

RESEARCH ARTICLE

Leopard in a tea-cup: A study of leopard habitat-use and human-leopard interactions in north-eastern India

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Abstract

There is increasing evidence of the importance of multi-use landscapes for the conservation of large carnivores. However, when carnivore ranges overlap with high density of humans, there are often serious conservation challenges. This is especially true in countries like India where loss of peoples' lives and property to large wildlife are not uncommon. The leopard (*Panthera pardus*) is a large felid that is widespread in India, often sharing landscapes with high human densities. In order to understand the ecology of leopards in a human use landscape and the nature of human-leopard interactions, we studied (i) the spatial and temporal distribution and the characteristics of leopard attacks on people, (ii) the spatial variability in the pattern of habitat use by the leopard, and (iii) the spatial relationship between attack locations and habitat use by leopards. The study site, located in northern West Bengal, India, is a densely populated mixed-use landscape of 630 km², comprising of forests, tea plantations, agriculture fields, and human settlements. A total of 171 leopard attacks on humans were reported between January 2009 and March 2016, most of which occurred within the tea-gardens. None of the attacks was fatal. We found significant spatial clustering of locations of leopard attacks on humans. However, most of the attacks were restricted to certain tea estates and occurred mostly between January and May. Analysis of habitat use by leopards showed that the probability of use of areas with more ground vegetation cover was high while that of areas with high density of buildings was low. However, locations of leopard attacks on people did not coincide with areas that showed a higher probability of use by leopards. This indicates that an increased use of an area by leopards, by itself, does not necessarily imply an increase in attacks on people. The spatial and temporal clustering of attack locations allowed us to use this information to prioritize areas to focus mitigation activities in order reduce negative encounters between people and leopards in this landscape which has had a long history of conflict.

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Introduction

Protected Areas are vital for the conservation of biodiversity [1] but cover less than 12% of the global land area [2] and are often small in size relative to adjoining non-protected land use matrices [2,3]. The small size of most protected areas makes it difficult to conserve large carnivores that are wide ranging, thus highlighting the importance of multi-use landscapes for their conservation [4]. There is increasing evidence of large carnivore presence in rural and semi-urban landscapes in many parts of the world that creates both opportunities and challenges for conservation [5,6]. Currently, the ecological understanding of large carnivores in many countries is largely limited to protected areas and is therefore insufficient to allow us to plan management strategies to deal with their presence in human dominated landscapes [7].

India still retains most of its large carnivore species including the four large cats, the tiger (*Panthera tigris*), the lion (*Panthera leo*), the snow leopard (*Panthera uncia*), and the common leopard (*Panthera pardus*) despite having an extremely high human population density. All four species share space with humans in parts of their ranges [8–11] and this can potentially lead to conflict, which, if unresolved, may seriously undermine conservation goals and impact human lives and livelihoods [4].

Of the four large cats in India, the leopard is the most adaptable with a very wide distribution, occupying a diverse range of habitat types varying from pristine protected forests to edges of urban landscapes [12–14]. Their adaptability has created many situations for spatial overlap with humans across much of their range in India. Therefore, livestock losses to leopards are widespread and attacks on humans are not uncommon in some areas [15–17]. The reasons for attack on humans by large carnivores in some areas but not others are not well known, although historically, hunters have put forward theories that include old age or injury as a predisposition to man-eating [18]. Previous studies of attacks on humans by large carnivores have provided information on the temporal and spatial patterns of attacks [19] and use correlations between different variables and attack locations [20–22]. However, understanding the reasons for the attack is difficult given that they are rare and unpredictable events. In one study, a strong correlation was found between translocation of leopards and attacks on people near the release sites indicating that such interventions might inadvertently exacerbate the severity of conflict in a densely populated country like India [15]. Further, it is a common assumption among the public and media that attacks by leopards on people will occur wherever leopards and humans co-occur.

In this paper, we investigate the spatial and temporal patterns of attacks on humans by leopards in a landscape predominated by tea gardens interspersed with forests, farms, and rural residences. We assessed the spatial habitat-use patterns of the leopards to understand the ecology of the species in a forest-production landscape mosaic. We also assessed if a higher probability of habitat use by leopards correlates with more frequent attacks on people, and we examined the nature of attacks on people to identify patterns that could be used to formulate management interventions to reduce future incidents in this region.

Materials and methods

Study area

This study was conducted in an area of ~630 km² located in Jalpaiguri district in the state of West Bengal, India (Fig 1). The study area consisted of villages and agricultural fields (21% of the area), tea estates (35%), forest (25%), river beds and fallow areas. It is largely a rural landscape with 80% of the population living in rural areas. Livestock rearing is a major occupation with 23% of the population being dependent on domestic animals such as cattle, goats, pigs

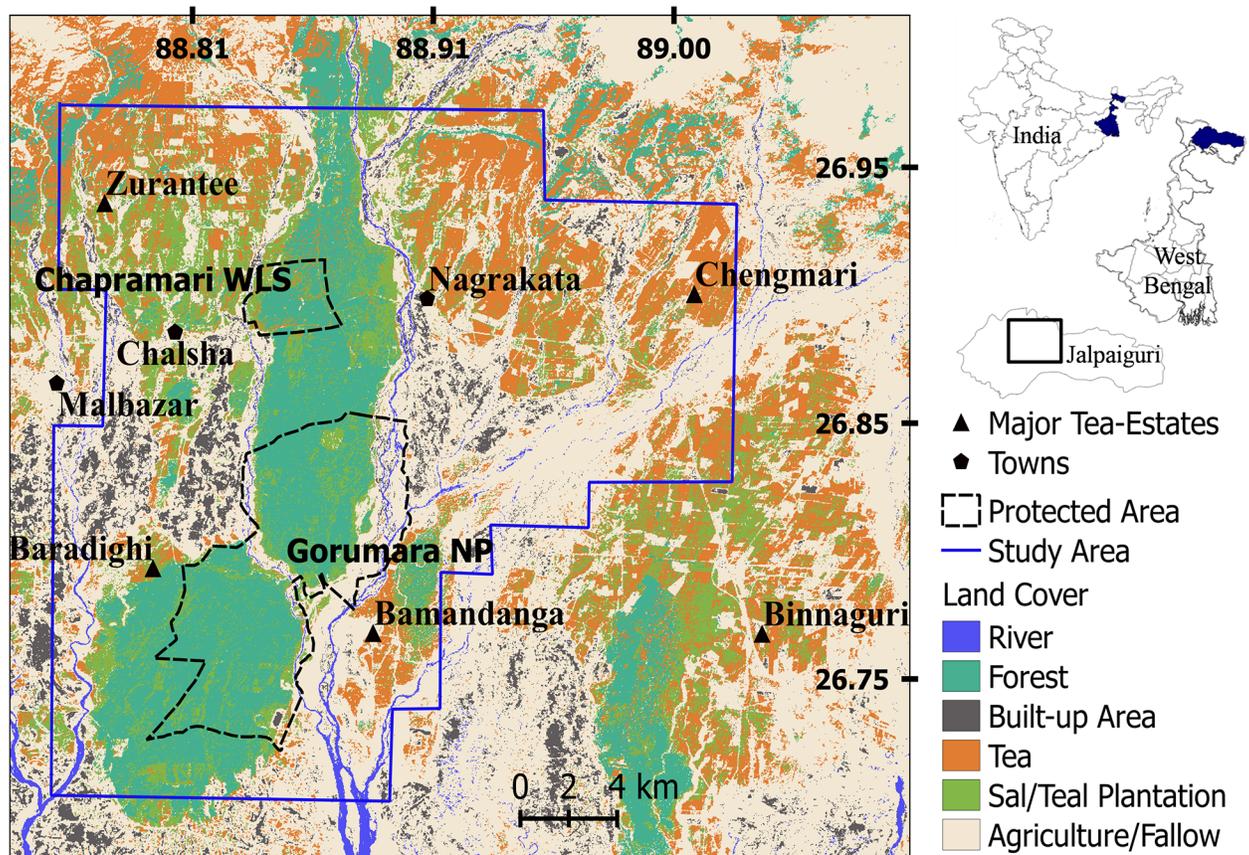


Fig 1. Map showing location of study area, sampled area, prediction area and land cover types in northern West Bengal, India.

