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Prey-Predator Dynamics of Apex Carnivores at Parambikulam Tiger Reserve, India

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Abstract
Large carnivores are vital regulators of forest ecosystems, influencing prey populations and maintaining ecological balance through top-down control. In India, the Parambikulam Tiger Reserve (PKTR), situated in the Western Ghats, harbours a rich assemblage of apex predators, including Tiger, leopard, and dhole, alongside a diverse ungulate prey base such as sambar, spotted deer, and wild boar. Despite their ecological importance, limited experimental data exist on predator-prey dynamics in PKTR. In this study, we investigated diet composition and prey selection of large carnivores within PKTR through the field study by examining the scat and direct sightings. The findings suggest that sambar and chital constitute the primary prey biomass. Also, the study showed differences in the prey preference with seasons. The results highlight the critical role of apex carnivores in regulating ungulate populations and maintaining trophic stability.
Keywords: *Apex predators, carnivores, scat analysis, ecosystem*

INTRODUCTION

The interaction between prey and predators is essential for maintaining ecological equilibrium as it influences population dynamics, behaviour, and evolution of species. Predators have played an important role in preventing the monopolisation of the major single-prey environmental requisites (Paine, 1966). The presence of predators indirectly benefits plant ecosystems and promotes biodiversity across various trophic levels, sustaining trophic cascades (Ripple et al., 2014). In order to prevent overgrazing and boost vegetation recovery and heterogeneity, apex predators like the tiger (Panthera tigris), leopard (Panthera pardus) and dhole (Cuon alpinus) practice top-down control over herbivore populations (Karanth & Johnsingh, 1983; Sunquist, 1995). These species differ in body size, hunting strategies, and prey selection, leading to niche partitioning and reduced interspecific competition (Hayward et al., 2014). In a natural ecosystem, large carnivores and herbivores are connected by a complex web of interspecific interactions. The distribution and number of species within an environment are largely determined by these interactions. Certain interactions between large carnivore and herbivore species will eventually disappear or reappear in some ecosystems due to the fast changes in their range and abundance that these species are experiencing on a global scale (Say-Sallaz, 2021). In India, sympatric large carnivores often share overlapping prey bases, especially medium to large ungulates such as sambar deer (Rusa unicolour), chital or spotted deer (Axis axis), gaur (Bos gaurus), and also smaller mammals, primates and arboreal or small ground vertebrates. Diet analysis from Indian reserves highlights sambar and chital as the most preferred prey of dholes and leopards, while tigers consistently show preference for large-bodied ungulates (Borah et al., 2009; Hayward et al., 2012). Beyond ungulates, opportunistic predation on small mammals, primates, and arboreal species such as flying squirrels has also been reported (Karanth and Sunquist, 1995). Although these species contribute less to carnivore biomass intake, they provide dietary flexibility, especially in areas where large ungulates are scarce, and thus support predator persistence. Large carnivores need expansive habitats as they are the top of the trophic level in ecosystems (Ripple et al., 2014). They serve a variety of functions and are the keystone species. By controlling the prey population and the number of meso-predators through intraguild competition and predation, they contribute to the preservation of ecological balance and the structure of natural communities (Carter et al., 2015). Large carnivores are under severe threat globally due to habitat destruction, shortage of prey species, and conflicts with humans and livestock (Karanth and Chellam, 2009). Therefore, understanding the diet of large predators is essential for long-term population management. Scat analyses provide information on prey consumed by large predators, which ultimately determines the prey distribution.

Study Area

Parambikulam Tiger Reserve (PKTR), the second Tiger reserve of Kerala State, is situated in Palghat district, Kerala, India. PKTR is located within the Anamalai Hills of Western Ghats (76.58-76-83°E 410-33-10-43°N). PKTR is surrounded by the Nemmara Reserve Forest, including Nelliampathy Hills to the north, Anamalai Tiger Reserve to the east, Sholayar Reserve Forest to the south, and Chalakkudy Reserve Forest to the west. The present study was carried out in the erstwhile Parambikulam Wildlife Sanctuary. The major vegetation types of PKTR are tropical evergreen deep forest, tropical semi-evergreen forest, southern moist deciduous forests, grasslands and teak plantations.

