

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

Craig Packer^{1,2}, Shweta Shivakumar³, Vidya Athreya³, Meggan E. Craft⁴, Harshawardhan Dhanwatey⁵, Poonam Dhanwatey⁵, Bhim Gurung⁶, Anup Joshi⁷, Hadas Kushnir⁸, John D. C. Linnell⁹, & Nicholas M. Fountain-Jones⁴

1. Dept. of Ecology, Evolution and Behavior, Univ. Minnesota, St. Paul, MN 55108, USA
2. School of Life Sciences, Univ. KwaZulu-Natal, Pietermaritzburg, 3209, South Africa
3. Wildlife Conservation Society-India, #551, Rajiv Gandhi Nagar, 7th Main Road, Kodigehalli, Bengaluru, Karnataka 560097, India.
4. Dept. of Veterinary Population Medicine, Univ. Minnesota, St Paul, MN 55108, USA
5. Tiger Research and Conservation Trust, Nagpur 440010, India
6. Nepal Tiger Trust, Bharatpur-27, Meghauly, Chitwan, Nepal
7. Conservation Sciences Program, University of Minnesota, St. Paul, MN 55108, USA
8. United States Agency for International Development, Washington, DC, USA
9. Norwegian Institute for Nature Research, PO Box 5685 Torgard, NO-7485 Trondheim, Norway

Email addresses: Craig Packer (packer@umn.edu), Shweta Shivakumar (envishweta@gmail.com), Meggan Craft (craft@umn.edu), Harshawardhen Dhanwatey (hdhanwatey@hotmail.com), Poonam Dhanwatey (pdhanwatey@hotmail.com), Bhim Gurung (guru0023@umn.edu), Anup Joshi (joshi002@umn.edu), Hadas Kushnir (hadaskushnir1@gmail.com), Vidya Athreya (vidya.athreya@gmail.com), John Linnell (john.linnell@nina.no), Nicholas Fountain-Jones (nfj@umn.edu)

Running title: Spatiotemporal patterns of attacks on humans

Keywords: Panthera, human-wildlife conflict, spatiotemporal clustering, space-time scan, anthropogenic landscape, attacks on humans, big cats

Type of Article: Letter

Abstract: 152 words

Main text: 3599 words

Number of references: 31

Number of figures: 3

Number of tables: 1

Corresponding author: Craig Packer, Dept. EEB, 1987 Upper Buford Circle, St. Paul, MN 55108. Tel: 612-625-5729 Fax: 612-624-6777 packer@umn.edu

39 **Abstract**

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

56

57

58 **Introduction**

59 Despite dramatic declines in carnivore populations over the past century (Ripple, et al.
60 2014), lion (*Panthera leo*), leopard (*Panthera pardus*) and tiger (*Panthera tigris*) attacks on
61 humans elicit highly negative responses that present a profound conservation challenge in many
62 parts of Asia and Africa. Nearly a thousand people were attacked by African lions in southern
63 Tanzania between 1990-2010 (Kushnir et al. 2010), between 1999-2005 over a thousand people
64 were attacked by leopards in India's Maharashtra State (Athreya, et al. 2011), and tiger attacks
65 persist in Nepal (Gurung et al. 2008) and India (Werbeck 2017). Worldwide, by far the most
66 common form of human-carnivore conflict is livestock depredation (Inskip & Zimmermann
67 2009; Miller et al. 2015), thus intensive conflict-mitigation efforts have primarily focused on
68 safeguarding sheep, goats and cattle (e.g., Hazzah, et al. 2014). However, such efforts can have
69 unintended consequences, as in the case of a large-scale translocation of leopards from a region
70 with widespread livestock attacks that subsequently increased the risk and severity of attacks on
71 humans near the release sites (Athreya, et al. 2011). Though attacks on humans are
72 comparatively rare, safeguarding human life is paramount, both morally, as there is no
73 justification for accepting persistent threats to human safety, and politically, as loss of life
74 generates intense responses that undermine public support for conserving endangered species.

75 On a global scale, natural habitats have become increasingly encroached by land
76 conversion and anthropogenic activity (DiMinin, et al. 2016), and wildlife species have also
77 colonized areas where they had historically been absent (Gehrt et al. 2010), intensifying conflicts
78 deriving from the ecology and human dimension of shared space (Carter & Linnell 2016;
79 Chapron et al. 2014). Human provocation (e.g., sport hunting or cub capture, as in the case of
80 tiger attacks in the Russian Far East, Goodrich et al. 2010) may generate isolated incidents, but

81 many other carnivore attacks are clustered in space and time, involving dozens of victims over
82 spans of weeks or months (Saberwal et al. 1994; Kerbis Peterhans & Gnoske 2001; Packer et al.
83 2005; Gurung et al. 2008; Goodrich et al. 2010; Athreya et al. 2011; Dhanwatey et al. 2013).
84 This pattern is generally assumed to result from specific individuals learning to recognize
85 humans as prey and subsequently attacking further victims before finally being captured or killed
86 (e.g., “serial human-killers,” Gurung, et al. 2008). However, attacks mostly occur at night or
87 with few witnesses (Packer, et al. 2011), and local people seldom, if ever, contact these animals
88 in other contexts, so individual recognition is impossible, and the propensity of an individual
89 attacking repeatedly is almost always inferred rather than confirmed, leaving open an alternative
90 explanation that ecological circumstances may elicit attacks on humans by several different
91 individuals in the same location at the same time.

92 For example, hundreds of lion attacks in southern Tanzania occurred in jurisdictions
93 where widespread conversion of natural habitat to subsistence agriculture had largely eliminated
94 “normal” lion prey and supported high levels of nocturnal mammalian crop pests (Packer, et al.
95 2005). Lion attacks here were clearly clustered into discrete outbreaks associated with high-risk
96 landscape variables (Kushnir, et al. 2014). Lion attacks in India’s Gir National Park were also
97 clustered in areas of high human activity and presumed to increase during droughts (Saberwal et
98 al. 1994). Leopard attacks in Junnar, India, spiked after large-scale translocations into unfamiliar
99 habitats (Athreya et al. 2011), and non-lethal attacks in tea gardens in West Bengal resulted from
100 leopards reacting defensively to approaching tea workers (Kshetry et al. 2017).

101 Attack outbreaks are also likely to be affected by the social system of each carnivore
102 species. Lions live in groups called “prides” that provide opportunities for social learning
103 (Borrego & Gaines 2016), thus if any one pride member starts attacking humans, pride-mates

104 may also adopt the behavior. In contrast, each solitary leopard or tiger could only learn the
105 behavior from its mother rather than from its neighbors. Thus, lion outbreaks would be expected
106 to persist for longer periods and eventually include more victims than leopard or tiger outbreaks.

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

117

118 **Materials and Methods**

119 *Spatiotemporal patterns in attacks.* We tested for the existence of discrete spatiotemporal
120 clusters using SaTScan (Kulldorf, 1997). High-risk clusters were identified by comparing the
121 observed number of attacks within a null-value window, using a space-time permutation model
122 (Kulldorff et al. 2005). Space-time scan methods evaluate surveillance data across a geographic
123 region through a series of time intervals using a cylindrical window with a circular geographic
124 base centered on each location (the radius varying from zero to an upper predetermined limit)
125 and with height corresponding to time (Gaudart, et al. 2006, Robertson, et al. 2010). Space-time
126 permutation is routinely used by public health agencies to detect geographical areas with

127 ongoing spatiotemporal clusters of infectious diseases or cancers (Kulldorff, 2001). For example,
128 identifying new outbreak clusters of tuberculosis (rather than individuals with reactivated latent
129 forms) allowed British public health agencies to focus control efforts in London (Smith et al,
130 2017). This method only requires the location and date of each attack and makes no assumptions
131 about the fine-scale distribution of at-risk humans across the survey area (Kulldorff et al. 2005),
132 whereas methods such as log-Gaussian Cox processes (Diggle et al, 2012) assume the at-risk
133 population distribution is either known or is uniform across the landscape (Kulldorff et al. 2005)
134 which is rarely the case. Not only do space-time scan methods require fewer assumptions, but
135 they also generally outperform spatiotemporal methods and are easier to perform (Mathes et al
136 2017), and the SaTScan software is freely available with a graphic user interface requiring
137 minimal epidemiological training (<https://www.SaTScan.org/>).