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and poultry for their livelihood. Six percent of the population depends on small and marginal agriculture for their livelihood while an equal percentage of people work as agricultural laborers (www.jalpaiguri.gov.in accessed on October 2016). The region receives an average annual rainfall of 3160 mm, has an average altitude of 200 m, with an overall human population density of 701 persons per km² (according to 2011 census, <http://jalpaiguri.gov.in/html/census.html>, accessed on October 2016).

The forests are part of the East Himalayan biodiversity hotspot [23] and includes two Protected Areas; Gorumara National Park (80 km²) and Chapramari Wildlife Sanctuary (9.5 km²) and the Reserve Forests of Jalpaiguri Forest Division (35 km²). The major forest types are Northern Tropical Semi-Evergreen and Tropical Moist Deciduous [24]. Despite being small in size Gorumara National Park and Chapramari Wildlife Sanctuary are home to the endangered one-horned rhinoceros (*Rhinoceros unicornis*), Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*), sambar (*Rusa unicolor*), chital (*Axis axis*), rhesus macaque (*Macaca mullata*) and a host of diverse fauna and flora [25]. The leopard is the only large carnivore present in the study area and reports of livestock depredation, attacks on humans and retaliatory killing by humans are not uncommon [25]. The landscape underwent large-scale alterations in the late 1800s when British tea planters cleared vast stretches of forests for tea cultivation resulting in the present landscape of small and fragmented forest patches connected via tea plantations. The permissions to carry out field studies in the forested areas were provided by the West Bengal Forest Department. Permission to work in the tea-estates was obtained from the Doorg

Branch of the Indian Tea Association. Fieldwork in the villages and agricultural fields did not require permits since these areas are accessible to the general public. However, prior to working in any village, we informed the villagers and/or land owners about the surveys. The field surveys involved recording of leopard signs such as scat, scrape, and pugmark that were observed, and did not involve capturing or handling of either the leopard or any endangered or protected species.

Patterns of encounters and conflict levels

In order to understand the characteristics of leopard attacks on people, we used compensation records for the Jalpaiguri District maintained by the Forest Department. Of the 352 leopard attacks on people that were reported between January 2009 and March 2016, 171 occurred within our study area of 630 km². Of these, we interviewed 89 victims to ascertain the characteristics of the attack. We used all the 171 attack incidences to map the attack locations either by visiting the actual site of attack (for the 89 interviews) or using the centroid of the tea-estate or village where the attack occurred as an approximate location of the attack.

We digitized all the villages and tea estates in the study area and found that the mean distance between the centre point of the tea-estate/village and its boundary was ~997 m (SE ±41m) indicating that the estimated location of attacks had a maximum error of 1 km. QGIS version 2.0 (<http://qgis.osgeo.org> accessed on May 2016), Google hybrid layers from the OpenLayers plugin, and the district map of Jalpaiguri were used to digitize the villages and tea estates, and map the centroids of the villages.

To identify the spatial clusters of attacks on people by leopards, we used all the 171 attack locations to generate kernel density maps using the HEATMAP plugin (http://docs.qgis.org/2.0/en/docs/user_manual/plugins/plugins_heatmap.html, accessed on May 2016) in QGIS version 2.0. In order to generate a kernel density map or 'hotspots' of leopard attack locations, we used a radius of 2.8 km around each attack location, which corresponded to a mean home range size of a leopard of 25 km² [8]. We used the biweight method for obtaining kernel density estimates as it gives more weight to points which are nearby compared to points that are far away from each other [26].

The extent of spatial clustering in the location of leopard attacks on humans was determined using Ripley's K function test, which is a descriptive statistic for detecting spatial clustering. A point process (such as location of attacks) is said to be clustered when the resultant k function ($K_{obs}(r)$) is greater than the k function of a random point process ($K_{theo}(r)$) [27]. We performed 200 simulations of the K function and plotted them against the random process with 95% confidence intervals at distances varying from 0-8000m. The wide distance bin of 8000 m was used to check for scale dependent cluster patterns which may appear due to the choice of the scale alone rather than any real clustering phenomenon.

Detailed information about the leopard attacks on people such as time, location and activity of the person during the attack was obtained by interviewing the affected people using semi-structured questionnaires. The questionnaires were approved by the Dissertation Advisory Committee of the National Centre for Biological Sciences, Tata Institute of Fundamental Research, and we obtained oral consent from respondents before administering the interview. We opted for oral consent rather than written consent since the victims/respondents were illiterate and unaccustomed to handling forms. The objective of obtaining this information from them was explained and no personal details of the respondents were noted or used in the analysis or presented in the results and this procedure was approved by the Dissertation Advisory Committee and Institutional Review Board.

We investigated the temporal trends of leopard attacks on humans using the full dataset of 171 attacks that occurred between January 2009 and March 2016. We aggregated the number of attacks over the months as well as across the day, to identify seasonal and diurnal patterns in attacks.

Recent research has shown that attacks on people can also be related to the release of translocated leopards in nearby areas [15]. There have been occasional translocations in our study area and we used the Forest Department records on captures and releases of leopards to test for correlations between attacks and translocations in the study area using the Auto Correlation Function (ACF). The month of the attack or translocation event was used in the analysis. As the records maintained by the forest department did not have co-ordinates of actual release sites, we were unable to perform any kind of spatial analysis to understand the impacts of leopard translocation and attacks on humans.

Identifying spatial variability in leopard habitat use

To assess the habitat use of leopards, we sampled 408 km² within the study area (of 630 km²) which was divided into 4 km² cells or sites to record the presence or absence of leopard signs [13,28]. The cell size was selected to be greater than the mean daily movement of leopards [8] so that each site could be treated as an independent sampling unit to estimate the probability of habitat-use [29,30] and such that multiple cells would constitute the home range of one animal. Thus, the smaller cells size would capture the variability in space-use within a home range or in other words, the habitat-use patterns [31,32]. Leopard signs such as scat, scrape, claw marks and pugmarks were recorded as detected or not detected for every 200 m segment (spatial replicates) along the sampled trails. A minimum of 2 km of sampling effort was allocated per cell (the sampling protocol is detailed in S1 File).

To identify factors influencing habitat use by leopards we used an occupancy modeling framework because it accounts for imperfect detection and uses presence-absence data for robust estimates of probability of use (Ψ) [33]. We used an extension of the standard occupancy model [34], which allows the use of spatially correlated replicates [35] and analyses were carried out using the program PRESENCE version 6.4 [36]. This approach also allowed us to estimate the probability of detecting leopard signs (p_t) since leopard signs are hard to detect and some signs may have been undetected during sampling, which could potentially lead to biased estimates of habitat use [37]. Since the ability to detect signs is related to the substrate type, which is itself a function of the landcover at each 200m segment (spatial replicate), we included the landcover type of each spatial replicate as a covariate which may influence the probability of detection in the habitat-use models.

Program R [38] and the package ‘ggplot2’ [39] were used in developing the remotely sensed covariates and for exploratory analyses to assess habitat use by leopards. The details of covariate development procedures are provided in the supplementary information (S2 File) and their expected relation to the response variable, i.e. habitat use, is provided in Table 1.

Table 1. Covariates used in habitat selection models and the expected relationship with site use by leopards.

Covariate	Source	Expected Relation	Reference
Wild Prey encounter rate	Ground Based	+	[44,45]
Domestic Prey Encounter rate	Ground based	+	[46,47]
Human encounter rate	Ground based	-	[48,49]
Distance to forest	Remotely Sensed	-	[22,50]
Ground Vegetation Cover	Remotely Sensed	+	[51]
House Density/ Human presence	Remotely Sensed	- / +	[14]

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Covariates related to habitat use were checked for correlations using a pair-wise correlation matrix and only non-correlated ($r < 0.5$) covariates were used in the same model. The model building approach was similar to Doherty et al. 2010, whereby covariates that influenced probability of detecting signs (p_t) were selected first while maintaining a constant model for probability of use (Ψ) [40]. We then used the top ranked detection covariate (covariate model with the lowest AIC score) as a constant for building models that influenced probability of use [41]. Models for probability of use were developed using the covariates in Table 1 and models that did not converge were dropped from the candidate set of models. The null (intercept-only) model without any covariates was also included for comparison. The best models were selected based on AIC scores and estimates of the probability of use (Ψ) were obtained by model averaging (including all models where $\Delta AIC < 2$) [42,43].

