1 **TITLE**

2 Using environmental niche modelling to investigate the importance of ambient temperature in

3 human-crocodilian attack occurrence for two species of crocodilian

4

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26   **ABSTRACT**

27   Crocodilians are distributed widely through the tropics and sub-tropics, and many species

28   pose a substantiated threat to human life. This has important implications for human safety

29   and crocodilian conservation. Understanding the drivers of crocodilian attacks on people

30   could help minimise future attacks and inform conflict management. Crocodilian attacks

31   follow a seasonal pattern in many regions; however, there has been limited analysis of the

32   relationship between fine-scale contemporaneous environmental conditions and attack

33   occurrence. Here, we use methods from environmental niche modelling to explore the

34   relationships between abiotic predictors and human attack occurrence at a daily temporal

35   resolution for two species: the Nile crocodile (*Crocodylus niloticus*) in South Africa and

36   Eswatini (formerly Swaziland), and the American alligator (*Alligator mississippiensis*) in

37   Florida, USA. Our results indicate that ambient daily temperature is the most important

38   abiotic temporal predictor of attack occurrence for both species, with attack likelihood

39   increasing sharply when daily average temperatures exceed 18°C and peaking at 28°C. It is

40   likely that this relationship is explained partially by human propensity to spend time in and

41   around water in warmer weather, but also by the effect of temperature on crocodilian hunting

42   behaviour and physiology, especially the ability to digest food. We discuss the potential of

43   our findings to contribute to the management of crocodilians, with benefits for human safety

44   and conservation, as well as the application of environmental niche modelling to

45   understanding human-wildlife conflicts with both ectotherms and endotherms.

46

47   **Key words:** human-wildlife conflict; human-crocodilian conflict; spatiotemporal modelling;

48   environmental niche modelling; crocodilian conservation; conservation management

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50

51 **INTRODUCTION**

52 Managing conflicts involving wildlife is a serious challenge worldwide, especially when the

53 target species poses a direct threat to human life (Woodroffe, Thirgood, & Rabinowitz,

54 2005). Over large regions of the tropics and subtropics, crocodilians are responsible for more

55 attacks on humans per year than any other large carnivore, with incidents reported for 65

56 countries (CrocBITE 2018). They also attack domestic animals such as livestock and dogs,

57 damage fishing nets, burrow through earthen dam walls, and cause general disruption to

58 movement and livelihoods by restricting the use of waterways that are required for travel,

59 fishing, and household chores (Aust et al. 2009, Lamarque et al. 2009).

60

61 Successfully mitigating harmful human-crocodilian interactions has important implications

62 not just for human safety but also conservation. Negative impacts on humans have resulted in

63 retaliatory killings and exacerbated issues such as overharvesting and habitat destruction

64 (Fukuda et al. 2015), which can have wider consequences for ecosystems. As the apex

65 predator of the aquatic environments they inhabit, and as carnivores with very varied diets,

66 crocodilians play a key role in local food webs, affecting abundance and behaviour of prey

67 species in ways that can influence the function and community structure of ecosystems (Van

68 der Ploeg et al. 2011). They also transport nutrients from land to water by preying on land

69 animals, or across ecosystems, as in cases where they travel to feed in estuarine areas before

70 returning to freshwater areas. Crocodilians are also ecosystems engineers, modifying their

71 environment by digging dens, holes and tunnels, and creating nest sites. Alligator holes, for

72 instance, retain water during dry seasons and serve as refuges for other aquatic species

73 (Crocodilian Species List, 2009).

74

75   Understanding the drivers of crocodilian attacks can help minimise future incidents and

76   inform conflict management. Previous analysis of crocodilian attack patterns has focused on

77   identifying high-risk human demographics and behaviours; however, there has been limited

78   analysis of abiotic environmental predictors of attack patterns, such as temperature and

79   rainfall (Brien et al. 2017; Das & Jana, 2017; Fukuda et al. 2015). There are strong theoretical

80   grounds for this, since temperature constrains crocodilian hunting behaviour via effects on

81   ectotherm physiology, especially metabolic function (Lance 2003; Seebacher & Franklin

82   2005; Hutton 1987). Similarly, people's propensity to expose themselves to crocodilian-

83   inhabited waterways is likely correlated with environmental conditions. Accordingly, despite

84   crocodilian attacks occurring year-round in many tropical regions (e.g., India and

85   Bangladesh), documented attack patterns are highly seasonal across Australia (Brien et al.

86   2017) and are correlated with mean monthly rainfall and temperature in South Africa and

87   Eswatini, as well as in the southern United States (Pooley 2015; Woodward et al 2014). To

88   date, studies have only explored the contribution of abiotic factors at a coarse temporal and

89   spatial resolution. In particular, they have exclusively used average monthly or seasonal data,

90   which does not capture the impact of climatic changes across days. Furthermore, this data is

91   used to represent regional environmental conditions, but it has typically been sourced from

92   single weather stations, limiting the ability to capture variation across space.

93

94   Here, we use environmental niche modelling methods to examine the relationships between

95   abiotic and biotic variables and human-crocodilian attack occurrence at a greater spatial and

96   temporal resolution than in previous studies. Environmental niche modelling describes

97   methods for inferring the occurrence of biological phenomena in environmentally-

98   heterogeneous areas and has previously been utilised to analyse human conflict with jaguars

99   in Brazil and Mexico (Carvalho et al. 2015; Zarco-González et al. 2013), wolves in Iran

100   (Behdarvand et al. 2014), leopards in Pakistan (Kabir et al. 2014), and monkeys in India

101   (Beisner et al. 2015). Crocodilian attacks can theoretically be thought of as an entity that can

102   only occupy a specific environmental niche defined by particular biophysical limits; thus, it

103   might be possible to use environmental niche modelling to illustrate the likelihood of attack

104   occurrence over time in a heterogeneous environment.

105

106   We focus on two species of crocodilian that come into regular conflict with humans: the east

107   African Nile crocodile (*Crocodylus niloticus*) in South Africa and Eswatini, which is

108   estimated to be responsible for more human fatalities per year than all other crocodilians

109   combined (Dunham el al. 2010; Wallace et al. 2011), and the American alligator in Florida

110   (*Alligator mississippiensis*), which is one of few indigenous predators that poses a

111   substantiated threat to human life in the southernmost states of the USA (Woodward et al.