138 Spatiotemporal clusters were identified from a significant excess of cases occurring
139 within a geographic area over a continuous period of time. Assuming a relatively stable at-risk
140 population size of humans and predators over the duration of the study, the space-time clusters
141 represent locations/times of increased attack risk while integrating both purely spatial and purely
142 temporal clusters. To ensure that these clusters were not merely the product of new human
143 settlements or sudden increases in carnivore population sizes, we checked each cluster for signs
144 of rapid growth in human habitation and found (and removed) one case where translocated
145 leopards had been released into an area. As many study areas only recorded the month of the
146 attack, we used month as the unit of time in our analysis, otherwise, the SaTScan default values
147 were used. Tests for statistical significance were based on a Poisson generalized likelihood ratio,
148 using a bootstrap inference (9999 permutations). The null hypothesis of “no cluster” was rejected

149 when the simulated P value was less than or equal to 0.05. Appendix 1 provides a step by step
150 vignette of the space-time permutation model in SaTScan version 9.4.

151 We applied these statistics on 319 lion attacks in a 42,500 km² area of southern Tanzania
152 between 1989-2008 (see Kushnir et al. 2014), 67 leopard attacks between 1993-2003 in 4,100
153 km² of Pune District (PU) of Maharashtra State in India, 329 leopard attacks between 2004-2014
154 in 19,100 km² of Himachal Pradesh State (HP), India, 94 tiger attacks between 2005-2010 in
155 2,400 km² of Maharashtra State (MH), and 88 tiger attacks in 2,300 km² around Chitwan
156 National Park in Nepal (NP) between 1979-2006 (Gurung, et al. 2008) (data in Table 1). All
157 attacks had first been reported to governmental agencies and were subsequently verified through
158 follow-up interviews conducted by members of independent research teams.

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

169 *Landscape simulation analysis.* We used a simulation and bootstrap procedure to test
170 whether attack clusters were associated with 19 classes of anthropogenic landscape features at 10
171 km x 10 km resolution from the year 2000 (henceforth referred to as the “anthrome”) as defined

172 by Ellis et al (2010). Anthrome classifications were derived via a decision-rule model based on
173 long-term estimates of human population density and percentage cover in urban, crop and
174 pasture lands (for classifications see Appendix 2). Further, as land conversion is known to alter
175 prey abundance and potentially increase the chances of lion attacks (Kushnir et al. 2014), we
176 included high levels of tree-cover loss as a variable (defined as > 30% loss between 2000 and
177 2012) measured at 30m x 30m resolution (Hansen, et al. 2013). Using the random points and
178 buffer tools in ArcGIS 10.2, we simulated 100 clusters based on average cluster size for each
179 species (Table 1) across southeastern Tanzania (lions) and in the area around Chitwan National
180 Park in Nepal and in Maharashtra India (tigers). Statistical significance was not calculated for
181 leopards in this analysis as most clusters (4 of 5) were too small to attain robust estimates from
182 the coarse-grained 100-km² anthrome data, and, although the tree-loss data were measured at a
183 suitable scale of resolution, the small size of most observed clusters meant that the proportions of
184 tree loss in each leopard cluster were often negligible.

185 The simulated clusters were bound by suitable habitat for lions (Bauer et al. 2015) and
186 tigers (IUCN, 2016) within grids sized to reflect the spatial extent of attacks reported by wildlife
187 authorities for each species (500 km²: lions, 300 km²: leopards (HP), and 150 km²: tigers and
188 leopards (PU). Each grid was positioned in the landscape based on the centroid of attack
189 locations. We then extracted the proportion of tree cover loss and of each anthrome category for
190 the observed clusters and for the 100 simulated clusters using the isectpolyrst tools in Geospatial
191 Modeling Environment (Beyer 2012). The 100 simulated values of each tree loss or anthrome
192 factor were compared to average values from the observed clusters by applying a bootstrap
193 sampling method with replacement (10,000 iterations) to the simulated data. P-values were

194 calculated by comparing the mean of simulation bootstrap samples to the mean of the observed
195 values (μ , see Appendix 3 for code).

196 *Landscape Heterogeneity.* To assess whether physical dimensions of species-typical
197 attack-clusters were imposed by geographical constraints, we developed a simple fractal
198 heterogeneity metric based on the number of adjacent 100-km² cells belonging to the same
199 anthrome classification. Highly heterogeneous landscapes would form complex checkerboard
200 patterns where each adjacent cell differs from its neighbor, whereas homogeneous landscapes
201 would be characterized by large numbers of adjacent cells with the same anthrome classification.

202

203 **Results**

204 Our space-time scan analysis revealed that attacks on humans showed clear signs of
205 spatiotemporal clustering (Fig. 1, Table 1). However, the dimensions of these “outbreaks”
206 varied between species. Lion outbreaks included significantly more attacks (Fig. 2a), persisted
207 over marginally longer time intervals (Fig. 2b), and extended over significantly greater radii (Fig.
208 2c) than either leopard or tiger outbreaks. About 50% of lion attacks could be classified as
209 belonging to discrete outbreaks, whereas only ~17-28% of leopard attacks and 23-48% of tiger
210 attacks resolved into outbreaks (Fig. 2d).

211 GIS analysis of the attack locations revealed a strong association with the habitat
212 classifications defined in Appendix 2. Lion attacks occurred significantly more often than
213 expected in woodlands populated with 10-100 people/km² (“residential woodlands”) and less
214 often than expected in woodlands occupied by only 1-10 people/km² (“populated woodlands”)
215 (Fig.3a; Appendix 4); lion attacks were also more common in areas of recent tree loss (Appendix
216 5). Although largely restricted to areas adjacent to the tiger reserves in both Nepal and India,

217 tiger attacks were again more common than expected in residential woodlands (Figs. 3b&c;
218 Appendix 4), and tiger attacks in Maharashtra were also associated with mixed settlements.
219 Although leopard attack clusters were too small to test for statistical significance, leopard attacks
220 in both sites largely occurred in agricultural villages (>100 people/km²) that are watered by
221 rainfall rather than by irrigation (“rainfed villages”) and leopard attacks in Himachal Pradesh
222 frequently occurred in “rainfed croplands” with 10-100 people/km² (Figs. 3d&e).

223 To test whether geography might have constrained the radius of attack clusters in each
224 species, we measured the fractal heterogeneity of comparable, relevant landscape features in the
225 different study areas. In leopards, attacks at both sites were most common in rainfed villages,
226 and the landscape heterogeneity metric was notably higher in rainfed villages in Himachal
227 Pradesh than in Pune (Appendix 6b). Consistent with landscape heterogeneity constraining
228 attack-cluster radii, leopard outbreaks were smaller in HP (1.2 km) than in PU (4.4 km) though
229 this difference was not statistically significant. For lions in Tanzania and tigers in Maharashtra,
230 attacks were most common in residential woodlands, and the heterogeneity metric for this habitat
231 was essentially identical in the two study areas (Appendix 6a). However, the median attack-
232 cluster radius in lions (23 km) was far higher than in the tiger outbreaks in Maharashtra (4.1 km),
233 even though lion and tiger outbreaks in these two areas might be expected to experience similar
234 constraints from landscape heterogeneity.

