



# Species-specific spatiotemporal patterns of leopard, lion and tiger attacks on humans

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## Abstract

1. Large carnivores of the genus *Panthera* can pose serious threats to public safety. Although the annual number of attacks on humans is rare compared to livestock depredation, such incidents undermine popular support for wildlife conservation and require immediate responses to protect human life.
2. We used a space–time scan method to perform a novel spatiotemporal analysis of 908 attacks on humans by lions, leopards, and tigers to estimate the risks of further attacks in the same locales.
3. We found that a substantial proportion of attacks were clustered in time and space, but the dimension of these outbreaks varied between species. Lion outbreaks included more human fatalities, persisted for longer periods of time, and extended over larger areas than tiger or leopard outbreaks.
4. *Synthesis and applications.* Our analysis reveals the typical spatiotemporal patterns of past lion, leopard, and tiger attacks on humans. In future, this technique could be used by relevant agencies to warn local people of risks from further attacks within a certain time and distance following an initial incident by each species. Furthermore, the approach can help identify areas requiring management interventions to address such threats.

## KEYWORDS

anthropogenic landscape, attacks on humans, big cats, human–wildlife conflict, *Panthera*, space–time scan, spatiotemporal clustering

## 1 | INTRODUCTION

Despite dramatic declines in carnivore populations over the past century (Ripple et al., 2014), lion *Panthera leo*, leopard *Panthera pardus*, and tiger *Panthera tigris* attacks on humans elicit highly negative responses that present a profound conservation challenge

in many parts of Asia and Africa. Nearly, a thousand people were attacked by African lions in southern Tanzania between 1990 and 2010 (Kushnir, Leitner, Ikanda, & Packer, 2010), between 1999 and 2005 over a thousand people were attacked by leopards in India's Maharashtra State (Athreya, Odden, Linnell, & Ullas Karanth, 2011), and tiger attacks persist in Nepal (Gurung, Smith, McDougal, Karki,

& Barlow, 2008) and India (Werbeck, 2017). World-wide, by far the most common form of human–carnivore conflict is livestock depredation (Inskip & Zimmermann, 2009; Miller, Jhala, Jena, & Schmitz, 2015), thus intensive conflict-mitigation efforts have primarily focused on safeguarding sheep, goats, and cattle (e.g., Hazzah et al., 2014). However, such efforts can have unintended consequences, as in the case of a large-scale translocation of leopards from a region with widespread livestock attacks that subsequently increased the risk and severity of attacks on humans near the release sites (Athreya et al., 2011). Though attacks on humans are comparatively rare, safeguarding human life is paramount, both morally, as there is no justification for accepting persistent threats to human safety, and politically, as loss of life generates intense responses that undermine public support for conserving endangered species.

On a global scale, natural habitats have become increasingly encroached by land conversion and anthropogenic activity (DiMinin et al., 2016), and wildlife species have also colonized areas where they had historically been absent (Gehrt, Riley, & Cypher, 2010), intensifying conflicts deriving from the ecology and human dimension of shared space (Carter & Linnell, 2016; Chapron et al., 2014). Human provocation (e.g., sport hunting or cub capture, as in the case of tiger attacks in the Russian Far East, Goodrich, Seryodkin, Miquelle, & Bereznuik, 2010) may generate isolated incidents, but many other carnivore attacks are clustered in space and time, involving dozens of victims over spans of weeks or months (Athreya et al., 2011; Dhanwatey et al., 2013; Goodrich et al., 2010; Gurung et al., 2008; Kerbis Peterhans & Gnoske, 2001; Packer, Ikanda, Kissui, & Kushnir, 2005; Saberwal, Gibbs, Chellam, & Johnsingh, 1994). This pattern is generally assumed to result from specific individuals learning to recognize humans as prey and subsequently attacking further victims before finally being captured or killed (e.g., “serial human–killers,” Gurung et al., 2008). However, attacks mostly occur at night or with few witnesses (Packer, Swanson, Ikanda, & Kushnir, 2011), and local people seldom, if ever, contact these animals in other contexts, so individual recognition is impossible, and the propensity of an individual attacking repeatedly is almost always inferred rather than confirmed, leaving open an alternative explanation that ecological circumstances may elicit attacks on humans by several different individuals in the same location at the same time.

For example, hundreds of lion attacks in southern Tanzania occurred in jurisdictions where widespread conversion of natural habitat to subsistence agriculture had largely eliminated “normal” lion prey and supported high levels of nocturnal mammalian crop pests (Packer et al., 2005). Lion attacks here were clearly clustered into discrete outbreaks associated with high-risk landscape variables (Kushnir, Olson, Juntunen, Ikanda, & Packer, 2014). Lion attacks in India’s Gir National Park were also clustered in areas of high human activity and presumed to increase during droughts (Saberwal et al., 1994). Leopard attacks in Junnar, India, spiked after large-scale translocations into unfamiliar habitats (Athreya et al., 2011), and non-lethal attacks in tea gardens in West Bengal resulted from leopards reacting defensively to approaching tea workers (Kshetry, Vaidyanathan, & Athreya, 2017).

Attack outbreaks are also likely to be affected by the social system of each carnivore species. Lions live in groups called “prides”

that provide opportunities for social learning (Borrego & Gaines, 2016); thus, if any one pride member starts attacking humans, pride-mates may also adopt the behaviour. In contrast, each solitary leopard or tiger could only learn the behaviour from its mother rather than from its neighbours. Thus, lion outbreaks would be expected to persist for longer periods and eventually include more victims than leopard or tiger outbreaks.

Regardless of the underlying cause, these spatiotemporal clusters can be considered as analogous to outbreaks of infectious disease, allowing the use of epidemiological approaches to characterize the temporal and spatial patterns of carnivore attacks on humans. We use a space–time scan method (Gaudart et al., 2006; Robertson & Nelson, 2010) to demarcate discrete clusters of lion, leopard and tiger attacks on humans in Tanzania, India, and Nepal. We then use geographic information system (GIS) to identify landscape features that are most commonly associated with attack clusters in each species. By comparing the location and timing of successive attacks by the three species, we estimate attack-risks in space and time following an initial incident and assess whether species-specific outbreak patterns arise from their contrasting social systems or result from the geographical constraints of their respective landscapes.

