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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

49

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 et 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 ($14.87 \pm$
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 $34.85 \pm$
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 crocodylians 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 crocodylian population
283 density data, or other proxies for human-crocodylian 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 crocodylian 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 crocodylian behaviour, attack likelihood may increase with ambient
308 temperature for physiological reasons. As ectotherms, the ability of crocodylians 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 crocodylian physiology (Mazzotti et
317 al., 2016; Seebacher & Franklin, 2005).

318

319 A related hypothesis proposes that increased attacks at higher temperatures reflect heightened
320 crocodylian 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 crocodylians. 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 occurred. 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 crocodylians, 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 crocodylian attack
416 seasonality is determined predominantly by temperature in regions where fluctuations are
417 large enough to have significant impacts on crocodylian 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

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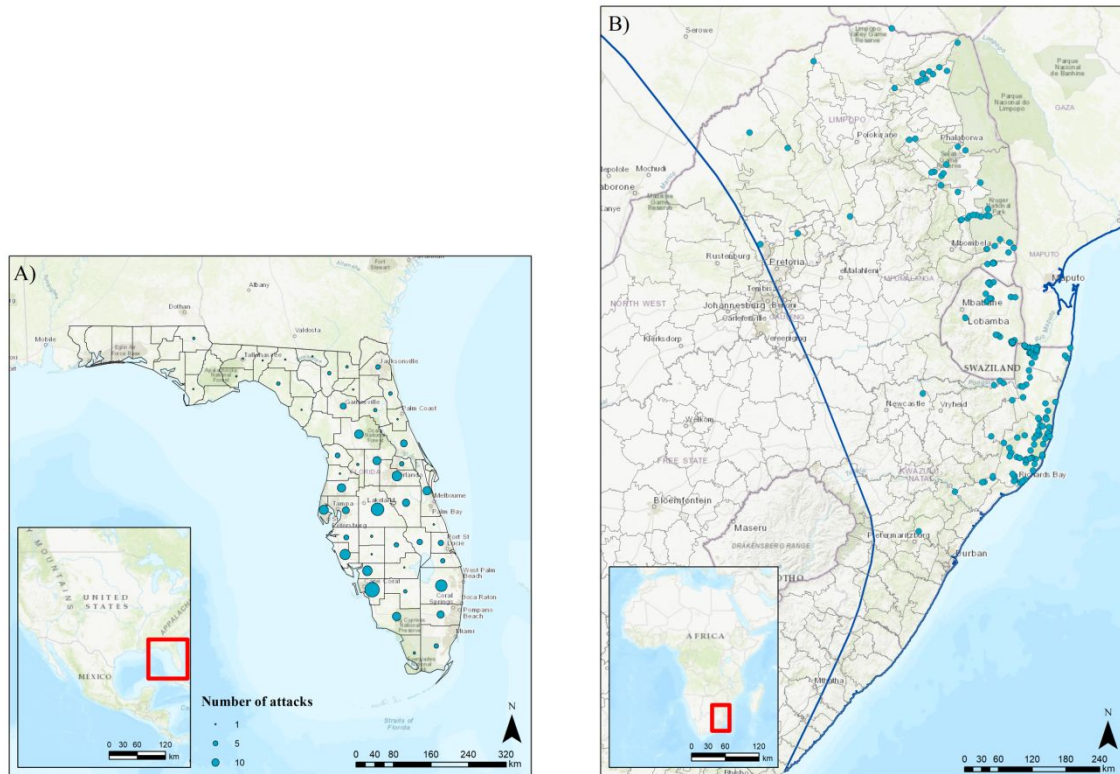
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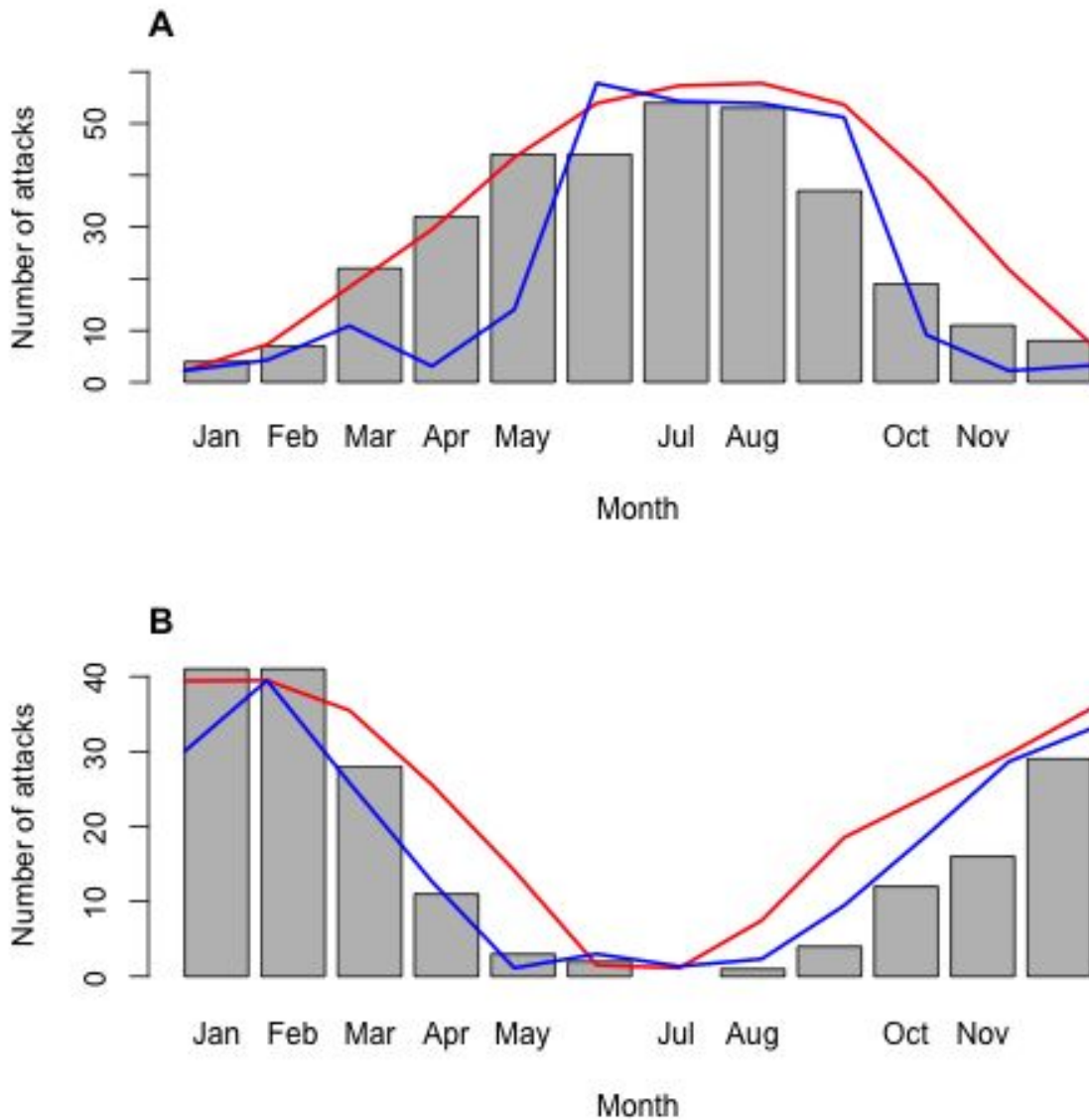
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Table and Figures



