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Indian Leopard *Panthera pardus fusca*: A Comprehensive Review of Current Ecological Knowledge and Research Efforts Across Its Range

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ABSTRACT

Leopards are most widespread member of family Felidae and have nine subspecies across the world. We reviewed the literature on the Indian leopards to summarize the extent of research efforts and current ecological understanding. We reviewed 105 studies published from 1960 to 2018 in 55 journals, and summarized the knowledge on evolution and taxonomy, status and distribution, abundance and density, feeding habits, spatial ecology, activity pattern, human-leopard conflict, interspecific interactions and habitat. Most of the studies were from protected areas as compared to non-protected areas while only three studies were conducted in ex-situ conditions. Human-wildlife conflict along with feeding habits were the most studied aspects while spatial and temporal ecology and behavior were the least studied aspects. Already lost 70% of its historical range, Indian leopards presently have patchy distribution. High densities of leopards were visible in prey rich areas. Leopard's diet was dominated by wild ungulates in PA's while in human dominated landscape, dogs and livestock were dominant. Indian leopards have smaller home ranges as compared to the African relatives. Leopards show activity peaks during down and dusk time of the day. Cover was an important factor affecting the presence of leopards. Leopards coexist with other large predator by fine adjustment in use of space time and food. Human-leopard conflict was one of the most studied aspect. Studies shows site dependency of conflict. Most severe conflict was livestock depredation. Important factor affecting conflict were occupation of humans, husbandry practices, change in land use pattern and successful conservation in some areas. Present policies to manage conflict seem insufficient. Feeding and behavioral plasticity makes leopards successful survival of human dominated landscapes. Apart from conflict and dietary studies, there is a lack of studies on ecological aspects such as population size, spatial ecology, interspecific interactions, habitat and behavior. These studies are needed to improve our understanding of their ecology for effective conservation. There is also an urgent need to look into the policies regarding management of human-wildlife conflict.

Key Words: Leopard; Density; Feeing Habit; Human-leopard Conflict; Mitigation Measures; India.

INTRODUCTION

Explosion in human population has drastically affect the status of wildlife conservation through different activities like habitat destruction, fragmentation and illegal killing of wildlife. Impact of these activities are disproportionate i.e. higher on some species or group of species as compared to other which make these species important concern for conservation (Cardillo et al. 2005). Large felids are one such group which is highly threatened and has faced a decline in range due to habitat destruction and fragmentation, prey decline, human-big cats conflict and illegal killing (Nowell and Jackson 1996). Because of situated at higher trophic level, being charismatic, embedded in culture and have high economic values, large carnivores are always subject to research across their range. But this work seems to be biased in terms of some particular species (Ghosal et al. 2013) or biased towards some ecological aspect (Balme et al. 2014). This disproportionality creates gaps in scientific understanding of some species which further affects the decision making on conservation issues. For example, much of scientific research on leopards has been biased towards the two subspecies i.e. African leopards (*Panthera pardus pardus*) and Indian leopards (*Panthera pardus fusca*) while other critical endangered species such as Amur leopard (*Panthera pardus orientalis*) and Persian leopard (*Panthera pardus saxicolor*) have received very little attention (Jacobson et al. 2016).

Leopard is one of the most widespread member of large felids group. Being generalist in resource requirement and high behavioral adaptability make this species able to survive from optimal to sub-optimal conditions. Taxonomically subdivided into nine sub-species (Miththapala et al. 1996), Indian leopard, one of the subspecies of leopards, has its distribution restricted to Indian sub-continent only and is one of the major co-predators along with the tiger and Asiatic lion. This subspecies has already lost more than half of its historical range and also is in severe conflict with humans (Jacobson et al. 2016). Jacobson et al. (2016) while conducting a review on status and distribution of leopards found that Indian leopard is one of the most studied subspecies after the African leopard. The studies on African leopards were reviewed by Balme et al. (2014) and the status and distribution of leopards collectively were reviewed by Jacobson et al. (2016). However, the ecology of Indian leopard has never been reviewed except a comparative assessment of studies on large felids in India by Ghosal et al. (2013). Here, we review the scientific studies on leopards conducted from 1960 to 2018. We are particularly interested in the amount of research effort that has been put into different ecological aspects and an assessment of the current state of ecological knowledge of Indian leopards.

METHODS

In order to quantify the research effort our data were earlier published studies. We searched Google Scholar using the keywords such as leopards, Indian leopards, and large carnivores from 1960 to 2018. We searched first five pages of the Google Scholar in each year from 1960 to 2018 included in peer-reviewed journals only. We further classified studies on different aspects of ecology such as evolution and taxonomy, status and distribution, abundance and density, feeding habits, spatial ecology, activity pattern, human-leopard conflict, interaction and coexistence with other large carnivores and habitat.

RESULTS

We found 106 studies related to the leopard in Indian subcontinent from 1960 to March 2018. Studies show substantial increase during these years but peaked especially from 2006 onwards. When segregated in relation to countries maximum studies were from India followed by Nepal, Bhutan and Pakistan. Further, maximum studies were conducted on human-leopard conflict (29.25 %) followed by feeding habits, status and distribution, abundance and density, genetics, inter-specific interactions, spatial ecology, activity pattern, behavior, habitat and only one study was conducted on prey predator relationship and there is only one review available (Figure 1). We classified one study as other published on semen characteristic of leopard. These studies were published in 55 different journals. Most of the studies were conducted inside the PA (53%) while less studies were conducted in human dominated areas (23%). Only three studies were conducted in ex-situ conditions. Nearly equal number of studies were conducted on multispecies assemblage (52%) in comparison with exclusive studies on leopard (48%).