## 2 | MATERIALS AND METHODS

### 2.1 | Spatiotemporal patterns in attacks

We tested for the existence of discrete spatiotemporal clusters using SaTScan (Kulldorff, 1997). High-risk clusters were identified by comparing the observed number of attacks within a null-value window, using a space–time permutation model (Kulldorff, Heffernan, Hartman, Assunção, & Mostashari, 2005a). Space–time scan methods evaluate surveillance data across a geographic region through a series of time intervals using a cylindrical window with a circular geographic base centred on each location (the radius varying from zero to an upper predetermined limit) and with height corresponding to time (Gaudart et al., 2006; Robertson & Nelson, 2010). Space–time permutation is routinely used by public health agencies to detect geographical areas with ongoing spatiotemporal clusters of infectious diseases or cancers (Kulldorff, 2001). For example, identifying new outbreak clusters of tuberculosis (rather than individuals with reactivated latent forms) allowed British public health agencies to focus control efforts in London (Smith, Maguire, Anderson, Macdonald, & Hayward, 2017). This method only requires the location and date of each attack and makes no assumptions about the fine-scale distribution of at-risk humans across the survey area (Kulldorff et al., 2005a), whereas methods such as log-Gaussian Cox processes (Diggle, Moraga, Rowlingson, & Taylor, 2013) assume the at-risk population distribution is either known or is uniform across the landscape (Kulldorff et al., 2005a) which is rarely the case. Not only do space–time scan methods require fewer assumptions, but they also generally outperform spatiotemporal methods and are easier to perform (Mathes et al., 2017), and the SaTScan software is freely available with a graphic user interface requiring minimal epidemiological training (<https://www.SaTScan.org/>).

**TABLE 1** Summary of attack data

Species	Total attacks	No. of clusters	Total # attacks clustered	Prob. of an outbreak	Median attacks per cluster	Median cluster radius (km)	Median duration per cluster (months)	High-risk landscapes
Lions	319	6	155	50%	28	23.10	11	Residential woodlands <sup>a</sup> and recent tree loss <sup>a</sup>
Tigers (NP)	88	5	42	48%	7	5.06	2	Residential woodlands <sup>a</sup>
Tigers (MH)	94	4	22	23%	6	4.07	2	Residential woodlands <sup>a</sup> and mixed settlement <sup>a</sup>
Leopards (HP)	329	6	50	28%	6	1.16	2	Rainfed villages and residential rainfed croplands
Leopards (PU)	78	4	27	17%	5	4.36	2.5	Rainfed villages

Note. NP, Nepal; MH, Maharashtra; HP, Himachal Pradesh; PU, Pune.

<sup>a</sup>Statistically significant landscape classes.

Spatiotemporal clusters were identified from a significant excess of cases occurring within a geographical area over a continuous period of time. Assuming a relatively stable at-risk population size of humans and predators over the duration of the study, the space–time clusters represent locations/times of increased attack risk while integrating both purely spatial and purely temporal clusters. To ensure that these clusters were not merely the product of new human settlements or sudden increases in carnivore population sizes, we checked each cluster for signs of rapid growth in human habitation and found (and removed) one case where translocated leopards had been released into an area. As many study areas only recorded the month of the attack, we used month as the unit of time in our analysis, otherwise, the SaTScan default values were used. Tests for statistical significance were based on a Poisson generalized likelihood ratio, using a bootstrap inference (9,999 permutations). The null hypothesis of “no cluster” was rejected when the simulated P value was less than or equal to 0.05. Supporting Information Appendix S1 provides a step by step vignette of the space–time permutation model in SaTScan version 9.4.

We applied these statistics on 319 lion attacks in a 42,500 km<sup>2</sup> area of southern Tanzania between 1989 and 2008 (see Kushnir et al., 2014), 67 leopard attacks between 1993 and 2003 in 4,100 km<sup>2</sup> of Pune district (PU) of Maharashtra State in India, 329 leopard attacks between 2004 and 2014 in 19,100 km<sup>2</sup> of Himachal Pradesh state (HP), India, 94 tiger attacks between 2005 and 2010 in 2,400 km<sup>2</sup> of Maharashtra state (MH), and 88 tiger attacks in 2,300 km<sup>2</sup> around Chitwan National Park in Nepal (NP) between 1979 and 2006 (Gurung et al., 2008; data in Table 1). All attacks had first been reported to governmental agencies and were subsequently verified through follow-up interviews conducted by members of independent research teams.

Inclusion of each incident in the final dataset required information on date and GPS coordinates. Note that while GPS coordinates may have occasionally been taken within a few hundred metres of the precise location of an attack, any mismeasurements at this scale would not have affected our results, as we have reported spatial estimates to the nearest tenth of a kilometre, and space–time permutation scan statistics have been shown to be minimally affected by inaccuracy in spatial data (Malizia, 2013). A Kruskal–Wallis test was used to test for differences in the spatiotemporal patterns of attack for each species (i.e., attacks per cluster, cluster radius, and cluster duration in months). Dunn post hoc tests for multiple comparisons were used to compare species. Information on group composition was available in most cases, but not a requisite for inclusion in the analysis.

