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Response of leopards to re-introduced tigers in Sariska Tiger Reserve, Western India

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Tigers got exterminated from Sariska Tiger Reserve before 2005. After that, five tigers were reintroduced to Sariska during 2008 to 2010. The present study compared the abundance, site occupancy and temporal activity pattern of leopard before and after tiger re-introduction. The population of leopard was estimated by mark-recapture technique using camera traps during 2008 to 2010 in an effective trapping area of 223.3 km². Before tiger re-introduction (2008), the leopard density was estimated to be 7.6±0.6 (SE) /100 km² and after tiger reintroduction it was 6.2±0.8 /100 km² (2009) and 3.1±0.4 /100 km² (2010). It was observed that the density of leopard declined significantly (Two sample T-Test; P = 0.0002) from 2008 to 2010. Rate of site occupancy was calculated through site-wise capture history of leopard obtained from camera traps. Before tiger re-introduction the probability of site utilization of leopard was 0.75, while after tiger re-introduction probabilities of site utilization of leopard and tiger were estimated at 0.54 and 0.52 respectively and the co-occurrence of both the species was 0.51. Temporal activity patterns of tiger and leopard were investigated from photo captures. Prior to the release of tigers, mean activity time of leopard was 20: 57 h (95% CI 20: 19 to 22: 53) but shifted to 22: 35 h (21: 02 to 01: 25 h) after tiger release (Watson's U² test: p<0.005). The present study showed that there was a decline in the leopard population after tiger re-introduction and considerable segregation between the two carnivores along the spatial and temporal axes.

Key words: Competition, density, leopard, population, reintroduction, spatial distribution, temporal activity, tiger.

INTRODUCTION

Competition in carnivores may result in reduced fecundity, growth or energy stores of individuals and reduced density and/or an altered age structure at a population level (MacNally, 1983; Petren and Case, 1998). Substantial data shows that large carnivores can limit the density of smaller carnivores by stealing food (Gorman et al., 1998), monopolizing areas of high prey density (Johnson and Franklin, 1994), competing for food (Hayward and Kerley, 2008), or by direct aggression and predation (Palomares and Caro, 1999). For example, studies showed that lions (*Panthera leo*) and/or hyenas

(*Crocuta crocuta*) affect wild dogs (*Lycaon pictus*) through partial exclusion from preferred habitat (Creel et al., 2001) and direct killing (Ginsberg et al., 1995). Consequently, wild dog densities are low where the densities of lions or hyenas are high (Creel and Creel, 1996) and local extinctions are more likely to occur where competition is intense (Vucetich and Creel, 1999). Brown and Maurer (1986) suggested that the ecological advantages of large body size, such as greater energy efficiency, greater mobility and more efficient homeostatic mechanisms, enable large bodied species to use a greater range of habitats. Also, large species can dominate resource use within habitats (Jones and Barmuta, 1998).

Tigers (*Panthera tigris*) and leopards (*Panthera pardus*) are sympatric in several parts of Asia. Karanth and Sunquist (1995, 2000) studied prey selection and

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interactions between these large cats in Nagarahole, India, where the densities of both species were reported high (Karanth, 1993, 1995), and their prey base is rich and diverse in terms of species and sizes (Karanth and Sunquist, 1992). The authors observed similar patterns between the species in space use and activity patterns (Karanth and Sunquist, 2000), but differences in prey selection with respect to prey size (Karanth and Sunquist, 1995). Similar differences are found in the preferred weight range throughout the entire distributions of tigers and leopards (Hayward et al., 2006, 2012).

A small population of tigers (10 to 12 individuals) got exterminated from Sariska Tiger Reserve (Sariska) due to poaching in 2004 (Sankar et al., 2009). Subsequently, leopard took over the entire tiger habitat, which was the best habitat available in Sariska and became the top predator (Sankar et al., 2009). The re-introduction of tigers from Ranathambore Tiger Reserve (RTR) to Sariska TR was envisaged by translocating initial population of five tigers (two males and three females) during 2008 to 2010 (Sankar et al., 2010). Accordingly, two tigers (male and female) in 2008, a tigress in 2009 and two tigers (male and female) in 2010 were reintroduced in Sariska. It was imperative to study the responses of resident leopards to re-introduced tigers in the study area. In Sariska, studies on prey selection of leopard and re-introduced tigers showed that both the carnivores preferred wild prey species such as sambar (Rusa unicolor) and chital (Axis axis) in similar manner (Mondal et al., 2011; Sankar et al., 2010) and size and sex classes of prey species consumed by leopard and tiger were not investigated. Based on photo-capture rate through camera traps and pugmark evidences of leopard before and after tiger re-introduction, it was assumed that there might be some change in site utilization and activity pattern of leopard, which are accounted for in the present study.