112   2014). We discuss the potential of our findings to contribute to the management of

113   crocodilians, especially in subtropical and temperate areas where climatic conditions are

114   similar to those in our study regions. We also highlight the benefits for human safety and

115   conservation arising from this study, as well as the potential application of environmental

116   niche modelling to the analysis of human conflict with other species, including ectotherms

117   and endotherms.

118

119   **METHODS**

120   **Attack and biophysical data**

121   Information on attacks by Nile crocodiles in South Africa and Eswatini (1951-2016) was

122   obtained from archival searches including the personal archive of Tony (A.C.) Pooley

123   (conservation warden responsible for crocodile attacks in Natal Province, c.1966-84, who

124   was active in investigations until c.2003), attack records kept at the St Lucia Crocodile

125   Centre, provincial and national newspapers (print and online) in KwaZulu-Natal and South

126   Africa, and the *Times of Swaziland* archive in Mbabane, Eswatini. Online searches used the

127   search term 'crocodile' paired with 'attack', 'bite' or 'victim', in English and Afrikaans.

128   Information on American alligator attacks in Florida (1971-2014) was provided by the Fish

129   and Wildlife Conservation Commission (FWC) (FWC 2016). Incidents involving a bite were

130   reported to the FWC by telephone by victims or their families, medical caregivers, or law

131   enforcement agencies. In most instances post 1970, FWC law enforcement officers conducted

132   investigations and interviewed victims and witnesses. Attacks by crocodilians were excluded

133   if they were not witnessed or lacked forensic support, if spatial or temporal data were lacking,

134   or if they were classified as provoked.

135

136   The attack records had different spatial resolutions: geographical coordinates were available

137   for the Nile crocodile attacks (Figure 1A). Whereas, for the American alligator attacks, the

138   Florida county in which the attack occurred was recorded (Figure 1B). ArcGIS (version 10.4)

139   was used to ensure Nile crocodile attack coordinates fell within the International Union for

140   Conservation of Nature (IUCN) predicted distribution of Nile crocodiles in South Africa and

141   Eswatini (IUCN 1996), and within 1km of a waterbody (Defence Mapping Agency 2003).

142   Figure 1 shows the distribution of crocodile attacks in South Africa and Swaziland, and

143   alligator attacks in Florida.

144

145   We compiled a dataset of biotic and abiotic environmental predictors that could be spatially

146   and temporally linked to attacks. These included the climatic variables: daily average

147   temperature, daily rainfall, and monthly average rainfall (20-year averages). Historic data

148   were not available for crocodile and alligator population densities across the study regions,

149   but human population density was included as a biotic predictor because the majority of

150   attacks in our study areas were on local residents (Woodward et al. 2014, Pooley 2015). Year

151   and month were also included to account for temporal trends.

152

153   Formatting of abiotic covariates was achieved in R version 3.4.2 (R Core Team 2017) and

154   ArcGIS version 10.4. Daily rainfall and minimum and maximum temperature data were

155   obtained from the National Oceanic and Atmospheric Administration (NOAA 2017). We

156   gathered data from all weather stations within a 300 km perimeter of the distribution (IUCN

157   1996) of Nile crocodiles in South Africa and Eswatini (n = 514), and all stations within

158   Florida (n = 1131). To account for collinearity, average temperature was calculated from

159   minimum and maximum values. For the Nile crocodile dataset, missing temperature data

160   were linearly interpolated when the gap between records did not exceed three days,

161   increasing coverage by 9.99%. Average monthly rainfall was calculated as means from all

162   dates within each month. Climatic variables were linked to each Nile crocodile attack record

163   from the closest NOAA station. Temperature measurements were adjusted based on the

164   difference between the attack elevation and station elevation (Fick & Hijmans 2017),

165   according to the temperature lapse rate defined by the International Civil Aviation

166   Organization (ICAO 2017). Mean climatic values were calculated for each county in Florida

167   from all encompassed stations and were linked to attack records according to date and

168   county.

169

170   Human population density in South Africa was estimated for the magisterial district

171   encompassing each attack from the closest of seven historical censuses (1951, 1960, 1970,

172   1980, 1991, 1996, 2001; digitised and geo-referenced by Giraut & Vacchiani-Marcuzzo,

173   2009). The annual human population density of Eswatini was estimated by the United

174   Nations Population Division (UN 2017). Florida county human population densities were

175 estimated using contemporaneous data from the year of the attack provided by the Office of

176 Economic and Demographic Research (OEDR 2017). In addition, the total wetland area in

177 each county, taken to be a measure of potential alligator habitat (and used when selecting

178 background points, see below), was estimated from the National Wetlands Inventory, US

179 Fish & Wildlife Service (U.S. Fish and Wildlife Service, 2017).

180

181 The final crocodile dataset comprised 188 attacks recorded in South Africa and Eswatini

182 between September 1951 and December 2016. The final alligator dataset comprised 335

183 attacks recorded from Florida between September 1971 and December 2014. Both datasets

184 included daily average temperature, daily rainfall, monthly average rainfall, human

185 population density, month, and year as variables for modelling.

186

187 **Background points**

188 Attack records constitute 'presence only' data, and there is no reliable measure of human-

189 crocodilian exposure to quantify when attacks did not occur. However, when absence data

190 are not available, models can be used with 'background' points that are randomly sampled to

191 characterise the null distribution of each variable in the model (Elith & Leathwick 2009;

192 Barbet-Massin et al. 2012).

193

194 Background point sampling influences the results of environmental niche models (Barbet-

195 Massin et al 2012; Phillips et al 2009). Therefore, we used two background sampling

196 methods for each species to compare and assess the influence of background point sampling

197 on the results (background sampling method A, and background sampling method B). Each

198 method was used to create datasets of 10,000 background points for Nile crocodiles and

199 American alligators that could be sampled for model fitting. For background sampling

200   method A, we stratified background point sampling according to where attacks have been

201   reported. 10,000 Nile crocodile attack coordinates were randomly sampled and randomly

202   assigned dates between 1951 and 2016, and 10,000 American alligator background points

203   were randomly sampled from Florida counties proportionate to their number of reported

204   attacks and randomly assigned dates between 1971 and 2014. For background sampling

205   method B, we sampled background points across the species predicted ranges. 10,000 Nile

206   crocodile background points were randomly selected as coordinates that fall on water bodies

207   within the IUCN distribution of Nile crocodiles in South Africa and Swaziland, and 10,000

208   American alligator background points were sampled from all counties in Florida (Woodward

209   et al 2014). To make this method comparable between the species, the probability of a

210   Florida county being sampled was proportionate to its total wetland area (i.e., counties with

211   more wetland area had a proportionally higher probability of selection). Covariates were

212   linked to background points following the same process as for attack records.