235 Data on group size were strikingly different between the three species. Out of 310
236 attacks where group composition could be estimated, 72% involved two or more adult lions, 20%
237 involved a lone male and 8% involved a lone female. In contrast, all 88 tiger attacks in Nepal
238 involved a lone adult (Gurung, et al. 2008), as was also the case in the leopard attacks in Pune.
239

240 **Discussion**

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

250 Our analysis was designed, first, to determine whether lion, leopard and tiger attacks
251 typically occurred in discrete outbreaks and, second, to characterize the dimensions of these
252 outbreaks in time and space. All three species showed non-random “clusters” of attacks on
253 humans, but patterns differed considerably between species. Nearly half of all lion attacks in
254 Tanzania and tiger attacks in Nepal occurred within well-defined bursts of activity (Fig. 1a, c),
255 whereas the majority (72-83%) of tiger attacks in Maharashtra and leopard attacks were widely
256 dispersed (Fig. 1b, d, e). As predicted, lion outbreaks included more victims, persisted for longer
257 periods, and extended over broader radii than either leopard or tiger outbreaks (Fig. 2a, b, c).

258 We investigated the landscape features associated with outbreaks for two reasons. First,
259 to assess whether anthropogenic activities increased the risks of carnivore attacks. Lion and tiger
260 outbreaks were disproportionately located in residential woodlands habitat with 10-100 people
261 per square kilometer, and lions also attacked more people in areas with recent loss of tree cover
262 (Fig. 3a,b). At a local level, leopard attacks in both study areas were over-represented in rainfed

263 villages; in Himachal Pradesh, attacks were also more common in rainfed croplands with 10-100
264 people per km² (Fig. 3d). Second, to determine whether differences in habitat heterogeneity in
265 Asia and Africa may have accounted for the differences in attack radii between the three species.
266 While the higher landscape heterogeneity in rainfed-village habitat in Himachal Pradesh may
267 have played a role in the slightly smaller outbreak radii in Himachal Pradesh compared to
268 leopard outbreaks in Pune, heterogeneities were virtually identical in residential woodlands in
269 Tanzania and Maharashtra, and the lion outbreaks in Tanzania were spread over far greater areas
270 than tiger attacks in Maharashtra (Table 1). Thus, spatial constraints imposed by the respective
271 environments in India, Tanzania and Nepal are unlikely to have played a major role in the
272 contrasting spatial dimensions of attack clusters between the three species. Note that while it is
273 possible that our analysis may have failed to capture relevant landscape changes over the
274 timespan of the study, the tree-loss data measured changes from 2000-2012, and the attack
275 outbreaks spanned from 1995–2013 so any mismatch was unlikely to have been substantial.

276 Our datasets were too limited to make strong inferences about the underlying factors that
277 elicited attacks on humans in the three study species. For example, even though there was an
278 effect of tree loss on lion attacks in Tanzania, we cannot say whether these occurred because the
279 areas had recently been settled or because of effects on the lions' usual prey in the disturbed
280 habitats. However, the majority of cases appeared to involve the deliberate targeting of humans:
281 65% of 815 lion attacks reported across all of Tanzania between 1990 and 2004 were fatal
282 (Packer et al. 2005), as were 100% of the 88 tiger attacks in Nepal (Gurung, et al. 2008), and
283 62% of 95 tiger attacks reported here for Maharashtra. Fatality rates are not known for the
284 leopard data, but 54% of 52 classifiable attacks in Pune were considered predatory, and half the
285 attacks in both Pune (51%, n=61) and Himachal Pradesh (54%, n=297) occurred at night, when

286 76% of the attacks in Pune were considered predatory (n=21 classifiable night-time attacks vs.
287 39% of 31 classifiable daytime attacks, $P=0.0111$, two-tailed, Fisher test). In contrast, there were
288 no mortalities in the daytime attacks described by Kshetry, et al. (2017) where leopards reacted
289 defensively to inadvertent encounters with workers on tea plantations.

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

303 While this scenario may help to explain the contrasting scale of discrete outbreaks, it
304 does not address why so many leopard attacks in both study areas and tiger attacks in
305 Maharashtra occurred in apparent isolation from each other. One possible explanation – at least
306 for leopards, where human fatalities appear to have been rare – is that a higher proportion of
307 attacks involved reactions to disturbance (as described by Kshetry et al. 2017) rather than
308 unprovoked attempts to capture humans as prey. Indeed, a substantial proportion of leopard

309 attacks in Pune occurred during the daytime, when only about 40% of cases were considered
310 predatory (see above).

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

322 Note that there are several general limitations of space-time permutation approaches.
323 First, although we found circles to be the most suitable configuration for defining attack clusters,
324 long and narrow outbreaks may not be accurately identified (Kulldorf et al, 2004). We found no
325 evidence for this pattern in our data, but it could exist where, say, attacks are restricted to the
326 outer edge of a large urban area. Second, if attacks are homogeneously distributed across an
327 entire survey area, space-time models will only detect localized perturbations in risk (Kulldorf et
328 al., 2005). However, the SaTScan method is the best option for detecting localized clusters in
329 areas where little information is available on the human or wildlife populations. Finally note that
330 while the tree-loss data largely matched the timescale of our datasets, longer-term studies may
331 span periods of substantial (and undocumented) anthropogenic changes.

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

342

343 **Acknowledgements**

344 We thank the National Science Foundation for financial support (grants DEB-1354093 to
345 C.P. and DEB-1413925 to N.M.F.-J. and M.E.C.). The Himachal Pradesh project was conducted
346 in collaboration with the Wildlife Wing of the Himachal Pradesh Forest Department and Wildlife
347 Conservation Society - India. All research was conducted with relevant permission from the
348 wildlife authorities in India, Nepal and Tanzania. We thank Julio Alvarez for early advice on the
349 SatScan method. We also thank Johan du Toit, Craig Tambling and the anonymous referee for
350 their comments.

351 **Authorship statement:** CP designed the study, NMFJ analyzed the spatiotemporal data, SS,
352 VA, HD, PD, BG, HK and JDCL collected data for the study, AJ provided GIS layers, and CP,
353 VA, MC, AJ, JDCL, NMFJ contributed to the writing of the manuscript. All authors have
354 approved this manuscript for publication.