Since the cell size we used for assessing habitat use (4 km^2) is a relatively small area in relation to the size of a leopard home range, we tested if covariates in adjacent cells influenced leopard site use by including the mean covariate value from the first order neighboring cells as a predictor in our models. In this way, we could also overcome potential spatial autocorrelation of the covariates that were used for habitat use estimation. We used the model averaged estimates to extrapolate the results to un-sampled cells adjoining the sampled area. This was done so that we could, more reliably assess the spatial relationship between location of leopard attacks and the probability of habitat use. Un-sampled cells that adjoined the sampled areas alone were used for prediction to avoid extrapolating the model to areas farther from those that were sampled.

Relationship between leopard attacks and habitat-use

We examined whether sites where leopards had attacked people coincided with areas of high probability of use by the leopard. This was done by using the presence or absence of leopard attack at a particular site (4 km^2) as a response variable and modeling it as a function of the probability of habitat use of that site using Generalized Linear Models (GLM). Additionally, we used multivariate Generalized Linear Model to investigate if any of the covariates influencing the probability of habitat use also influenced presence or absence of attack.

A binomial distribution was used for the response variable (presence or absence of attack) in the GLM. Null deviance, residual deviance, and Pseudo R^2 values ($1 - \text{Residual deviance} / \text{Null deviance}$) were used to assess absolute fit of the model, and AIC scores were used to assess the relative fit of the models. We did not need to account for issues related to imperfect detection of attacks since all incidents of leopard attacks on people are reported and records are maintained by the West Bengal Forest Department, thereby minimizing the chance of false positives.

Results

Temporal and spatial patterns of leopard attacks on humans

None of the 171 leopard attacks on humans reported in the study area between January 2009 and March 2016 were fatal. During this period 24 people on an average ($n = 171$) were attacked by leopards each year with significantly higher incidences of leopard attacks reported in 2009 ($\chi^2 = 59.409$, $df = 7$, $p < 0.0005$) (Fig 2a). Most of the attacks occurred in the tea-gardens between January and May (83 of 89 attacks) and this period coincides with the lean season in tea production when activities like pruning, irrigation, and uprooting of old and diseased tea plants are carried out (Fig 2b). This result was substantiated using Pearson's correlation between month wise leopard attacks on people and monthly tea production ($r = -0.71$).

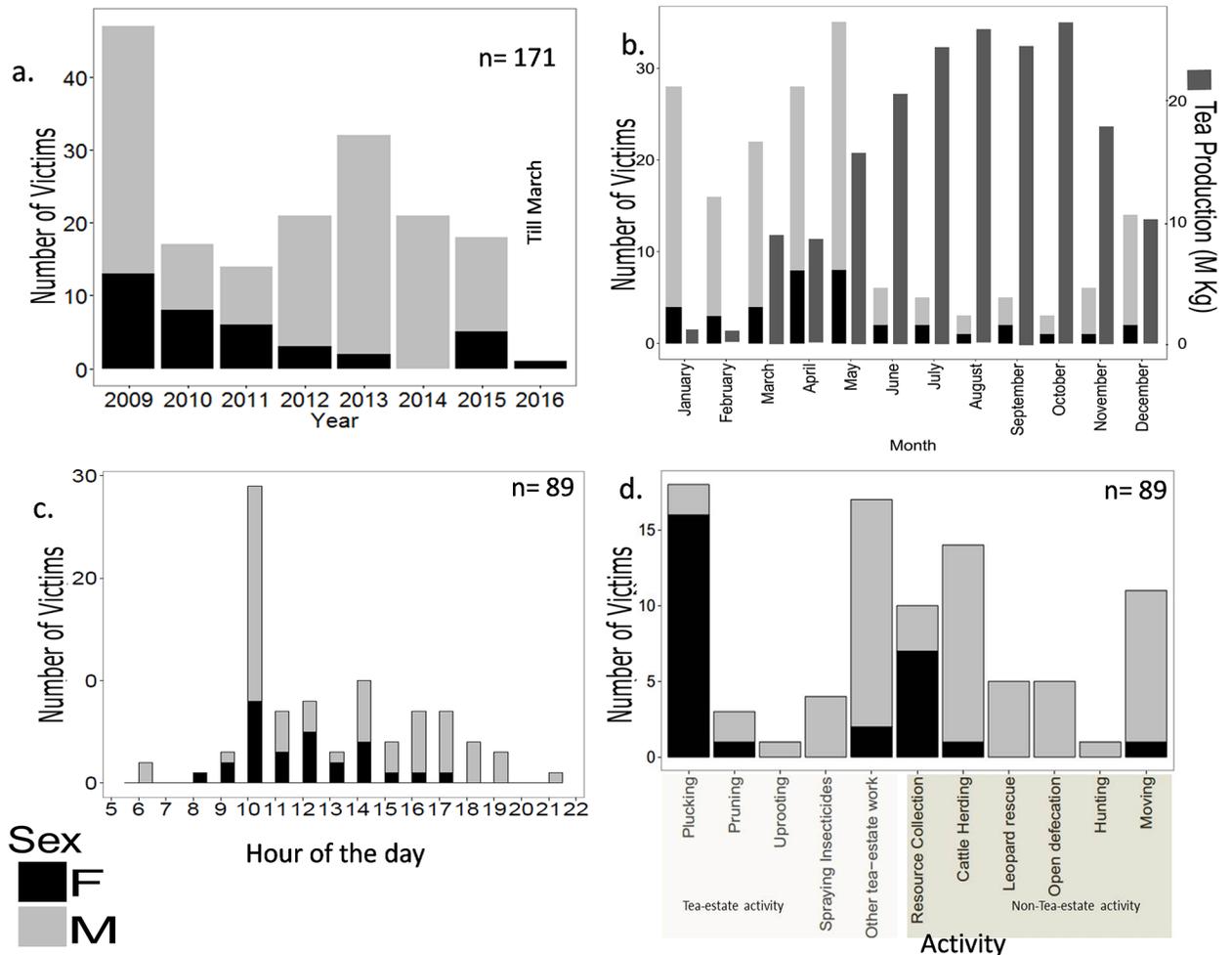


Fig 2. Graphs showing temporal trends in leopard attacks on people, (a) numbers of leopard attacks per year, (b) monthly distribution of attacks and peak tea production, (c) time of day of attack and (d) activity of the victim prior to the attack.

<https://doi.org/10.1371/journal.pone.0177013.g002>

The majority of leopard attacks on people occurred between 10:00 AM and 02:00 PM (Fig 2c) and men were attacked more frequently than women ($\chi^2 = 52.778$, $df = 1$, $p < 0.0005$) (Fig 2c).

Twenty percent of the leopard attacks on people occurred while they were plucking tea leaves and mostly women were injured during this activity since plucking is mostly done by women workers, 18% while carrying out other tea estate related activities, 16% while herding livestock, 11% while moving about in the tea estate and 9% while collecting forest products ($n = 89$; Fig 2d). On an average the victims were 30 years old ($n = 89$) with 95% of the victims belonging to the age category from 20–40 years. The only cases of children being attacked ($n = 2$, age < 10 years), occurred when they were herding livestock within the tea-gardens. The attacks showed significant spatial clustering (Fig 3).

The Auto Correlation Function (ACF) plots indicated a weak but statistically significant correlation between leopard attacks and leopard translocations in the study area with the correlation lasting up to two months from an instance of translocation or attack event (S1 Fig).