213

214   **Model fitting**

215   Spearman's Rank correlation was calculated between all variables prior to model fitting

216   (Supplementary table 1). We first assessed attack seasonality for both species by calculating

217   Spearman's Rank correlations between the total number of attacks per month, and average

218   monthly temperature and average monthly rainfall, calculated using the background datasets.

219   We analysed attack patterns at a finer spatial and temporal resolution using boosted

220   regression trees (BRT). BRTs were fit to express nonlinearities in the data (Elith et al. 2006).

221

222   We sampled background points from the background datasets following guidelines set out by

223   Barbet-Massin et al. (2012). BRTs had an equal ratio (1:1) of background points to attacks.

224   BRTs were fit with 10-fold cross validation, as recommended by Miller (2015), and model fit

225   was evaluated as the mean area under curve (AUC) of the receiver operating characteristics

226   (ROC) plot. BRT model parameters that maximised ROC were selected. Each BRT had a

227   learning rate of 0.005, a tree complexity of 5, and a bag fraction of 0.5. The number of

228   boosted trees varied for each model but were selected to minimise holdout deviance. BRT

229   model contribution was assessed based on the number of times the variable is selected for

230   splitting, weighted by the squared improvement to the model as a result of each split, and

231   averaged over all trees (Friedman & Meulman 2003). Background point sampling affects

232   ROC and variable importance; therefore, we used a bootstrapping technique where each

233   model was fit 100 times with independently sampled background points, and variable

234   importance and ROC were measured across each iteration. All analyses were conducted in R

235   v.3.4.2 (R Core Team 2017) and BRTs were fit using the 'gbm' package v.2.1.3 (Ridgeway

236   2017).

237

238   **RESULTS**

239   Attack frequency shows a seasonal pattern for both species (Figure 2). There is a significant

240   correlation between number of attacks and mean monthly temperature over the study period

241   for both alligators (rho(10) = 0.95, p < 0.001) in Florida, and crocodiles (rho(10) = 0.98, p <

242   0.001) in South Africa and Swaziland. There is also a significant correlation between number

243   of attacks and mean monthly rainfall for alligators (rho(10) = 0.82, p < 0.001) and crocodiles

244   (rho(10) = 0.95, p < 0.001).

245

246   We fit BRTs to predict attack occurrence as a function of daily average temperature, daily

247   rainfall, monthly average rainfall, human population density, year, and month for both

248   species. BRTs were fit over 100 iterations with background points sampled from two datasets

249   for each species: one stratified by attack locations (background dataset A), and the other

250   sampled from across the species predicted ranges (background dataset B). The crocodile

251   BRTs had a mean cross-validation ROC value (± 1 s.d) of 0.83 ± 0.02 using background

252   dataset A, and 0.85 ± 0.01 using background dataset B. The alligator BRTs had a mean cross-

253   validation ROC value (± 1 s.d) of 0.69 ± 0.02 using background dataset A, and 0.77 ± 0.02

254   using background dataset B.

255

256   With background point sampling stratified by attack locations (background dataset A), daily

257   average temperature is the most important predictor of attack occurrence based on model

258   contribution for both Nile crocodiles (41.16 ± 3.73) and American alligators (42.97 ± 4.16),

259   and this was consistent for each model fitting iteration (Figure 3). The distributions of model

260   contribution overlap for daily rainfall, monthly average rainfall, human population density,

261   year, and month for both species, highlighting the variability introduced by background

262   sampling (Figure 3). However, on average, the second and third most important predictors of

263   Nile crocodile attack occurrence are human population density (17.86 ± 2.58), and monthly

264   average rainfall (14.80 ± 2.71), and of American alligator attack occurrence are year (14.87 ±

265   1.98), and human population density (11.90 ± 1.95).

266

267   With background points sampled across the species predicted ranges (background dataset B),

268   daily average temperature and human population density are the strongest predictors of attack

269   occurrence. For American alligators, mean BRT contribution was 32.34 ± 3.42 and 34.85 ±

270   3.44 for daily average temperature and human population density respectively. For Nile

271   crocodiles, mean BRT contribution was 49.42 ± 3.83 and 16.93 ± 2.67 for daily average

272   temperature and human population density respectively. The relative increase in the strength

273   of human population density as a predictor when background points are sampled across the

274   species predicted ranges (background dataset B) compared with when sampling is stratified

275   by attack location (background dataset A) is likely due to an increase in attack likelihood

276   variance across space. This would increase the relative importance of the covariate that is the

277   strongest spatial predictor. In our case, this is human population density, which varies greatly

278   across state country and magisterial district. Notably, human population density has a non-

279   linear relationship with attack occurrence across the predicted ranges of both species. This is

280   likely due to the patchy distribution of crocodilians and humans, since attacks are heavily

281   dependent on the relative local abundance of *both* species and can only occur when there is

282   exposure between the two. The lack of historical fine-scale human and crocodilian population

283   density data, or other proxies for human-crocodilian exposure rates, likely limits the accuracy

284   of our models, and it is possible that the inclusion of further covariates would affect the

285   relative importance of predictors.

286

287   BRTs indicate that the probability of attack occurrence increases for Nile crocodiles and

288   American alligators as temperature increases. BRT partial dependence plots highlight the

289   relationship between daily average temperature and attack likelihood after accounting for the

290   average effects of all other variables in the model. These indicate that attack likelihood

291   sharply increases when daily average temperature exceeds 18°C for both species, and that it

292   plateaus after approximately 28°C (Figure 4). It is important to note here that this does not

293   mean attacks could not occur at temperatures below 18°C. For example, the minimum daily

294   average temperature linked to Nile crocodile and American alligator attacks in our dataset

295   were 10.63°C and 12.5°C respectively.

296

297   **DISCUSSION**

298   Using environmental niche modelling, we explored the influence of abiotic and biotic

299   environmental variables on crocodilian attack occurrence at a finer spatial and temporal

300   resolution than in previous studies. Three key findings emerged for both Nile crocodiles and

301   American alligators. First, temperature was the most important abiotic temporal predictor of

302   attack occurrence. Second, attack likelihood increased sharply when daily average

303   temperature exceeded 18°C. Third, the probability of attacks was highest above 28°C, where

304   it plateaued. Below, we discuss three non-mutually exclusive hypotheses that may explain

305   these findings.