355 **Data accessibility**

356 Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.bt5j6k4>

357
358

359 **References**

- 360 Athreya, V., Odden, M., Linnell, J.D.C. & Ullas Karanth, K. (2011). Translocation as a tool for
 361 mitigating conflict with leopards in human-dominated landscapes of India. Conservation
 362 Biology, 25, 133-141.
- 363 Beyer, H. B. L. (2012). Geospatial Modelling Environment.
 364 <http://www.spatial ecology.com/gme/> [accessed Jan 2017]
- 365 Borrego, N. & Gaines, M. (2016). Social carnivores outperform asocial carnivores on an
 366 innovative problem. Animal Behaviour 114, 21-26.
- 367 Carter, N. H., & Linnell, J. D. C. (2016). Co-Adaptation is key to coexisting with large
 368 carnivores. Trends in Ecology & Evolution, 31(8), 575–578.
 369 <http://doi.org/10.1016/j.tree.2016.05.006>
- 370 Chapron, G., Kaczensky, P., Linnell, J. D. C., Arx, von, M., Huber, D., Andrén, H., et al. (2014).
 371 Recovery of large carnivores in Europe's modern human-dominated landscapes. Science,
 372 346(6216), 1517–1519. <http://doi.org/10.1126/science.1257553>
- 373 Dhanwatey, H. S., Crawford, J. C., Abade, L. A. S., Dhanwatey, P. H., Nielsen, C. K., & Sillero-
 374 Zubiri, C. (2013). Large carnivore attacks on humans in central India: a case study from
 375 the Tadoba-Andhari Tiger Reserve. Oryx, 47(02), 221–227.
 376 <http://doi.org/10.1017/S0030605311001803>.
- 377 DiMinin, E., Slotow, R., Hunter, L.T.B., Montesino Pouzols, F., Toivonen, T., Verburg, P.H.,
 378 Leader Williams, N., Petracca, L., & Moilanen, A. (2016). Global priorities for national
 379 carnivore conservation under land use change. Scientific Reports 6,
 380 doi:10.1038/srep23814.
- 381 Ellis, E.C., Goldewijk, K.K., Siebert, S., Lightman, D., & Rmankutty, N. (2010). Anthropogenic
 382 transformation of the biomes, 1700 to 2000. Global Ecol. Biogeogr. **19**, 589–606.
- 383 Gaudart, J., B. Poudiougou, A. Dicko, S. Ranque, O. Toure, I. Sagara, M. Diallo, S. Diawara, A.
 384 Ouattara, M. Diakite, O.K Doumbo (2006). Space-time clustering of childhood malaria at
 385 the household level: a dynamic cohort in a Mali village. BMC Public Health **6**, 286.
 386 **DOI:** 10.1186/1471-2458-6-286
- 387 Gehrt, S.D., S.P.D. Riley & B.L. Cypher (2010). Urban Carnivores. Johns Hopkins University
 388 Press.
- 389 Goodrich, J. M., Seryodkin, I., Miquelle, D. G., & Bereznuik, S. L. (2010). Conflicts between
 390 Amur (Siberian) tigers and humans in the Russian Far East. Biological Conservation, 1–
 391 9. <http://doi.org/10.1016/j.biocon.2010.10.016>
- 392 Gurung, B., Smith, J.L.D., McDougal, C., Karki, J.B., & Barlow, A. (2008). Factors associated
 393 with human-killing tigers in Chitwan National Park, Nepal. Biological Conservation,
 394 141, 3069-3078.
- 395 Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau,
 396 D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L.,
 397 Justice, C.O., & Townshend, J.R.G. (2013). High-resolution global maps of 21st century
 398 forest cover change. Science 342, 850–3.
- 399 Hazzah, L., Dolrenry, S., Naughton, L., Edwards, C.T.T., Mwebi, O., Kearney, F., & Frank, L.
 400 (2014). Efficacy of two lion conservation programs in Maasailand, Kenya. Conservation
 401 Biology 28, 851–860. DOI: 10.1111/cobi.12244
- 402 Inskip, C., & Zimmermann, A. (2009). Human-felid conflict: A review of patterns and priorities
 403 worldwide. Oryx, 43(1), 18–34 doi:10.1017/S003060530899030X

404 IUCN (2016). *The IUCN Red List of Threatened Species. Version 2016-3.*
405 <<http://www.iucnredlist.org>>. Downloaded on 07 December 2016.

406 Kerbis Peterhans, J.C., Gnoske, T.P. (2001) The science of ‘Man-eating’ among lions (*Panthera*
407 *leo*) with a reconstruction of the natural history of the ‘Man eaters of Tsavo.’ J. E. Afr.
408 Nat. Hist. 90: 1–40.

409 Kshetry, A. Vaidyanathan, S., Athreya, V. (2017). Leopard in a tea-cup: A study of leopard
410 habitat-use and human-leopard interactions in north-eastern India. PLoS One 12(5):
411 w0177013. DOI: 10.1371/journal.pone.0177013

412 Kulldorff, M. (1997). A spatial scan statistic. Communications in Statistics: Theory and
413 Methods, 26, 1481-1496.

414 Kulldorff, M., Heffernan, R., Hartman, J., Assunção, R.M., & Mostashari, F. (2005). A space-
415 time permutation scan statistic for the early detection of disease outbreaks. PLoS
416 Medicine, 2, 216-224.

417 Kushnir H., Leitner, H., Ikanda, D., & Packer, C. (2010). Human and ecological risk factors for
418 unprovoked lion attacks on humans in southeastern Tanzania. Human Dimensions of
419 Wildlife 15, 315-331.

420 Kushnir, H., Olson, E., Juntunen, T., Ikanda, D., & Packer, C. (2014). Using landscape
421 characteristics to predict risk of lion attacks in southeastern Tanzania. African Journal of
422 Ecology. 52, 524-532. DOI: 10.1111/aje.12157

423 Kushnir, H., & Packer, C. (in press). Reality vs. Perception: How rural Tanzanians view risks
424 from man-eating lions.

425 Malizia, N. (2013). Inaccuracy, uncertainty and the space-time permutation scan statistic.
426 PLoS-One doi.org/10.1371/journal.pone.0052034

427 Miller, J.R.B., Jhala, Y.V., Jena, J., & Schmitz. O.J. (2015). Landscape-scale accessibility of
428 livestock to tigers: implications of spatial grain for modeling predation risk to mitigate
429 human-carnivore conflict. Ecology and Evolution 5, 1354-1367. Doi: 10.1002/ece.1440

430 Packer, C., Ikanda, D., Kissui, B., & Kushnir, H. (2005). Ecology: Lion attacks on humans in
431 Tanzania. Nature 436, 927-928.

432 Packer, C., Shivakumar, S., Athreya, V., Craft, M.E., Dhanwatey, H., Dhanwatey, P., Gurung,
433 B., Joshi, A., Kushnir, H., Linnell, J.D.C., & Fountain-Jones. N.M. (2018) Data from:
434 Species-specific spatiotemporal patterns of leopard, lion and tiger attacks on humans
435 Dryad Digital Repository. <https://doi.org/10.5061/dryad.bt5j6k4>

436 Packer, C., Swanson, A., Ikanda, D., & Kushnir, H. (2011). Fear of darkness, the full moon and
437 the lunar ecology of African lions. PLoS One. doi:10.1371/journal.pone.0022285

438 Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger,
439 J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D.,
440 & Wirsing, A.J. (2014). Status and ecological effects of the world’s largest carnivores.
441 Science 343, DOI: 10.1126/science.1241484

442 Robertson, C., & Nelson, T.A. (2010). Review of software for space-time disease surveillance.
443 Int. J. Health Geographics 9, 16. DOI: 10.1186/1476-072X-9-16

444 Saberwal, V. K., Gibbs, J. P., Chellam, R., & Johnsingh, A. (1994). Lion - human conflict in the
445 Gir Forest, India. Conservation Biology 8, 501–507

446 Slovic P. 1987. Perception of Risk. Science 236(4799):280-285.

447 Werbeck, N. (2017). Dramatic pictures reveal clashes between people and tigers.
448 <http://www.nationalgeographic.com/photography/proof/2017/02/human-vs-tiger-conflict/>
449

