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## Can an herbivore affect where a top predator kills its prey by modifying woody vegetation structure?

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16 **Abstract**

17 In large mammal communities, little is known about modification of interspecific  
18 interactions through habitat structure changes. We assessed the effects of African  
19 elephants (*Loxodonta africana*) on features of woody habitat structure that can affect  
20 predator-prey interactions. We then explored how this can influence where African lions  
21 (*Panthera leo*) kill their prey. Indeed, lions are stalk-and-ambush predators and habitat  
22 structure and concealment opportunities are assumed to influence their hunting success.  
23 During two years, in Hwange National Park, Zimbabwe, kill sites (n=167) of GPS-  
24 collared lions were characterized (visibility distance for large mammals, distance to a  
25 potential ambush site and presence of elephant impacts). We compared characteristics of  
26 lion kill sites with characteristics of random sites (i) at a large scale (i.e, in areas  
27 intensively used by lions, n=418) and (ii) at the microhabitat scale (i.e., in the direct  
28 surrounding available habitat, < 150m, n = 167). Elephant-impacted sites had a slightly  
29 higher visibility and a longer distance to a potential ambush site than non-impacted sites,  
30 but these relationships were characterized by a high variability. At large scale, kill sites  
31 were characterized by higher levels of elephant impacts compared to random sites. At  
32 microhabitat scale, compared to the direct nearby available habitat kill sites were  
33 characterized by a reduced distance to a potential ambush site. We suggest a conceptual  
34 framework whereby the relative importance of habitat features and prey abundance could  
35 change upon the scale considered.

36 **Key words:** *ecosystem engineer, indirect effects, apex predator, megaherbivores,*  
37 *predator-prey relationships.*

38 **Introduction**

39 Species within an ecosystem are linked by a network of interspecific interactions (e.g.  
40 predation, competition, facilitation), which ultimately drives ecosystem functioning  
41 (Wardle et al. 2004). There is an increasing awareness that these interactions are dynamic  
42 and can be mediated by abiotic (e.g. climate change - Tylianakis et al. 2008, van der  
43 Putten et al. 2010) and biotic factors (e.g. parasitism - Hatcher et al. 2006, non-lethal  
44 effects of predators that mediate interspecific prey competition - Preisser & Bolnick  
45 2008). In these cases, the interaction between two species can be modified by a third  
46 species (hereafter “interaction modification”, Wootton 1993). This process can arise from  
47 a change of a plastic trait of one of the two main species interacting (i.e. trait-mediated  
48 interaction modification) or through alteration of the environment in which the  
49 interaction takes place (i.e. environment-mediated interaction modification, Wootton  
50 1993, 2002, Dambacher & Ramos-Jiliberto 2007).

51 Questions have arisen about how habitat changes (diversity and/or physical  
52 structure) may affect interspecific interactions (Petren & Case 1998). In the current  
53 context of biodiversity loss, many studies have focused on anthropogenic alterations of  
54 the habitat (e.g. Tylianakis et al. 2007), but other ecosystem engineer species (Jones et al.  
55 1994) can affect habitats (Crooks 2002), and ultimately interspecific interactions  
56 (Marquis & Lill 2007). Arditi et al. (2005) even designated ecosystem engineer species as  
57 “interaction modifiers” due to their capacity to modulate their environment. Interaction  
58 modifications were shown to drive community dynamics in systems with few species  
59 (Werner & Peacor 2003, Preisser et al. 2007, Abrams 2010). There is now growing  
60 impetus from other recent works to address the challenges of detecting, measuring and

61 testing the potential role of interaction modifications in complex systems such as natural  
62 communities (e.g. Wootton 1994, Peacor & Werner 2001, Okuyama & Bolker 2007).  
63 Such an understanding is key to improve our ability to forecast how ecosystems will  
64 respond to global changes (Kéfi et al. 2012) as interaction modifications are often  
65 identified as the cause of unexpected responses to perturbation (Terry et al. 2017 and  
66 references therein).

67       The African elephant (*Loxodonta africana*) is an ecosystem engineer (Bond 1994).  
68 While the effects of elephants on vegetation structure through their foraging activity start  
69 to be well understood (review in Guldmond & van Aarde 2008), the consequences of  
70 elephant-induced vegetation changes on the whole ecosystem remain unknown as a  
71 diversity of indirect effects is documented (Pringle 2008, Valeix et al. 2011, Coverdale et  
72 al. 2016). In particular, little is known about the environment-mediated modifications of  
73 predator-prey relationships by elephants. Yet, elephants affect the vegetation structure,  
74 especially in the understory (Coverdale et al. 2016, Ferry 2018). Further, predation is  
75 mediated by physical features of habitats (Bell 1991, Kauffman et al. 2007) and has  
76 cascading effects down the food chain (Estes et al. 2011). To our knowledge, two studies  
77 highlighted elephant-induced modification of predator-prey relationships. Tambling et al.  
78 (2013) showed that elephants, by fragmenting very dense vegetation, improve access for  
79 lions, which may ultimately lead to an increased predation by lions on the small prey  
80 hiding in this very dense vegetation. Fležar et al. (2019) simulated elephant-induced  
81 habitat change at two spatial scales: (i) at the “patch” scale, by comparing high-quality  
82 grassland sites with high visibility against ones with low visibility (due to dense woody  
83 vegetation) and (ii) at the “within-patch” scale by adding coarse woody debris, potential

84 escape impediment for prey, in open areas. They then assessed the perceived predation  
85 risk by different herbivores. They revealed different responses of prey at the two scales  
86 and argue that depending on the scale, elephants' impact on the risk landscape could be  
87 both to hamper kill success (by opening up vegetation, improving visibility and lowering  
88 ambush opportunity) as well as facilitate kill success (by dropping woody debris that may  
89 lower visibility and create escape impediments). Elephants are thus able to modify  
90 predator-prey interactions by altering habitats and different manifestations of elephant-  
91 induced changes on the vegetation (e.g., visibility and coarse woody debris) could act at  
92 different spatial scales.

93         Here, we investigated whether elephants, through their impacts on vegetation  
94 structure (that lead to changes in visibility distance for large mammals and changes in the  
95 distance to a potential ambush site), can influence predator-prey interactions between  
96 African lions (*Panthera leo*) and their prey in a woody savanna ecosystem. Lions are  
97 stalk-and-ambush predators that rely on features of the habitat providing concealment  
98 (typically dense vegetation) to approach and attack their prey (Hopcraft et al. 2005,  
99 Loarie et al. 2013, Davies et al. 2016). Therefore, habitat characteristics are expected to  
100 play an important role in selecting areas that may increase hunting success (the *ambush-*  
101 *habitat* hypothesis - Hopcraft et al. 2005). This has been illustrated in Kruger National  
102 Park, South Africa, where lions kill their prey within nine meters of a potential ambush  
103 site (Loarie et al. 2013). Elephants are thus likely to affect where lions hunt and/or  
104 successfully hunt (i.e. kill) their prey.