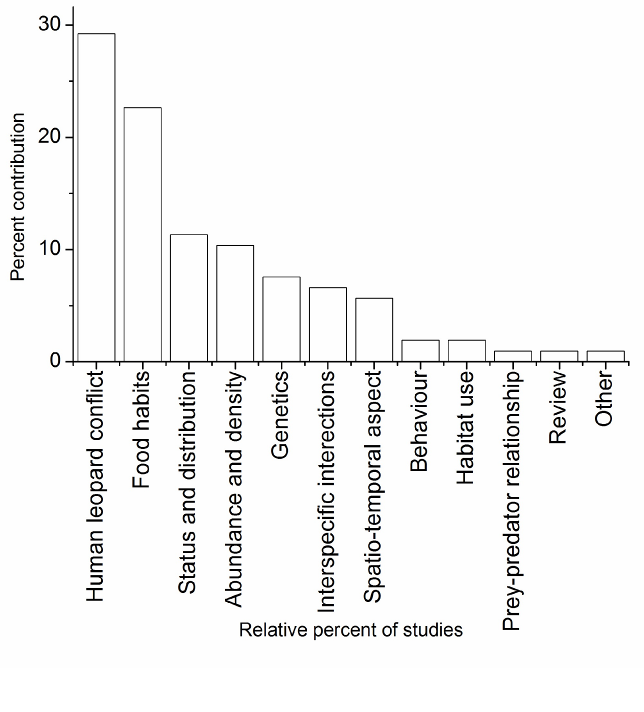

Figure 1. Distribution of various aspects of leopard ecology studied during 1960 to 2018

Evolution and Taxonomy

Leopards belong to the family Felidae and have monophyletic evolution and diverged from the common ancestor around 2-3 million years ago (Ma) (O'brien and Johnson 2007). Modern leopard originated about 0.471 ± 0.102 Ma and Asian leopard around 0.169 ± 0.049 (Uphyrkina et al. 2001). Earlier thought to be 27 sub species of leopards around the world and four in Indian subcontinent, using genetic analysis Miththapala et al. (1996) were able able to identify nine subspecies of leopards among which one is African (*P.p. pardus*) and eight are Asian subspecies (*P.p fusca* in India; *P.p. orientalis* in Russian far east; *P.p. nimr* in Arabian Peninsula; *P.p. japonensis* in North China; *P.p. kotiya* in Sri Lanka; *P.p. delacouri* in South China; *P.p. melas* in Java; *P.p saxicolor* in Central Asia). Uphyrkina et al. (2001) also assess the genetic diversity in the leopards and found that Indian leopard possessed intermediate diversity (0.69) as compared to African leopard (0.80) and higher diversity than in Sri Lankan (0.48) and Amur leopard (0.35).

Status and Distribution

Leopards in Indian subcontinent are distributed broadly ranging from high altitude mountains of Kashmir and Bhutan (Wang and Macdonald 2009a, Noor et al. 2017) to evergreen forest of India (Ramesh et al. 2012c). We found eight studies which particularly assessed the status and distribution of leopards in multispecies assemblages using sign surveys and direct sightings (Gaston et al. 1983, Waite et al. 2007, Bali et al. 2007, Kumara et al. 2012) or using relative abundance index from camera trapping (Datta et al. 2008, Ramesh et al. 2012c, Navya et al. 2014, Palei et al. 2015). Our literature review found the confirmed presence of leopards in forty-eight protected areas of the Indian subcontinent out of which forty are in India, four are in Nepal, two in Bhutan and two in Pakistan. We also found presence of leopards in eight places outside protected area in India. Possibly, the present distribution is quite underestimated since our literature included only peer-reviewed journals and left out the grey literature. But present results are conservative regarding the distribution of leopards. Jacobson et al. (2016) generated a map of leopard's distribution across its range. They found that Indian leopard has already lost 70-72% of its historical range with extant range of 1,066,600 km^2. Persisting in forty-nine patches of forest, Indian leopard has only 11% of the present range as protected. Later study also indicates fragmented range of Indian leopard with continued forest range presently occurring in Terai arc landscape and Western Ghats landscape only. Only national level study of the range of Indian leopard to assess the distribution of multiple species was by Karanth et al. (2009) who found that leopard was one of the widely distributed carnivore across India with natïve occupancy 0.52. Johnsing and Negi (2003) assessed the status of leopards in the landscape of Corbett and Rajaji Tiger Reserve using sign surveys and Athreya et al. (2015) in Karnataka using the secondary information from news articles while assessing the status of human-leopard conflict found that leopards were widely distributed in both the landscape. Much of the information regarding the status and distribution of leopards is from protected areas and only few studies were there from outside the protected areas (Bali et al. 2007, Navya et al. 2014).