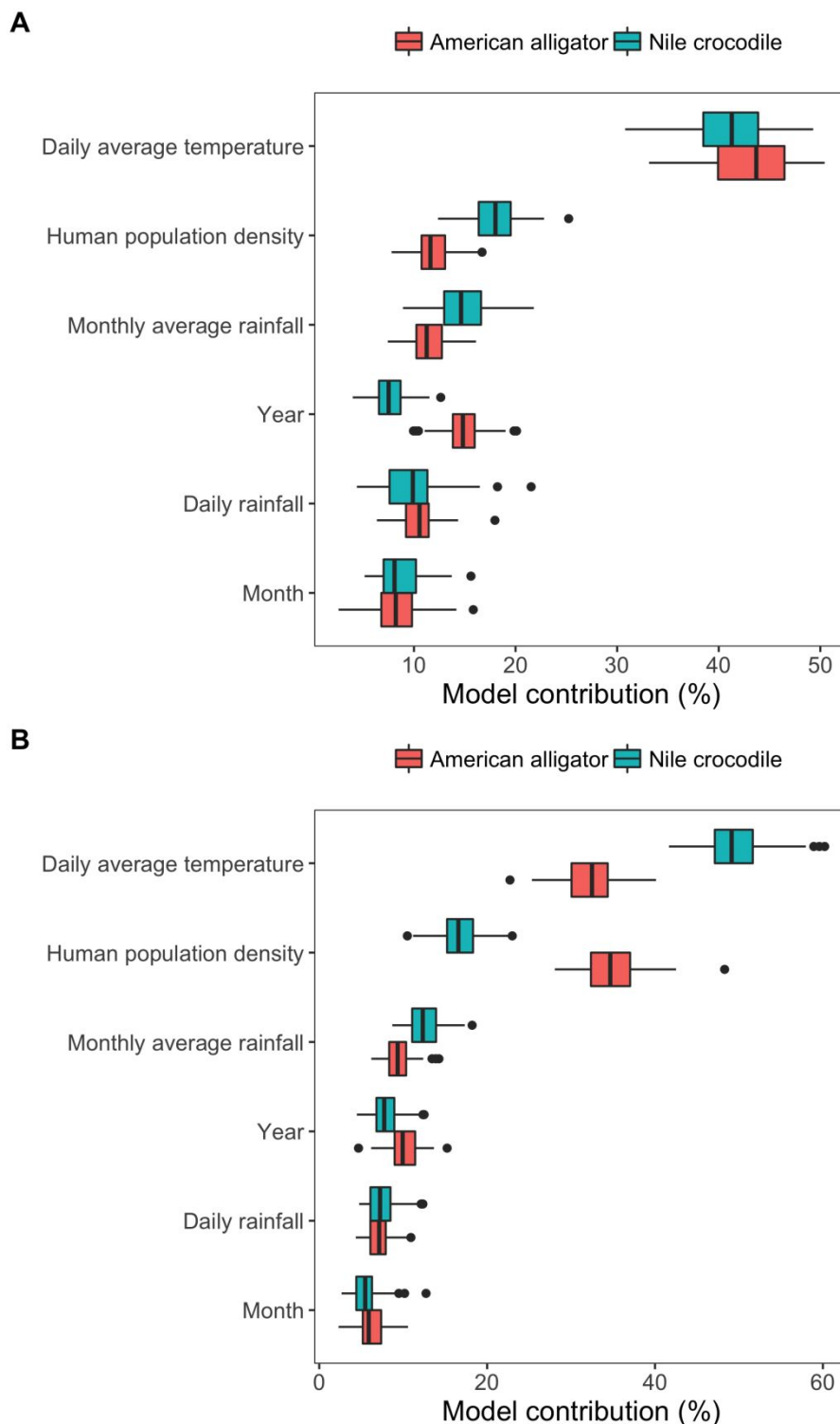
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Figure 1 – Map of A) American alligator attacks in Florida, USA, between 1971 and 2014 ($n = 335$). The size of the blue circle is proportionate to the number of recorded attacks in each county (which are outlined in black). There are 67 counties in Florida. Map of B) Nile crocodile attack coordinates in South Africa and Swaziland between 1951 and 2016 ($n = 188$). The blue line outlines the distribution of Nile crocodiles (IUCN 1996).