105         The aim of this study is two-fold: (1) to assess whether elephant impacts on  
106 woody vegetation are associated with an increased visibility and a change in the distance

107 to a potential ambush site, and (2) to test the hypothesis that lions kill less in areas  
108 impacted by elephants (as we expect them to be more successful hunters in areas with  
109 denser vegetation thus greater opportunities for concealment). This second aim was  
110 investigated at two different scales: (i) we first compared lion kill sites with random sites  
111 in areas intensively used by lions to assess if among all habitats used by lions, kill sites  
112 were characterized by denser vegetation and less elephant impacts (the “large” scale  
113 hereafter), and (ii) we then compared the characteristics of lion kill sites with  
114 characteristics of the direct surrounding available habitat (< 150 m) to assess if lions  
115 killed more in closed microhabitats that were less impacted by elephants (the  
116 “microhabitat” scale hereafter). Together, the results will allow an assessment of the  
117 extent to which elephants can induce environment-mediated trophic interaction  
118 modification between lions and their prey in woodland savannas and if this modification  
119 is scale-dependent.

120

## 121 **Materials and methods**

122 Study site - Hwange National Park covers ~15 000 km<sup>2</sup> of semi-arid dystrophic (low  
123 nutrient soil) savanna in western Zimbabwe (19°00' S, 26°30' E). The vegetation is  
124 primarily woodland and bushland savanna. The east and southern parts of the park are  
125 dominated by open wooded savannas on Kalahari sands, primarily teak woodland  
126 (*Baikiaea plurijuga*) and *Combretum/Terminalia* woodlands. Batoka basalt and Karoo  
127 sediments in the north and north-west of the park are dominated by *Colophospermum*  
128 *mopane* woodlands interspersed with grassland vleis. The long-term mean annual rainfall  
129 is ~ 600 mm, which falls primarily between October and April. The surface water

130 available to animals is found in natural as well as artificial waterholes. The study area is  
131 located in the northern region of Hwange National Park (~7 000km<sup>2</sup>) where lion density  
132 is estimated around 4.3 individuals/100 km<sup>2</sup> (Loveridge et al. 2016), and elephant density  
133 is estimated above 2 individuals/km<sup>2</sup> (Chamaillé-Jammes et al. 2008).

134 Data – We collected data between 2014 and 2015 from 12 female and 15 male lions from  
135 different coalitions and prides equipped with 2D size AWT GPS radio-collars. The lions’  
136 locations were available hourly and for some lions every two hours, day and night.

137 Potential lion kills were attained by identifying clusters of coordinates that had more than  
138 4 hours of sequential locations within a defined proximity (150 m, see also Tambling et  
139 al. 2010). In the field, these clusters were searched for a carcass or the remains of a  
140 carcass and classified as kill sites based on the evidence of a kill. We confirmed lion kills  
141 when the presence of a carcass was associated with indications of a hunt / struggle from  
142 animal tracks (observed by skilled field trackers) and / or broken and tramped vegetation  
143 and / or from the condition of any remaining hide bearing claw and bite marks typical of  
144 lion predation. Carcasses found were classified to species based on the body size of the  
145 animal killed and the presence of identifiable material, such as horns, jaws, bones, and  
146 hair. We made the assumption that the kill site is a good proxy of the environment within  
147 which the lion decided to start the hunt, as lion is a stalk-and-ambush predator attacking  
148 and killing prey at short distances (van Orsdol 1984, Haas et al. 2005). This assumption  
149 has been made in several previous works (Davidson et al. 2012, 2013, Loarie et al. 2013,  
150 Davies et al. 2016). In total, 705 clusters were monitored among which 167 were  
151 identified as kill sites and 538 were not (called “non-kill sites” hereafter). For the 167 kill  
152 sites and for 251 non-kill sites, we identified a paired random site (with a random

153 direction, a random distance between 50 and 150m from the kill for kill sites and from  
154 the GPS point identified as the start of the cluster for non-kill sites). In total, 418 random  
155 sites were characterized and represented habitats intensively used by lions. Among these  
156 random sites, 167 were associated to a kill site and represented the direct surrounding  
157 available habitat. For each kill site, non-kill site and random site, we measured the  
158 distance to a potential ambush site (DPAS hereafter, a potential ambush site was any  
159 habitat feature able to conceal a lying lion, i.e. most of the time a dense bush in the study  
160 ecosystem) and the visibility. Visibility at each site was assessed by using two 50 cm x  
161 50 cm white boards. The two boards were set so that one board was at 10–60 cm  
162 (representative of the height of a crawling lion) and the other was at 100–150cm  
163 (representative of a standing lion). One person stood at the location of the kill or at the  
164 centre of the random site, while another person held the boards, walked away from the  
165 centre in the four cardinal directions and recorded the distance at which the person at the  
166 centre of the site could not see each board anymore. The four distances obtained from the  
167 four cardinal directions were then averaged (“visibility” hereafter). As lions are more  
168 successful at capturing prey when attacks are launched at short distance (<7.6m for  
169 Thomson’s gazelle, 15m for wildebeest and zebras, Haas et al. 2005), elephant impacts  
170 were assessed within a 25m radius of the kill for the kill sites, of the random point for the  
171 random sites and of the GPS point identified as the start of the non-kill sites. The extent  
172 of elephant impact was determined by the definition of five classes of percentage of trees  
173 impacted by elephants (broken, coppiced and/or uprooted): class 0: no impact; class 1: [1-  
174 25%]; class 2: [26%-50%]; class 3: [51%-75%]; and class 4 : [76%-100%].

175 *Analyses* –Proximity to water is commonly thought to influence the level of herbivore  
176 impacts on the vegetation (i.e. the “piosphere effect”, Lange 1969), but this has recently  
177 been debated in wild protected areas (Chamaillé-Jammes et al. 2009). We therefore  
178 preliminarily checked the existence of a link between distance to water and the existence  
179 of elephant impacts on the vegetation and found that sites (random sites and kill sites)  
180 impacted by elephants were not located closer to waterholes than sites not impacted by  
181 elephants (Kruskal-Wallis test,  $\chi^2 = 5.51$ ,  $df = 3$ ,  $p\text{-value} = 0.14$ ).

182 *Effect of elephants on woody habitat structure* - Visibility at 100-150 cm was highly  
183 correlated to visibility at 10-60cm ( $r = 0.91$ ,  $t = 75$ ,  $df = 1121$ ,  $p < 0.001$ ), so only results  
184 on the visibility at 10-60 cm (visibility hereafter) were considered in the subsequent  
185 analyses. We assessed the effect of the level of elephant impacts on (1) the visibility with  
186 a simple linear model performed on log-transformed visibility data and on (2) the DPAS  
187 with a truncated linear regression as data distribution was left truncated at 0 m on log-  
188 transformed DPAS data (‘truncreg’ package from open source Software R 3.3.1 R.  
189 Development Core Team, 2014). All kill sites, all non-kill sites and all random sites were  
190 included in this analysis to best describe the link between the level of elephant impact  
191 and the vegetation characteristics.