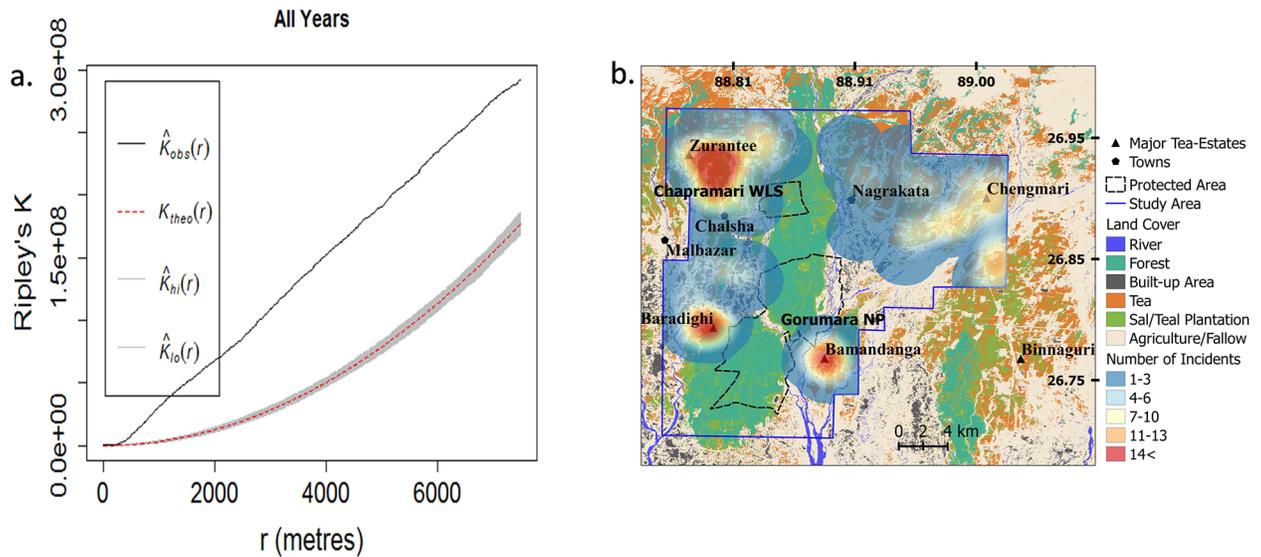


Fig 3. Maps showing (a) Ripley's K Plots for clustering of attack locations and (b) clusters of location of leopard attack on people between January 2009 and March 2016 in northern West Bengal, India. $K_{obs}(r)$: Ripley's k function of attack locations, $K_{theo}(r)$: Ripley's K function for random process.

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Patterns of habitat use

A total of 370 km was walked to survey for signs with an average survey effort per cell of 3.4 (± 0.5) km. Leopard signs were detected in 50% of all the sampled cells ($n = 102$), but after accounting for imperfect detection, 68% (null model) of the cells were found to be used by leopards. The overall probability of detecting leopard signs was 0.18 ($SE \pm 0.09$) and the mean probability of site use in the landscape was 0.75 (Range: 0.04–0.98) ($SE \pm 0.13$, Range: 0.02–0.29) indicating that leopards were widespread and common throughout the study site.

The best model for detection probability (p_i) included the covariate land cover ($p_r(\text{landcov})$) and this was retained building the habitat-use models (Table 2).

Since we did not obtain a single best model estimating the probability of habitat use, we model averaged using all models with $\Delta AIC < 2$. The covariates encounter rate of wild, domestic, small, medium and large prey, distance to river, distance to nearest forest patch and encounter rate of humans were not present in the top models. The model averaged estimates of site use by leopards were negatively influenced by the density of houses within the sampled

Table 2. Model comparisons to identify ecological and anthropogenic covariates influencing leopard habitat-use in northern West Bengal, India.

Model	AIC	ΔAIC	AIC wt	Model Likelihood	K	-2loglik
$\Psi(\text{house.D} + \text{house.nbr} + \text{gv}, \theta^0(\cdot), \theta^1(\cdot), p_i(\text{landcov}))$	701.58	0	0.35	1	9	683.58
$\Psi(\text{house.D} + \text{house.nbr} + \text{gv} + \text{gv.nbr}, \theta^0(\cdot), \theta^1(\cdot), p_i(\text{landcov}))$	703.29	1.71	0.15	0.43	10	683.29
$\Psi(\text{house.nbr}, \theta^0(\cdot), \theta^1(\cdot), p_i(\text{landcov}))$	703.38	1.8	0.14	0.41	7	689.38
$\Psi(\text{house.D} + \text{house.nbr}, \theta^0(\cdot), \theta^1(\cdot), p_i(\text{landcov}))$	703.52	1.94	0.13	0.38	8	687.52
$\Psi(\cdot, \theta^0(\cdot), \theta^1(\cdot), p_i(\cdot))$	736.95	35.37	0	0	5	726.95

Ψ : Probability of habitat-use; house.D: density of houses/buildings; house.nbr: mean density of houses/buildings in neighboring cells; θ^0 : probability of leopard presence in a replicate conditional on absence in the previous replicate; θ^1 : probability of leopard presence in a replicate conditional on presence in the previous replicate; p_i : probability of detecting leopard sign in a replicate conditional on presence in the replicate; gv: mean Mahalanobis distance from highest ground vegetation cover pixel; gv.nbr: mean gv in neighboring cells; landcov: land cover type in the replicate; K: number of parameters.

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cell (Cumulative AIC Weight of Covariate or Relative Importance: 0.63) and mean density of houses of neighboring cells (Cumulative AIC weight of Covariate: 0.77). It was positively influenced by ground vegetation cover of the focal cell (Cumulative AIC weight of covariate: 0.49) and the mean ground vegetation cover of neighboring cells (Cumulative AIC weight of covariate: 0.15) [52]. We quantified distance to high ground vegetation cover as the predictor (S2 File) hence a negative relation between the response and the predictor indicates a positive relation between habitat-use probability and ground vegetation cover. We used the third quartile and above to define the high probability of use (range 0.89–0.99) and our results showed that 51 out of the 102 cells that were sampled had high probability of use by leopards and nearly 25% of these high-use sites fell outside the forested area (Fig 4). The model averaged beta estimates for each covariate are provided in the supporting information (S3 File).

Comparing attack levels with habitat use

The generalized linear models showed that the number of leopard attacks on humans was not significantly predicted by leopard habitat-use ($\beta_0 = 0.11, p = 0.72; \beta_\psi = -1.26, p = 0.005$; Pseudo $R^2 = 0.04, n = 159, AIC = 201.12$). The four covariates that influenced habitat use namely, density of buildings, mean density of buildings in neighboring cells, ground vegetation cover, and mean ground vegetation cover in neighboring cells, were all included in a model, which only weakly explained the presence or absence of attacks at a site (Pseudo $R^2 = 0.26, AIC = 160.49$). There was no support for any relation between sites with attacks and sites with high probability of habitat use.