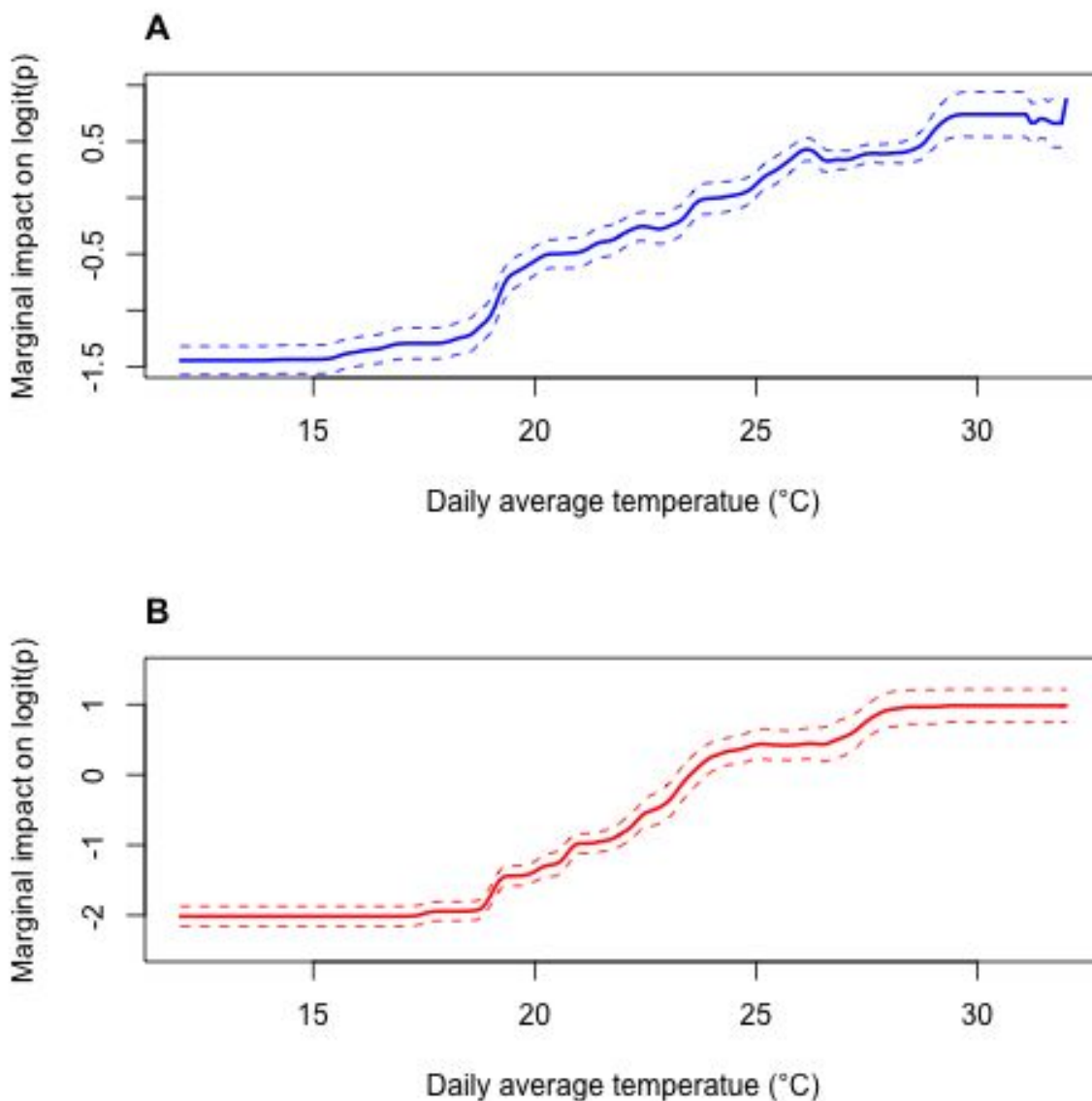
612
 613 **Figure 2** – Seasonal variations in the incidence of attacks by A) American alligators in
 614 Florida between 1971 and 2014, and B) Nile crocodiles in South Africa between 1951 and
 615 2016. Average monthly rainfall and temperature of background points (n = 10,000) are
 616 shown in blue and red respectively.