## 2.2 | Landscape simulation analysis

We used a simulation and bootstrap procedure to test whether attack clusters were associated with 19 classes of anthropogenic landscape features at 10 × 10 km resolution from the year 2000 (henceforth referred to as the “anthrome”) as defined by Ellis, Goldewijk, Siebert, Lightman, and Rmankutty (2010). Anthrome classifications were derived via a decision-rule model based on long-term estimates of human population density and percentage

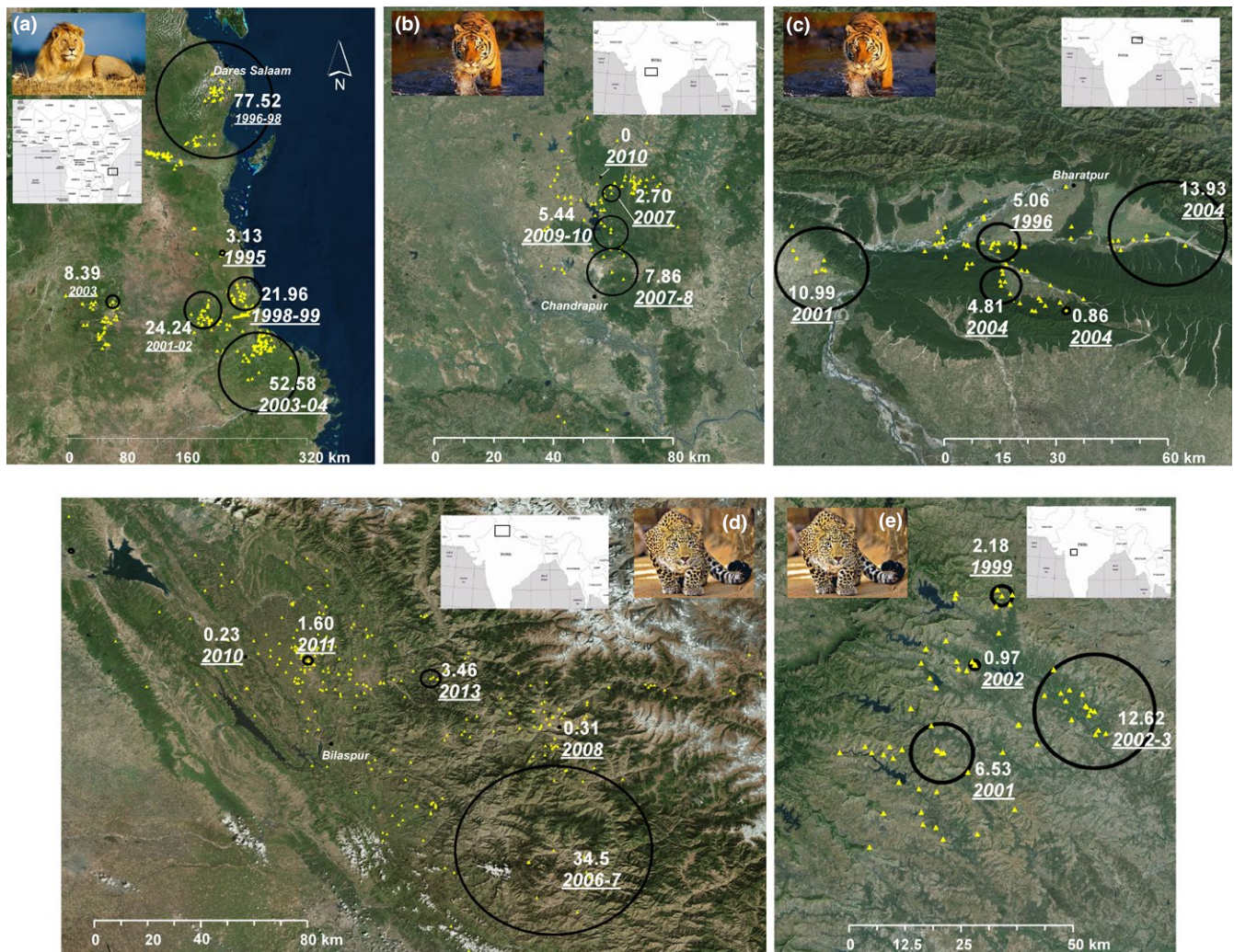
cover in urban, crop and pasture lands (for classifications see Supporting Information Appendix S2). Furthermore, as land conversion is known to alter prey abundance and potentially increase the chances of lion attacks (Kushnir et al., 2014), we included high levels of tree-cover loss as a variable (defined as >30% loss between 2000 and 2012) measured at  $30 \times 30$  m resolution (Hansen et al., 2013). Using the random points and buffer tools in ArcGIS 10.2, we simulated 100 clusters based on average cluster size for each species (Table 1) across southeastern Tanzania (lions) and in the area around Chitwan National Park in Nepal and in Maharashtra, India (tigers). Statistical significance was not calculated for leopards in this analysis as most clusters (4 of 5) were too small to attain robust estimates from the coarse-grained 100-km<sup>2</sup> anthrome data, and, although the tree-loss data were measured at a suitable scale of resolution, the small size of most observed clusters meant that the proportions of tree loss in each leopard cluster were often negligible.

The simulated clusters were bound by suitable habitat for lions (Bauer et al. 2015) and tigers (IUCN, 2016) within grids sized

to reflect the spatial extent of attacks reported by wildlife authorities for each species (500 km<sup>2</sup>: lions; 300 km<sup>2</sup>: leopards [HP]; and 150 km<sup>2</sup>: tigers and leopards [PU]). Each grid was positioned in the landscape based on the centroid of attack locations. We then extracted the proportion of tree cover loss and of each anthrome category for the observed clusters and for the 100 simulated clusters using the *isectpolyst* tools in Geospatial Modeling Environment (Beyer, 2012). The 100 simulated values of each tree loss or anthrome factor were compared to average values from the observed clusters by applying a bootstrap sampling method with replacement (10,000 iterations) to the simulated data. Values of *p* were calculated by comparing the mean of simulation bootstrap samples to the mean of the observed values ( $\mu$ , see Supporting Information Appendix S3 for code).