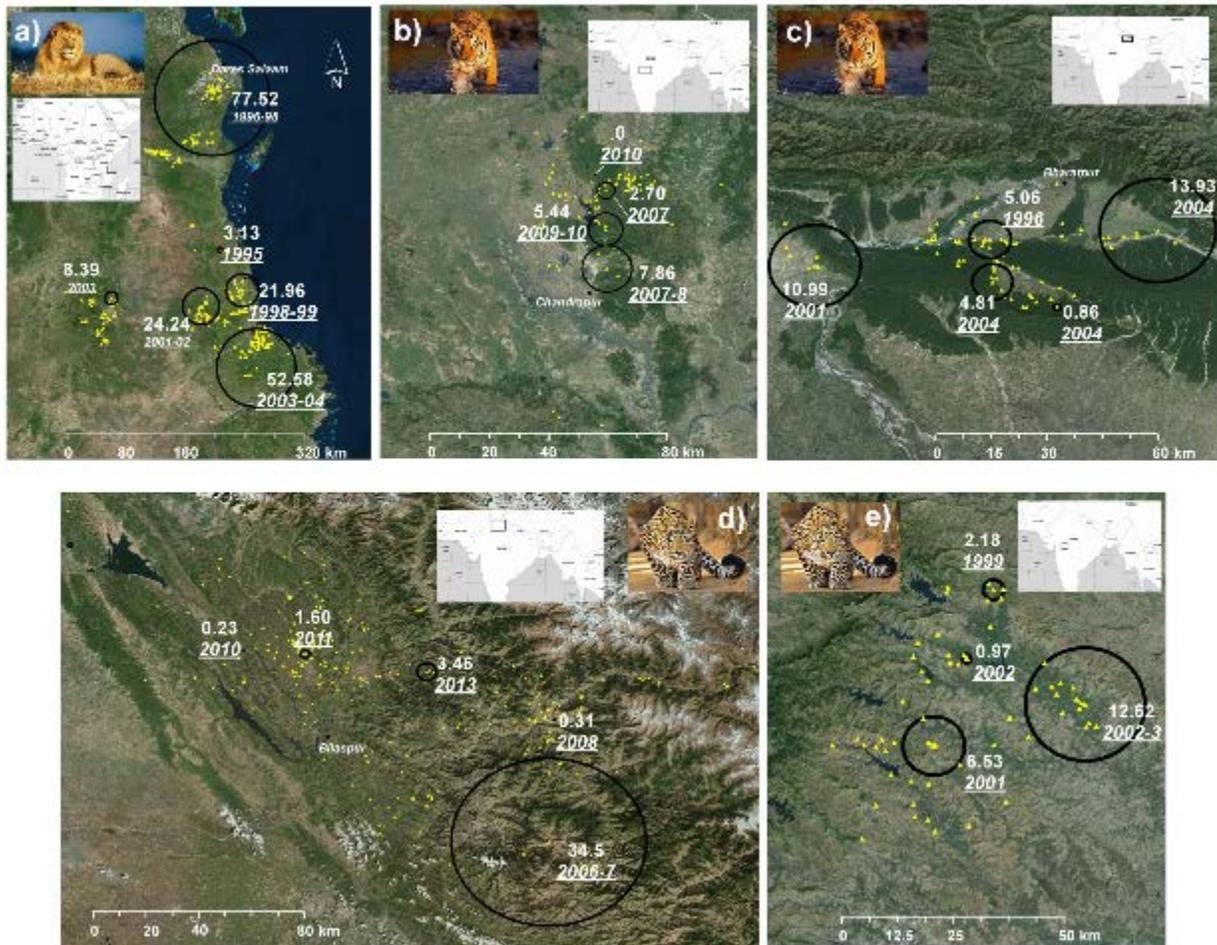
450
451
452
453
454

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* and recent tree loss*
Tigers (NP)	88	5	42	48%	7	5.06	2	Residential woodlands*
Tigers (MH)	94	4	22	23%	6	4.07	2	Residential woodlands* and mixed settlement*
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

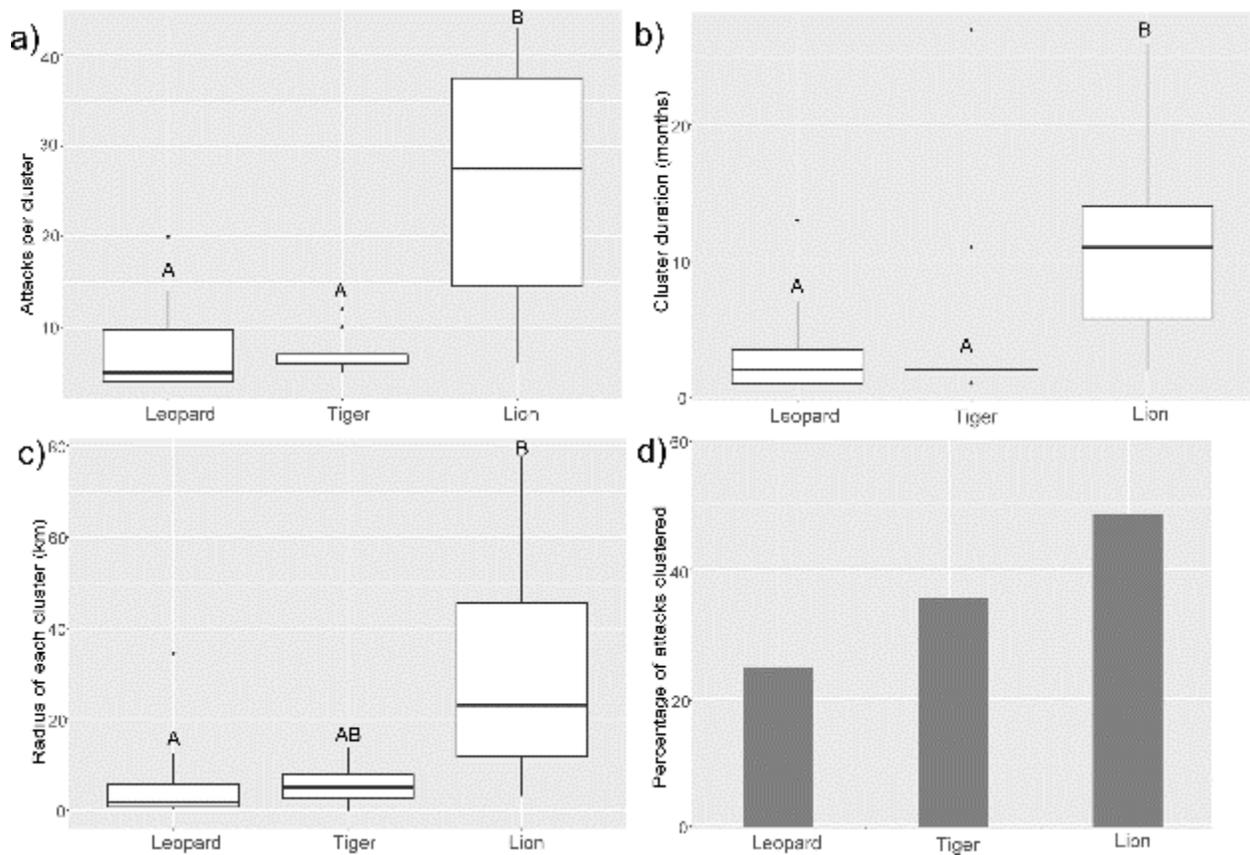
455
456
457
458

NP: Nepal, MH: Maharashtra, HP: Himachal Pradesh, PU: Pune
*Statistically significant landscape classes.



