3.1	0.7	1.6	6.3	_	
Dietary overlap*	().54		0.94		

^{*}Pianka Index.

to large ungulates after tiger extermination from Sariska (Sankar et al. 2009; Mondal et al. 2011). In the present study, it was found that, leopard and tiger consumed the prey species in similar way. Both leopard and tiger showed similar preference except for the arboreal prey species common langur, as common langur was preferred by leopard but avoided by tiger due to its less capability to climb tree (Figure 6). Ranathambore Tiger Reserve and Sariska Tiger Reserve both lies in Aravalli hills with similar habitat condition, environmental condition and prey base. The re-introduced tigers in Sariska TR consumed largely sambar (41.7%), chital (26.2%) and nilgai (10.7%), which are very similar to the previous study in Ranathambore Tiger Reserve (original habitat of re-introduced tigers), where tigers found to consume largely chital (45.7%), sambar (36.9%) and nilgai (3.3%) (Bagchi et al. 2003). Because of the presence of around 10,000 livestock population in the study area, the contribution of livestock in tiger diet is higher in Sariska TR (19.4%) than Ranthambore Tiger Reserve (5.5%), as there is no village situated inside Ranathambore Tiger Reserve. A high overlap (94%) was observed between leopard and tiger diet in the present study, though in the previous study the diet overlap was only 54% (Sankar & Johnsingh 2002). The standardized diet niche breadth of leopard (0.51) was observed much higher than tiger (0.31) in the previous study in the study area (Sankar & Johnsingh 2002), as leopard was largely dependent on small to medium sized prey species and had broader prey spectrum. But in the present study, the standardized diet niche breadth of leopard (0.36) and tiger (0.30) are similar (Figure 7).

Leopards have been found to coexist with other large canivores across most of their range. In Asia, it shares its habitat with the tiger, Asiatic lion and dhole (Karanth & Sunquist 1995, 2000). In Zaire, Central Africa, Hart et al. (1996) found the leopard coexisting with the golden cat (Felis aurata) by specializing on different prey. In Nagarhole, Karanth & Sunguist (2000) found that the tiger, leopard and dhole selectively killed different prey in terms of species, size and age-sex classes, allowing for the co-existence of all three predators. Leopards are opportunists and are flexible in diet; their ability to feed on both small and large prey, to climb trees and scavenge (Johnsingh 1983) may help them survive in highly disturbed habitat where prev species are scarce. Tigers, on the other hand, are not good climbers, limiting their ability to hunt arboreal prev. Unlike the study of Arivazhagan et al. (2007) and Seidenstickker & Lumpkin (1996), where leopards are more likely to move through open terrain and raid villages for domestic prey and tigers depend upon large ungulate prey (Ramakrishnan et al. 1999), in Sariska both the predators utilized the prey species in same manner and tiger consumed more domestic cattle (19.4%) than leopard (7.1%).

Available studies in India reported high dietary overlap amongst leopard, wild dog and tiger (Johnsingh 1983; Karanth & Sunquist 1995; Ramesh et al. 2008). Similar to present study, the dietary overlap between leopard and tiger was observed 94% in Nagarhole Tiger Reserve (Karanth & Sunquist 1995) and 82% in Mudumalai Tiger Reserve (Ramesh et al. 2008). Evidences suggest that among large sympatric carnivores, the larger carnivores can prey on broader size ranges of prey classes due to

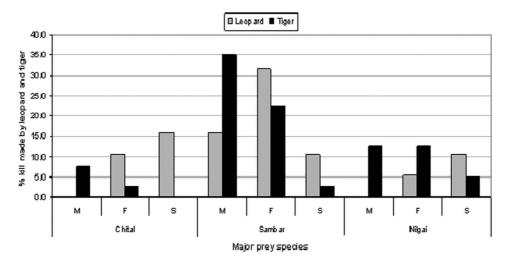


Figure 8. Age and sex classes of large herbivores observed by kill records of leopard (n=29) and tiger (n=40) in Sariska Tiger Reserve, Rajasthan, India. M=Male, F=Female, and S=Subadult.

their prey handling capabilities (Gittleman 1983). In Chitawan National Park where tigers and leopards co-exist, tigers were recorded utilizing a much wider range of prey sizes than leopards (Seidensticker 1976). The wild ungulate density in the intensive study area (102 individuals/km²) is one of the highest reported density in Indian sub-continent (Mondal 2011) and adequate to support both leopard and reintroduced tiger population in the study area (Sankar et al. 2009). Though leopards and tigers utilized the same prey species in the study area, but there is a difference between the sex and size classes of prey species, as observed by kill records. Present study showed that tiger and leopard killed chital, sambar and nilgai but leopards largely killed females and fawns while tigers largely killed adult males and females (Figure 8). From the present study it was understood that, when there was a large number of tigers (12-16) in the study area (1988-1990), leopard was dependent on lesser bodied prey species and occupied broader diet niche breadth than tiger (Sankar & Johnsingh 2002). But after the extermination of tigers, diet of leopard completely shifted to large bodied ungulates (Mondal et al. 2011). After the re-introduction of tiger in the study area, both the predators utilized the prey species in a similar manner and showed similar preference towards large ungulates. The dietary overlap between leopard and tiger was also increased from 54% (1988-1990) to 94% (present study). There was a noticeable difference observed in the selection of sex and age class of prey species by these two predators, as leopard largely hunted fawns and females of large ungulates, while tiger largely hunted adult males, as observed by kill records (Figure 8). At present, there are only six reintroduced tigers in Sariska TR. With the increase in the number of re-introduced tigers a clearer picture of prey utilization and dietary interaction between these two top predators in the study area is expected.

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