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Figure 3 – Boxplots of variable contribution for boosted regression trees (BRTs) for Nile crocodile (blue) and American alligator (red) attack occurrence. BRTs were fit 100 times with a ratio of 1:1 presence to background points sampled from two background datasets: background dataset A (A), and background dataset B (B). Background dataset A contains background points sampled from attack locations over the study periods. Background dataset B contains background points sampled across the species predicted ranges over the study periods.



629
 630 **Figure 4** – Boosted regression tree (BRT) partial dependence plots showing the marginal
 631 impact of daily average temperature (x-axis) on attack likelihood (y-axis) for American
 632 alligators (A) and Nile crocodiles (B) after accounting for the average effects of all other
 633 variables in the model. The mean (solid lines) and standard errors (dashed lines) were
 634 calculated across all 100 model fitting iterations. Y-axes are on the logit scale and are centred
 635 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

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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.

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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.

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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
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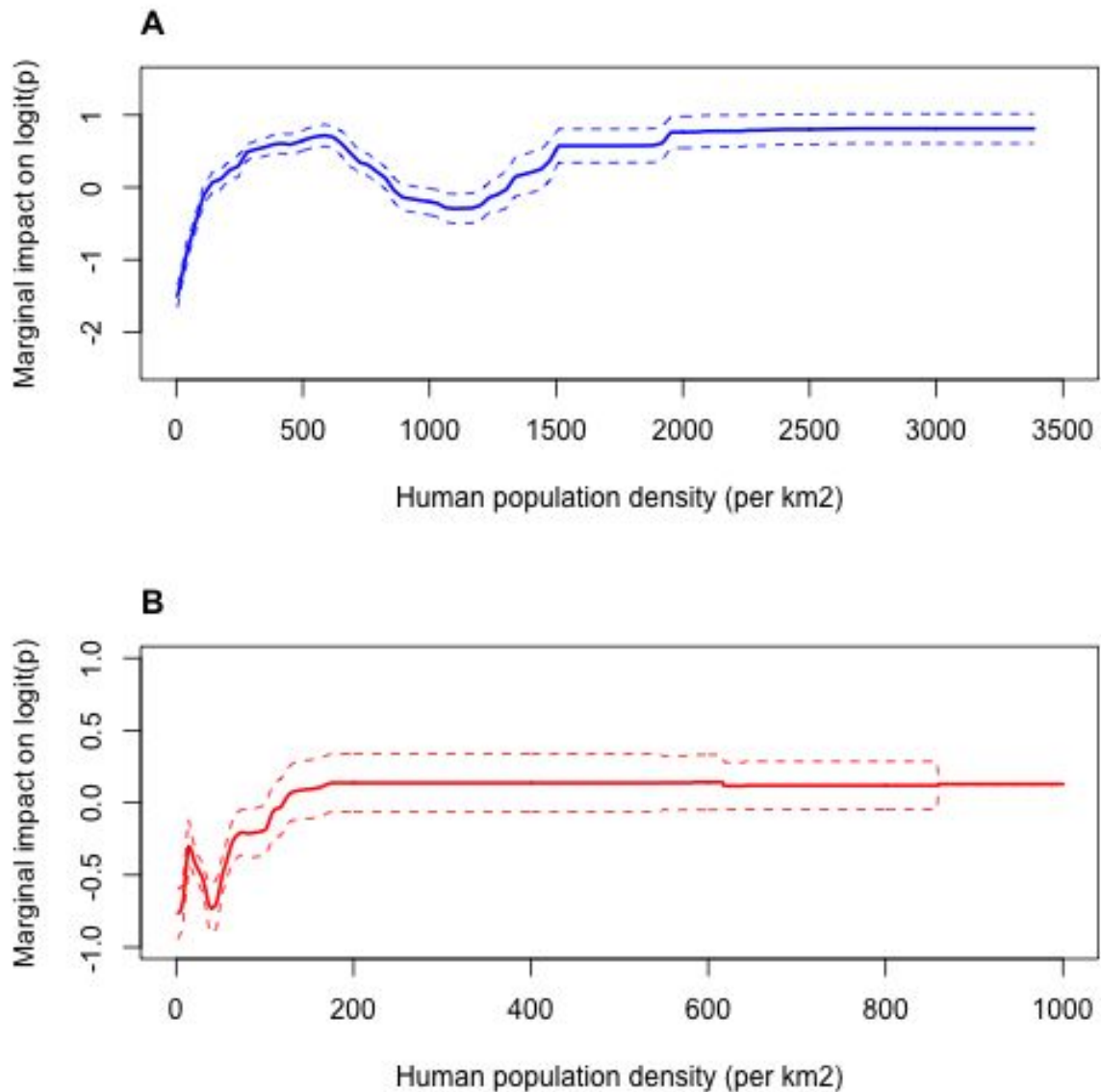
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658 **Supplementary table 2** -- Model contribution of BRT predictors with different methods for
 659 background point sampling. Method A: background points were sampled stratified by attack
 660 locations. Method B: background points were sampled across the species predicted ranges.
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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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Supplementary figure 1 – Boosted Regression Tree (BRT) partial dependence plots showing the marginal impact of human population density (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 (filled line) 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.