MATERIALS AND METHODS

Tiger, leopard and wild dog scats were collected whenever encountered in the intensive study area. A total of 280 scats from tigers, 221 scats from leopards, and 243 scats from wild dogs were collected and analysed. The animal trails were monitored for scat collection. Tiger, leopard, and wild dog scats were distinguished from one another by the size of the scats and the presence of ancillary signs, such as pugmarks (Sunquist 1981; Karanth and Sunquist 1995), as well as other evidence, including the diameter of the scat, scrapes, and claw marks. Tiger scats were found to be less coiled and have a larger distance between two successive constrictions as a single piece of scat, when compared to leopards, which are mostly coiled and have a similar distance between constrictions (Johnsingh, 1983).Collected scats were taken on a sieve and rinsed with running water. The separated prey remains, such as hair, teeth, claws and bones, were taken for examination. A total of 20 hairs were randomly picked from each scat for slide preparation. With the help of a compound stereoscopic microscope under 400x magnification, the hairs were examined. Based on the general appearance of the hair, including its colour, relative length, relative width, texture, and medullary width as described by Moore et al. (1974) and Mukherjee et al. (1994), the prey species were identified.

RESULTS

The prey-predator relationship of various herbivores like barking deer, sambar deer, spotted deer, etc., with carnivores like the Tiger, Leopard and wild dog was examined (Fig. 1) through scat analysis.

Wild Dog Scat Analysis

The mean frequency of hairs of different prey species found in wild dog scat was analysed (Tables 1 & 2). The major prey species of wild dog were sambar deer (13.60±2.88), spotted deer (5.60±0.89), wild boar (3.00±1.22), barking deer (2.40±1.14), hare (2.40±1.14), porcupine (1.25±1.32), and Langur (0.40±0.55). In the dry season, wild dog scat contained more A. axis hairs (6.60±1.14). Simultaneously, Sambar deer hair was found to decrease in the wild dog scat in the dry season. Wild dog scat analyses showed significant differences in spotted deer's hair in different seasons. Langur, hare, and porcupine hairs in the wild dog scat also showed significant differences with seasons (Table 1). The two-way ANOVA of prey animal hairs and seasons showed significant differences (Table 2).




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Figure 1. Photographs showing the Prey-predator relationship

Table 1. Wild Dog Scat Analysis. *P< 0.05, ** P< 0.01

Prey Animals	Winter		Dry		Wet		Overall		F-Value
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Barking Deer	2.40	1.14	2.80	1.30	1.80	0.84	2.33	1.11	2.310
Spotted Deer	5.60	0.89	6.60	1.14	3.00	1.00	5.07	1.83	37.597**
Wild Boar	3.00	1.22	4.20	0.84	2.80	1.48	3.33	1.29	4.398*
Sambar Deer	13.60	2.88	12.40	1.82	13.80	1.92	13.27	2.19	1.265
Flying Squirrel	0.00	0.00	0.20	0.45	0.40	0.55	0.20	0.41	2.701
Langur	0.40	0.55	1.00	1.00	0.00	0.00	0.47	0.74	6.577**
Hare	2.40	1.14	3.20	1.30	1.20	0.84	2.27	1.33	9.243**
Porcupine	1.25	1.32	2.11	1.35	0.82	0.75	1.39	1.14	8.257**

Table 2. Two-way ANOVA of animal hairs found and seasons in wild dog scat in Parambikkulam Tiger Reserve. *P<0.05, **P<0.01

	Sum of squares	dF	Mean square	F value
Main effects (combined)	1861.60	20.00	93.08	61.082**
Animal hairs	1800.00	6.00	299.99	196.87**
Season	19.79	2.00	9.90	6.494**
2-way interactions (Hair & season)	41.81	12.00	3.48	2.286*
Model	1554.40	1.00	1550.40	1020.100**
Residual	1989.60	104.00		
Total	3544.00	105.00		

Leopard Scat Analysis

The mean frequency of hairs of different prey species of leopard scats showed Sambar deer (4.53 ± 2.59 SD) as the major prey species (Table 3-4).