### 2.3 | Landscape heterogeneity

To assess whether physical dimensions of species-typical attack clusters were imposed by geographical constraints, we developed



**FIGURE 1** Spatiotemporal clusters (circles) of (a) lion attacks in southeastern Tanzania; (b) tiger attacks in Maharashtra, India, and (c) central Nepal; (d) leopard attacks in Himachal Pradesh, India, and (e) Pune, India. Yellow symbols reflect the location of attacks. Values within or next to each cluster indicate cluster radius (km) and the year the outbreak started

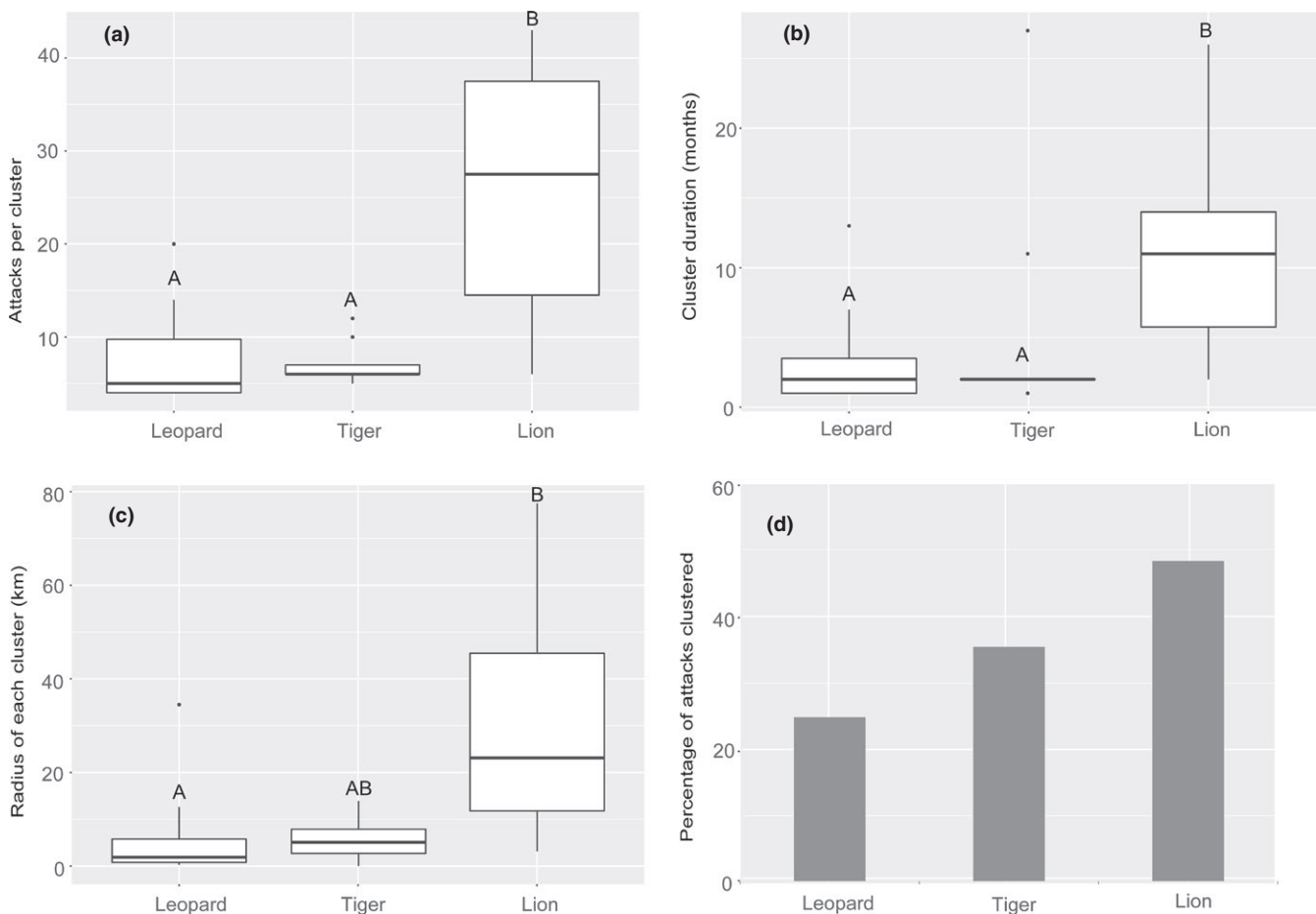
a simple fractal heterogeneity metric based on the number of adjacent 100-km<sup>2</sup> cells belonging to the same anthrome classification. Highly heterogeneous landscapes would form complex checkerboard patterns where each adjacent cell differs from its neighbour, whereas homogeneous landscapes would be characterized by large numbers of adjacent cells with the same anthrome classification.