306

307   From the perspective of crocodilian behaviour, attack likelihood may increase with ambient

308   temperature for physiological reasons. As ectotherms, the ability of crocodilians to digest

309   food and to hunt is dependent on ambient temperatures (Emshwiller & Gleeson, 1997;

310   Seebacher & Franklin 2005; Hutton 1987). For instance, in alligators, digestive efficiency

311   increases significantly as body temperature rises from 25°C to 31°C (Coulson & Coulson,

312   1986), and they stop eating when ambient temperatures drop below 16°C (Lance, 2003).

313   Hossain et al. (2013) found comparable patterns for captive saltwater crocodiles. In our study,

314   a remarkably similar relationship was evident, including comparable minimum and maximum

315   temperature thresholds, which offers strong support for the hypothesis that ambient

316   temperature influences attack patterns via its effect on crocodilian physiology (Mazzotti et

317   al., 2016; Seebacher & Franklin, 2005).

318

319   A related hypothesis proposes that increased attacks at higher temperatures reflect heightened

320   crocodilian aggression during the breeding season, mediated either by the effect of

321   testosterone on male behaviour or female nest-guarding (Pooley et al 1992). However, studies

322   on alligators indicated that testosterone was not correlated with attack frequency (Woodward

323   et al. 2014), and the limited research on hormones and breeding undertaken on captive Nile

324   crocodiles suggests that heightened hormone levels and breeding occur during the late winter

325   months, when attack occurrence is low (Kofron 1990; pers. comm. Myburgh 2018.)

326   Similarly, in the USA, limited data suggest elevated testosterone levels in the early breeding

327   season (February-March) that decline sharply over summer (Hamlin et al. 2011). Moreover,

328   for Nile crocodiles, nest-guarding in most regions occurs in the hottest months, meaning

329   many of the larger adult females are not hunting and remain on or near their nests, reducing

330   the likelihood of attacks by these animals (Pooley 1982; Kofron, 1990; Combrink et al.

331   2017).

332

333   From a human behavioural perspective, attack likelihood may increase with ambient

334   temperature as a result of people spending more time in and around water in hot weather,

335   increasing encounters with crocodilians. In South Africa and Eswatini, nearly half of all

336   attacks occurred on weekends and holidays, suggesting that human activity patterns are

337   important. In further support of this, data collected from our study area in southern Africa

338   suggest that Nile crocodile attacks occur most often during activities such as crossing rivers,

339   domestic chores, fishing, and swimming (Pooley et al, in press), and similar observations

340   have been made in Australia (Wallace, Leslie, & Coulson 2011). This hypothesis is clearly

341   applicable to temperature-dependent activities, such as swimming, but is less so for river

342   crossing and domestic chores, which occur year-round (although they may differ in duration

343   and method at different temperatures). Unfortunately, due to the lack of direct data on human

344   activity levels for the full duration of the study periods, we are currently unable to quantify

345   how changes in human behaviour contribute to attack patterns. However, this highlights an

346   interesting area for future work.

347

348   Variable importance and predictive accuracy (measured as ROC) of the models was

349   influenced by how background points were sampled. Predictive accuracy and the relative

350   importance of human population density as a predictor were increased for the American

351   alligator attack model when background points were sampled from across all counties in

352   Florida (stratified by total wetland area), as opposed to stratified by counties in which attacks

353   have occured. This is likely due to spatial variation in attack likelihood between counties,

354   which is captured by human population density due to the close association between human

355   population density and county. This is supported by the non-linear relationship observed

356   between attack likelihood and human population density across Florida. Spatial variation in

357   attack likelihood is likely a result of the patchy distribution of American alligators across

358   their predicted range and resulting variation in human-crocodilian exposure rates.

359   Our findings have implications for crocodilian conservation. In particular, improving our

360   understanding of the climatic conditions under which negative interactions between people

361   and crocodilians are more common could inform future strategies for conflict management,

362   including educating local communities in high-risk areas about the relationship between

363   temperature and attack occurrence. They might also discourage antagonistic approaches that

364   threaten crocodilian welfare, such as removal, extermination, and nest destruction

365   (Woodward et al. 2014). Behavioural modification strategies are likely to be more practical

366   for irregular activities that can be scheduled during the winter, such as dam repair (see

367   CrocBITE, 2018 for reports of attacks on divers). However, the use of crocodilian-inhabited

368   waterways for domestic chores and livelihoods could also be modified by organising essential

369   activities during cooler periods. As with all conflict-mitigation strategies, this comes with the

370   caveat that attacks may still possible at colder temperatures due to individual variation in

371   crocodilian behaviour and physiology or the risk of accidental encounters (e.g., stumbling

372   upon a nest or treading on a crocodilian). This is especially true when temperatures fall at

373   dawn, dusk, or during the night, as crocodilian activity often increases during these periods

374   and humans or other prey are more vulnerable to attack because of poor lighting conditions

375   (CrocBITE, 2018). More generally, in regions with less seasonal temperature variation,

376   crocodilian behavioural modification of the kind described above will be less pronounced.

377   For example, in India and Bangladesh, daily average temperature rarely drops below 23°C,

378   which is well within the comfortable physiological range for crocodilian hunting (Das &

379   Jana, 2017).

380   Seasonal limitations on crocodilian attacks linked to temperature may be affected markedly

381   by predicted trends in global warming. For instance, average temperatures in Africa are

382   predicted to increase by as much as 5-8% by 2050-2100 (Munzhedzi, 2018; Ziervogel et al.

383   2014). This is likely to facilitate more regular crocodilian hunting, potentially to the point that

384   it becomes commonplace throughout the year, as it is in contemporary equatorial Africa,

385   India and Bangladesh. Ongoing monitoring of the influence of temperature changes on

386   crocodile behaviour in the coming years and their effect on attack patterns will be important.

387   Our findings also have implications beyond crocodilian conflict management. The finding

388   that crocodilian attack patterns appear to be influenced by inherent physiological constraints

389   that are common to all ectotherms suggests that similar methods could be applied to

390   understanding conflict with other species. For example, snakes commonly bite humans, their

391   pets, and livestock, and The World Health Organization (2018) estimates that around 5

392   million snakebites occur annually, resulting in between 81,000 and 138,000 deaths. This issue

393   has been neglected in the literature, resulting in the slow development of mitigation strategies

394   (Mohapatra et al. 2011). However, like crocodilians, there is both theoretical and

395   observational evidence that behaviour in snakes is influenced by climatic factors, including

396   temperature constraints on metabolism (Saint Girons 1980; Wang et al. 2002). Accordingly,

397   it has been reported that seasonal snakebite patterns peak in the summer months in countries

398   such as Bangladesh (Rahman et al. 2010) and Nepal (Longkumer et al. 2017). Our methods

399   could also be applied to local issues that affect small communities, such as attacks by

400   Komodo dragons on people, pets, and livestock in Indonesia. These attacks are reported to

401   have affected 33.3% of people in a study of affected areas (Ardiantiono et al. 2015).