192 *Lion kill site characteristics* - For the subsequent analyses, non-kill sites were excluded  
193 as they could have represented any lion’s activity (e.g., resting site). These sites could  
194 have been under selection by lions (e.g., habitat with higher woody cover for shadow  
195 preferred) and thus led to a bias in our results/interpretation. At the large scale, we  
196 compared the characteristics of lion kill sites with characteristics of the habitats of all the  
197 random sites (associated to kill sites and to non-kill sites), representing areas intensively

198 used by lions. We used logistic regressions to develop resource selection functions (RSF),  
199 with the dependent variable being 1 for kill sites and 0 for random sites. We performed a  
200 first logistic regression to assess if lions kill more in low visibility environments where  
201 prey can be closely approached thanks to low DPAS. For this first logistic regression, the  
202 explanatory variables are visibility and DPAS. No strong correlation was observed  
203 between these two variables, which were therefore kept for the analyses (Pearson's  
204 correlation coefficient visibility-DPAS = 0.38). We performed a second logistic  
205 regression to assess if the level of elephant impacts on vegetation structure influences  
206 lion kill site location. In this second logistic regression, the explanatory variable was the  
207 level of elephant impacts. A model selection was performed using the function "dredge"  
208 ('MuMin' package) using the Bayesian Information Criterion (BIC) for a compromise  
209 between the explanatory power and the parsimony of the models and model averaging  
210 was performed on all the models (Burnham & Anderson 2004). Variables considered as  
211 important were those for which  $\beta \pm 1.96*SE$  did not include zero. At the microhabitat  
212 scale, we compared the characteristics of lion kill sites with the characteristics of the  
213 direct surrounding available habitat (represented by the random site associated to each  
214 kill site). A paired Generalized Estimating Equations (GEE) model was performed using  
215 the package "gee" to remove all the variability between the different pairs and focus only  
216 of the variability within each pair (Liang & Zeger 1986). We conducted the same two  
217 regression analyses as above. For this analysis, the quasi-likelihood criterion (QIC) was  
218 used (Liang & Zeger 1986) and a model averaging was performed on all the models. As  
219 no difference between lion sexes was observed (Online Resource 1), all kill sites  
220 identified were used and pooled together independently of whether the kill site was found

221 using GPS-collar data from a female or a male lion. Further, our data did not allow  
222 assessing if the collared individual was the one that made the kill, and male and female  
223 lions were regularly observed together (70.1% of all lions' observations) in Hwange  
224 National Park at the time of the study.

225

226

## 227 **Results**

228 Kills were not evenly distributed over the different classes of shrub layer cover and over  
229 the different prey species (Online Resource 2). The main prey of lions were greater kudu  
230 *Tragelaphus strepsiceros* (27%), followed by African buffalo *Syncerus caffer* (20%) and  
231 plains zebra *Equus quagga* (12 %, Online Resource 2). DPAS and visibility at kills for  
232 each prey species are presented in Online Resource 3.

233

234 Effect of elephants on woody vegetation structure – For each class of level of elephant  
235 impacts (0: no impact; 1: [1-25%]; 2: [26%-50%]; 3: [51%-75%]; and 4: [76%-100%]),  
236 the number of study sites (including all kill sites, non-kill sites and random sites) was  
237 respectively: 453, 275, 205, 132, and 55. The log-visibility increased as the level of  
238 elephant impacts increased (estimate  $\pm$  SE =  $0.14 \pm 0.015$ ,  $t = 9.04$ ,  $p < 0.001$ , Table 1a,  
239 Fig. 1a), and the log-transformed DPAS also increased as the level of elephant impacts  
240 increased (estimate  $\pm$  SE =  $0.17 \pm 0.02$ ,  $t = 7.5$ ,  $p < 0.001$ ), Table 1b, Fig. 1b). On  
241 average, there was a difference of 14m for the visibility (mean<sub>Level 0</sub> = 16.7m, mean<sub>Level 4</sub>  
242 = 30.7m) and 3m for the DPAS (mean<sub>Level 0</sub> = 2.4, mean<sub>Level 4</sub> = 5.4m) between habitats

243 not impacted by elephants and those with the highest level of elephant impacts. It is  
244 noteworthy that there exists a high variability in the visibilities and the DPAS (Fig. 1).  
245  
246 Lion kill site characteristics - In the first analyses at large scale, comparing kill sites to  
247 the all the random sites, representing available habitat in areas intensively used by lions,  
248 we revealed that the level of elephant impacts was the only variable to explain lion kill  
249 site characteristics (Table 2a). Lion kills were located in habitats with higher levels of  
250 elephant impacts (estimate  $\pm$  SE =  $0.27 \pm 0.09$ , Fig. 2a, see Online Resource 4 for raw  
251 data). At the microhabitat scale, when we compared the characteristics of lion kill sites to  
252 the characteristics of the direct surrounding habitat (within-pair comparison approach),  
253 we revealed that the DPAS was the only variable to explain lion kill site characteristics  
254 (Table 2b). Lion kill sites were preferentially located in habitats characterized by a  
255 reduced DPAS compared to the direct nearby available habitat (estimate  $\pm$  SE =  $-0.44 \pm$   
256  $0.19$ , Fig. 2b). In the kill sites, the mean DPAS value was 5.86 m, whereas it was 7.56 m  
257 in the random sites representing a decrease of 1.7 m (22% of the mean DPAS value of  
258 random sites).

259

260

## 261 **Discussion**

262 In this study, we first assessed the effects of elephants on features of woody habitat  
263 structure that can be key for the ecology of predator-prey interactions, i.e. visibility and  
264 distance to a potential ambush site. Elephant-induced vegetation changes tended to be  
265 associated with an increase in visibility (as observed by Valeix et al. 2011). Regarding

266 distance to a potential ambush site, elephants could either increase it (e.g., by removing  
267 large bushes or by reducing the crown diameter of bushes – see Ferry 2018) or reduce it  
268 (e.g., by uprooting or breaking trees, which can create ambush sites behind the trunk,  
269 branches and foliage on the ground). Overall, in Hwange National Park, elephant-induced  
270 vegetation changes tended to be associated with an increase in distance to a potential  
271 ambush site. Even though these average differences were not very large, they can make a  
272 difference in dense habitats considering the hunting behaviour of lions, which kill their  
273 prey close to dense vegetation (e.g. within 9 meters of a potential ambush site - Loarie et  
274 al. 2013). Hence, elephants, by altering visibility and distance to potential ambush site,  
275 are likely to affect where lions choose to hunt and/or where they hunt successfully in  
276 woodland. Following the *ambush-habitat* hypothesis (Hopcraft et al. 2005), we initially  
277 expected lions to kill more in habitats with lower level of elephant impacts and  
278 characterized by lower visibility and a shorter distance to potential ambush site, thus  
279 more favourable to lion hunting success (Fig. 3A– expected pattern). This assumption can  
280 appear to be in opposition with the results from Tambling et al. (2013) and Davies et al.  
281 (2016). This can be explained by the fact that, in these studies, habitats not impacted by  
282 elephants were actually so dense (average distance to cover < 1 m) that lions were not  
283 able to move and hunt inside this dense vegetation, which could be therefore used as a  
284 refuge by small prey species (e.g., the duiker *Sylvicapra grimmia*).