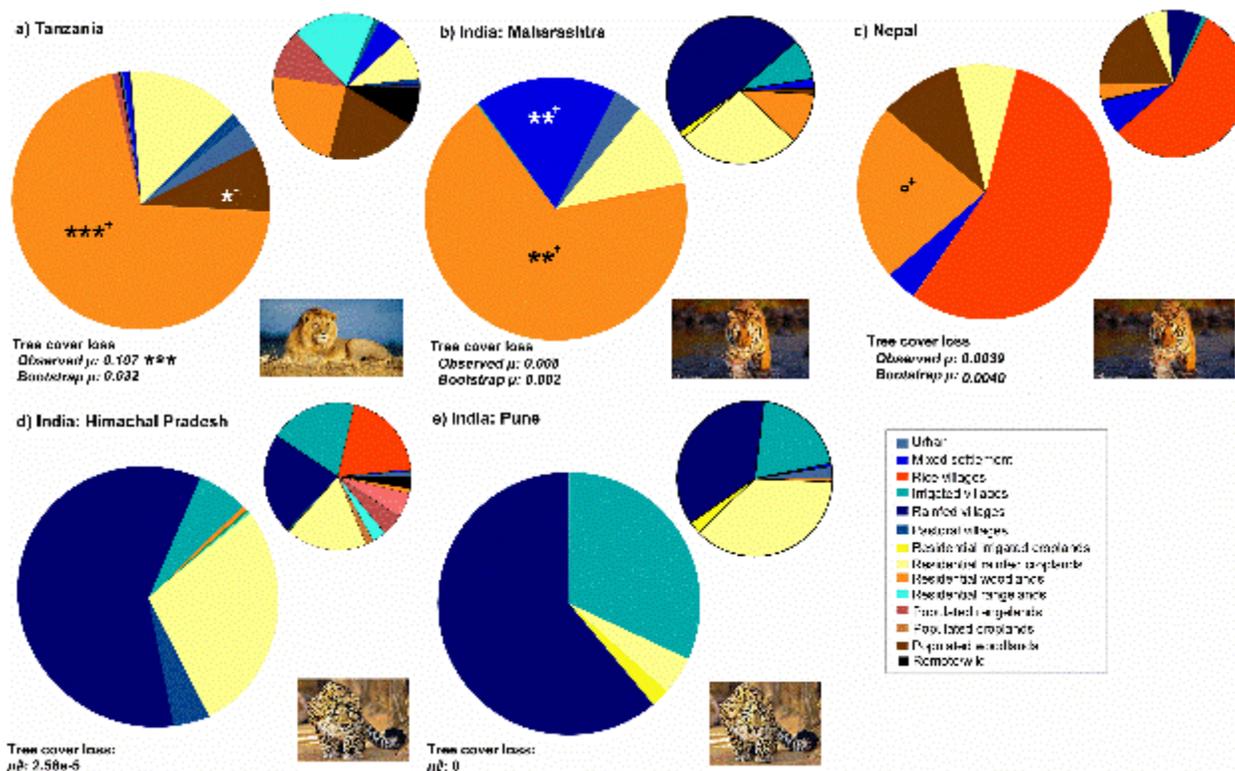
460
 461
 462
 463
 464
 465
 466
 467

Fig. 1: Spatio-temporal 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.



468
 469 **Fig. 2:** Spatio-temporal characteristics of attack clusters in each species. a) Average number of
 470 attacks per cluster for each species (Kruskal-Wallis chi-square = 9.54, $P = 0.0008$). b) Average
 471 duration of attack clusters (Kruskal-Wallis chi-square = 5.85, $P = 0.054$), c) Average radius of
 472 attack clusters (Kruskal-Wallis chi-square = 7.22, $P = 0.027$). “A” and “B” above respective
 473 boxplots designate significant (Benjamin-Hochberg adjusted $P < 0.05$) post hoc groupings, AB
 474 indicates that this group was not significantly different from groups ‘A’ or ‘B’. d) Percentage of
 475 attacks classified within spatio-temporal clusters for leopards, tigers and lions.

476
 477
 478



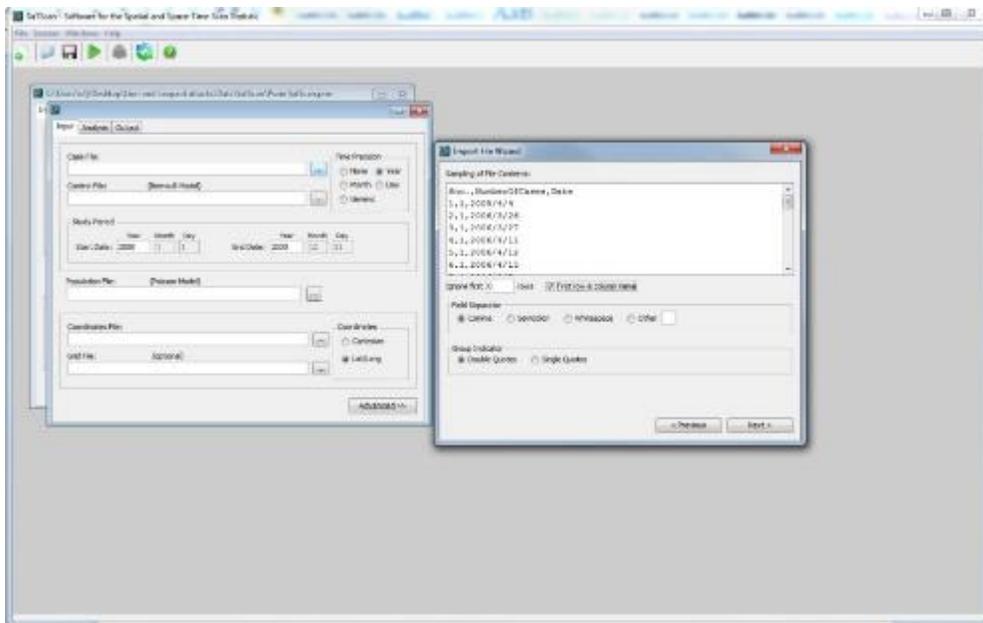
479
 480 **Fig. 3:** Proportion of anthropogenic landscape classifications (large pie charts) and the
 481 surrounding landscapes (small pie charts) for attack clusters for (a) lions, (b/c) tigers and (d/e)
 482 leopards. Effects of tree-cover loss between 2000 and 2012 are listed at the bottom left corner of
 483 each panel; $\mu\#$: mean derived from the area around the attack clusters (see *Methods*). Statistical
 484 significance was determined by simulation and a bootstrap procedure (observed μ versus
 485 bootstrap, see *Methods*). \circ : $P = 0.05-0.1$, $*$: $P = 0.01-0.05$, $**$: $P < 0.01$, $***$: $P < 0.0001$. $-$:
 486 observed mean was significantly smaller than the bootstrap estimate, $+$: observed mean was
 487 significantly larger. Leopards (d/e) were excluded from the bootstrap analysis due to the small
 488 size of clusters relative to landscape features.