402   In addition, the current approach of linking attacks by endothermic predators to spatial

403   variables such as topography and urban land use (Carvalho et al. 2015; Zarco-González et al.

404   2013; Behdarvand et al. 2014; Kabir et al. 2014) could be expanded to include abiotic

405   predictors. The heat dissipation hypothesis suggests that activity in large species, including

406   dangerous predators such as tigers, lions, hunting dogs, and bears, will be limited during

407   hotter periods due to the difficulty of thermoregulating (Creel et al. 2016; Smith & Kok,

408   2006; Ghoddousi et al. 2016). A recent study exploring injuries and fatalities caused by large

409   mammals in Nepal found that attacks on humans by elephants, rhinoceros, and tigers were all

410   significantly higher in the winter, potentially indicating increased aggression among both

411   predators and large herbivores at colder temperatures when vigorous activity becomes less

412   problematic (Acharya et al. 2016). As with previous work on crocodilians, Acharya et al.

413   used monthly climatic data that only offered a coarse temporal resolution. Our methods,

414   therefore, could provide a template for the future study of human-endotherm conflict.

415   In conclusion, our findings offer strong support for the hypothesis that crocodilian attack

416   seasonality is determined predominantly by temperature in regions where fluctuations are

417   large enough to have significant impacts on crocodilian behaviour. We provide the first

418   evidence of this at a high spatial and temporal resolution. Our analysis demonstrates that

419   attacks increase predictably across a given temperature range and appear to be constrained by

420   a biologically-relevant threshold. This has the potential to inform conflict management and

421   conservation. The strong theoretical grounding for the temperature-physiology relationship

422   suggests that our approach could be promising in casting light on the dynamics of human

423   conflict with other species, including both ectotherms and endotherms.