Abundance and Density

We found 11 studies where densities and abundance of the leopards were estimated at different areas (Harihar et al. 2009, Wang and Macdonald 2009a, Kalle et al. 2011, Mondal et al. 2012b, Borah et al. 2013, Athreya et al. 2013, Goswami and Ganesh 2014, Selvan et al. 2014, Thapa et al. 2014, Jhala et al. 2014, Goldberg et al. 2015). Most of these studies used camera trapping as a tool under mark-recapture framework. We compared the study using only ½ MMDM approach rather than recent SCCR approach because former approach provides more studies to comparison. Densities of leopards in the Indian subcontinent range from 1.04 leopards $(100\ km)^{-2}$ (Wang and Macdonald 2009a) to 14.99 ± 6.9 leopards $(100\ km)^{-2}$ in Rajaji Tiger Reserve (Harihar et al. 2009). We found only single effort in human dominated landscape to assess the densities of leopards by Athreya et al. (2013) where leopard density was 6.4 ± 0.78 leopard 100 km^2. A single study from Sariska Tiger Reserve, India by Mondal et al. (2012b) also provides long term data set answering the questions pertaining to the survivorship of leopard. Many of the studies on abundance and density have been conducted in multi-species assemblages, especially tiger and dhole. Since densities of large carnivores are affected by prey base (Karanth et al. 2004, Periquet et al. 2015), leopard densities were higher in areas where prey base was high; e.g., Rajaji Tiger Reserve has wild ungulates prey density of about 72.6 individuals km^{-2} as compared to Pakke Tiger Reserve (17.9 individuals km^{-2} ; Table 1).

Table 1. Densities of leopards in Indian subcontinent.

S.N.	Site	Density/100km^2 ±SE	Method	Reference
1.	Bori Wildlife Sanctuary, India	8.0±2.5	1/2 MMDM	Edgaonkar 2008
2.	Sariska Tiger Reserve, India	7.0±0.2	1/2 MMDM	Sankar et al. 2008
3.	Rajaji Tiger Reserve, India	14.99 ± 6.9	1/2 MMDM	Harihar et al. 2009
4.	Jigme Singye Wangchuck National Park, Bhutan	1.04	1/2 MMDM	Wang and Macdonald 2009
5.	Mudumalai Tiger Reserve, India	28.91±7.22	1/2 MMDM	Kalle et al. 2011
		13.17±3.15	SECR	
6.	Sariska tiger reserve, India	6.0±0.5	1/2 MMDM	Mondal et al. 2011
		7.1±2.0	SECR	
7.	Manas National Park, India	11.30±2.90	1/2 MMDM	Borah et al. 2013
		3.40±0.82	SECR	
8.	Akole tehsil, Maharashtra, India	6.4±0.78	1/2 MMDM	Athreya et al. 2013
9.	Manas National Park, India	1.86	RAI based	Goswami and Ganesh 2014
10.	Pakke Tiger Reserve, India	2.99 ± 1.13	1/2 MMDM	Selvan et al. 2014
		2.82 ± 1.2	SECR	
11.	Parsa Wildlife Reserve, Nepal	5.61±1.30	1/2 MMDM	Thapa et al. 2014
		3.78±0.85	SECR	
12.	Dachigam National Park, J&K, India	2.11±1.06	1/2 MMDM	Habib et al. 2014
13.	Mukundra Hills Tiger Reserve, India	11.22±3.14	SECR	Jhala et al. 2015
14.	Kuno Wildlife Sanctuary, India	9.12±1.92	SECR	Jhala et al. 2015
15.	Phen Wildlife Sanctuary, India	8.49±1.91	SECR	Jhala et al. 2015
16.	Umred Karhandla Wildlife Sanctuary, India	6.32±1.79	SECR	Jhala et al. 2015
17.	Kawal Tiger Reserve, India	2.23±0.84	SECR	Jhala et al. 2015
18.	Gir Protected Area, India	17.89	Scat surveys	Zehra et al. 2016

Only one study was conducted on methodological issue regarding estimation of leopard abundance in Bhutan by Goldberg et al. (2015). Later study addressed the issue of spatial and temporal scales in camera trapping. Using various temporal scales in sampling intervals they found that minimum time interval should be used while framing the sampling occasion assessing the leopard abundance through camera trapping. They evaluate abundance estimation with models including two different covariates i.e. distance and sex and found that when includes sex as a covariate estimates of abundance increased substantially as compared to the distance model in SECR framework.