Table 3. Leopard scat analysis. *P< 0.05, ** P< 0.01

Prey Animals	Winter		Dry		Wet		Overall		F-Value
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Barking deer	0.40	0.55	1.40	1.14	0.80	0.84	0.87	0.92	3.717*
Spotted deer	4.20	1.64	2.40	1.14	3.40	1.14	3.33	1.45	5.179*
Wild boar	3.80	2.77	3.60	2.97	4.00	2.00	3.80	2.43	0.660
Flying squirrel	0.40	0.55	1.20	0.84	0.00	0.00	0.53	0.74	12.601**
Sambar deer	14.60	2.51	11.00	1.58	12.00	2.45	4.53	2.59	7.878**
Langur	2.20	1.48	6.60	3.05	0.60	0.55	3.13	3.20	27.610**
Hare	0.40	0.55	1.40	0.89	0.20	0.45	0.67	0.82	10.731**

Porcupine	1.28	0.72	1.92	0.85	0.95	0.81	1.38	0.79	13.391
Gaur	2.12	1.32	1.78	0.76	2.12	0.56	2.00	0.88	

Barking deer constituted a mean frequency (0.87 ± 0.92), Wild Boar (3.80 ± 2.43), spotted deer (3.33 ± 1.45), Gaur (2.00 ± 0.88), Langur (3.13 ± 3.20), Hare (0.67 ± 0.82), and Porcupine (1.38 ± 0.79). Two-way ANOVA of the hair of prey animals found in the leopard at different seasons were done. It shows significant variations in prey animals' hairs in different seasons (Table 4).

Table 4. Two-way ANOVA of animal hairs found and seasons in Leopard scat in Parambikkulam Tiger Reserve. *P<0.05, **P<0.01

	Sum of squares	**dF**	**Means square**	**F value**
Main effects (combined)	1734.00	20	86.70	31.941**
Animal hairs	1584.00	6	263.99	97.261**
Season	16.93	2	8.47	3.119*
2-way interactions (Hair & season)	133.07	12	11.09	4.085**
Model	1962.00	104	1325.00	488.17**
Residual	228.00	84	2.71	
Total	3287.00	105		

Tiger Scat Analysis

The mean frequency of hairs of different prey species found in Tiger Scats was analysed (Table 5). The major prey species of Tiger Scats was Sambar deer (17.00±2.30). Tiger Scat contained a mean frequency of spotted deer hair (4.60±1.45), wild boar (3.60±0.64), barking deer (2.13±1.92), langur (1.33±1.59), hare (2.20±0.94), Porcupine (1.48±1.47), and gaur (7.00±1.27). Here in this analysis, spotted deer occupy the third position as the prey animal (Table 5-6).

Table 5. Tiger Scat Analysis. *P< 0.05, ** P< 0.01.

Prey Animals	**Winter**		**Dry**		**Wet**		**Overall**		**F-Value**
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Barking Deer	1.80	2.17	3.40	2.07	1.20	0.84	2.13	1.92	4.500*
Spotted Deer	4.80	0.01	4.60	1.14	4.40	1.67	4.60	1.45	0.185
Wild Boar	4.44	2.19	3.20	1.03	2.20	1.30	3.60	0.64	1.976
Sambar Deer	0.00	0.00	0.80	0.84	0.20	0.45	0.33	0.62	6.500**
Flying Squirrel	16.60	1.82	15.40	2.07	19.00	1.58	17.00	2.30	11.228**
Langur	0.80	0.84	3.00	1.58	0.20	0.45	1.33	1.59	21.574**
Hare	2.60	1.14	2.20	0.84	1.80	0.84	2.20	0.94	2.000
Porcupine	1.21	1.31	2.11	2.18	1.12	0.92	1.48	1.47	6.271
Gaur	6.28	1.23	7.21	1.75	7.52	0.82	7.00	1.27	6.782**

Table 6. Two-way ANOVA of animal hairs found and seasons in the Tiger scat in Parambikkulam Tiger Reserve. *P<0.05, **P<0.01

	Sum of squares	**dF**	**Means square**	**F value**
Main effects (combined)	2085.90	1	2085.10	1035.600**
Animal hairs	2930.10	6	488.34	242.44**
Season	2.46	2	1.23	0.61
2-way interactions (Hair & season)	74.34	12	6.15	3.076**
Model	3006.90	20	150.34	74.698**
Residual	169.20	84	2.01	
Total	5262.00	105		

Habitat analysis of wild dog scats

The frequency of wild dog scat collected from different habitats was analysed (Table 7-8). Most of the wild dog scats were collected from moist deciduous forest habitats and from grassland habitats (12.6±3.8 and 12.6±2.7, respectively). Teak plantations (5.53±1.1, semi-evergreen (1.13±1.0), and evergreen habitat (0.138±0.3). Two-way ANOVA was done between habitats from which dog scats were collected and across seasons. It showed significant variations (Table 8).