424   **Author contributions**
425
426   SP and GP conceived of the study; SP collected the attack data; GP and JJW collected the
427   environmental and spatial data and prepared the data for analysis; GP and ST carried out the
428   analyses; TMMV and GP wrote the manuscript; all authors contributed to revisions of the
429   manuscript.
430
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432
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434   Commission for alligator attack data. Prior to this study, SP worked on early ideas on the
435   seasonality of crocodile attacks related to biophysical variables with Joshua Potter (cited).
436
437   **Conflicts of Interest**
438
439   None
440
441   **Ethical standards**
442
443   This work complies with Oryx's Code of Conduct for authors. The research did not involve
444   human or animal test subjects nor the collection of specimens.
445
446   **References cited**
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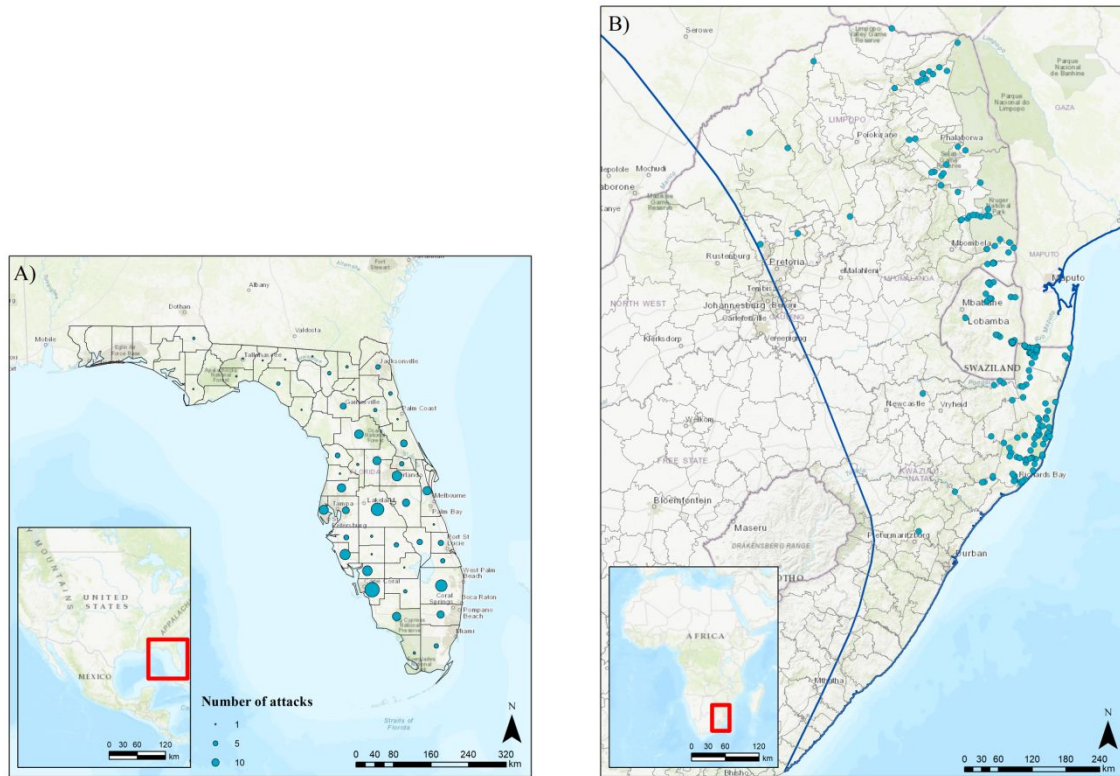
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599 **Table and Figures**
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605 **Figure 1 –** Map of A) American alligator attacks in Florida, USA, between 1971 and 2014 (n
606 = 335). The size of the blue circle is proportionate to the number of recorded attacks in each
607 county (which are outlined in black). There are 67 counties in Florida. Map of B) Nile
608 crocodile attack coordinates in South Africa and Swaziland between 1951 and 2016 (n =
609 188). The blue line outlines the distribution of Nile crocodiles (IUCN 1996).
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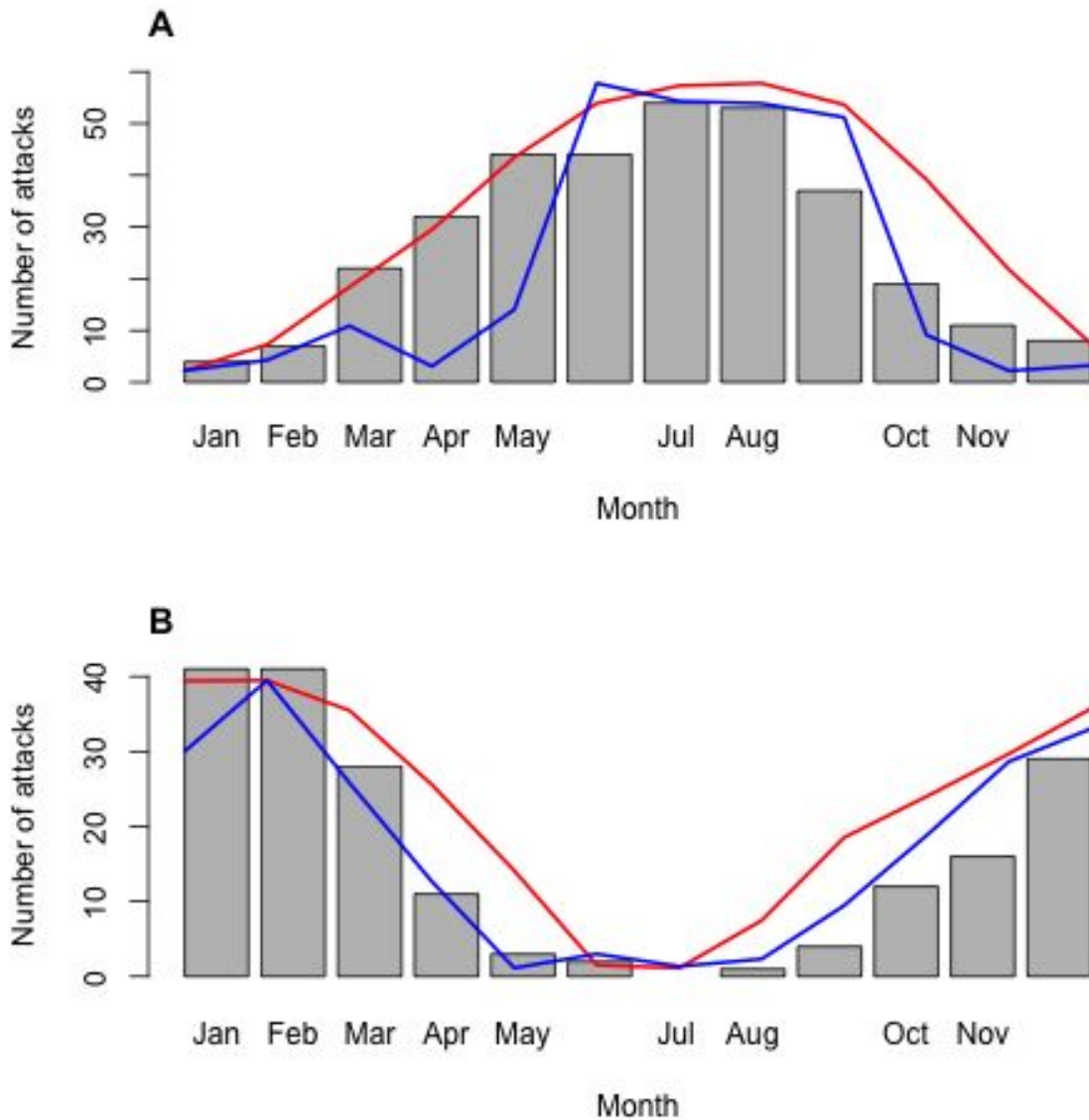