Feeding Habits

Feeding habits is one of the most addressed ecological work pertaining to leopards after conflict might due to involvement of less logistics and cost. We found 23 studies pertaining to the food habits of Indian leopards (Seidensticker 1976, Johnsingh 1992, Mukherjee et al. 1994, Karanth and Sunquist 1995, Ramakrishnan et al. 1999, Sankar and Johnsingh 2002, Edgaonkar and Chellam 2002, Andheria et al. 2007, Ahmed and Khan 2008, Edgaonkar 2008, Odden and Wegge 2009, Achyut and Kreigenhofer 2009, Mondal et al. 2011, Ramesh et al. 2012a, Kumaraguru et al. 2012, Koirala et al. 2012, Selvon et al. 2013, Shehzad et al. 2015, Sidhu et al. 2015, Athreya et al. 2016, Kshettry et al. 2018, Zehra et al. 2017). Since leopards are shy and hard to monitor in the field, most of the studies have used scats as a measure of feeding habits. Hayward et al. (2007) found that leopards preyed upon more than hundred prey species across their range. Studies on Indian leopards follow the same pattern where leopard's diet ranges up to twenty-one prey species (Ramesh et al. 2012a). These number might be more but most of the studies have categorized small mammals and birds under one group which results in an underestimation of prey species. Wild ungulates were most frequently consumed prey, among them chital and sambar were dominated in most of the dietary studies (Johnsingh 1992, Karanth and Sunquist 1995, Ramakrishnan et al. 1999, Sankar and Johnsingh 2002, Andheria et al. 2007, Ahmed and Khan 2008, Odden and Wegge 2009, Mondal et al. 2011, Ramesh et al. 2012a, 2012b, Selvon et al. 2013, Zehra et al. 2017). While in Human dominated landscape domestic dogs, cattle and domestic goats contributed maximum in the diet of leopards (Athreya et al. 2016, Shehzad et al. 2014, Kshettry et al. 2018). Optimal foraging theory predicts that most profitable prey is the one which can be killed without getting injured also called as model prey. Hayward et al. (2007) found that leopards preferred prey between the weight range 10-40 kg. Prey species within this range required less handling time and subsequently low chance of getting injured which makes prey of this weight range as model prey. Further, prey availability, cover, prey defense, presence of competitor and group size of prey seem to be major factors which can affect the predation process (Gittleman 1989). Leopard in the Indian subcontinent feeds on numerically abundant prey species of appropriate weight range. High prey densities result in lesser searching time and also increase in encounter rate of prey which might result in killing of numerically abundant prey of appro-priate size since issue of handling cannot be ruled over. For example, in Gir, Gujarat and Chitwan, Nepal where prey densities are really higher (>50 chital km^{-2}), leopards dominantly feed on the chital. Apart from being numerically abundant and having optimal weight for handling, chital preference for flatter areas (Khan et al. 1996) puts less energetic constraint on leopards predating chital rather killing a species in undulating or hilly terrain. In a nutshell, Indian leopards become energy maximizer while when prey density of optimal range prey goes down leopards become number maximizer and increase their dietary breath (Rama-krishnan et al. 1999).

Leopards can kill prey larger than their size which is very much visible by dominance of sambar in the diet of leopard but it is quite possible that leopards might kill young one of sambar which come under their model prey weight range. Further sambar lives in small group which also makes them vulnerable to predation by leopards. Presence of smaller mammals in the diet of leopards indicate the opportunistic behavior of leopards and also strategy to receive rewards at each encounter of prey.

Every field method has its advantages and disadvantages. Scat analysis being less expensive is highly used but it does not provide information on the process of food eaten, either predated or scavenged or snatched. Also it does not provide fine information regarding the age and sex of individuals killed. Few studies have used kill monitoring to study the diet of leopards (Seidensticker 1976, Johnsingh 1992, Karanth and Sunquist 1995, Odden and Wegge 2009, Kumaraguru et al. 2012). Seidensticker (1976) in Chitwan found that leopards predate majorly on chital while many of the kills range between 25 and 50 kg. Karanth and Sunquist (1995) in Nagarhole found that leopard kills relatively younger chital as compared to adult individuals possibly because the young might be inexperienced to avoid the predators. Odden and Wegge (2009) through radio tracking of three individuals found that adult chital male was dominant in the diet of leopards. Later study also found that leopard's daily food intake was 4.7±0.3 per capita.

In human dominated landscapes leopards feed dominantly on dogs (Athreya et al. 2016), goats and smaller livestock (Miller et al. 2016a). Both dogs and goat and young livestock are smaller prey which are numerically abundant as well which lacks anti-predator strategies and hence easy prey. Also in human dominated landscape prey should be dragged to safer refuges and consumed quickly to avoid human disturbance. Smaller prey such as dog and goats in human dominated landscapes provide this opportunity of less handling time.

Spatial Ecology

Spatial ecology is one of the least addressed subject in the case of Indian leopard. We found only four studies where information regarding the spatial ecology of leopard is available (Sunquist 1983, Odden and Wegge 2005, Mondal et al. 2013a, Odden et al. 2014). Indian leopard's home ranges were consistently smaller ranging from 8 km^2 to 62 km^2 (Mondal et al. 2013a, Odden et al. 2014,) and much small as compared to the African studies (Reviewed in Marker and Dickman 2005). Home ranges in case of large carnivores are found to be inversely related to prey availability (Marker and Dickman 2005). Present Indian studies follow the pattern where resource rich areas such as in Chitwan have smaller home ranges (reviewed in Odden and Wegge 2005) compared to other protected areas such as Sariska in India where prey availability was not as high as Chitwan. Difference between home ranges of male and female is reflected in some studies (reviewed in Odden and Wegge 2005; but see Marker and Dickman 2005). Intersexual overlap in home ranges were evident in studies of Indian leopard where male showed more overlap with female home ranges as compared to overlap with the same sex (Odden and Wegge 2005). Interestingly, only study conducted in human dominated landscape in India by Odden et al. (2014) found much smaller home ranges of leopards (8.35 km^2) compared to the protected areas. High resources availability in terms of anthropogenic food resources and year round availability of some crucial resources such as water might be responsible for such smaller ranges (Odden et al. 2014, Salek et al. 2015). Since carnivores are territorial, therefore densities of conspecific may affect the home rang size in carnivores. Salek et al. (2015) conducted a review and found that carnivores' home ranges were negatively correlated to their densities. But presently there is no such study on Indian leopard. Fattebert et al. (2015) found no decline in home ranges of males as compared to females. Later study found evidence for dispersal regulated strategy, that female leopards decrease their home range size in response to increased density while males maintain large home ranges. These results suggested a more complex pattern in spatial organization of large carnivores.