### 3 | RESULTS

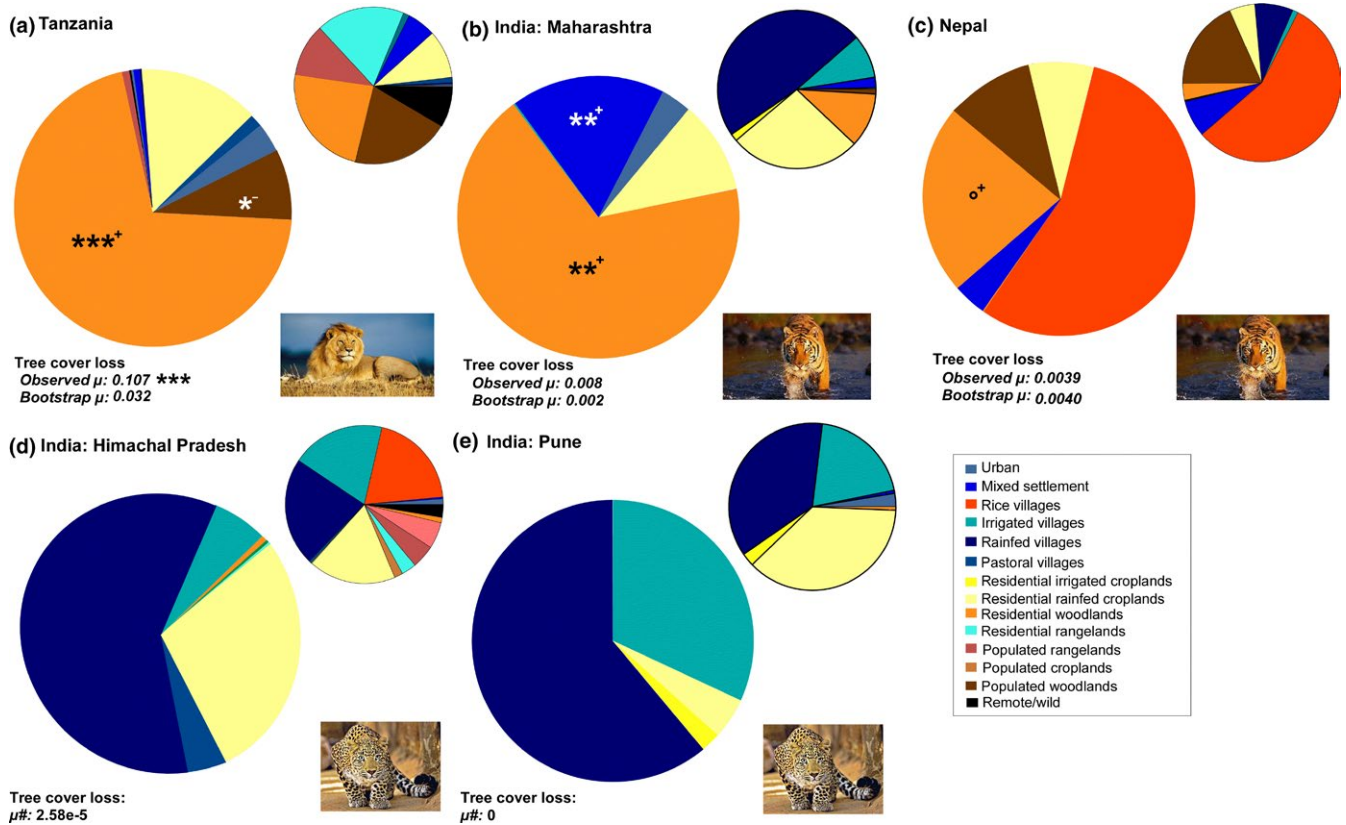
Our space-time scan analysis revealed that attacks on humans showed clear signs of spatiotemporal clustering (Figure 1; Table 1). However, the dimensions of these “outbreaks” varied between species. Lion outbreaks included significantly more attacks (Figure 2a), persisted over marginally longer time intervals (Figure 2b), and extended over significantly greater radii (Figure 2c) than either leopard or tiger outbreaks. About 50% of lion attacks could be classified as belonging to discrete outbreaks, whereas only ~17%–28% of

leopard attacks and 23%–48% of tiger attacks resolved into outbreaks (Figure 2d).

GIS analysis of the attack locations revealed a strong association with the habitat classifications defined in Supporting Information Appendix S2. Lion attacks occurred significantly more often than expected in woodlands populated with 10–100 people/km<sup>2</sup> (“residential woodlands”) and less often than expected in woodlands occupied by only 1–10 people/km<sup>2</sup> (“populated woodlands”; Figure 3a; Supporting Information Appendix S4); lion attacks were also more common in areas of recent tree loss (Supporting Information Appendix S5). Although largely restricted to areas adjacent to the tiger reserves in both Nepal and India, tiger attacks were again more common than expected in residential woodlands (Figure 3b,c; Supporting Information Appendix S4), and tiger attacks in Maharashtra were also associated with mixed settlements. Although leopard attack clusters were too small to test for statistical significance, leopard attacks in both sites largely occurred in agricultural villages (>100 people/km<sup>2</sup>) that are watered by rainfall rather than by irrigation (“rainfed villages”) and leopard attacks in



**FIGURE 2** Spatiotemporal characteristics of attack clusters in each species. (a) Average number of attacks per cluster for each species (Kruskal–Wallis  $\chi^2 = 9.54$ ,  $p = 0.0008$ ). (b) Average duration of attack clusters (Kruskal–Wallis  $\chi^2 = 5.85$ ,  $p = 0.054$ ), (c) Average radius of attack clusters (Kruskal–Wallis  $\chi^2 = 7.22$ ,  $p = 0.027$ ). “A” and “B” above respective boxplots designate significant (Benjamini–Hochberg adjusted  $p < 0.05$ ) post hoc groupings, AB indicates that this group was not significantly different from groups “A” or “B.” (d) Percentage of attacks classified within spatiotemporal clusters for leopards, tigers and lions



**FIGURE 3** Proportion of anthropogenic landscape classifications (large pie charts) and the surrounding landscapes (small pie charts) for attack clusters for (a) lions, (b/c) tigers, and (d/e) leopards. Effects of tree-cover loss between 2000 and 2012 are listed at the bottom left corner of each panel;  $\mu\#$ : mean derived from the area around the attack clusters (see Section 2). Statistical significance was determined by simulation and a bootstrap procedure (observed  $\mu$  vs. bootstrap, see Section 2). °  $p = 0.05$ – $0.1$ , \*  $p = 0.01$ – $0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.0001$ . ° observed mean was significantly smaller than the bootstrap estimate, °+ observed mean was significantly larger. Leopards (d/e) were excluded from the bootstrap analysis due to the small size of clusters relative to landscape features

Himachal Pradesh frequently occurred in “rainfed croplands” with 10–100 people/km<sup>2</sup> (Figure 3d,e).

To test whether geography might have constrained the radius of attack clusters in each species, we measured the fractal heterogeneity of comparable, relevant landscape features in the different study areas. In leopards, attacks at both sites were most common in rainfed villages, and the landscape heterogeneity metric was notably higher in rainfed villages in Himachal Pradesh than in Pune (Supporting Information Appendix S6b). Consistent with landscape heterogeneity constraining attack-cluster radii, leopard outbreaks were smaller in HP (1.2 km) than in PU (4.4 km) though this difference was not statistically significant. For lions in Tanzania and tigers in Maharashtra, attacks were most common in residential woodlands, and the heterogeneity metric for this habitat was essentially identical in the two study areas (Supporting Information Appendix S6a). However, the median attack-cluster radius in lions (23 km) was far higher than in the tiger outbreaks in Maharashtra (4.1 km), even though lion and tiger outbreaks in these two areas might be expected to experience similar constraints from landscape heterogeneity.