Theory and empirical data suggested that behavioral factors may play a role in tiger-leopard co-existence in Seidensticker certain circumstances. (1976) and McDougal (1988) observed indications of avoidance of tiger by leopard Chitwan National Park, Nepal. Furthermore, theoretically the size difference between tigers and leopards, their similar feeding habits, and their close taxonomic relatedness are strong indicators of a high risk of intra-guild predation (Donadio and Buskirk, 2006; Palomares and Caro, 1999; Polis et al., 1989). Empirical studies have demonstrated that an inferior competitor may avoid interference competition by inhabiting "competition refuges", areas where encounters with the superior opponent are less frequent (Durant, 1998; Odden et al., 2010; Saleni et al., 2007; Woodroffe Other competitors and Ginsberg, 2005). avoid interference competition by partitioning their activity times (Hayward and Slotow, 2009). Two main types of refuges are reported in the literature; some species avoid conflicts by inhabiting the margins of their competitors'

home ranges, whereas others seek out areas within the ranges of their opponents that are low in resource density, thereby, reducing the probability of inter-specific encounters (Odden et al., 2010; Woodroffe and Ginsberg, 2005). According to Creel et al. (2001), a sound approach of detecting avoidance due to interference competition among carnivores requires objective methods of mapping habitat quality for the competitors and of recording their spatial distributions. In the present study, the noninvasive method of camera trapping technique under a mark-recapture framework was used for: (a) estimation of population of leopard before and after tiger reintroduction, (b) site utilization of leopard and tiger in the study area and (c) temporal activity pattern of leopard and tiger.

MATERIALS AND METHODS

Study area

The study area is the Sariska Tiger Reserve (Sariska), 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 in the semi-arid part of Rajasthan (Rodgers and 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 to 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 and Seth, 1968). Apart from leopard and tiger, other carnivores present are striped hyena (Hyaena hyaena), jackal (Canis aureus), jungle cat (Felis chaus), common mongoose (Herpestes edwardsi), small Indian mongoose (Herpestes auropunctatus), ruddy mongoose (Herpestes smithi), palm civet (Paradoxurus hermaphroditus), small Indian civet (Viverricula indica) and honey badger (Mellivora capensis). In 2009, desert cat (Felis silvestris) was reported from Sariska (Gupta et al., 2009). Prey species of leopards and tigers in the area include chital (A. axis), sambar (R. unicolor), nilgai (Boselaphus tragocamelus), common langur (Seminopithecus 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 still 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).

Estimation of population of leopard before and after tiger reintroduction

To estimate the population of leopard, camera trapping was used under a mark-recapture framework (Karanth, 1995). A



Figure 1. Geographic location of Sariska Tiger Reserve and location of camera traps in the intensive study area.

comprehensive overview of camera trapping tigers and leopards for the purpose of estimating abundance is given by Karanth (1995) and Karanth and Nichols (1998). Camera trapping was done in the study area from December, 2007 to June, 2008, from January to June, 2009 and from January to May, 2010. A preliminary survey was carried out during November to December 2007 in the intensive study area of 160 km² in the National Park by surveying available trails. Indirect signs such as spoor and scats of leopard were identified and marked using a handheld Global Positioning System. The entire study area was divided into two 80 km² blocks and each block was subdivided into 20 grids of 2×2 km². A pair of cameras was placed in each 2×2 km² grid (Figure 1). Camera traps were placed on the basis of leopard evidence (spoor, scats) on the trails. Forty units of analog and digital cameras were used which worked on passive infrared motion/ heat sensors. The camera traps were equipped with 35 mm lens and date and time of each photograph were recorded. The camera delay was kept at minimum (15 s) and sensor sensitivity was set high. A total of 40 locations were selected for the placement of camera traps in the study area. Camera traps were operated for 117 consecutive nights in 2008, 130 in 2009 and 85 in 2010. The main concern was to cover the area fairly completely, in the sense that it would be difficult for a tiger or leopard in the sampled area to travel about and not encounter at least one camera trap (Karanth and Nichols, 2002). Every two nights were considered as a single occasion, resulting in 59 occasions and effort of 4680 trap nights in 2008, 65 occasions and effort of 5200 trap nights in 2009 and 43 occasions and 3400 trap nights in 2010. Individual leopard obtained from



Figure 2. Number of individual leopard photographed and number of leopard photographs with increasing number of sampling occasions in Sariska Tiger Reserve to evaluate sampling adequacy in 2008.

camera trap photographs were identified by a combination of distinguishing characters, such as position and shape of rosettes on flanks, limbs and forequarters (Schaller, 1967; Karanth, 1995). Any photograph with a distorted perspective or which lacked clarity, were discarded (n = 3). Every leopard captured was given a unique identification code like L1, L2, and L3 etc.