Dispersal ecology is important in order to understand the population dynamics and to understand the social interaction among large carnivores. In case of Indian leopard, only one study is available conducted by Sunquist (1983) in Chitwan, Nepal. A later study on the basis of three radio-collared leopards found that dispersal starts at an age between 15 to 18 months. Leopards in Chitwan reach independency around an age of 13-18 months. But no study has been conducted how male and female leopards disperse and what factors affect this process. Much robust studies have been carried out with large sample size on African leopards to address the dispersal ecology. Fattebert et al. (2015) on the basis of 35 individual leopards found that dispersal starts at and age of 13.6±0.4 months. Male individuals dispersed at a farther distance as compared to females (11.0±2.5) while female's dispersal distances were low and showed philopatry. Among all the collared individuals sex biased dispersal was reported, all males dispersed while all females settled near the mother home ranges. Dispersal distance in case in the later study was in response to mate competition while in case of females it was inversely density dependent.

In nutshell, leopard's spatial ecological studies in Indian continent are based on small sample size which put constraints to draw a general conclusion and provide fine level understanding. We appreciate that there are some studies which are able to generate at least base line data regarding the spatial ecology of Indian leopard.

Activity Pattern

After spatial ecology, activity pattern was one of the least studied subject in case of Indian leopard. Few studies have been conducted on the activity pattern of leopards in Indian subcontinent. Most of the studies of activity pattern were carried out in order to examine the interspecific interactions or to study the spatial ecology (Odden and Wegge 2005, Ramesh et al. 2012b, Odden et al. 2014, Carter et al. 2015, Karanth et al. 2017, Noor et al. 2018). Camera trapping and radio collaring were the methods used in these studies. Studies within protected areas show plasticity in the activity patterns of leopards. Leopard's activity ranges from diurnal to nocturnal but major peaks were in during early morning hours or late evening hours (Karanth and Sunquist 2000, Odden and Wegge 2005, Ramesh et al. 2012, Carter et al. 2015, Noor et al. 2018). While studies carried out in the human dominated landscape found that leopards were dominantly nocturnal (Odden and Wegge 2014, Carter et al. 2015). Theory of activity patterns revolves around bottom up or top down theory (Hayward and Slotow 2009). Bottom up process predicts that predator will follow the prey while top down theory predicts that predator will avoid the activity of the larger competitor. But human disturbance seems to be another major factor that could affect the activity pattern of leopards and is largely reflected in human dominated landscape (Carter et al. 2015). Daytime temperature is another important abiotic factor which affects the activity pattern of leopards. Most of the above stated studies show a decline in activity peak of leopards during mid-day time when temperature is highest. But impact of this factor has not been quantified yet.

We found a single study on the activity budget of the leopard in Zoological Park (Mallapur and Chellam 2002). Despite large use of camera trapping in ecology in the Indian subcontinent, only few studies quantified the activity pattern of leopards. Camera traps are effective means to study the pattern such as activity of space use in low density areas also but radio telemetry can provide a comparatively finer level information in relation to age and sex which is presently lacking in case of Indian leopard.