285 In this study, we were limited on the inferences we could make because of two main  
286 limitations in our data. The first one is that we were not able to identify hunts in which  
287 lions failed, which prevented us from assessing whether there were more kills in a habitat  
288 because lions hunted more in this habitat or had a higher hunting success there. The

289 second limitation is the lack of information about the contextual abundance and  
290 distribution of herbivores during the hunt, which could influence the kill site location as  
291 expected under the *prey-abundance* hypothesis. To partly fill these gaps, we suggest a  
292 conceptual framework with different scenarios that could explain the patterns observed  
293 based on three different parameters: the probability of prey presence, the probability to  
294 hunt (depending either on prey presence or on habitat openness), and the probability to  
295 kill a prey (i.e. to hunt successfully) (Fig. 3B). *Patterns 3,9* and *11* represent our initial  
296 hypothesis, without assumption on prey distribution and with the probability to hunt  
297 and/or kill being linked to habitat features only (following the *ambush-habitat*  
298 hypothesis, with more hunt/kills in habitats less impacted by elephants, less open).

299         Contrary to our expectations, at the large scale, when we compared the  
300 characteristics of lion kill sites to the characteristics of random sites in areas intensively  
301 used by lions, kills were more located in woody habitats characterized by higher levels of  
302 elephant impacts, but we did not detect a selection for a lower visibility and a shorter  
303 distance to a potential ambush site. This result suggests that other factors than habitat  
304 structural features drive lion hunting behaviour at this scale, such as the presence and  
305 abundance of prey (i.e., the *prey-abundance* hypothesis, Hopcraft et al. 2005). If this is  
306 the case, it assumes that herbivores select habitats impacted by elephants (representing all  
307 the even numbered patterns in Fig. 3). This selection pattern may arise from (i) a  
308 coincidence with elephants and other herbivores using the same habitats, (ii) a reduced  
309 perceived risk of predation in elephant-impacted habitats due to the higher visibility  
310 caused by elephants in these habitats for all herbivore species (Underwood 1982, Valeix  
311 et al. 2011), and/or (iii) a facilitative effect of elephants that may increase browse

312 availability at lower heights within reach of smaller browsers by stimulating tree  
313 coppicing, a mechanisms known as “browsing lawns” (Rutina et al. 2005, Fornara & du  
314 Toit 2007). Hence, the fact that lion kills were preferentially found in elephant-impacted  
315 habitats at the large scale could be explained by a selection for areas where prey are  
316 abundant (*patterns 6, 8, 14 and 16*, Fig. 3) and elephants could be considered as  
317 interaction modifiers if they influence prey habitat selection. Evidences about the role of  
318 elephants in other herbivore woody habitat selection at this scale still need to accumulate  
319 (e.g., herbivore distribution data thanks to camera traps placed on contrasted elephant-  
320 impacted habitats).

321         At the microhabitat scale (the within-pair comparison between a kill site and its  
322 paired random site), results revealed that lion kills were not preferentially located in  
323 habitats impacted by elephants anymore. At this scale, lion kill sites were preferentially  
324 located in habitats characterized by a shorter distance to a potential ambush site (*patterns*  
325 *3, 4, 7-16*, Fig. 3), supporting here our hypothesis of the role of prey catchability  
326 (*ambush-habitat* hypothesis). Interestingly, the visibility did not seem to be a factor as  
327 important as the distance to a potential ambush site. An explanation could be that,  
328 whatever the visibility, the presence of a few large bushes / broken trees as potential  
329 ambush sites is sufficient to lead to a higher probability of kill even in woody habitats  
330 with a high visibility. Finally, when combining the two different scales, the only patterns  
331 to explain the observed pattern (Fig 3A – observed pattern) with both more kills in  
332 impacted habitat at the large scale and more kills in closed habitat at the microhabitat  
333 scale are *Patterns 8, 14 and 16*. These patterns share the same processes: prey select  
334 elephant-impacted habitats and a higher probability to hunt in habitat with more prey

335 (*prey-abundance* hypothesis). However, they differ in terms of probability to hunt or to  
336 kill in closed habitats. *Pattern 8* needs a higher probability to kill in closed habitats,  
337 *Pattern 14* needs a higher probability to hunt in closed habitats and *Pattern 16* needs both  
338 of them, suggesting therefore that lions are influenced by habitat structure during the  
339 hunting process at the microhabitat scale (*ambush-habitat* hypothesis).

340       Therefore, our results suggest that the main driver of kill site location for lions is  
341 likely to be prey abundance at a first scale of selection, and prey catchability at the scale  
342 of the direct nearby available habitat (<150 m). As suggested in previous studies, the  
343 *prey-abundance* and the *ambush-habitat* hypotheses are not exclusive and could interact  
344 with one another to explain lion hunting behaviour (Davidson et al. 2012). Therefore, by  
345 affecting the woody vegetation structure, elephants could play an important role in the  
346 intensity of predator-prey relationships although in complex ways, as they could act on  
347 both predators and prey's behaviour, with different mechanisms involved depending on  
348 the scale considered (as suggested by Fležar et al. 2019). We encourage future research to  
349 confirm that herbivores select woody habitats impacted by elephants because of the  
350 elephant's engineering process and not because of simple coincidence or shared  
351 resources. Further, a focus on identifying unsuccessful hunts will be needed to  
352 disentangle the roles of the probability to hunt and the probability to kill in closed  
353 habitats. This would ultimately help to know which process is influenced by the  
354 vegetation structure during the lion hunting behaviour in woodland areas. This task is  
355 both conceptually and practically a challenging one, although perhaps it can be  
356 accomplished through the deployment of GPS-collars with integrated tri-axial  
357 accelerometer-magnetometer (see for example Fröhlich et al. 2012, Wilmers et al. 2017).

358           Despite remaining questions regarding the underlying mechanisms, our study  
359 suggests that elephants have the potential to influence predator-prey interactions in their  
360 ecosystem. In a context of rapidly changing elephant populations worldwide (Chase et  
361 al., 2016), it is of importance to understand their indirect role on interspecific  
362 interactions. Our results reinforce the idea that elephants, through ecosystem engineering,  
363 could act on a multitude of broad-scale ecological processes in wooded savannas (Kerley  
364 & Landman 2006). Further, whereas previous studies of ecosystem engineers have  
365 highlighted their effects on other species abundance and richness (Jones et al. 1997), our  
366 findings demonstrate the importance of their indirect effect on interspecific interactions  
367 (see also Arditi et al. 2005, Marquis & Lill 2007 and references therein). Finally, we  
368 highlighted the importance of multi-scale consideration in interspecific interactions and  
369 their modification (see also Fležar et al. 2019). We therefore hope these findings will  
370 promote studies on interaction modification, with a multi-scale component (Tylianakis &  
371 Morris 2017) in large mammal communities.