Occasion wise capture history of each individual was generated in an X matrix format (Otis et al., 1978) for the analysis of population estimation. Population closure test was performed using software CAPTURE (Otis et al., 1978; Rexstad and Burnham, 1991). The density of leopard was calculated by four different methods such as full MMDM, half MMDM, spatially explicit Inverse Prediction density (IP dens) and spatial maximum likelihood density (ML dens) using program DENSITY 4.1 (Efford et al., 2004) and SPACECAP (Singh et al., 2010).

Spatial distribution of leopard and tiger

Spatial distribution of leopard and tiger were studied through photographic evidences obtained from camera trapping study and later used in a Geographical Information System (GIS) domain to understand site-utilization of both the species. The number of photographs per 100 trap nights was calculated in each camera trapping grid $(2 \times 2 \text{ km}^2)$ for both species. This data was then projected in GIS along with the Sariska map to get a visual interpretation of site utilization of leopard and tiger in the study area. One binary matrix of camera trap locations against photocaptures was prepared for tiger and leopard (before and after tiger release) from camera trap data. This matrix was then analyzed for presence/absence site utilization in program PRESENCE 4.0 (Hines, 2006) following single session two species model. The detection probabilities of leopard and tiger in the study area in the presence or absence of either species were analyzed using the program PRESENCE 4.0 (Hines, 2006).

Temporal activity pattern of leopard and tiger

Temporal activity pattern of leopard and tiger was studied thorough the photographic time evidence obtained from camera traps. In total the camera traps yielded 81 and 64 leopard photographs before and after tiger release respectively along with 27 tiger photographs. These photographs were further pooled (Hayward and Hayward, 2007) into following categories for leopard and tiger: 9:01-12:00 hrs, 12:01 to 15:00 h, 15:01 to 18:00 h, 18:01 to 21:00 h, 21:01 to 0:00 h, 0:01 to 3:00 h, 3:01 to 6:00 h and 6:01 to 9:00 h. Peak activity period (95% CI) and peak activity time were analyzed in program ORIANA (Andersen et al., 2000).

RESULTS

Estimation of population of leopard before and after tiger re-introduction

The camera trapping study resulted in a total of 81 photographs of 17 individual leopards in 2008, 64 photographs of 14 individual leopards in 2009 and 31 photographs of 8 individual leopards in 2010, based on the number of individuals identified from the rosette pattern. Effective trapping area (ETA) and density (D) was calculated by different methods using program DENSITY 4.1 (Efford et al., 2004). The 40 trapping locations covered a minimum convex polygon area of 118 km² and an effective trapping area (ETA) of 223.8, 223.1 and 250.3 km² with a buffer of half mean maximum distance moved model (1/2 MMDM) in 2008, 2009 and 2010 respectively.

The number of individual leopard was found to stabilize after the 37^{th} occasion (74 days) of camera trapping in 2008, hence, it was inferred that a minimum of 80 days camera trapping is necessary to capture the entire leopard population in the study area (Figure 2). As population estimation was done separately between years, it was found to be geographically and demographically closed for the sample period in 2008 (P = 0.06), 2009 (P = 0.07) and 2010 (P = 0.08). The overall model selection test based on discriminant functions using the model selection algorithm of program

Estimates -	Pre-release of tigers	Post-release of tigers (2009)	
	2008	2009	2010
Population (Mh Jackknife)	17.9 (3.0)	16.3 (3.3)	9.0 (1.5)
Population (Mh Chao)	18.6 (2.2)	18.2 (4.9)	8.0 (0.7)
Population (Mo Null)	17.0 (0.6)	14.0 (0.6)	8.0 (0.3)
Density (MMDM/2)	7.6 (0.6)	6.2 (0.8)	3.1 (0.4)
Density (Max likelihood)	8.0 (2.0)	5.7 (1.5)	3.3 (1.2)
Density (Bayesian)	7.4 (1.3)	5.2 (0.8)	2.3 (0.5)



Figure 3. Spatial distribution of tiger and leopard based on camera trap photo-captures in the study area of Sariska Tiger Reserve.