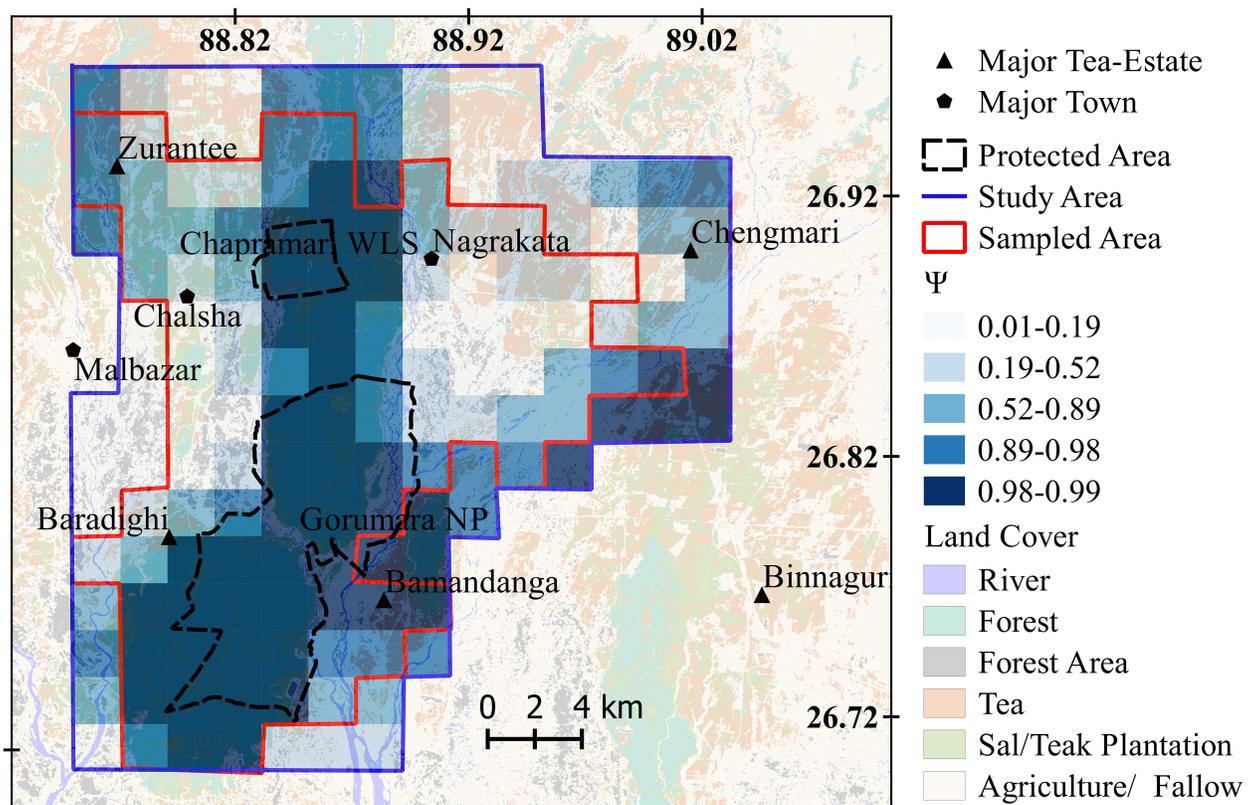


Fig 4. Map showing probability of habitat use (Ψ) by leopards in the study area in northern West Bengal, India.

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Discussion

Conserving carnivores in human dominated landscapes is associated with various challenges. While large carnivore ranging habits make it inevitable that they will share space with humans, their presence in any human dominated landscape will be associated with damage to human property and sometimes even attacks on humans [15,46]. Therefore, conservation of large carnivores in human dominated landscapes requires balancing of the safety of humans and their livestock with carnivore conservation goals [4,53]. Our study site is a mosaic of anthropogenic habitats dominated by tea gardens and villages, interspersed with small Protected Areas with populations of large, potentially dangerous wild animals such as leopards, elephants, rhinos and gaur [25]. The tea gardens were established by the British in the 1850's [54], and have remained largely unchanged since then. There are reports of leopard presence as well as attacks on people in these areas since the colonial times of the early 1900s [55]. Leopard attacks on people appear to have increased in the district since 1993, with 121 attacks reported between 1993–1997, 243 cases between 2001 and 2008, and 353 cases between 2009 and 2016 [25]. However, within the seven-year period between January 2009 and March 2016, the year 2009 had the highest reports of leopard attacks on people in our study area as much as 83% higher than the average in the same period. Seventy-five percent of the attacks by leopards occurred between January and May that also coincides with large-scale activities in the tea plantations like pruning of tea bushes and irrigation where entire sections of tea gardens are disturbed.

Leopard attacks on people occurred in the tea gardens during the day when most of the tea-garden employees were at work in the plantations. The attacks have been largely on adults and none of them resulted in the death of the victim. Men were attacked more frequently than women and this could be related to the different nature of work that men and women do in the plantations. Although both men and women are engaged in plucking tea leaves, men are mainly involved in pruning and irrigation work where people work in small groups within the plantation. Activities such as plucking tea and resource collection (drift wood, fodder for livestock) are mostly done by women who are usually in larger groups during these activities. Attacks on children have occurred while they were herding cattle since mostly the children are associated with this activity.

There have been relatively few detailed studies of the exact circumstances of attacks on humans for other species / locations. Instances of human deaths by other large carnivores like tigers are reported from the Sunderbans in West Bengal but the circumstances behind these deaths remain unknown [56]. The characteristics of attacks have been studied in a few cases like for tiger attacks in Chitwan in Nepal where male victims outnumbered female victims, and most of the attacks occurred during the day while victims were herding cattle, collecting fodder/grass, or when the victim accidentally disturbed tigers at kill sites [57]. In contrast, attacks by lions in Tanzania occurred mostly at night when people were herding cattle, hunting for bushmeat, protecting crops from herbivores, or sleeping in makeshift beds in the open [58]. The results of our study indicate that leopard attacks on people are localized and mainly occur within the tea gardens during daylight hours while people are engaged in tea-estate activities. Even among the tea gardens, the number of attacks had substantial variation between years.

A tea garden in the southwestern region of the study area reported high number of attacks in 2009 with very little or no attacks in the subsequent years. Discussion with the manager of the particular tea garden revealed that following the high number of attacks in 2009, they had restarted the practice of making loud noises prior to commencing work in the gardens. The British planters practiced this in the colonial period in an attempt to warn wild animals of the

imminent presence of people to prevent accidental encounters. Whether this practice has resulted in a decrease in attacks needs to be tested systematically.

The lack of relationship between clustering of leopard attacks and habitat-use patterns by revealed that mere presence of suitable leopard habitat and leopards does not imply that attacks will occur. Not all tea gardens in the region reported attacks on people although leopard signs were found there during our surveys.

A reason that could lead to an increase in leopard attacks on humans is the capture and translocation of leopards from an attack site. This management strategy to mitigate conflict, which arises due to public and political pressure and is a common practice in our study site and captured leopards are usually released into the nearby Protected Areas within the landscape (West Bengal Forest Department, Annual Forest Report 2013). A correlation, albeit weak, was seen between the months of attacks and translocation. A more detailed analysis with larger datasets of captures and releases of leopards in this region would help us to understand the role of translocations in leopard attacks on humans in the study area.

Similar tea-garden landscapes in southern India rarely report leopard attacks on the tea garden workers although leopards are present [59]. This could be due to taller tea plants and the undulating terrain in southern India, which allows a clear view of the floor and also provides very little cover for the leopards to rest during the day (AK personal observation). This is unlike the tea-gardens in West Bengal where the tea shrubs are shorter and much denser, and the terrain is flat.

The habitat-use analysis indicate that leopards are ubiquitous in the landscape and we found high availability of dense ground vegetation and low human presence (low density of houses) to be the strongest positive predictors of leopard habitat-use. Habitat attributes such as availability of prey or distance to forest patch or rivers did not influence how leopards used the landscape. Livestock density outside of the forests was extremely high at 342 animals per km² and density of wild prey was at 56 animals per km² in the forested areas indicating the high prey biomass that is potentially available to the leopards in the landscape [60]. Also, an extensive network of rivers and ground vegetation provided by tea bushes explains the lack of influence of the distance to rivers and forest patches on habitat selection as reported in other studies [61,62]. Our study also found that built-up areas and agricultural lands show lower usage by leopards. Although agricultural landscapes in other parts of India report leopards [8], they occur in areas with good irrigation and tall crops like sugarcane that are grown throughout the year. In our study area crops such as rice paddy and maize are grown only during the monsoons (June-September). The land is left fallow during the non-cropping season and is usually devoid of any vegetation cover, thus making it an unsuitable habitat for leopards for most parts of the year. On the other hand, numerous instances of leopard cubs being found within the tea gardens (AK personal observation) indicates that leopards den in the dense cover provided by the tea bushes which is also the area with the most number of attacks (93% of all attacks occurred in tea gardens).

Our study underscores the potential value that human-dominated landscapes can have for the persistence of a threatened large felid, but also highlights the problems that are associated with shared spaces. The results of our work indicate that there are defined hotspots of conflict within the landscape and most of these attacks are restricted to certain parts of the year. The spatial and temporal clustering in attacks provides a unique opportunity to test mitigation methods to reduce human-leopard conflict. Our study also highlights the plasticity in habitat use in leopards which has been reported in historical records but rarely studied [7,55]. Despite the large number of leopard attacks on humans in this landscape, the non-fatal nature of attacks tends to suggest these are defensive rather than predatory in nature. This implies that if the leopards are warned early of human presence they could be given time to move away,

thereby reducing the number of human casualties. Such an approach has been adopted in one of the estates with apparently a good measure of success. Further experimentation and innovations in developing systems to avoid conflict should help ensure safety of humans while allowing leopards to use shared spaces.