Table 7. Habitats from which wild dog scats were collected. *P< 0.05, ** P< 0.01

Prey Animals	Winter		Dry		Wet		Overall		F-Value
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Evergreen	0.00	0.00	0.40	0.55	0.00	0.00	0.13	0.35	6.000**
semi-evergreen	1.00	0.71	1.80	1.30	0.60	0.89	1.13	1.06	4.200*
Moist deciduous forest	15.40	1.67	14.60	1.82	7.80	1.64	12.60	3.87	66.886**
Grassland	11.80	1.64	0.40	1.14	15.80	1.92	12.67	2.79	34.422**
Teak plantations	5.80	1.30	5.40	0.55	5.40	1.67	5.53	1.19	0.375

Table 8. Two-way ANOVA of animal hairs found and seasons in wild dog scat in Parambikkulam Tiger Reserve *P<0.05, **P<0.01

	Sum of squares	dF	Means square	F value
Main effects (combined)	2439.80	14	74.27	106.260**
Habitats	2182.10	4	545.51	332.63**
Season	10.11	2	5.05	3.08
2-way interactions (Hair & season)	247.63	8	30.95	18.874**
Model	3084.80	1	3084.80	1881.000**
Residual	98.40	60	1.65	
Total	5623.00	75		

Habitat analysis of leopard scats

The mean frequency of leopard scats collected from different habitats was analysed (Table 9-10). Most of the leopard scats were collected from moist deciduous forests (21.20± 4.78). The second most scats were collected from grasslands (5.71±1.68). From Teak plantations (3.93±2.19), from semi-evergreen (2.40±1.18), from evergreen (1.40±1.35). Two-way ANOVA was done between different habitats from which leopard scats were collected and different seasons (Table 10). The difference between habitats from leopard scats collected was significant. Seasonal differences from which leopard scats were collected were non-significant.

Table 9. Habitats from which leopard scats were collected. *P< 0.05, ** P< 0.01.

Prey Animals	Winter		Dry		Wet		Overall		F-Value
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Evergreen	1.20	1.30	2.60	1.14	0.40	0.55	1.40	1.35	12.682**
semi-evergreen	2.60	1.52	2.40	1.14	2.20	1.10	2.40	1.18	0.281
Moist deciduous forest	18.20	1.92	18.80	2.49	26.60	3.91	21.20	4.78	29.411**

Grassland	5.20	1.30	6.50	1.29	5.60	2.30	5.71	1.68	1.461
Teak plantations	5.60	2.51	4.00	1.58	2.20	0.84	3.93	2.19	10.279**

Table 10. Two-way ANOVA of animal hairs found and seasons in the Leopard scat in Parambikkulam Tiger Reserve. *P<0.05, **P<0.01.

	Sum of squares	**dF**	**Means square**	**F value**
Main effects (combined)	3293.80	11	299.43	15.278**
Habitats	1281.90	4	320.47	16.352**
Season	5.83	2	2.92	0.149
2-way interactions (Hair & season)	2143.00	5	428.60	21.869*
Model	2821.50	1	2821.50	143.97**
Residual	1117.10	57	19.60	
Total	7834.00	69		

Habitat analysis of Tiger scats

The mean frequency of tiger scats collected from different habitats was analysed (Table 11-12). Most of the tiger scats were collected from the moist deciduous forest (12.20±4.26), Teak plantations (3.53±1.55), semi-evergreen (3.13±2.07), and grasslands (2.40±1.35). Surprisingly, from evergreen habitats, tiger scats were collected (1.80±1.57).

Table 11. Habitats from which Tiger scats were collected. *P< 0.05, ** P< 0.01.