372

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374

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### 389 **Literature cited**

390 Abrams PA (2010) Implications of flexible foraging for interspecific interactions: lessons  
391 from simple models. - *Funct. Ecol.* 24: 7–17. doi: 10.1111/j.1365-

392 2435.2009.01621.x

393 Arditi R, Michalski J, Hirzel AH (2005) Rheagogies: modelling non-trophic effects in  
394 food webs. *Ecol. Complex.* 2:249-258. doi: 10.1016/j.ecocom.2005.04.003

395 Bell WJ (1991) Searching behavior: the behavioural ecology of finding resources -

396 Chapman & Hall, New York.

397 Bond WJ (1994) Keystone species. – In *Biodiversity and ecosystem function* (eds ED

398 Schulze, HA Mooney), pp 237-253. Springer Berlin Heidelberg.

399 Burnham KP, Anderson DR (2004) Multimodel Inference. - *Sociol. Methods Res* 33:

400 261–304. doi: 10.1177/0049124104268644

401 Chamailié-Jammes S, Fritz H, Valeix M, Murindagomo F, Clobert J (2008) Resource

402 variability, aggregation and direct density dependence in an open context: the

403 local regulation of an African elephant population. - *J. Anim. Ecol.* 77: 135–144.  
404 doi: 10.1111/j.1365-2656.2007.01307.x

405 Chamailé-Jammes S, Fritz H, Madzikanda H (2009) Piosphere contribution to landscape  
406 heterogeneity: a case study of remote-sensed woody cover in a high elephant  
407 density landscape. - *Ecography* 32: 871–880. doi: 10.1111/j.1600-  
408 0587.2009.05785.x.

409 Chase MJ et al. (2016) Continent-wide survey reveals massive decline in African  
410 savannah elephants. - *PeerJ* 4: e2354. doi: 10.7717/peerj.2354

411 Coverdale TC et al. (2016) Elephants in the understory: opposing direct and indirect  
412 effects of consumption and ecosystem engineering by megaherbivores. - *Ecology*  
413 97: 3219–3230. doi: 10.1002/ecy.1557

414 Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions:  
415 the role of ecosystem engineers. - *Oikos* 97: 153–166. doi: 10.1034/j.1600-  
416 0706.2002.970201.x

417 Dambacher JM, Ramos-Jiliberto R (2007) Understanding and predicting effects of  
418 modified interactions through a qualitative analysis of community structure. - *Q.*  
419 *Rev. Biol.* 82: 227–250. Doi: 10.1086/519966

420 Davidson Z, Valeix M, Loveridge AJ, Hunt JE, Johnson PJ, Madzikanda H, Macdonald  
421 DW (2012) Environmental determinants of habitat and kill site selection in a large  
422 carnivore: scale matters. - *J. Mammal.* 93: 677–685. doi: 10.1644/10-mamm-a-  
423 424.1

424 Davidson Z, Valeix M, Van Kesteren F, Loveridge AJ, Hunt JE, Murindagomo F,  
425 Macdonald DW (2013) Seasonal diet and prey preference of the African lion in a

426 waterhole-driven semi-arid savanna. PLoS ONE 8: e55182. doi:  
427 10.1371/journal.pone.0055182

428 Davies AB, Tambling CJ, Kerley GI, Asner GP (2016) Effects of Vegetation Structure  
429 on the Location of Lion Kill Sites in African Thicket - PLoS ONE 11: e0149098.  
430 doi: 10.1371/journal.pone.0149098

431 Estes JA et al. (2011) Trophic Downgrading of Planet Earth. - Science 333: 301–306.  
432 doi:10.1126/science.1205106

433 Ferry N (2018) Processes involved in the functioning of large mammal communities: the  
434 role of the African elephant in the ecology of predator-prey relationships. PhD.  
435 University of Lyon, France.

436 Fležar U et al. (2019) Simulated elephant-induced habitat changes can create dynamic  
437 landscapes of fear. Biological Conservation 237: 267-279. doi:  
438 10.1016/j.biocon.2019.07.012

439 Fornara DA, du Toit JTD (2007) Browsing lawns? Responses of *Acacia nigrescens* to  
440 ungulate browsing in an African savanna. - Ecology 88: 200–209. doi:  
441 10.1890/0012-9658(2007)88[200:blroan]2.0.co;2

442 Fröhlich M, Berger A, Kramer-Schadt S, Heckmann I, Martins Q (2012) Complementing  
443 GPS Cluster Analysis with Activity Data for Studies of Leopard (*Panthera*  
444 *pardus*) Diet. S. Afr. J. Wildl. Res. 42: 104–110. doi: 10.3957/056.042.0208

445 Guldemon R, van Aarde R (2008) A Meta-Analysis of the Impact of African Elephants  
446 on Savanna Vegetation. - J. Wildl. Manag. 72: 892–899. doi: 10.2193/2007-072

447 Haas SK, Hayssen V, Krausman PR (2005) *Panthera leo*. Mamm. Species, 1-11.

448 Hatcher MJ, Dick JT, Dunn AM (2006) How parasites affect interactions between  
449 competitors and predators. – *Ecol. Lett.* 9: 1253–1271. doi: 10.1111/j.1461-  
450 0248.2006.00964.x

451 Hopcraft JGC, Sinclair ARE, C Packer (2005) Planning for success: Serengeti lions seek  
452 prey accessibility rather than abundance. *J. Animal Ecol.* 74: 559–566. doi:  
453 10.1111/j.1365-2656.2005.00955.x

454 Jones CG, Lawton JH, Shachak M (1994) Organisms as Ecosystem Engineers. - *Oikos*  
455 69: 373-386. doi: 10.2307/3545850

456 Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as  
457 physical ecosystem engineers. - *Ecology* 78: 1946–1957. doi: 10.1890/0012-  
458 9658(1997)078[1946:paneoo]2.0.co;2

459 Kauffman MJ, Varley N, Smith DW, Stahler DR, MacNulty DR, Boyce MS (2007)  
460 Landscape heterogeneity shapes predation in a newly restored predator-prey  
461 system. – *Ecol. Lett.* 10: 690–700. doi:10.1111/j.1461-0248.2007.01059.x

462 Kéfi S et al. (2012) More than a meal... integrating non-feeding interactions into food  
463 webs. – *Ecol. Lett.* 15: 291–300. doi:10.1111/j.1461-0248.2011.01732.x

464 Kerley GI, Landman M (2006) The impacts of elephants on biodiversity in the Eastern  
465 Cape Subtropical Thickets: elephant conservation. - *South Af. J. of Science*, 102:  
466 395-402.