CAPTURE identified Mh (heterogeneity model) as the most appropriate model in our study. With Mh (jackknife) estimator, the leopard population (N) was estimated at 17.9 ± SE 3.0 in 2008 (before tiger release), 16.3 ± SE 3.3 in 2009 and 9.0 \pm SE 1.5 in 2010 (after tiger release) (Table 1). The estimated population of leopard with other models such as Mh (Chao) and Mo are given in Table 1. For estimation of density of leopard in the study area, half normal detection function fitted the best for both maximum likelihood approach and Bayesian approach. The density of leopard estimated using maximum likelihood approach was 8.0 individual/ 100 km² (SE 2.0) in 2008 (before tiger release), 5.7 individual/ 100 km² (SE 1.5) in 2009 and 3.3 individual/ 100 km² (SE 1.2) in 2010 (after tiger release). The estimated density of leopard following Bayesian approach was 7.4 individual/ 100 km² (SE 1.3) in 2008 (before tiger release), 5.2 individual/ 100 km^2 (SE 0.8) in 2009 and 2.3 individual/ 100 km^2 (SE 0.5) in 2010 (after tiger release). Density of leopard calculated with half MMDM model is given in Table 1. It was observed that the density of leopard (using Bayesian approach) declined significantly (Two samples T-Test; P = 0.0002) from 2008 to 2010.

Spatial distribution of leopard and tiger in the study area

The capture rate of leopard and tiger per 100 trap nights in each grid was calculated and projected on Sariska grid map through color gradient (Figure 3). It was found that the grids with maximum tiger photo-captures were largely

 Table 1. Population and density estimation of leopard before and after tiger release in Sariska Tiger Reserve between 2008 and 2010.



Figure 4. Temporal activity of leopard and tiger in Sariska Tiger Reserve between 2008 and 2010.

 Table 2. Activity period of tiger and leopard (before and after tiger release) in Sariska Tiger Reserve between 2008 and 2010.

Variable	Leopard before tiger release	Leopard after tiger release	Tiger
Mean peak activity	20:57 h	22:35 h	03:02 h
Peak activity period	20:19 – 22:53 h	21:02 – 01:25 h	01:15 – 04:37 h
U ² value	0.869 (P<0.005)	0.342 (P<0.005)	0.520 (P<0.005)

avoided by leopard that selected areas where tiger occurrence is less. Site utilization of both the species was estimated with site-wise capture records. Before release of the tiger in 2008, the probability of site utilization of leopard was 0.75 in the study area. But after tiger release the site utilization of leopard and tiger were 0.55 and 0.53 respectively in the absence of either species, while that of both leopard and tiger together was 0.51. The detection probability of leopard was estimated to be 0.36 in the absence of tiger and it was 0.07 when tiger is present. Detection probability of leopard and tiger together was only 0.008 when both the species were utilizing the same area.

Temporal activity pattern of leopard and tiger

Leopard was found to be most active in the evening between 18:00 to 21:00 h before tiger release and it was

shifted to late evening that is, 21:00 to 0:00 h after tiger release (Figure 4). Tiger showed a bimodal activity pattern with a minor and major peak. The major peak of tiger activity was observed after midnight 0:00 to 3:00 h and the minor peak was between 18:00 to 21:00 h. The leopard activity was found very low after midnight between 0:00 to 3:00 h, when tiger was most active. The mean peak activity time of leopard was 20:57 and 22:35 h before and after tiger release respectively (Watson's U² test: P<0.005), while mean peak activity time of tiger was 03:02 h (Table 2).