Prey Animals	**Winter**		**Dry**		**Wet**		**Overall**		**F-Value**
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Evergreen	2.20	1.48	2.80	1.48	0.40	0.55	1.80	1.57	11.202**
semi-evergreen	4.00	2.24	4.00	2.00	1.40	0.55	3.13	2.07	8.177**
Moist deciduous forest	17.20	2.59	9.20	1.64	10.20	2.59	12.20	4.26	39.829**
Grassland	3.00	0.71	1.20	0.84	3.00	1.58	2.40	1.35	9.851**
Teak plantations	3.60	1.14	4.80	1.48	2.20	0.84	3.53	1.55	13.607**

Table 12. Two-way ANOVA of animal hairs found and seasons in Tiger scat in the Parambikkulam Tiger Reserve. *P<0.05, **P<0.01.

	Sum of squares	**df**	**Means square**	**F value**
Main effects (combined)	1213.10	12	101.10	20.849**
Habitats	698.28	4	174.57	36.001**
Season	156.19	2	78.10	16.105**
2-way interactions (Hair & season)	541.61	5	90.26	18.616**
Model	1402.30	1	1402.30	289.19**
Residual	300.46	62	4.45	
Total	3110.00	75		

DISCUSSION

The Southeast Asian forests have a multi-predator system, which includes the tiger, dhole and leopard. The dhole is a social canid, and the other two big cats are solitary. Based on their physiological demands and competitive abilities, tigers (180 – 245kg) are considered to be top predators, followed by leopards (46-65kg) and dholes (10-21kg) (Steinmetz et al., 2013). Dholes have been widely studied with tigers and leopards under various environmental conditions to determine the mechanisms of intraguild competition in the Indian peninsula.

The present study in Parambikulam Tiger Reserve indicates that dholes are highly dependent on sambar deer. It was surprising that the dholes preyed upon sambar deer, rather than spotted deer. The spotted

deer is the most common ungulate in the study area over other prey species. The Dhole diet contains a higher percentage composition of wild pig and barking deer in Nepal (Aryal et al., 2015) and spotted deer in the tropical deciduous forest (Swaminathan et al., 2002; Andheria et al., 2007). The dhole in Parambikulam Tiger Reserve were found in packs of 5 to 14 individuals. So, they prefer sambar deer for maximising the energy intake per unit time. Also, the studies from Nagarhole suggest that with a higher tiger density, dhole prey upon smaller prey species like spotted deer (Karanth and Sunquist, 1995). Larger prey are hunted by larger packs of dholes, and the success rate was high.

As expected, from our study, Parambikulam Tiger Reserve showed that large-bodied prey constitutes most of the tiger diet and is in accordance with the majority of the existing studies (Sunquist, 1981; Biswas and Sankar, 2002). Overall, the data suggest that sambar deer, spotted deer and wild pig are the most predated prey species across PKTR. Sambar deer is known to be present in higher density in the undulating terrains of the Shivalik–Bhabhar habitat (Johnsingh and Goyal, 2005) and therefore became the major prey species. However, livestock, being large-bodied prey, was not consumed by tigers in Parambikulam Tiger Reserve. This is due to the very low livestock abundance in the area.

Leopards are versatile predators known for their non-selective hunting habits, targeting a wide range of prey species, focusing on medium-sized mammals, birds, and livestock (Karanth & Sunquist, 1995; Andheria et al., 2007; Ramesh et al., 2009). Leopard's diet consists of 9 different prey species. In the diet, about 57% was spotted deer, sambar deer and common langur together, which was somewhat similar to the findings reported from Nagarhole (Karanth and Sunquist, 1995). In Sariska (Sankar and Johnsingh, 2002), 47% of the leopard diet was constituted of sambar deer, common langur and spotted deer. The leopard preferred sambar deer, spotted deer, wild pig and common langur in Parambikulam Tiger Reserve. Both tiger and leopard showed a preference for sambar deer in the study area. But they hunt sambar deer at different times (hours) of the day, as the leopard is nocturnal and the tiger is crepuscular in behavioural habits.

However, when resources are scarce, species might show fine-scale adjustments in spatiotemporal activity patterns to allocate resources and avoid competition from the dominant carnivore (Rayan & Linkie, 2016; Karanth et al., 2017). The social structuring in carnivores is influenced by prey abundance, composition and distribution (Périquet et al., 2015). The larger groups can consume the prey instantly and defend the prey effectively without attracting other consumers (Carbone et al., 2005). The dominant predator in the system is competitively and effectively suppressed by the larger pack of subordinates (Periquet et al., 2015).

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