467 Lange RT (1969) Piosphere—sheep track and dung patterns. *J. of Range Management*  
468 22, 396–400

469 Liang KY, Zeger SL (1986) Longitudinal data analysis using generalized linear models. -  
470 *Biometrika* 73: 13–22. doi: 10.1093/biomet/73.1.13

471 Loarie SR, Tambling CJ, Asner GP (2013) Lion hunting behaviour and vegetation  
472 structure in an African savanna. - *Animal Behav.* 85: 899–906. doi:  
473 10.1016/j.anbehav.2013.01.018

474 Loveridge AJ, Valeix M, Chapron G, Davidson Z, Mtare G, Macdonald DW (2016)  
475 Conservation of large predator populations: Demographic and spatial responses of  
476 African lions to the intensity of trophy hunting. - *Biol. Conserv.* 204: 247–254.  
477 doi: 10.1016/j.biocon.2016.10.024

478 Marquis RJ, Lill JT (2007) Effects of arthropods as physical ecosystem engineers on  
479 plant-based trophic interaction webs. - In: Ohgushi, T. et al. (eds), *Ecological*  
480 *Communities*. Cambridge University Press, pp. 246–274.  
481 doi:10.1017/cbo9780511542701.012

482 Okuyama T, Bolker BM (2007) On quantitative measures of indirect interactions. - *Ecol.*  
483 *Lett.* 10: 264–271. doi:/10.1111/j.1461-0248.2007.01019.x

484 Peacor SD, Werner EE (2001) The contribution of trait-mediated indirect effects to the  
485 net effects of a predator. - *Proc. Natl. Acad. Sci. USA PNAS* 98: 3904–3908. doi:  
486 10.1073/pnas.071061998

487 Petren K, Case TJ (1998) Habitat structure determines competition intensity and invasion  
488 success in gecko lizards. - *Proc. Natl. Acad. Sci. USA PNAS* 95: 11739–11744.  
489 doi: 10.1073/pnas.95.20.11739

490 Preisser EL, Bolnick DI (2008) The Many Faces of Fear: Comparing the Pathways and  
491 Impacts of Nonconsumptive Predator Effects on Prey Populations. - *PLoS ONE* 3:  
492 e2465. doi: 10.1371/journal.pone.0002465

493 Preisser EL, Orrock JL, Schmitz OJ (2007) Predator hunting mode and habitat domain  
494 alter nonconsumptive effects in predator–prey interactions. - Ecology 88: 2744–  
495 2751. doi: 10.1890/07-0260.1

496 Pringle RM (2008) Elephants as agents of habitat creation for small vertebrates at the  
497 patch scale. - Ecology 89: 26–33. doi: 10.1890/07-0776.1

498 R Development Core Team (2014) R a language and environment for statistical  
499 computing. Vienna, Austria: R Foundation for Statistical Computing,  
500 <http://www.r-project.org>

501 Rutina LP, Moe SR, Swenson JE (2005) Elephant *Loxodonta africana* driven woodland  
502 conversion to shrubland improves dry-season browse availability for impalas  
503 *Aepyceros melampus*. - Conserv Biol 11: 207–213. doi: 10.2981/0909-  
504 6396(2005)11[207:ELADWC]2.0.CO;2

505 Tambling CJ, Cameron EZ, du Toit JT, Getz WM (2010) Methods for Locating African  
506 Lion Kills Using Global Positioning System Movement Data. - J. Wildl. Manag.  
507 74: 549–556. doi:10.2193/2009-010

508 Tambling CJ, Minnie L, Adendorff J, Kerley GI (2013) Elephants facilitate impact of  
509 large predators on small ungulate prey species. - Basic Appl Ecol 14: 694–701.  
510 doi: 10.1016/j.baae.2013.09.010

511 Terry JCD, Morris RJ, Bonsall MB (2017) Trophic interaction modifications: an  
512 empirical and theoretical framework. – Ecol. Lett. 20: 1219–1230. doi:  
513 10.1111/ele.12824

514 Tylianakis JM, Tscharrntke T, Lewis OT (2007) Habitat modification alters the structure  
515 of tropical host–parasitoid food webs. - *Nature* 445: 202–205. doi:  
516 10.1038/nature05429

517 Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species  
518 interactions in terrestrial ecosystems. – *Ecol. Lett.* 11: 1351–1363. doi:  
519 10.1111/j.1461-0248.2008.01250.x

520 Tylianakis JM, Morris RJ (2017) Ecological networks across environmental gradients.  
521 *Annu Rev Ecol Evol Syst.*, 48.

522 Underwood R (1982) Vigilance Behaviour in Grazing African Antelopes. - *Behaviour* 79:  
523 81–107. doi: 10.1163/156853982x00193

524 Valeix M, Fritz H, Sabatier R, Murindagomo F, Cumming D, Duncan P (2011) Elephant-  
525 induced structural changes in the vegetation and habitat selection by large  
526 herbivores in an African savanna. – *Biol. Conserv.* 144: 902–912. doi:  
527 10.1016/j.biocon.2010.10.029

528 Van der Putten WH, Macel M, Visser ME (2010) Predicting species distribution and  
529 abundance responses to climate change: why it is essential to include biotic  
530 interactions across trophic levels. - *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*  
531 365: 2025–2034. doi: 10.1098/rstb.2010.0037

532 Van Orsdol KG (1984) Foraging behaviour and hunting success of lions in Queen  
533 Elizabeth National Park, Uganda. - *Afr. J. Ecol.* 22: 79–99. doi:10.1111/j.1365-  
534 2028.1984.tb00682.x

535 Wardle DA, Bardgett RD, Klironomos JN, Setälä H, Van Der Putten WH, Wall DH  
536 (2004) Ecological linkages between aboveground and belowground biota.  
537 *Science*, 304(5677), 1629-1633. doi: 10.1126/science.1094875

538 Wilmers CC, Isbell LA, Suraci JP, Williams TM (2017) Energetics-informed behavioral  
539 states reveal the drive to kill in African leopards. - *Ecosphere* 8: e01850. doi:  
540 10.1002/ecs2.1850

541 Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in  
542 ecological communities. - *Ecology* 84: 1083–1100. doi: 10.1890/0012-  
543 9658(2003)084[1083:AROTII]2.0.CO;2

544 Wickham H (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New  
545 York. ISBN 978-3-319-24277-4, <https://ggplot2.tidyverse.org>.