Human-Leopard Conflict

Leopard is one of the felids which is severely involved in conflict with humans (Inskipp and Zimmerman 2009). Due to behavioral and dietary flexibility leopards can persist in human dominated landscape at fairly high densities (Athreya et al. 2013). We found 30 studies which were related to leopard-human conflict and talk about patterns of human-leopard conflict, factors affecting the conflict and kill sites and spatial risk modelling by leopards and also on human perceptions towards leopards (Sekhar 1998, Pati et al. 2002, Vijayan and Pati 2002, Athreya 2006, Athreya et al. 2007, Tamang and Baral 2008, Chhangani et al. 2008, Dar et al. 2009, Nabi et al. 2009, Marker and Sivamani 2009, Kalaivanan et al. 2011, Karanth et al. 2012, Bhattacharjee and Parthasarathy 2013, Karanth et al. 2013a, 2013b, Shingote and Schuett 2013, Bhatia et al. 2013, Dhanwatey et al. 2013, Kala and Kothari 2013, Ghosal and Kjosavik 2015, Kabir et al. 2014, Kumar et al. 2015, Malviya and Ramesh 2015, Athreya et al. 2015, Pandey et al. 2016, Miller et al. 2016a, 2016b, Acharya et al. 2016, Garcia et al. 2016, Sidhu et al. 2017). Among later cited studies 55% were carried out in the multispecies assemblage while 45% were carried out exclusively on Indian leopard. Most of the studies used secondary data to assess the pattern of human leopard conflict (41.37%), followed by interviews of people (20.68%), interview and field work (10.34%), secondary data and field observation studies where data were procured from forest department (13.79%) used for characterizing kill sites and secondary data and interview (13.79%). Very few studies have been conducted on regional or country scale (Athreya et al. 2015, Acharya et al. 2016) in comparison to site specific studies. Leopard in later stated studies emerges as major livestock depredator and source of human injuries. Magnitude of the conflict vary in between site ranging from high conflict sites such as Binsar (Kala and Kothari 2013) where leopards were responsible for killing around 7-14 livestock per month to studies where low depredation has taken place (Sidhu et al. 2017). Most of the studies found that leopards predate upon livestock of medium weight such as cattle calves, goat, sheep and dogs. Preference for this weight range of leopards is also very much reflected in diet in natural areas. Not only scale of conflict but the timings of conflict also vary in between the sites. Some studies reported that livestock depredation occurs during night time dominantly (Kabir et al. 2014) while other studies reported mid-day and night (Malviya and Ramesh 2015) and afternoon and evening (Miller et al. 2016a) as major peak times of depredation. Distance from protected area and grazing inside the protected area reflected as major factors affecting the livestock depredation. Majority of studies stated livestock depredation increased during the drier months of the year. Crunch of resources during the lean season may push leopards towards the search of easy prey and other resources such as water. But at some sites, for example, Gir despite year round stable prey base (Zehra 2014), conflict occurs in surrounding areas that indicates involvement of more complex reasons and species ecology has a larger role to determine the cause of livestock depredation by leopards. Also Kshettry et al. (2017) found that leopard habitat use was not associated with human injuries; this strengthens the hypothesis that these interactions are not simple to understand. Site specificity also found in human injuries by leopards. Cause of human injuries seems to follow the kind of work victims are engaged. Karanth et al. (2013b) in their conflict study around three tiger reserve found that major of human injuries from predators were during the time of NTFP collection of grazing which results in frequent encounters of predators and hence conflict. Bhattacharjee and Parthasarathy (2013) in tea gardens of Jalpaiguri district of west Bengal found that peak time of human attacks by leopards was in January when males are engaged in tea pruning. Site specific factors affecting the livestock depredation was assessed by Miller et al. (2016a) in Kanha Tiger Reserve. Later studies found that leopards kill risk probability increased with increase in scrubland and open forest to moderately dense forest in comparison to tiger which needs dense forest to kill livestock. Further, livestock depredation also depends very much on the husbandry practices. Open grazing of cattle inside the protected areas results in more frequent encounters, hence greater predation of livestock than in case of stall feeding where livestock are guarded in the physical structure. Stall feeding is a costly strategy since it needs few cattle of better breed as compare to open grazing where numerically more livestock can be supported. In nutshell livestock depredation by leopards in the Indian subcontinent seems to be a complex issue where site specificity and other ecological conditions affect the level of depredation.

Leopards are one of the successful felid which can thrive in human dominated landscapes. Not much attention has been given in order to understand how leopards adapt and thrive in human dominated landscape and subsequently give rise to conflict except a single study carried out by Athreya (2012) in Maharashtra. Loss of habitat, prey along with improved conservation scenario are among most important factor describes the persistence of large carnivores in human dominated landscapes and hence conflict. Prey depletion and habitat fragmentation have forced large carnivores to use these attractive traps to fulfill their energetics requirements (Blecha et al. 2018). Further, strict law and high political will have given a chance to some of the large carnivore thrive again in some protected areas (Chapron et al. 2014, Meena et al. 2014). These conservation efforts biased largely towards tiger in Indian subcontinent have automatically benefitted leopards. Smaller size of protected area in the range of

Indian leopards not able to sustain high population which results in spillover of leopards in nearby areas which are multiuse human dominated matrix. Food and habitat are of paramount importance for any animal and hence, for large carnivores also. Dietary flexibility of leopards enables them to predate upon range of prey species in human dominated landscape includes domestic as wild prey. Human dominated landscapes provide super abundance of such foods items. Athreya et al. (2016) found that total prey density of leopard's potential prey was around 595 individuals/km^2 in Maharashtra, India. Apart from that human dominated landscapes provide year round stable resources such as water and provide an escape from competitive interactions by other large carnivores. Much of the human dominated landscape also provide refuge to leopards which is largely associated with the change in land use practices especially cropping pattern and agriculture practices around protected areas. Replacement of traditional crops by cash crops, especially sugarcane and mango orchards, has resulted in artificial forest type habitat for leopards in human dominated landscapes. Leopard is an ambush predator relying heavily upon cover. Sugarcane especially provides a dense cover to leopards along with low temperature during the daytime due to frequent irrigation; hence sugarcane results in attractive habitat for leopards. Studies have indicated that leopards also use these sugarcane fields as breeding habitat (Bhattacharjee and Parthasarathy 2013) which is indication of resident population of leopards in human dominated landscapes. Vijayan and Pati (2002) study around Gir found that replacement of traditional crops such as groundnut and wheat which cannot provide optimal cover for leopards frequently replaced by sugarcane and mango orchards due to involvement of less cost and protection and more monitory gain. These crops give suitable space for leopards and lions which results in human-leopard conflict. The agriculture practices are also an important determinant of conflict, especially for human injuries and killings. Hand cutting of dense crops such as sugarcane put the laborers in direct conflict with leopards. Zehra (2014) found that laborers used in crop harvesting on the periphery of Gir protected area come in direct conflict with leopards while cutting the fields where leopard take refuges. Also these laborers used to live near the crop field in shelters which lack doors. These conditions make them vulnerable to the leopards. There are several instances in Gir where leopards have killed these workers in the night time. Sometimes victims were dragged even from homes where doors were not present. Further, behavioral adaptability of leopards to avoid humans and maintaining small home ranges (Odden et al. 2014) also increase the chance of their persistence in human dominated landscape. Later study found that leopards avoid daytime activity of humans and remains active during the nighttime.