612
613　**Figure 2 –** Seasonal variations in the incidence of attacks by A) American alligators in
614　Florida between 1971 and 2014, and B) Nile crocodiles in South Africa between 1951 and
615　2016. Average monthly rainfall and temperature of background points (n = 10,000) are
616　shown in blue and red respectively.
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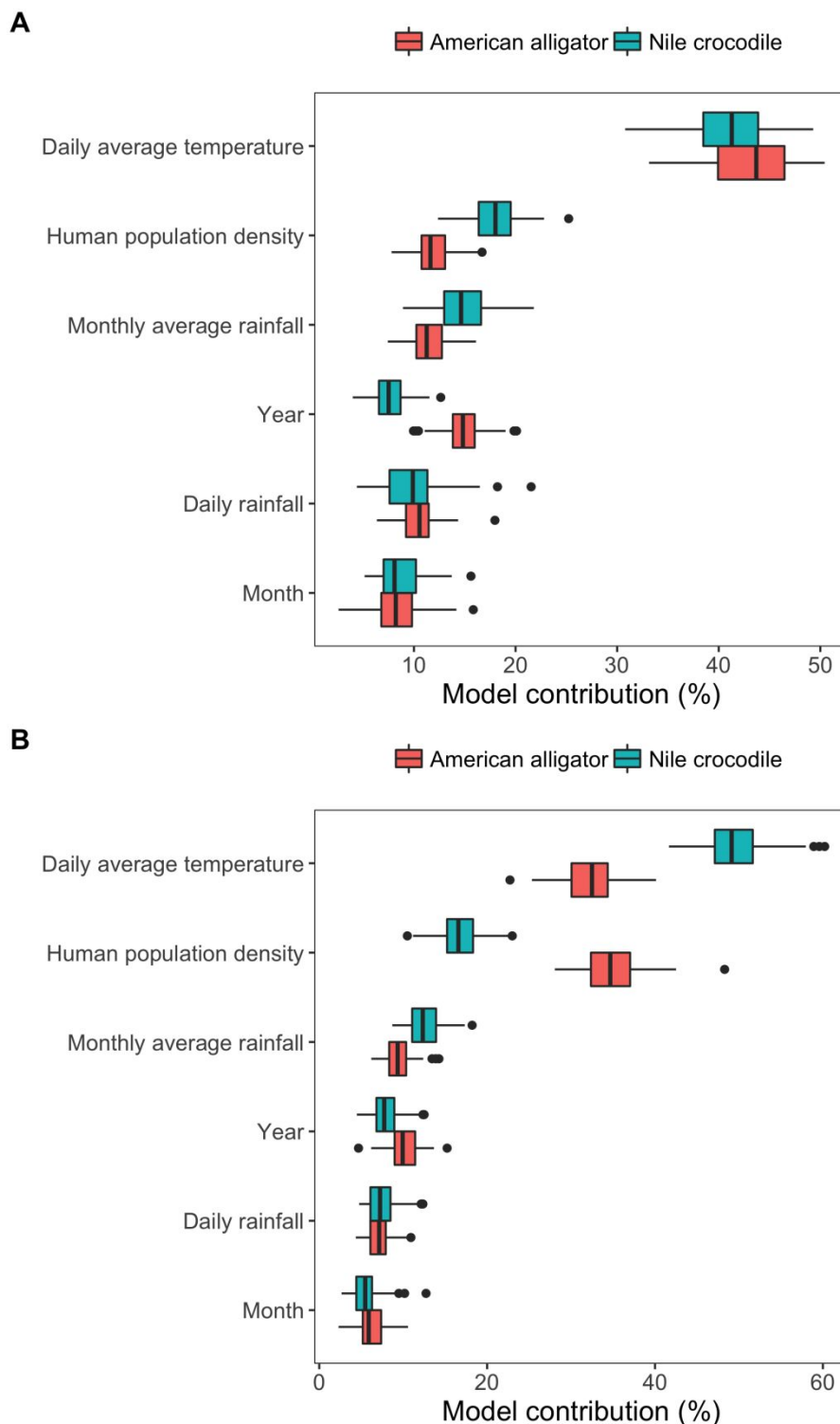
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621   **Figure 3** – Boxplots of variable contribution for boosted regression trees (BRTs) for Nile
622   crocodile (blue) and American alligator (red) attack occurrence. BRTs were fit 100 times
623   with a ratio of 1:1 presence to background points sampled from two background datasets:
624   background dataset A (A), and background dataset B (B). Background dataset A contains
625   background points sampled from attack locations over the study periods. Background dataset
626   B contains background points sampled across the species predicted ranges over the study
627   periods.
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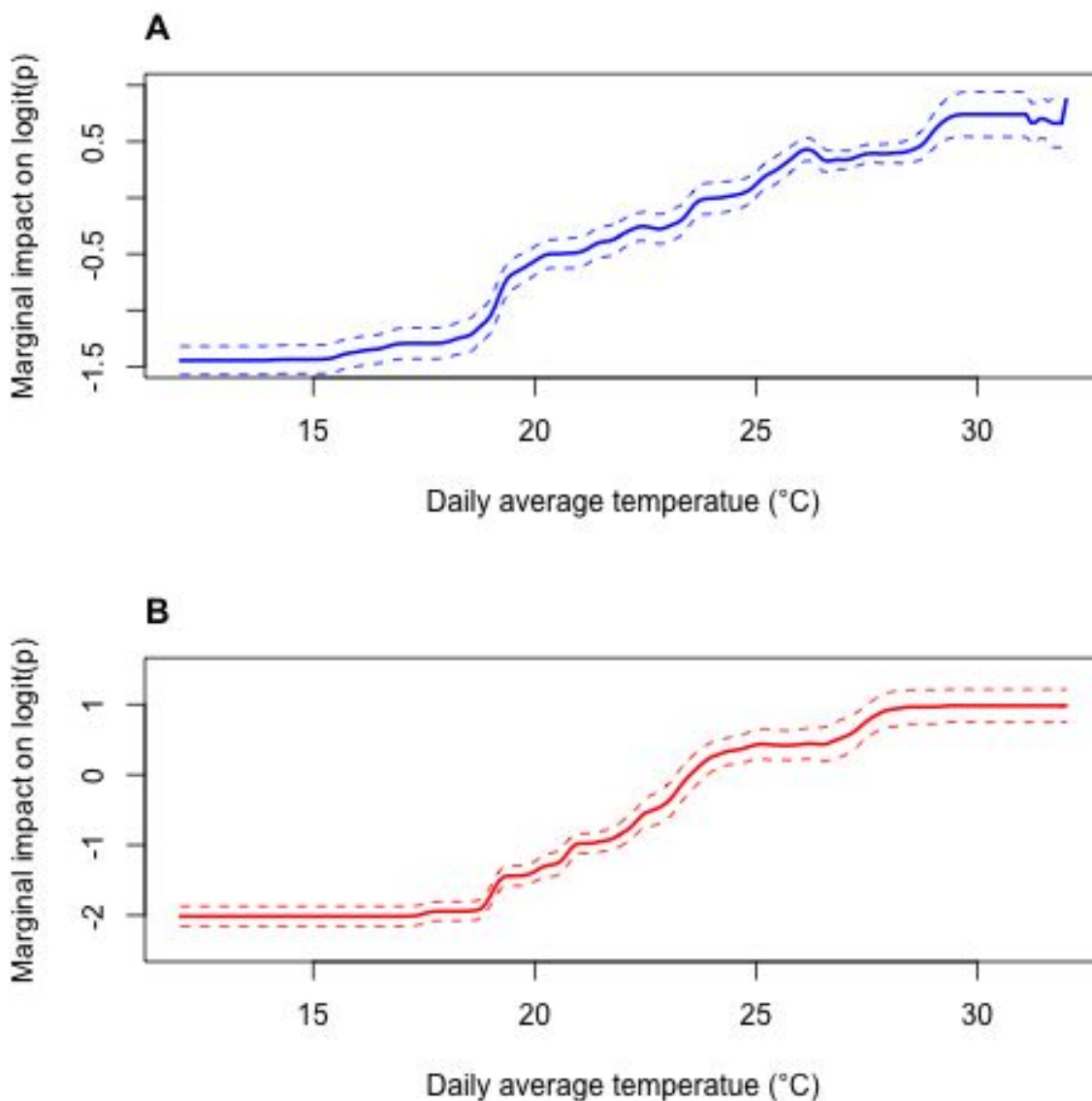
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Figure 4 – Boosted regression tree (BRT) partial dependence plots showing the marginal impact of daily average temperature (x-axis) on attack likelihood (y-axis) for American alligators (A) and Nile crocodiles (B) after accounting for the average effects of all other variables in the model. The mean (solid lines) and standard errors (dashed lines) were calculated across all 100 model fitting iterations. Y-axes are on the logit scale and are centred to have zero mean over the data distribution.