546 Wootton JT (1993) Indirect Effects and Habitat Use in an Intertidal Community:  
547 Interaction Chains and Interaction Modifications. – *Am. Nat.* 141: 71–89. doi:  
548 10.1086/285461

549 Wootton JT (1994) The Nature and Consequences of Indirect Effects in Ecological  
550 Communities. - *Annu. Rev. Ecol. Evol. Syst.* 25: 443–466. doi:  
551 10.1146/annurev.es.25.110194.002303

552 Wootton JT (2002) Indirect effects in complex ecosystems: recent progress and future  
553 challenges. – *J. Sea Res.* 48: 157–172. doi: 10.1016/S1385-1101(02)00149-1  
554

## Tables

**Table 1:** Estimated mean and confidence interval at 95% for each level of elephant impacts of (a) the visibility (m) and (b) the distance to a potential ambush site (DPAS) (m).

<b>a</b>	% of impacted trees	2.5%	Mean	97.5%
0	0	15.7	16.7	17.8
1	[1,25]	17.5	20.5	24
2	[26,50]	20	23.7	28
3	[51,75]	20.6	24.8	29.9
4	[76,100]	24	30.7	39.1
<b>b</b>	% impacted trees	2.5%	Mean	97.5%
0	0	2.1	2.4	2.7
1	[1,25]	2.5	3.5	4.7
2	[26,50]	3.5	4.8	6.5
3	[51,75]	3.2	4.5	6.3
4	[76,100]	3.5	5.4	8.1

**Table 2:** Logistic models examining (1) the effect of visibility (Vis) and distance to a potential ambush site (DPAS) on lion kill site location and (2) the effect of the level of elephant impacts (Ele) on lion kill site location. a) Approach at the large scale, comparing the characteristics of kill sites to characteristics of all random sites in areas intensively used by lions. b) Approach at the microhabitat scale, comparing the characteristics of kill sites to characteristics of paired random site representing the direct surrounding available habitat (< 150 m). Models are ranked according to their BIC or QIC. Model-averaged estimates for the variables  $\pm$  standard error are shown at the bottom of each table. Variables considered as important were those for which  $\beta \pm 1.96*SE$  did not include zero.

**a) Large scale - Kill sites VS All random sites**

(1) – *Kill sites / Random sites ~ DPAS + Vis*

	Candidate models	df	BIC	$\Delta i$	$w_i$	bcc $w_i$
1	Null	1	702.2	0.00	0.453	0.453
2	DPAS	2	702.7	0.45	0.361	0.814
3	Vis + DPAS	3	704.3	2.06	0.162	0.976
4	Vis	2	708.1	5.89	0.024	1

Variable	Average $\beta$	SE
Vis	0.22	0.25
DPAS	-0.06	0.13

(2) – *Kill sites / Random sites ~ Ele*

	Candidate models	df	BIC	$\Delta i$	$w_i$	bcc $w_i$
1	Ele	2	696.6	0	0.943	0.943
2	Null	1	702.2	5.62	0.057	1

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Variable	Average $\beta$	SE
Ele	0.25	0.09

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**b) Microhabitat scale - Kill site VS Paired random site**

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(1) – Kill site / Paired random site ~ DPAS + Vis

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	Candidate models	QIC	$\Delta i$	$w_i$	bcc $w_i$
1	Vis + DPAS	310.5	0.00	0.436	0.436
2	DPAS	310.6	0.13	0.408	0.844
3	Vis	312.7	2.22	0.144	0.988
4	Null	317.6	7.1	0.013	1

---

Variable	Average $\beta$	SE
Vis	-0.33	0.27
DPAS	-0.44	0.19

---

(2) – Kill site / Paired random site ~ Ele

---

	Candidate models	QIC	$\Delta i$	$w_i$	bcc $w_i$
1	Null	317.6	0	0.596	0.596
2	Ele	318.4	0.78	0.404	1

---

Variable	Average $\beta$	SE
Ele	0.004	0.07

1 **Figure legends**

2 Figure 1: Boxplot distribution of a) the visibility and b) the distance to a potential ambush  
3 site (DPAS) according to the five classes of level of elephant impacts, i.e. of percentage  
4 of trees impacted by elephants (broken, coppiced and/or uprooted): class 0: no impact;  
5 class 1: [1-25%]; class 2: [26%-50%]; class 3: [51%-75%]; and class 4 [76%-100%]. The  
6 notch represents the 95% confidence interval of the median. Points represent raw data  
7 using `geom_jitter` function from *ggplot2* package (Wikcham 2016).

8

9 Figure 2: (a) Relationship between the level of elephant impacts and the strength of this  
10 factor on lions' kill site location at the large scale. (b) Relationship between the log-  
11 transformed DPAS (for DPAS ranging from 0 to 50m) and the strength of this factor on  
12 lions' kill site location at the microhabitat scale. The selection strength is  
13  $\exp(\beta_0 + \beta_1 * \text{level of elephant impacts})$  at the large scale and  $\exp(\beta_0 + \beta_1 * \log(\text{DPAS} + 1))$   
14 at the microhabitat scale, where  $\beta_0$  is the intercept estimate and  $\beta_1$  is the estimated  
15 coefficient for the level of elephant impacts at the large scale and for  $\log(\text{DPAS} + 1)$  at the  
16 microhabitat scale. Dotted lines represent the standard errors.

17

18 Figure 3: A) Representation of the expected pattern under our initial hypotheses and the  
19 observed pattern. 1) Expected pattern - Under our initial hypotheses, we expected higher  
20 visibilities and DPAS in habitats with higher levels of elephant impacts, as well as more  
21 lion kill sites in habitats characterized by a lower visibility and a shorter DPAS, and thus  
22 more kills in non-impacted habitats. 2) Observed pattern - An increased visibility and  
23 DPAS were effectively observed with the increase of the level of elephant impacts but

24 not as strongly as expected (see the shape of the green area). At the large scale, lion kills  
25 were, unexpectedly, more in highly elephant-impacted habitats. At the microhabitat scale,  
26 lion kill sites were more in habitat characterized by a shorter DPAS. B) Representation of  
27 the different scenarios envisaged to explain the observed pattern. We played on the  
28 combination of three variables: the probability of prey presence, the probability that a  
29 hunt will occur (with lions hunting more in high prey abundance habitat and/or with lions  
30 hunting more in closed habitats), and 3) the probability of a kill, i.e. of a successful hunt  
31 (with lions having a higher success rate in closed habitat). Patterns 8, 14 and 16 appear to  
32 be the most likely to explain the observed pattern.