Conflict management in Indian subcontinent is majorly on the reactive basis which involved rescue of the animal and translocation to other sites on stress call and compensation schemes in case of livestock depredation or human injury and death. Translocation as strategy to reduce conflict has resulted in near complete failure in case of leopards. Zehra (2014) in Gir protected area found that some leopards were recaptured five times from the same location by forest department. Sometimes forest department itself not confident regarding the problematic individual identity. Translocation has not only been impractical to resolve the conflict but sometimes has resulted also in an increase in the level of conflict due to stress and new conditions at the site of translocation (Athreya et al. 2011). Once an established individual is removed from the site, some other disperser acquired that site which is new to the area and lack of experience in such individuals results in more conflict at such sites. Further, this translocation sometime results in conflict at the new site. This strategy seems only to shift the problem from one place to another. Compensation schemes are effective in maintaining the tolerance of the victims. Compensation is, however, long-time-taking procedure and there is difference in compensation paid and actual cost of livestock killed which leaves the victim with monetary loss (Karanth et al. 2013a, Sidhu et al. 2017) and might impact the tolerance level.

Interactions and Coexistence with Other Large Carnivores

Interspecific interactions among large carnivores that vary from trophic facilitation to competition can really affect the ecology of subordinate predators which ranges from change in patterns of space, time and food use to decline in population (Creel and Creel 1996, Harihar et al. 2011). We found eight studies which carryout to understand the interspecific interactions among leopards with tiger and dhole (Seidensticker 1976, Odden et al. 2010, Harihar et al. 2011, Ramesh et al. 2012b, Bhattarai and Kindlmann 2012, Lovari et al. 2014, Carter et al. 2015, Karanth et al. 2017). Apart from that few studies which focused on dietary habits have also assessed the overlap in diet with co-predators. Most of the studies used camera traps and scat analysis as a method to study the interactions. Most of the studies were site specific, with only a single study which compared the interaction at four sites in Southern India (Karanth et al. 2017). Studies look at food, diet and space as major axis to study the interactions. Among food habits leopards show extensive dietary overlap with tiger, lion and dholes also. High dietary overlap may be expected since all these predators make their diet from ungulates prey. Dietary overlap between tiger and leopards was higher in areas where there is less diversity in size of prey class especially larger prey (Wang and Macdonald 2009, Mondal et al. 2012a) as compared to area where more diversity in prey size class (Ramesh 2012a, Selvon et al. 2013). Asiatic lion is another large felid which coexists with leopards in Gir but despite its large size and group living behavior do not show much diversity in prey size in the presence of large sized prey as is seen in the case of Gir where both predators feed on most abundant prey chital and hence overlap in diet (Zehra et al. 2017). But this pattern was not visible in overlap among leopard and dhole. Large carnivore predation is very much limited by their own body size (Carbone et al. 1999). Seidensticker (1976) in Chitwan through radio-collaring also found that leopards kill medium size prey than the tigers. Tiger being largest felid is able to kill the large prey available as compared to leopards and dhole which are not much benefitted by the large sized prey. Feeding on one of the most available prey also results in dietary overlap between these predators. Despite high overlap leopards' diverse diet also helps them to coexist with other co-predators. Flexible in food habits, leopards switch their diet in response to densities of dominant competitor. For example, Harihar et al. (2011) in Rajaji Tiger Reserve, India found that leopards shifted their diet to livestock and smaller prey when tiger densities rose in the area due to Gujjars' relocation. Conclusively, all earlier studies mentioned that leopards segregated from other large carnivores in their diet in prey size classes where leopards feed on small to medium size prey while tiger and lion apart from medium sized prey also feed upon larger prey. But higher overlap in diet might be an indicator of current competition even in resource rich areas between leopards and other co predators. Looking at the high overlap in food, it is not seeming to be the major axis along with leopards segregate themselves from other large carnivores.

Studies have shown high overlap in activity pattern of leopards with tiger especially, but not with dhole (Ramesh et al. 2012b, Carter et al. 2015, Karanth et al. 2017). But the activity peak among large tiger and leopard vary in case of high temporal overlap which shows fine temporal partitioning among predators. Also activity pattern graphs show that leopards exploit wider temporal niche by remaining active during the daytime also which was not evident in case of tiger or dhole. Karanth et al. (2017) compared different PAs with resource gradients and found that prey availability seems to affect the activity pattern overlap among the tiger and leopard. Later study found that in the low prey availability areas predators tend to roam more for prey gathering and hence overlapped more in activity. Human disturbances may play a significant role in affecting the activity patterns of leopards (Odden et al. 2014, Carter et al. 2015). It is quite possible if daytime human disturbance is more than it may force carnivores to active during the less disturbed hour and subsequently results in high overlap. Carter et al. (2015) found that temporal overlap was highest among leopard and tiger in human dominated landscape. Same high overlap in food and activity is also not evident as main axis where leopards segregate with other large carnivores.