Data on group size were strikingly different between the three species. Out of 310 attacks where group composition could be estimated, 72% involved two or more adult lions, 20% involved a lone

male and 8% involved a lone female. In contrast, all 88 tiger attacks in Nepal involved a lone adult (Gurung et al., 2008), as was also the case in the leopard attacks in Pune.

## 4 | DISCUSSION

Typical of rare yet spectacular dangers (see Slovic, 1987), vulnerable communities greatly exaggerate their personal risks from carnivore attacks. For example, Kushnir and Packer (in press) found that 40% of people in the man-eating areas of southern Tanzania considered themselves to be at a similar personal risk from lion attacks as from HIV/AIDS, malaria or famine, even though the latter three hazards were each at least twenty times more likely. Perceptions that wildlife authorities value endangered species over human life can lead to protests and even riots, as in the case of a man-eating tiger in Ranthambore, India in 2015. Thus, we set out to provide tools that could be used by conservation agencies to anticipate the timing and location of future attacks by animals that are almost never seen between incidents.

Our analysis was designed, first, to determine whether lion, leopard, and tiger attacks typically occurred in discrete outbreaks and, second, to characterize the dimensions of these outbreaks in time and

space. All three species showed non-random “clusters” of attacks on humans, but patterns differed considerably between species. Nearly half of all lion attacks in Tanzania and tiger attacks in Nepal occurred within well-defined bursts of activity (Figure 1a,c), whereas the majority (72%–83%) of tiger attacks in Maharashtra and leopard attacks were widely dispersed (Figure 1b,d,e). As predicted, lion outbreaks included more victims, persisted for longer periods, and extended over broader radii than either leopard or tiger outbreaks (Figure 2a–c).

We investigated the landscape features associated with outbreaks for two reasons. First, to assess whether anthropogenic activities increased the risks of carnivore attacks. Lion and tiger outbreaks were disproportionately located in residential woodlands habitat with 10–100 people per square kilometre, and lions also attacked more people in areas with recent loss of tree cover (Figure 3a,b). At a local level, leopard attacks in both study areas were over-represented in rainfed villages; in Himachal Pradesh, attacks were also more common in rainfed croplands with 10–100 people/km<sup>2</sup> (Figure 3d). Second, to determine whether differences in habitat heterogeneity in Asia and Africa may have accounted for the differences in attack radii between the three species. While the higher landscape heterogeneity in rainfed-village habitat in Himachal Pradesh may have played a role in the slightly smaller outbreak radii in Himachal Pradesh compared to leopard outbreaks in Pune, heterogeneities were virtually identical in residential woodlands in Tanzania and Maharashtra, and the lion outbreaks in Tanzania were spread over far greater areas than tiger attacks in Maharashtra (Table 1). Thus, spatial constraints imposed by the respective environments in India, Tanzania and Nepal are unlikely to have played a major role in the contrasting spatial dimensions of attack clusters between the three species. Note that while it is possible that our analysis may have failed to capture relevant landscape changes over the time span of the study, the tree-loss data measured changes from 2000 to 2012, and the attack outbreaks spanned from 1995 to 2013 so any mismatch was unlikely to have been substantial.

Our datasets were too limited to make strong inferences about the underlying factors that elicited attacks on humans in the three study species. For example, even though there was an effect of tree loss on lion attacks in Tanzania, we cannot say whether these occurred because the areas had recently been settled or because of effects on the lions' usual prey in the disturbed habitats. However, the majority of cases appeared to involve the deliberate targeting of humans: 65% of 815 lion attacks reported across all of Tanzania between 1990 and 2004 were fatal (Packer et al., 2005), as were 100% of the 88 tiger attacks in Nepal (Gurung et al., 2008), and 62% of 95 tiger attacks reported here for Maharashtra. Fatality rates are not known for the leopard data, but 54% of 52 classifiable attacks in Pune were considered predatory, and half the attacks in both Pune (51%,  $n = 61$ ) and Himachal Pradesh (54%,  $n = 297$ ) occurred at night, when 76% of the attacks in Pune were considered predatory ( $n = 21$  classifiable night-time attacks vs. 39% of 31 classifiable daytime attacks,  $p = 0.0111$ , two-tailed, Fisher test). In contrast, there were no mortalities in the daytime attacks described by Kshetry et al. (2017) where leopards reacted defensively to inadvertent encounters with workers on tea plantations.

Strikingly, the majority (72%) of lion attacks involved two or more lions, whereas all of the leopard and tiger attacks were by single individuals. Taken together, the circumstantial evidence is consistent with the following scenario: for whatever reason an individual first attacks a human, about half of the lions, a quarter to half of the tigers, and a quarter of the leopards subsequently attack repeatedly (column 5 in Table 1). In leopards and tigers, these individuals continue to attack humans either until they are killed or abandon the behaviour, but their solitary habits do not allow the “cultural” spread of the behaviour to other members of the population. Thus, a leopard- or tiger-attack outbreak is usually brief and restricted to a single animal. In contrast, lions live in fission-fusion social groups (“prides”), and pride-mates often move together, so once one pride member attacks a human, its companions often adopt the same behaviour. But lions also forage alone, so pride-mates may attack separate victims during the same outbreak, and, thus, a lion outbreak will generally involve multiple individuals who continue attacking humans until the entire pride has been eliminated.

While this scenario may help to explain the contrasting scale of discrete outbreaks, it does not address why so many leopard attacks in both study areas and tiger attacks in Maharashtra occurred in apparent isolation from each other. One possible explanation—at least for leopards, where human fatalities appear to have been rare—is that a higher proportion of attacks involved reactions to disturbance (as described by Kshetry et al., 2017) rather than unprovoked attempts to capture humans as prey. Indeed, a substantial proportion of leopard attacks in Pune occurred during the daytime, when only about 40% of cases were considered predatory (see above).