33

**Figures**

*Figure 1*

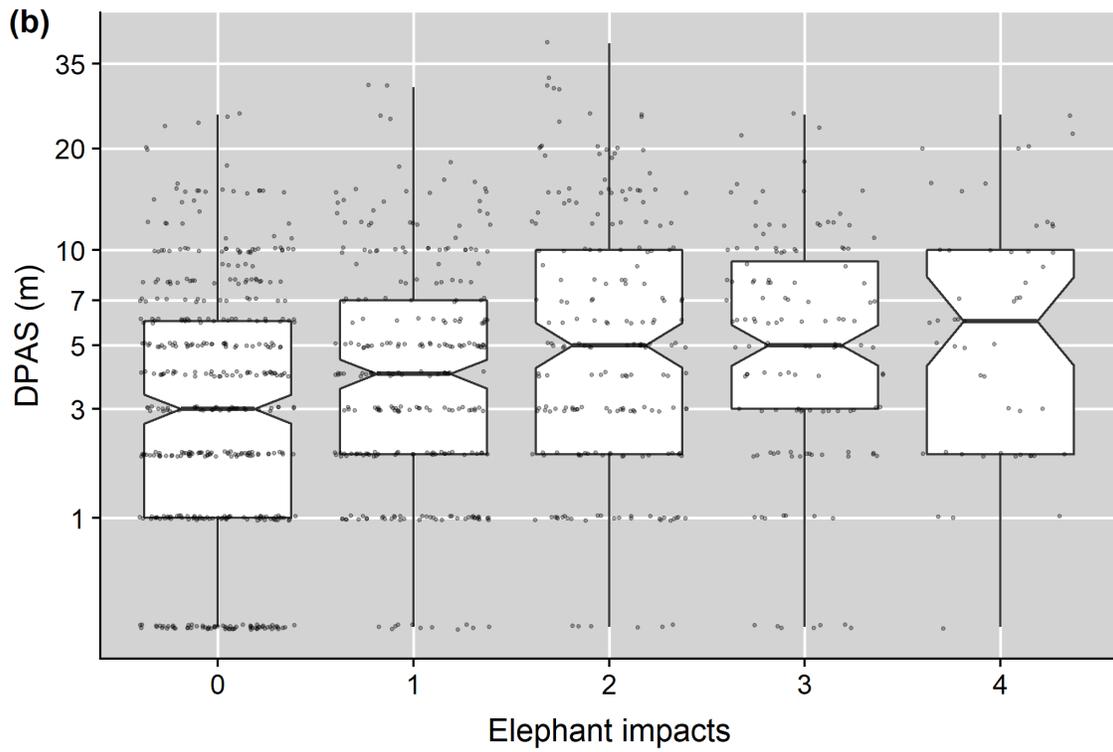
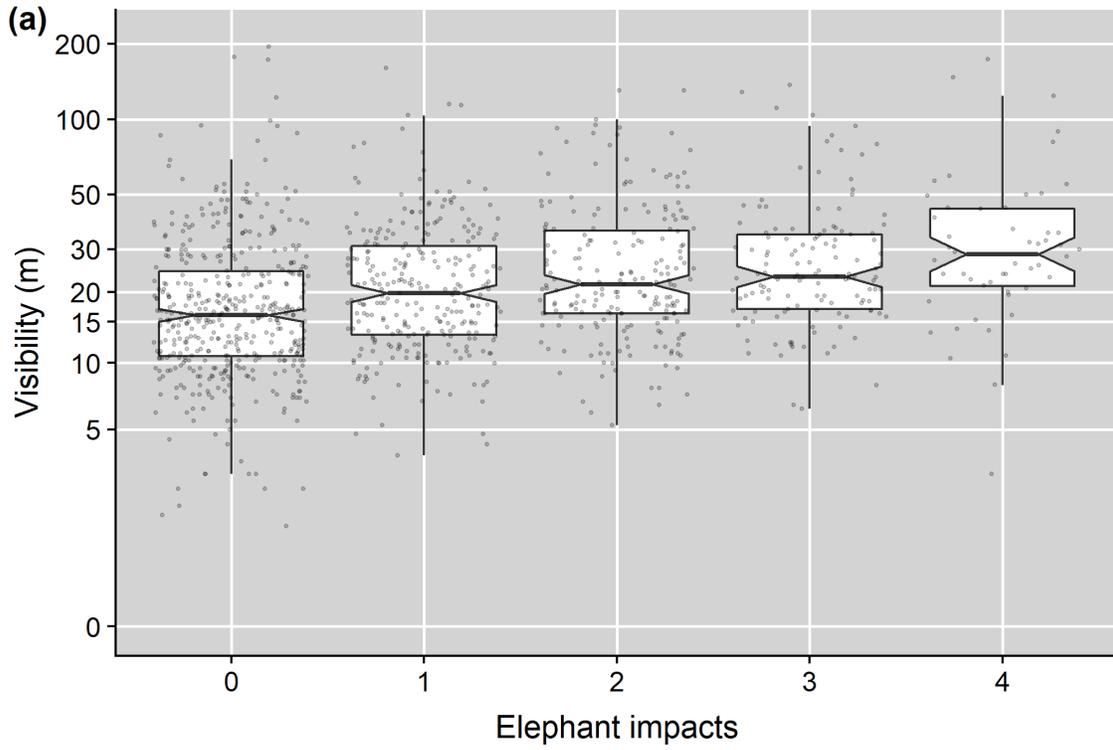


Figure 2

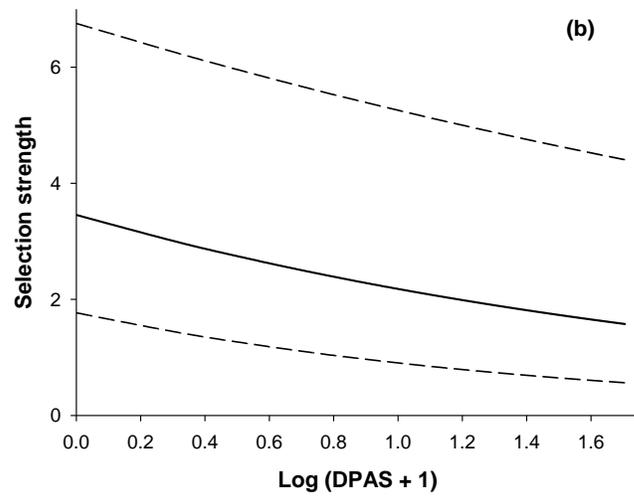
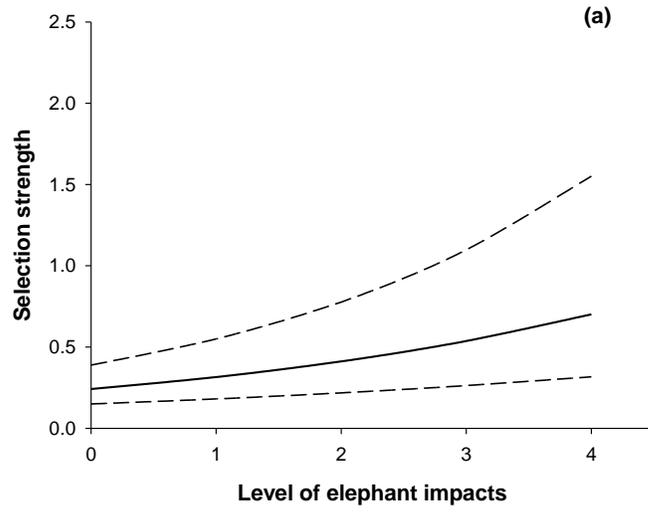


Figure 3