489
 490
 491
 492
 493
 494
 495
 496
 497
 498
 499
 500
 501
 502
 503
 504

505 **Appendix 1: SaTScan space time permutation method for detecting spatiotemporal clusters**
506 **of animal attacks.**

507
508 **Downloading and opening the software.** SaTScan is free software that can be run on Windows,
509 Mac OSX or Linux. The user must provide a password, name and organization details at the
510 following site: https://www.SaTScan.org/download_SaTScan.html. Launch the software from
511 the SaTScan shortcut on the desktop (or from the SaTScan folder) then select 'Create New
512 Session' from the menu. After the SaTScan analysis is complete, a kml file enables clusters to be
513 viewed in Google Earth, which can be downloaded here:
514 <http://www.google.com/earth/index.html>

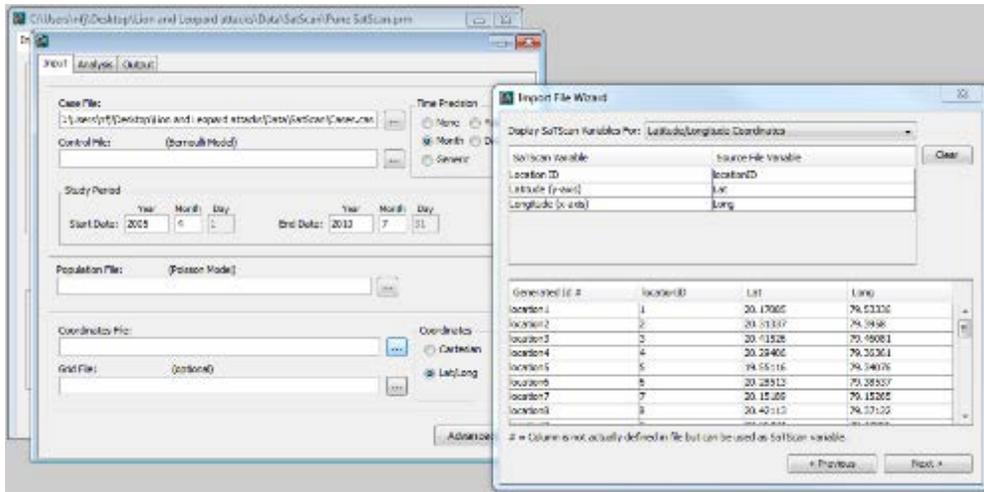
515
516 **Inputting the data.** The analysis requires a 'case file' and a 'coordinates' file. The example
517 dataset in this tutorial is from the lion attacks data in Tanzania. In the input tab, go to the Case
518 File box and open the SaTScan Import Wizard (the '...' button, Fig. A). Find the
519 'lionCaseFile.csv' file and check the 'First row is column name' option and otherwise keep the
520 default options (Fig. a). Note that these files are in comma separated (.csv) format.
521



522
523 **Fig. A:** Screenshot of the case-file importation stage.

524
525 Move to the next screen and select the 'space-time permutation model' from the 'Display
526 SaTScan Variables For' menu. Define each column by setting 'Sno' as the Location ID' (a
527 unique number associated with that attack), 'Number of Cases' as 'NumberOfCases' (always 1
528 as only one attack was recorded at each event), and data/Time as 'Date' (year/month day). Save
529 the imported data and complete the import process. On the input tab, set time precision to
530 'month,' start date at 1989/3, and end at 2009/1. Go to 'Coordinates File' and import as above.
531 Find the 'lionCoordinates.csv' and continue. Check the 'First row is column name' option and
532 leave the rest as default. Select 'Latitude/Longitude Coordinates' from the 'Display SaTScan

533 Variables For' menu and define the columns as 'Location ID' and 'Latitude' (Lat) and
 534 'Longitude' (Long). Save the file, making sure Lat/Long is checked in the 'Coordinates' box.
 535 See Fig. B.
 536

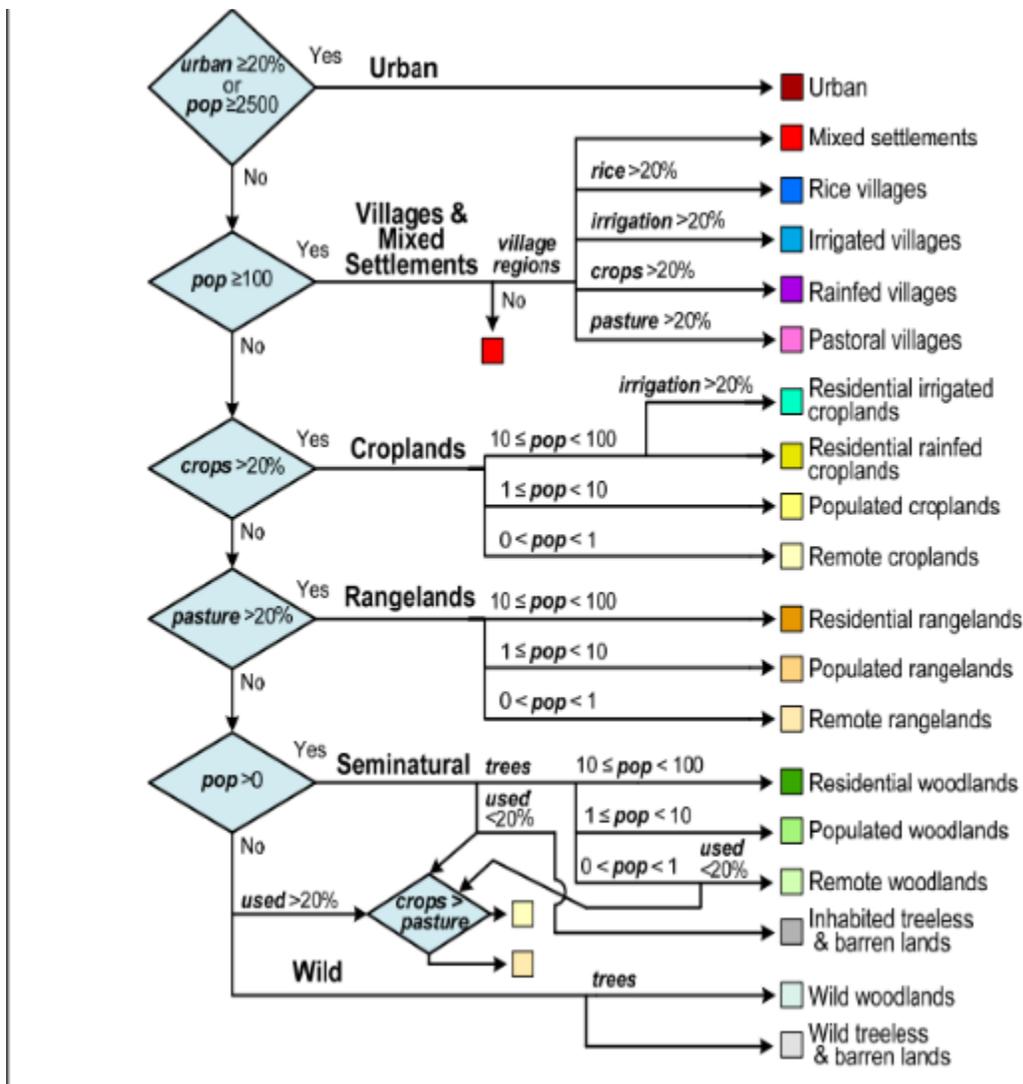


537
 538 **Fig. B:** Screenshot of the coordinate file importation stage.
 539

540 Go to the 'Analysis' tab and select the retrospective 'Space-Time' with the 'Space-Time
 541 Permutation' probability model. To identify areas with above-average attack rates, select 'High
 542 Rates.' Aggregate time by a length of 1 month. Alter the inference tab to set the number of
 543 replications to 9999. Select a file name for your results file and save. Choose your preferred
 544 geographic output and column output formats.
 545

546 **Running the analysis.** After setting all the parameters, select the triangular start button in the
 547 task bar. Any problems will be logged in this screen from each of the 9999 permutations. Once
 548 complete, all cluster information (with probabilities) will be provided on screen. Google Earth
 549 will open automatically, enabling visualization of the clusters.
 550