Supporting information

S1 File. Trail survey protocol. Data collection protocol during sign surveys.
(PDF)

S2 File. Covariate development.
(PDF)

S3 File. Model average estimates of covariates influencing probability of habitat use.
 Ψ : Probability of habitat-use; house.D: density of houses/buildings; house.nbr: mean density of houses/buildings in neighboring cells; θ^0 : probability of leopard presence in a replicate conditional on absence in the previous replicate; θ^1 : probability of leopard presence in a replicate conditional on presence in the previous replicate; p_i : probability of detecting leopard sign in a replicate conditional on presence in the replicate; gv: mean Mahalanobis distance from highest ground vegetation cover pixel; gv.nbr: mean gv in neighboring cells; landcov: land cover type in the replicate.
(PDF)

S1 Fig. Lag model comparing leopard translocations and attacks. Auto Correlation plot of month of leopard translocations and leopard attacks on people between January 2009 and March 2015.
(TIF)

S2 Fig. Covariate value comparison in sites with leopard attacks on people versus sites with no attacks. Box-plots showing (a). Density of houses (b). Mean density of houses in neighboring cells, (c). Distance to highest ground vegetation cover, and (d). Mean distance to high ground vegetation cover in neighboring cells in sites with leopard attacks and sites without leopard attack.
(TIF)

S3 Fig. Effect of human population, distance to forest and size of tea-plantation on occurrence of leopard attacks on people. Box-plots showing effect of (a). Human population (b). distance to forest patch and (c). size of tea-estate/village on the number of leopard attacks on people.
(TIF)

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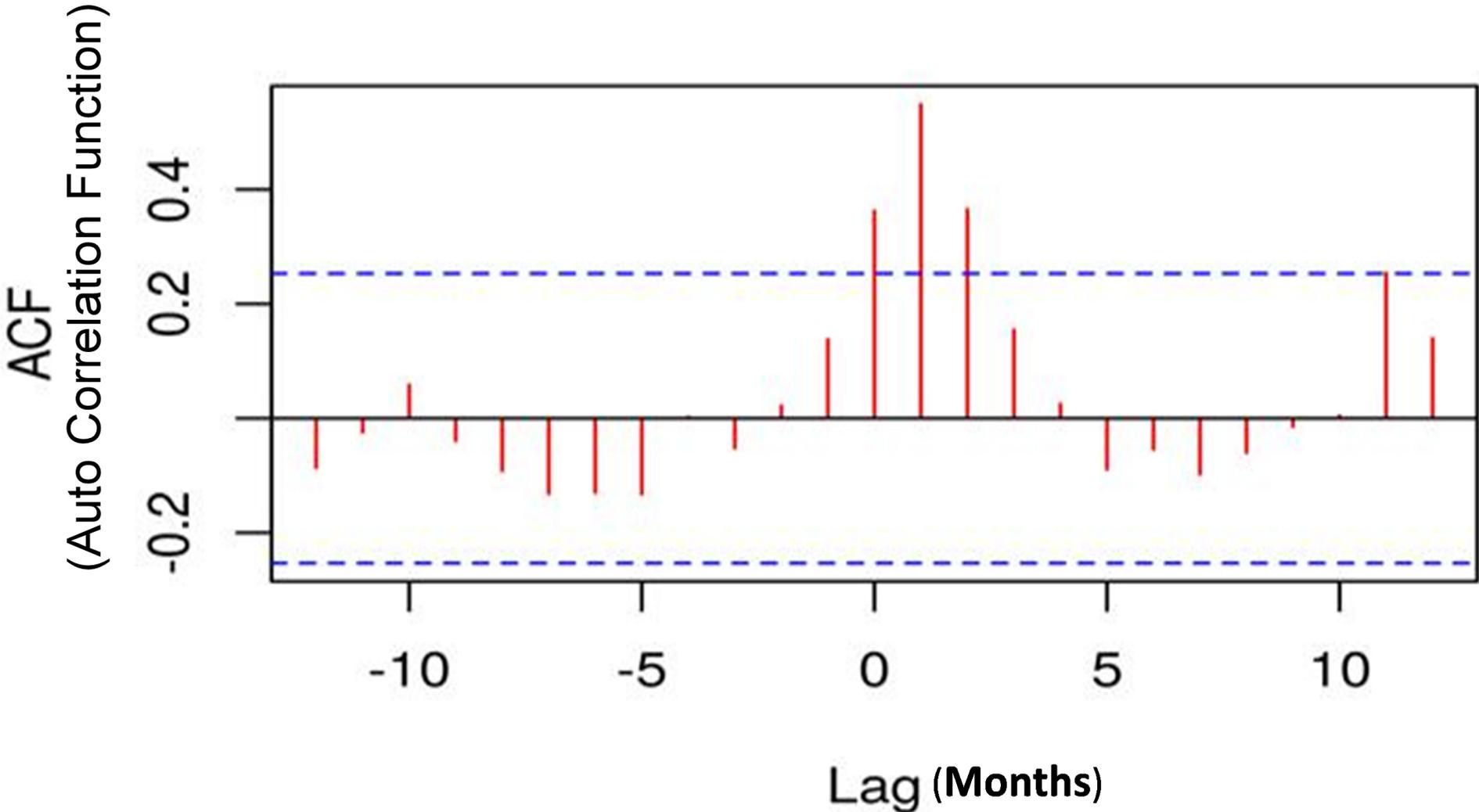
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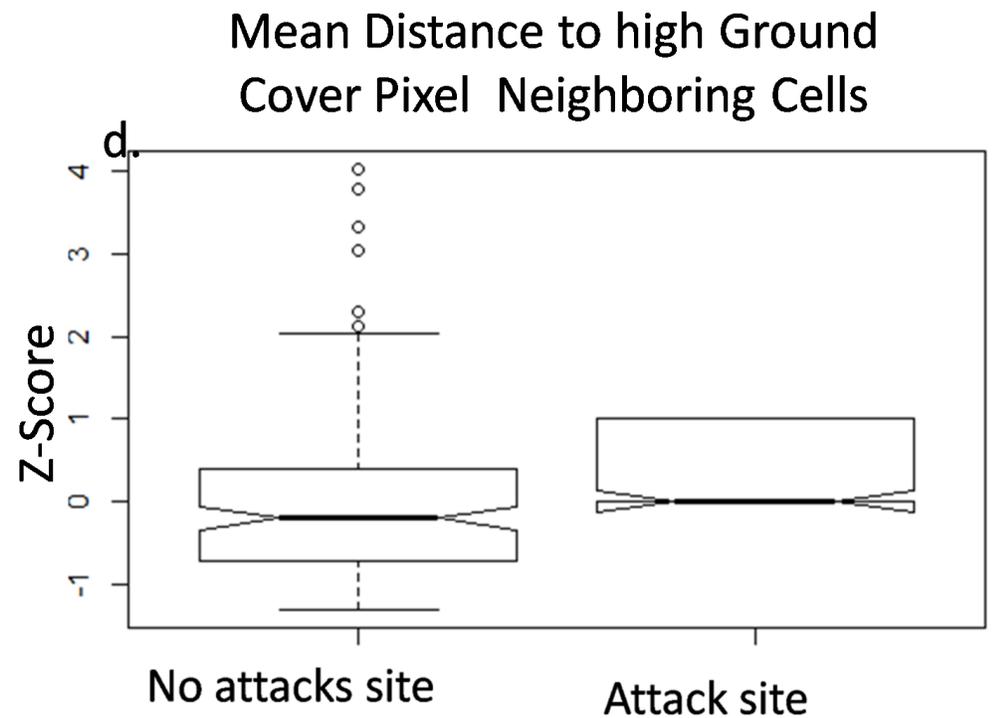
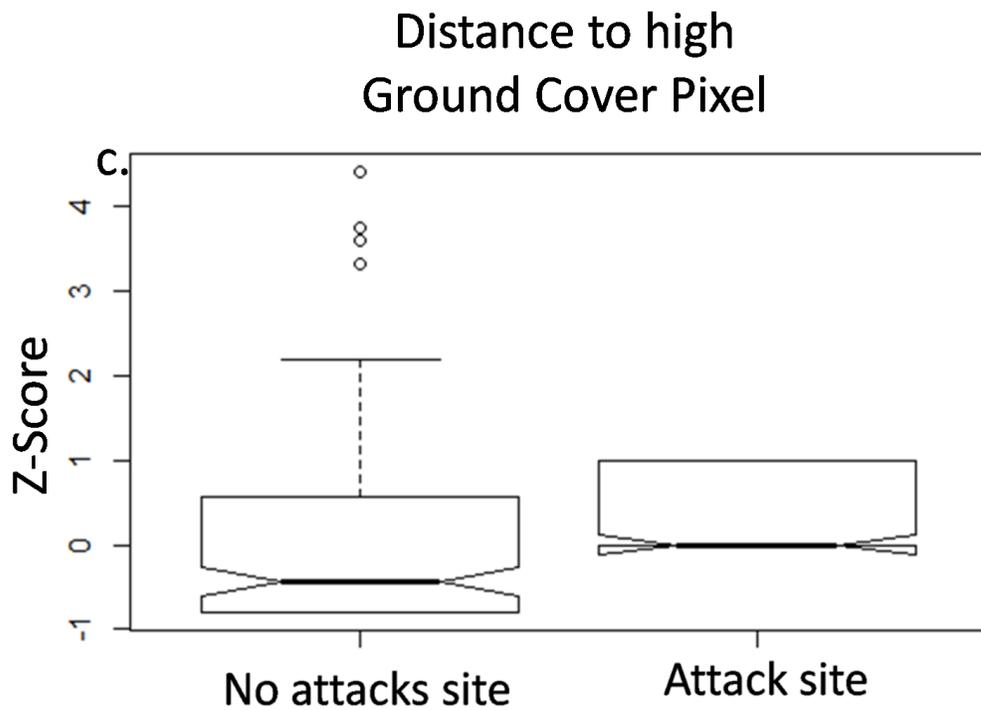
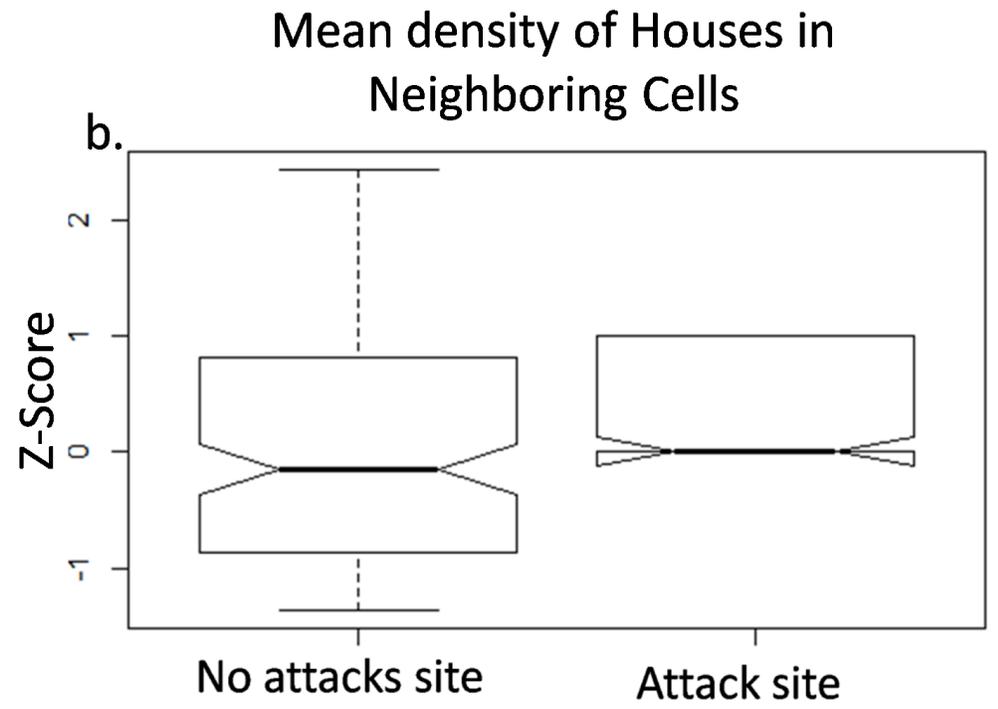
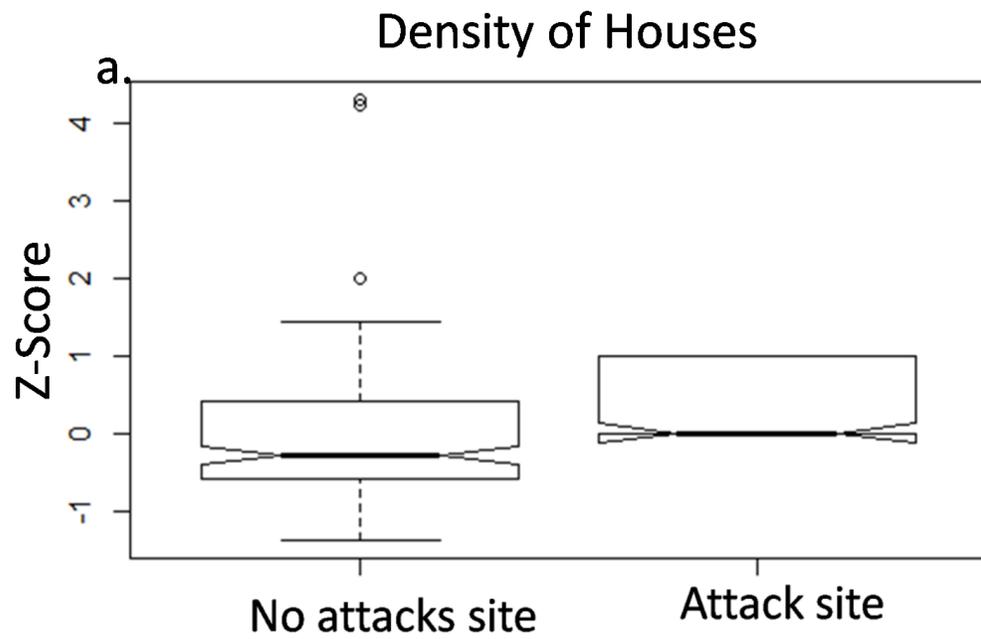
Translocation vs Attacks