Table 1 summarizes the spatiotemporal characteristics of leopard, lion, and tiger outbreaks. Given an initial attack, subsequent attacks are likely to follow a characteristic pattern in each species. Thus, as in tracking the spread of infectious disease, statistical techniques such as SaTScan could be used in real-time by relevant organizations to detect the onset of an outbreak and provide an early warning system to inform local inhabitants and park/wildlife management authorities so as to take action in anticipation of a potential cluster of further carnivore attacks. Longer term conflict-mitigation efforts could also be focused in these areas. We also recommend that wildlife agencies take care to collect dates and GPS coordinates for every incident within their jurisdiction: while we were able to utilize virtually all lion and tiger data, we were forced to exclude 87 leopard attacks from Himachal Pradesh (allowing consideration of only 329 out of 416 attacks).

Note that there are several general limitations of space-time permutation approaches. First, although we found circles to be the most suitable configuration for defining attack clusters, long and narrow outbreaks may not be accurately identified (Kulldorff, Heffernan, Hartman, Assunção, & Mostashari, 2005b). We found no evidence for this pattern in our data, but it could exist where, say, attacks are restricted to the outer edge of a large urban area. Second, if attacks are homogeneously distributed across an entire survey area, space-time models will only detect localized perturbations in risk (Kulldorff et al., 2005a). However, the SaTScan method is the best option for detecting localized clusters in areas where little information is available on the human or wildlife populations. Finally, note that while the tree-loss data largely matched

the time-scale of our datasets, longer term studies may span periods of substantial (and undocumented) anthropogenic changes.

We restricted our analysis to lions, tigers, and leopards because of the large sample size available on each species: although pumas, jaguars, and wolves are all known to attack humans, such incidents are too rare to provide similar insights. Attacks on livestock by lions, leopards and tigers are more common than on humans, but the human datasets are far more amenable to detailed statistical analysis because of the requisite record-keeping whenever a citizen is injured or killed by wildlife. Nevertheless, our statistical approach could certainly be applied wherever comprehensive detailed data exist on depredation of domestic animals and thus have general utility for characterizing outbreaks of livestock-killing by a wide range of felids (caracal, cheetah, jaguar, lynx, pumas, snow leopard, Inskip & Zimmermann, 2009; Miller et al., 2015), and other carnivore species (e.g., wolves, bears, etc.).

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## AUTHORS' CONTRIBUTIONS

C.P. designed the study; N.M.F.-J. analysed the spatiotemporal data; S.S., V.A., H.D., P.D., B.G., H.K., and J.D.C.L. collected data for the study; A.J. provided GIS layers; and C.P., V.A., M.C., A.J., J.D.C.L., and N.M.F.-J. contributed to the writing of the manuscript. All authors have approved this manuscript for publication.

## DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.bt5j6k4> (Packer et al., 2018).

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## REFERENCES

- Athreya, V., Odden, M., Linnell, J. D. C., & Ullas Karanth, K. (2011). Translocation as a tool for mitigating conflict with leopards in human-dominated landscapes of India. *Conservation Biology*, 25, 133–141. <https://doi.org/10.1111/j.1523-1739.2010.01599.x>
- Bauer, H., Nowell, K., Henschel, P., Funston, P., Chapron, G., Hunter, L., ... Packer, C. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences of the USA*, 112, 14894–14899. <https://doi.org/10.1073/pnas.1500664112>
- Beyer, H. B. L. (2012). Geospatial modelling environment. Retrieved from <http://www.spatial ecology.com/gme/>
- Borrego, N., & Gaines, M. (2016). Social carnivores outperform asocial carnivores on an innovative problem. *Animal Behaviour*, 114, 21–26. <https://doi.org/10.1016/j.anbehav.2016.01.013>
- Carter, N. H., & Linnell, J. D. C. (2016). Co-adaptation is key to coexisting with large carnivores. *Trends in Ecology & Evolution*, 31(8), 575–578. <https://doi.org/10.1016/j.tree.2016.05.006>
- Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andr n, H., & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346(6216), 1517–1519. <https://doi.org/10.1126/science.1257553>
- Dhanwatey, H. S., Crawford, J. C., Abade, L. A. S., Dhanwatey, P. H., Nielsen, C. K., & Sillero-Zubiri, C. (2013). Large carnivore attacks on humans in central India: A case study from the Tadoba-Andhari Tiger Reserve. *Oryx*, 47(02), 221–227. <https://doi.org/10.1017/S0030605311001803>
- Diggle, P. J., Moraga, P., Rowlingson, B., & Taylor, B. M. (2013). Spatial and spatio-temporal log-gaussian cox processes: Extending the geo-statistical paradigm. *Statistical Science*, 28, 542–563. <https://doi.org/10.1214/13-TS441>
- DiMinin, E., Slotow, R., Hunter, L. T. B., Montesino Pouzols, F., Toivonen, T., Verburg, P. H., ... Moilanen, A. (2016). Global priorities for national carnivore conservation under land use change. *Scientific Reports*, 6, 23814. <https://doi.org/10.1038/srep23814> <https://doi.org/10.1038/srep23814>
- Ellis, E. C., Goldewijk, K. K., Siebert, S., Lightman, D., & Rmankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, 19, 589–606.
- Gaudart, J., Poudiougou, B., Dicko, A., Ranque, S., Toure, O., Sagara, I., ... Doumbo, O. K. (2006). Space-time clustering of childhood malaria at the household level: A dynamic cohort in a Mali village. *BMC Public Health*, 6, 286. <https://doi.org/10.1186/1471-2458-6-286>
- Gehrt, S. D., Riley, S. P. D., & Cypher, B. L. (2010). *Urban carnivores*. Baltimore, MD: Johns Hopkins University Press.
- Goodrich, J. M., Seryodkin, I., Miquelle, D. G., & Bereznuik, S. L. (2010). Conflicts between Amur (Siberian) tigers and humans in the Russian Far East. *Biological Conservation*, 144, 584–592. <https://doi.org/10.1016/j.biocon.2010.10.016>
- Gurung, B., Smith, J. L. D., McDougal, C., Karki, J. B., & Barlow, A. (2008). Factors associated with human-killing tigers in Chitwan National Park, Nepal. *Biological Conservation*, 141, 3069–3078. <https://doi.org/10.1016/j.biocon.2008.09.013>
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Townshend, J. R. G. (2013). High-resolution global maps of 21st century forest cover change. *Science*, 342, 850–853. <https://doi.org/10.1126/science.1244693>
- Hazzah, L., Dolrenry, S., Naughton, L., Edwards, C. T. T., Mwebi, O., Kearney, F., & Frank, L. (2014). Efficacy of two lion conservation programs in Maasailand, Kenya. *Conservation Biology*, 28, 851–860. <https://doi.org/10.1111/cobi.12244>
- Inskip, C., & Zimmermann, A. (2009). Human-felid conflict: A review of patterns and priorities worldwide. *Oryx*, 43(1), 18–34. <https://doi.org/10.1017/S003060530899030X>
- IUCN. (2016). *The IUCN Red List of Threatened Species*. Version 2016-3. Retrieved from <http://www.iucnredlist.org>
- Kerbis Peterhans, J. C., & Gnoske, T. P. (2001). The science of 'Man-eating' among lions (*Panthera leo*) with a reconstruction of the natural history of the 'Man eaters of Tsavo'. *Journal of East African Natural History*, 90, 1–40. [https://doi.org/10.2982/0012-8317\(2001\)90\[1:TSOMAL\]2.0.CO;2](https://doi.org/10.2982/0012-8317(2001)90[1:TSOMAL]2.0.CO;2)
- Kshetry, A., Vaidyanathan, S., & Athreya, V. (2017). Leopard in a teacup: A study of leopard habitat-use and human-leopard interactions