DISCUSSION

After the extermination of tigers from Sariska in 2004, leopard occupied the entire Sariska National Park area (present study area), which was previously occupied by tigers. Sankar et al. (2009) also recorded comparatively high density of leopard (10.7/100 km²) in the study area before tiger release. The present study showed that there was a significant (P = 0.0002) decline in leopard population after the reintroduction of tigers in the study area. In regions of high tiger density, tigers are known to out-compete leopards (McDougal, 1988; Schaller, 1967). Radio-tracking studies on tiger and leopard indicate that leopards avoid areas frequented by tigers and occupy the periphery of parks near human settlements (Seidensticker, 1976). In the present study, photo capture rate of leopard and tiger showed that leopard avoided valley habitats which were frequented by tigers. Leopard largely occupied the peripheral hilly areas which are less frequented by tigers in the study area. In two occasions, re-introduced tigers killed two leopards in the study area due to confrontation between 2009 and 2010. A number of studies reported that, one species may occupy areas that do not overlap with the competitor species' home ranges, or they may use different habitats (Fuller and Keith, 1981; Major and Sherburne, 1987; Voigt and Earle, 1983). Red foxes (Vulpes vulpes) have been reported using the periphery of coyote (Canis latrans) home ranges or different habitats from coyotes where they occur sympatrically and coyotes have been recorded as using areas between wolf (Canis lupus) home ranges (Dekker, 1989; Harrison et al., 1989; Sargeant et al., 1987). European genets (Genetta genetta) and Egyptian mongooses (Herpestes ichneumon) avoid suitable habitats where densities of Iberian lynx (Lynx pardinus) are high (Palomares et al., 1996), as do wild dogs and cheetahs (Acinonyx jubatus) where lions are common (Durant, 1998; Mills and Gorman, 1997).

Based on photo capture time, it was found that leopard changed their mean peak activity period from 20.57 h before tiger release to 22:35 h after tiger release. Leopards became more active in the late evening in between two tiger activity peaks, which reflects a temporal segregation between these two sympatric large cats. Temporal segregation is a mechanism that ecologically similar species can use to avoid competition (Kronfeld-Schor and Dayan, 2003; Hayward and Slotow, 2009). Examination of our data suggests that temporal niche segregation may occur between leopard and tiger. One species may adjust its activity patterns to reduce encounters with competitor species (Litvaitis, 1992; Johnson et al., 1996). For example, in Kruger National Park, lions became active mainly at night, wild dogs in early morning, and cheetahs around the middle of the day (Mills and Biggs, 1993). Rudzinski et al. (1982) found that the activity of arctic foxes (Vulpes lagopus) decreased when red foxes were present. Nevertheless, clear temporal segregation has been found rarely in studies of resource partitioning between sympatric and potentially interacting carnivores (Litvaitis and Harrison, 1989; Major and Sherburne, 1987; Saleni et al., 2007).

The present study suggested that there is segregation along the spatial and temporal axis between these two

carnivores. The dietary segregations between leopard and tiger were observed in many study sites (Hayward et al., 2006, 2012), but in the present study area, both leopard and tiger utilized and preferred wild prey species (sambar and chital) in similar manner (Mondal et al., 2011; Sankar et al., 2010). Leopard responded to tiger presence in terms of (a) space (detection probability of leopard is 0.36 when tiger is not present and detection probability of leopard is 0.07 when tiger is present; similarly site utilization of leopard reduced from 0.75 to 0.55 after tiger release) and (b) time (peak activity period is shifted from 20:19 to 22:53 h to 21:02 to 01:25 h). The results reflected that there is inter-specific competition between leopards and re-introduced tigers in Sariska. The reintroduction efforts for carnivores should routinely include assessment of the potential effects of interspecific competition, as Gusset et al. (2008) assessed the effects of re-introduction of wild dogs in South Africa. Inter-specific social dominance can confer the right of first choice in food and space. The tiger, through inter-specific interactions, can reduce the abundance of leopards and in effect substitute ability in utilization of resources (MacArthur, 1972), and thereby secure a wider potential resource base (Schaller, 1967). The leopard, as subordinate, can derive no benefit from inter-specific competition with the tiger. For the leopard to co-exist with the larger cat in many areas of range overlap, it must have the ability to exist within a decreased niche breadth or else shift to areas where the tiger is absent. Selection pressure on the leopard is directed both towards specialization by reducing overlap with the tiger in use of resources and expansion of the fundamental niche in terms of areas and habitats it occupies (Eisenberg and Lokhart, 1972; Schaller, 1972; Seidensticker, 1976). In Kanha Tiger Reserve, leopards were resident only in areas where the tiger was absent. This inter-specific competition can have strong effects on the distribution and abundance of carnivores and should be an important consideration in their conservation. Studies of an ecologically and phylogenetically broad set of carnivore species show that the effects of competition on carnivore populations are sometimes difficult to predict (Creel et al., 2001; Palomares and Caro, 1999). The spatial and temporal factors, which can modify the effect of competition among carnivores, sometimes in ways are counter-intuitive under classical competition theory (Creel et al., 2001). At present, there are only five re-introduced tigers in Sariska TR. With the increase of number of reintroduced tigers, it is expected to get a clear picture of co-existence of tiger and leopard in Sariska TR.

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