Trail Survey Protocol:

A minimum of 2 km was surveyed in each cell, the trails included all roads and animal trails in forests and in case of tea estates, the entire estate was covered by walking in zigzag routes starting from one end of the tea-plantation along existing paths and ending in the diagonally opposite end. It was not possible to survey all routes in tea estates and villages because there were numerous paths and therefore only mud roads were surveyed where signs of pugmarks and scrapes were easily visible. Each trail was surveyed by two observers walking on both sides of the road/trail. GPS coordinates were noted at the beginning of each 200 m segment in the survey route. The 200 m segments were our spatial replicates within each cell. For every segment, presence or absence of leopard signs were noted and indirect signs were noted for prey species as well as for humans, the land cover at each segment was also noted. The available land cover categories were:

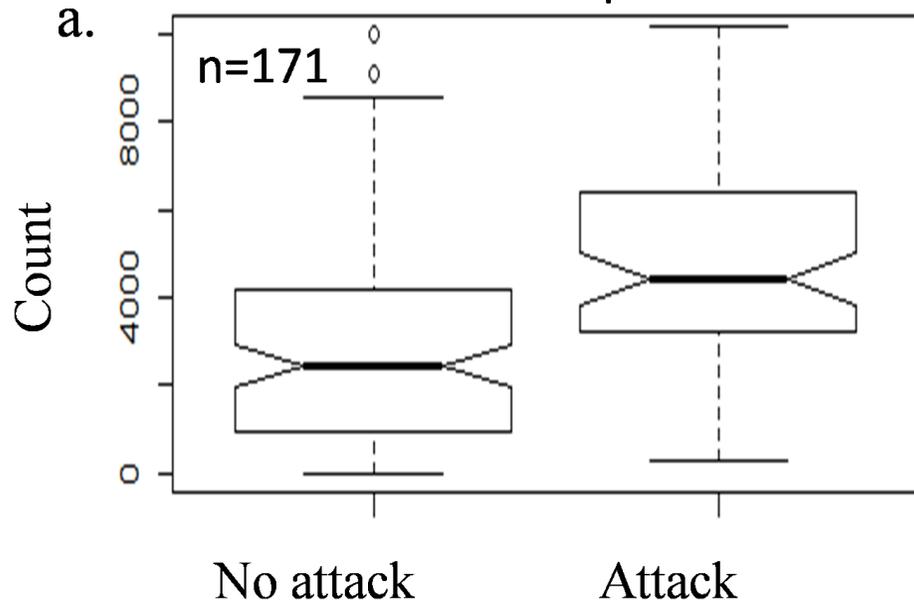
- i. Tea plantations
- ii. Human settlement
- iii. Moist deciduous forest
- iv. Sal/Teak plantation
- v. River bed