551 **Other resources.** Other tutorials for running SaTScan spatiotemporal models are located at:
 552 <https://www.SaTScan.org/tutorials.html>. SaTScan is also available as an R Package 'rsatscan'
 553 and a tutorial on performing the analysis in R are at:
 554 <https://www.SaTScan.org/rSaTScan/rSaTScan.html>

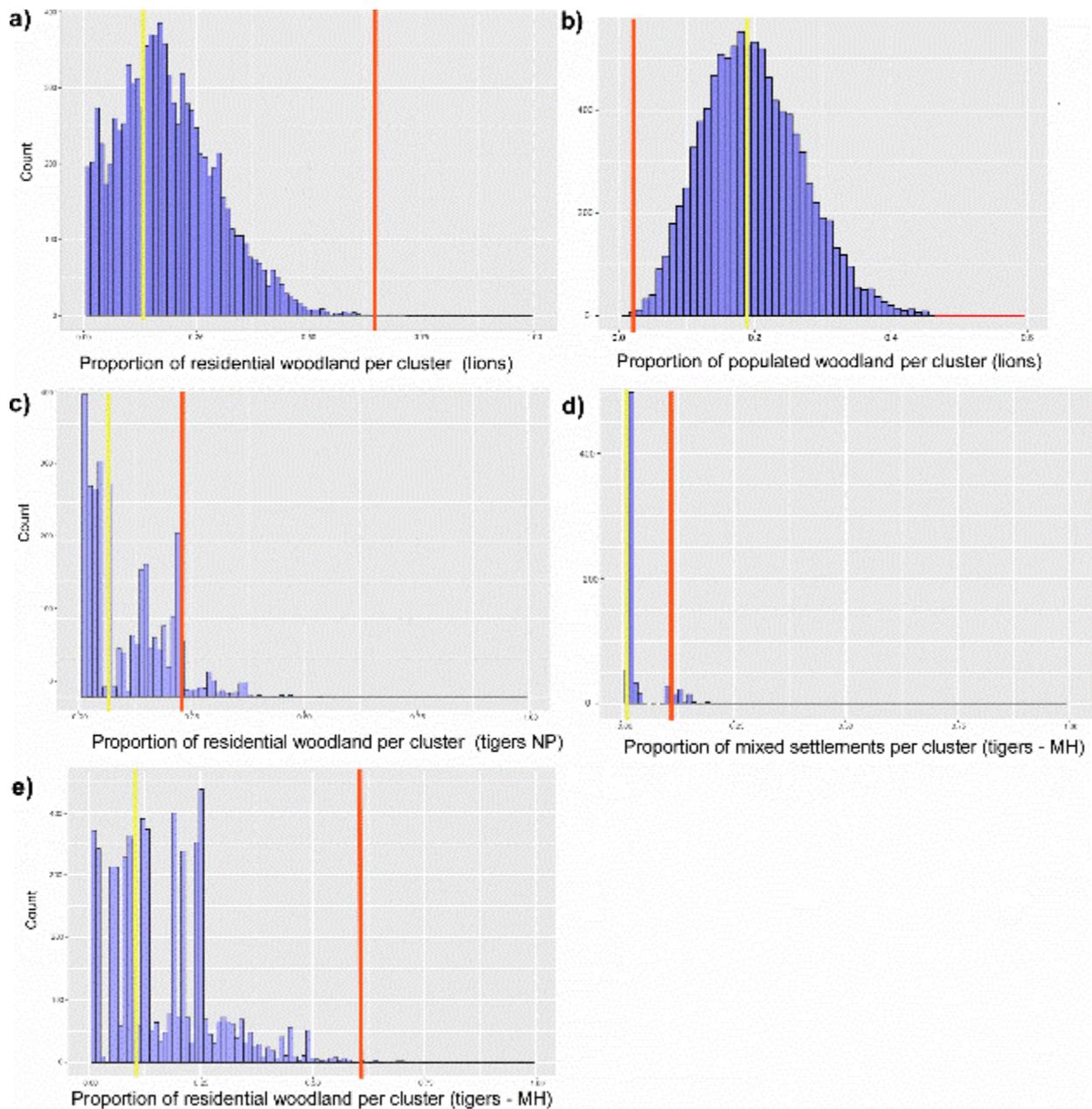


Appendix 2: Flow chart defining each anthropome variable (from Ellis et al 2010). Data inputs to the model are in italics: urban = % urban land cover, pop = population density (persons km²), rice = % cover by rice, irrigation = % land area irrigated, crops = % area covered by crops, pasture = % area covered by pastures, trees = areas of tree cover.

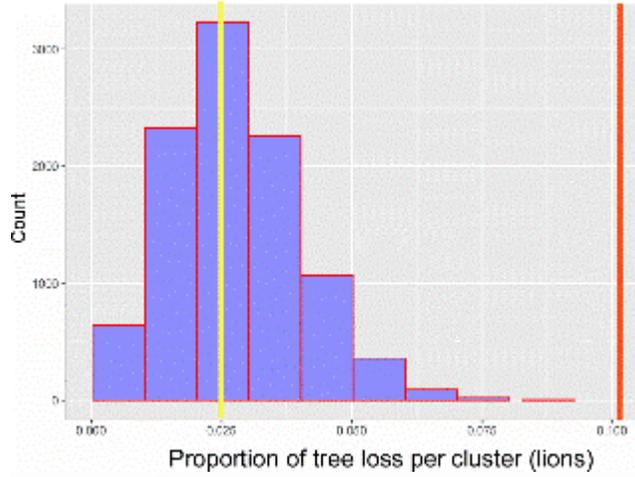
```
#Bootstrap Hypothesis Test
```

```
#function  
set.seed(123)  
nboot<- 10000  
bstrap <- rep(NA, nboot)  
for (i in 1:nboot){  
  bstrap[i] <- mean(sample(data, 5, replace=T))  
}  
#calculate probability  
(sum(bstrap < observed_mean) + sum(bstrap > ((bstrap_mean-  
observed_mean)+bstrap_mean)/10000
```

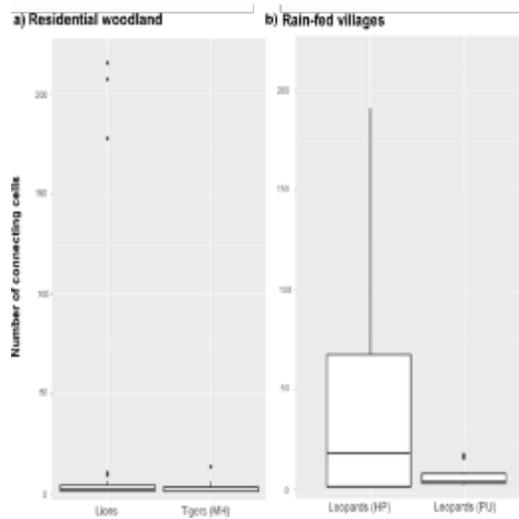
Appendix 3: Code for comparing the mean of simulation bootstrap samples to the mean of the observed values (μ). Data are available in Dryad.



Appendix 4: Histograms comparing the observed mean (red) versus bootstrap mean (yellow) for (a) residential woodlands and (b) populated woodlands in lion-attack clusters, (c) residential woodlands in tiger-attack (Nepal - NP) clusters, (d) mixed settlements, and (e) residential woodlands in tiger attack (Maharashtra- MH) clusters.



Appendix 5: Mean and distribution of bootstrap values from tree loss (lions).



Appendix 6: Box plots showing the average heterogeneity of (a) residential woodland landscapes for lion and tiger attacks (MH: Maharashtra) and (b) rainfed villages for leopard attacks in Himachal Pradesh (HP) and Pune (PU).