- in north-eastern India. *PLoS ONE*, 12(5), w0177013. <https://doi.org/10.1371/journal.pone.0177013>
- Kulldorff, M. (1997). A spatial scan statistic. *Communications in Statistics: Theory and Methods*, 26, 1481–1496. <https://doi.org/10.1080/03610929708831995>
- Kulldorff, M. (2001). Prospective time-periodic geographical disease surveillance using a scan statistic. *Journal of the Royal Statistical Society*, <https://doi.org/10.1111/1467-985X.00186>
- Kulldorff, M., Heffernan, R., Hartman, J., Assunção, R. M., & Mostashari, F. (2005a). A space-time permutation scan statistic for the early detection of disease outbreaks. *PLoS Medicine*, 2, 216–224.
- Kulldorff, M., Heffernan, R., Hartman, J., Assunção, R., & Mostashari, F. (2005b). A space-time permutation scan statistic for disease outbreak detection. *PLOS Medicine*, 2, e59. <https://doi.org/10.1371/journal.pmed.0020059>
- Kushnir, H., Leitner, H., Ikanda, D., & Packer, C. (2010). Human and ecological risk factors for unprovoked lion attacks on humans in south-eastern Tanzania. *Human Dimensions of Wildlife*, 15, 315–331. <https://doi.org/10.1080/10871200903510999>
- Kushnir, H., Olson, E., Juntunen, T., Ikanda, D., & Packer, C. (2014). Using landscape characteristics to predict risk of lion attacks in southeastern Tanzania. *African Journal of Ecology*, 52, 524–532. <https://doi.org/10.1111/aje.12157>
- Kushnir, H., & Packer, C. (in press). Reality vs. perception: How rural Tanzanians view risks from man-eating lions. *Frontiers in Ecology and Evolution*.
- Malizia, N. (2013). Inaccuracy, uncertainty and the space-time permutation scan statistic. *PLoS ONE*, 8, e52034. <https://doi.org/10.1371/journal.pone.0052034>
- Mathes, R. W., Lall, R., Levin-Rector, A., Sell, J., Paladini, M., Konty, K. J., ... Weiss, D. (2017). Evaluating and implementing temporal, spatial, and spatio-temporal methods for outbreak detection in a local syndromic surveillance system. *PLoS ONE*, 12, e0184419. <https://doi.org/10.1371/journal.pone.0184419>
- Miller, J. R. B., Jhala, Y. V., Jena, J., & Schmitz, O. J. (2015). Landscape-scale accessibility of livestock to tigers: Implications of spatial grain for modeling predation risk to mitigate human-carnivore conflict. *Ecology and Evolution*, 5, 1354–1367. <https://doi.org/10.1002/ece3.1440>
- Packer, C., Ikanda, D., Kissui, B., & Kushnir, H. (2005). Ecology: Lion attacks on humans in Tanzania. *Nature*, 436, 927–928. <https://doi.org/10.1038/436927a>
- Packer, C., Shivakumar, S., Athreya, V., Craft, M. E., Dhanwatey, H., Dhanwatey, P., ... Fountain-Jones, N. M. (2018). Data from: Species-specific spatio-temporal patterns of leopard, lion and tiger attacks on humans. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.bt5j6k4>
- Packer, C., Swanson, A., Ikanda, D., & Kushnir, H. (2011). Fear of darkness, the full moon and the lunar ecology of African lions. *PLoS ONE*, 6, e22285. <https://doi.org/10.1371/journal.pone.0022285>
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484. <https://doi.org/10.1126/science.1241484>
- Robertson, C., & Nelson, T. A. (2010). Review of software for space-time disease surveillance. *International Journal of Health Geographics*, 9, 16. <https://doi.org/10.1186/1476-072X-9-16>
- Saberwal, V. K., Gibbs, J. P., Chellam, R., & Johnsingh, A. (1994). Lion-human conflict in the Gir Forest, India. *Conservation Biology*, 8, 501–507. <https://doi.org/10.1046/j.1523-1739.1994.08020501.x>
- Slovic, P. (1987). Perception of risk. *Science*, 236(4799), 280–285. <https://doi.org/10.1126/science.3563507>
- Smith, C. M., Maguire, H., Anderson, C., Macdonald, N., & Hayward, A. C. (2017). Multiple large clusters of tuberculosis in London: A cross-sectional analysis of molecular and spatial data. *ERJ Open Research*, 3, 00098–2016. <https://doi.org/10.1183/23120541.00098-2016>
- Werbeck, N. (2017). Dramatic pictures reveal clashes between people and tigers. Retrieved from <http://www.nationalgeographic.com/photography/proof/2017/02/human-vs-tiger-conflict/>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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