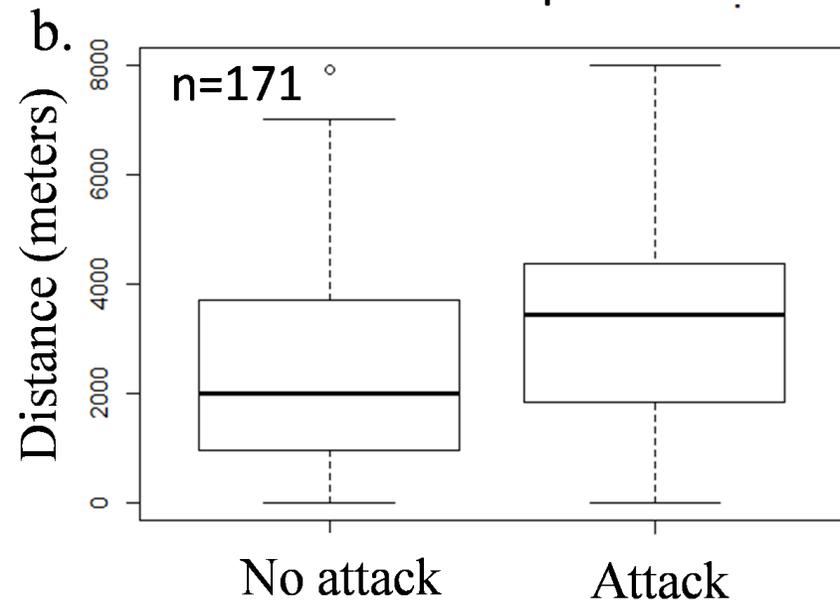
Covariate Development:

The ground based covariates included encounter rate (200 m^{-1}) of humans, goat, cattle, pig, dogs, rhesus macaque, peafowl, jungle fowl, sambar, chital and gaur. Domestic and wild prey species were grouped into size classes of small ($<10 \text{ kg}$), medium ($10\text{-}60 \text{ kg}$) and large ($100\text{-}1000 \text{ kg}$). Data on density of houses, distance to high ground vegetation pixels, distance between cell centroid and nearest river, and nearest forest patch were remotely sensed. Density of houses was also included as a proxy for human presence and was obtained by digitizing all houses in the study area using QGIS 2.0.1-Dufour software (<http://www.qgis.org/en/site>, accessed on September 2013) and the Google Hybrid layer plugin (https://plugins.qgis.org/plugins/openlayers_plugin, accessed on March 2014). A ground vegetation cover layer was developed using Mahalanobis distance from areas of high ground cover. We recorded areas with dense vegetation cover in the field using hand-held GPS device. This covariate was added as leopards are ambush predators and presence of ground vegetation cover could positively influence their site-use (Balme et al., 2007). We recorded coordinates of highest ground vegetation cover areas in field and 50 such points were recorded at a spacing of 500 m or more and these were used as the reference class. A raster stack was developed using LANDSAT 8 (www.usgs.gov) products comprising of the following rasters, the NDVI November 2013, NDVI April 2014, IR April 2014 and difference in NDVI between April 2014 and November 2013. The Mahalanobis distance between the spectral signature of the reference class (high ground vegetation cover points) and the spectral signatures of all other pixels in the study area was the resulting raster. The rivers and the forested areas in the study area were digitized over Google Earth plugin in QGIS (QGIS 2.0.1-Dufour software (<http://www.qgis.org/en/site>, accessed on September 2013) and Google Hybrid layer plugin (https://plugins.qgis.org/plugins/openlayers_plugin, accessed on March 2014). The centroids of the $2\text{km}\times 2\text{km}$ cells were obtained in QGIS and the distance between the cell centroids and nearest River or Forest edge was estimated using package Geosphere in R (Robert et al., 2014). All covariates were normalized to Z scores by subtracting mean and dividing by standard deviation before analyses (Schielzeth, 2010).

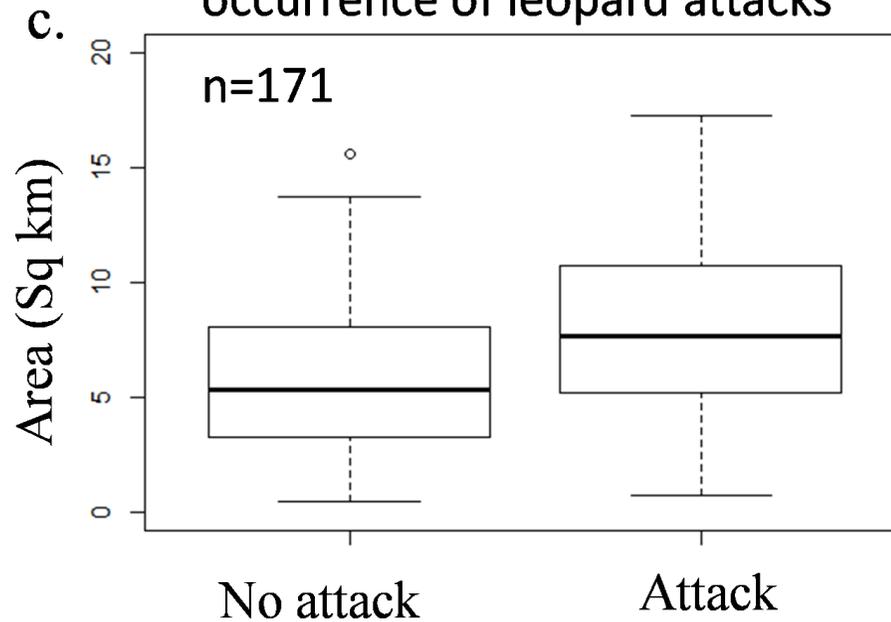
Effect of human population on occurrence of leopard attacks



Effect of distance to forest on occurrence of leopard attacks



Effect of area of tea-plantation on occurrence of leopard attacks



Model	Intercept	SE	$\beta_{\text{house.D}}$	SE	$\beta_{\text{house.nbr}}$	SE	β_{gv}	SE	$\beta_{\text{gv.nbr}}$	SE	Model Weight
$\Psi(\text{house.D}+\text{house.nbr}+\text{gv}), \Theta^0(.), \Theta^1(.), p_t(\text{landcov})$	2.25	2.18	-1.14	1.09	-3.12	2.60	-1.64	1.66			0.35
$\Psi(\text{house.D}+\text{house.nbr}+\text{gvt}+\text{gv.nbr}), \Theta^0(.), \Theta^1(.), p_t(\text{landcov})$	1.58	1.35	-1.19	1.01	-2.08	1.89	-0.91	1.14	-0.53	0.89	0.15
$\Psi(\text{house.nbr}), \Theta^0(.), \Theta^1(.), p_t(\text{landcov})$	1.60	0.73			-2.08	0.97					0.14
$\Psi(\text{house.D}+\text{house.nbr}), \Theta^0(.), \Theta^1(.), p_t(\text{landcov})$	1.35	0.73	-0.83	0.64	-1.64	0.97					0.13
Model Averaged Estimates	1.85	1.20	-1.09	0.62	-2.48	1.53	-1.42	0.77	-0.53	0.89	
AIC wt of covariate			0.63		0.77		0.49		0.15		

Ψ : Probability of habitat-use; house.D: density of houses/buildings; house.nbr: mean density of houses/buildings in neighboring cells; Θ^0 : probability of leopard presence in a replicate conditional on absence in the previous replicate; Θ^1 : probability of leopard presence in a replicate conditional on presence in the previous replicate; p_t : probability of detecting leopard sign in a replicate conditional on presence in the replicate; gv: mean Mahalanobis distance from highest ground vegetation cover pixel; gv.nbr: mean gv in neighboring cells; landcov: land cover type in the replicate.