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646 **Supplementary material**
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Variable	Daily average temperature	Daily rainfall	Monthly average rainfall	Human population density	Year	Month
Daily average temperature	1	0.282	0.507	0.08	0.03	0.236
Daily rainfall		1	0.361	0.045	0.039	0.07
Monthly average rainfall			1	0.002	-0.006	0.073
Human population density				1	0.342	-0.001
Year					1	0.001
Month						1

648
649 **Supplementary table 1A --** Spearman's Rank correlation between background covariates
650 used to model Nile crocodile attacks. 10,000 background points were sampled, stratified
651 according to where attacks have been reported.
652
653 **Supplementary table 1B --** Spearman's Rank correlation between background covariates (n
654 = 10,000) used to model American alligator attacks. 10,000 background points were sampled,
655 stratified according to where attacks have been reported.
656

Variable	Daily average temperature	Daily rainfall	Monthly average rainfall	Human population density	Year	Month
Daily average temperature	1	0.172	0.386	0.131	0.224	-0.200
Daily rainfall		1	0.360	0.167	0.254	0.004
Monthly average rainfall			1	0.168	0.215	-0.041
Human population density				1	0.647	-0.004
Year					1	-0.008

| Month						1

657

658 **Supplementary table 2 --** Model contribution of BRT predictors with different methods for
659 background point sampling. Method A: background points were sampled stratified by attack
660 locations. Method B: background points were sampled across the species predicted ranges.
661

Covariate	Nile Crocodile		American alligator	
	Method A BRT contribution (mean, sd)	Method B BRT contribution (mean, sd)	Method A BRT contribution (mean, sd)	Method B BRT contribution (mean, sd)
Daily average temperature	41.16 ±3.73	49.43 ±3.83	42.97 ±4.16	32.34 ±3.42
Human population density	17.86 ±2.58	16.93 ±2.67	11.90 ±1.95	34.85 ±3.44
Year	7.72 ±1.70	7.96 ±1.70	14.87 ±1.98	10.07 ±1.85
Monthly average rainfall	14.80 ±2.71	12.62 ±2.08	11.60 ±2.09	9.41 ±1.59
Daily rainfall	9.79 ±2.89	7.48 ±1.85	10.36 ±1.91	7.07 ±1.37
Month	8.67 ±2.25	5.58 ±1.65	8.30 ±2.24	6.26 ±1.69

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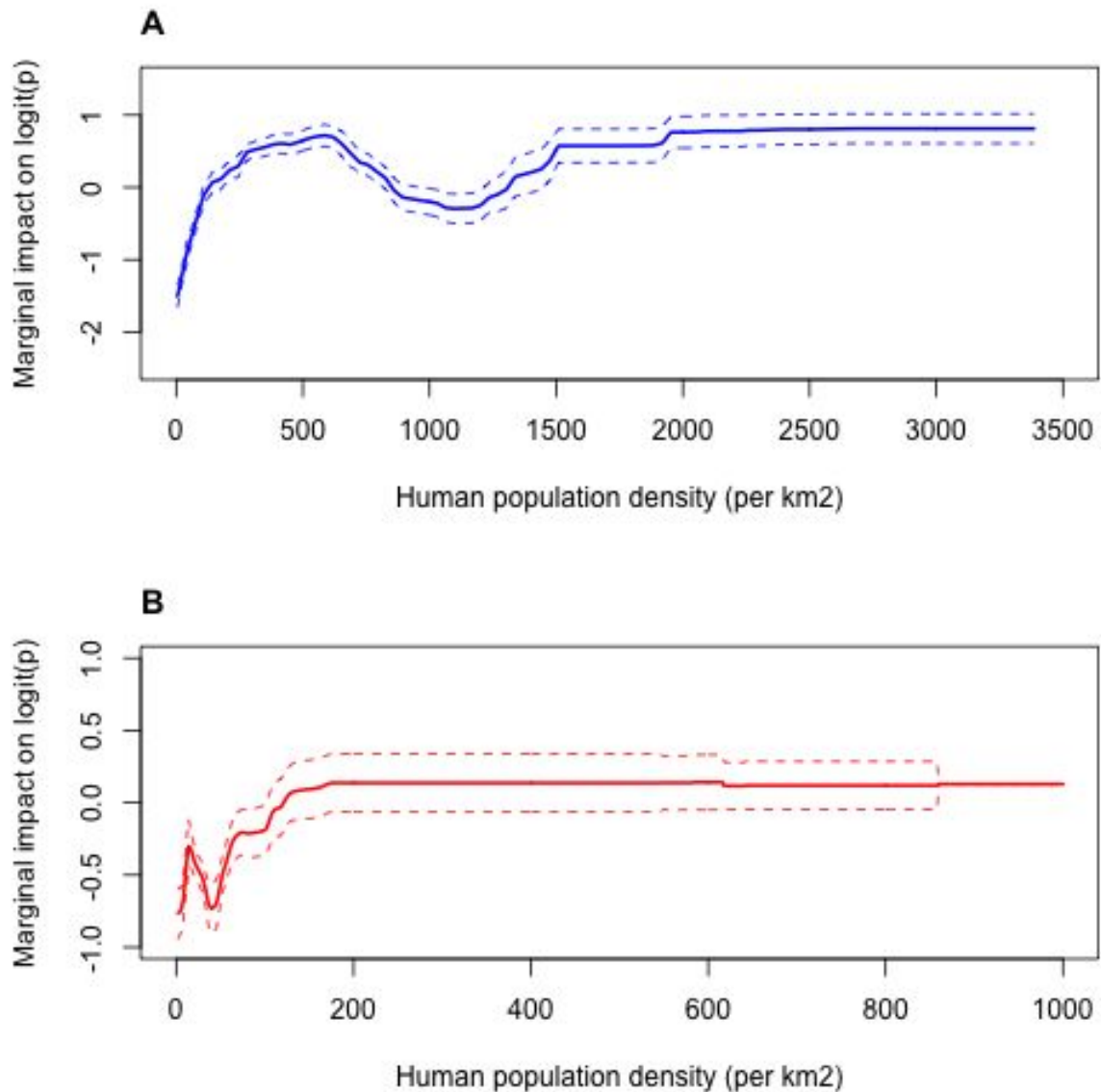
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665
666   **Supplementary figure 1 –** Boosted Regression Tree (BRT) partial dependence plots
667   showing the marginal impact of human population density (x-axis) on attack likelihood (y-
668   axis) for American alligators (A) and Nile crocodiles (B) after accounting for the average
669   effects of all other variables in the model. The mean (filled line) and standard errors (dashed
670   lines) were calculated across all 100 model fitting iterations. Y axes are on the logit scale and
671   are centred to have zero mean over the data distribution.
672