Spatial overlap among leopard, tiger and dhole was very much evident from the studies (Ramesh et al. 2012b, Karanth et al. 2017) despite that aggregated use may enhance the interference competition of leopard with other large carnivores. Some studies assessed the space use at a fine spatial scale while a few were carried out on larger space use by leopards (Seidensticker 1976, Odden et al. 2010). Role of the habitat along with the tree climbing ability of leopards seems to have greater role in avoiding larger carnivores by leopards in the protected areas and has not been much appreciated by the studies except by Karanth and Sunquist (2000). Areas with high habitat heterogeneity can result in change of prey distribution and can also provide the refuges to avoid the interference competition. Since both leopards and tiger are solitary felid and ambush predator, high habitat heterogeneity can also provide more hunting areas to sympatric predators by facilitating the fine scale avoidance of larger predator by leopards. In this fine scale avoidance tree climbing ability of leopards helps them out to insistently reduce the risk of getting killed by other large predators in case of direct encounters. Seidensticker (1976) also stated that in Chitwan high habitat heterogeneity allows leopards to remain close to tigers as compared to Kanha where tiger displaces leopards. Leopards and dhole have different hunting strategies and hence different hunting habitat is required by both the predators which can be the reason that despite overlap leopards coexist with dholes.

Interspecific interactions among leopards and other large carnivores vary at different sites. No single factor among food, space and time was clearly able to define the coexistence of leopards and other large carnivores. Leopards adjust in each of their axis at fine scale in order to coexist with other large carnivores. We agree with Odden et al. (2010) that there is no single key for coexistence. Further, large carnivores' impact on subordinate predators is context dependent (Haswell et al. 2017). Density of dominant large carnivores apparently affects the strategies of coexistence by subordinate carnivore. Leopards at higher densities of tigers use behavioral tactics such as fine scale habitat use and exploiting more temporal and feeding niche. Since proactive resource use might result in decrease in fitness, high overlap among time, space and food of leopards with other large co-predators suggest fine level reactive responses which help leopard to successfully coexist with the larger predators of their range.

Habitat

Worldwide leopards are adapted to different habitats ranging from high mountains in far east Russia to tropical rainforest of southern India. However, leopards show strong requirement towards the cover for feeding and resting requirements (Karanth et al. 2009). At the site specific level vegetation cover and terrain seemed to be important factors determining the presence of leopards (Athreya et al. 2015, Kshettry et al. 2017). Karanth and Sunquist (2000) using radio-collaring found that leopards use comparatively open cover to kill prey in comparison with tigers. Another study also found leopards make use of other factors such as water in killing behavior.

In human dominated landscapes, Kshettry et al. (2017) found that leopard presence was determined by dense ground cover as leopards avoid areas of high density. Cover in the form of irrigated cropland was also an important variable in leopard's presence in Karnataka district of India (Athreya et al. 2015). At country level there is only one study (Karanth et al. 2009) which is able to assess the leopard's presence along with other species. They found that evergreen, temperate and deciduous forest types were major determinant of leopards. These areas might act as a proxy for cover which is essential for leopards. Barren land was another predictor of leopard's presence across the country might be due to these lands provide refuges in the form of the resting sites with less human disturbance.

CONCLUSION

Major threat to conservation of leopard in Indian subcontinent is Human-Wildlife conflict which subsequently leads to retaliatory killing of leopards in these landscapes. Only eleven percent of present range of Indian leopard is protected (Jacobson et al. 2016) this makes human-wildlife on these landscapes of utmost importance. Present studies regarding human-leopard's conflict were mostly speaking about temporal pattern of human-leopard conflict using secondary data in Human-dominated landscape. Few studies have addressed the factors responsible for human–leopard conflict and whatsoever studies have been made on this aspect, are in multispecies assemblage. Kshettry et al. (2017) found that leopard attacks were not associated with their habitat use suggesting that leopards avoid humans. Recent study by Blecha et al. (2018) on pumas found that risk of foraging in human dominated landscape was hunger mediated. Do leopards have such kind of mechanism or they have totally adapted themselves in human dominated landscapes and become farm dwelling animals? What drives leopards to live in risk-sensitive areas is an important question for research. Studies have found that leopards live in high densities in human dominated areas but most important is to find if density can act as a better indicator of a good population or these areas are ecological traps where fitness is low as compared to natural populations? Or these landscapes are attractive ecological traps in terms of habitat and food? Or can they act as a sink habitat? These questions should be answered for the conservation of leopards in human dominated landscape.

Present management of human-leopard conflict in Indian subcontinent is on reactive basis. There is an urgent need to look into this and work out new management strategies. Karanth et al. (2009) in a country wide assessment found that protected areas were positively correlated with the presence of leopard which suggests strongly the importance of protected areas in leopard conservation. Inside the protected area, there is urgent need to estimate the population size of the population. Also the distribution of the Indian leopard is poorly understood, Jacobson et al. (2016) though determine the extent of distribution of leopards on the basis of published studies. But there might be many more areas where leopards are present, especially the non-protected areas where their presence has not been recorded. For example, Athreya et al. (2015) found the leopard's presence in half of the Karnataka state in India. Apart from that no study examined the prey-predator relationship in case of leopards except by Wegge et al. (2009) in Bardia. Habitat degradation and fragmentation is a threat to currently all felids. But no study has been yet able to understand the extent of habitat fragmentation or degradation in case of Indian leopard. Although there are studies on large landscapes using genetic techniques to study the impact of fragmentation in gene flow of leopards (Dutta et al. 2013a, 2013b). More studies are needed in this direction to understand the impact of land use change on leopard population.

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