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## Climate effects on prey vulnerability modify expectations of predator responses to short- and long-term climate fluctuations

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26

27 **1 Abstract**

28 Climate changes affect the distribution and abundance of organisms, often via changes in species  
29 interactions. Most animals experience predation, and a number of models have investigated how  
30 climate fluctuations can influence predator-prey dynamics by affecting prey abundance through  
31 changes in resource availability. However, field studies have shown that prey vulnerability is a key  
32 feature determining the outcome of predator-prey interactions, which also varies with climatic  
33 conditions, *via* changes in prey body condition or in habitat characteristics (e.g. vegetation cover). In  
34 this theoretical work, we explore, with large mammals of African savannas in mind, how the interplay  
35 between climate-induced changes in prey abundance and climate-induced changes in prey vulnerability  
36 affects the immediate and long-term responses of predator populations. We account for prey body  
37 condition and habitat effects on prey vulnerability to predation. We show that predictions on how  
38 predator abundance responds to climate fluctuations differ depending on how climate influences prey  
39 vulnerability (habitat characteristics vs. prey body condition). We discuss how species traits influence  
40 the relative importance of the different sources of vulnerability. For example, our results suggest that  
41 populations of cursorial predators (such as spotted hyaenas) are expected to fare better than populations  
42 of ambush predators (such as African lions) in African ecosystems that will be characterized by an  
43 aridification. This study highlights the importance of understanding, and accounting for, the  
44 vulnerability factors associated to a given predator-prey pair, and improves our comprehension of  
45 predator-prey relationships in a changing climate.

## 46 2 Introduction

47 The Earth's climate is changing rapidly, largely because of human activities (IPCC 2014a).  
48 Temperature is rising globally and will continue to do so, precipitation regimes are, or will be, locally  
49 altered, and extreme climatic events will become more common (IPCC 2014a). Climate changes  
50 already have ecological impacts and are, or will soon be, a major driver of species dynamics and  
51 survival (Maclean & Wilson, 2011; Pacifici et al., 2017). So far, most studies on the impacts of climate  
52 changes have focused on describing changes in population distribution and abundance (e.g. Martay et  
53 al., 2017; Parmesan et al., 1999), phenology and demography (e.g. Inouye et al., 2000; Moyes et al.,  
54 2011) or behaviour (Candolin & Wong, 2012). Even though these changes can sometimes emerge from  
55 the direct effect of climate on individuals, they often result from cascading effects occurring through  
56 biotic interactions, such as trophic interactions (e.g. Visser et al., 2006). Therefore, understanding how  
57 climate changes will affect species through their biotic interactions is fundamental to grasp the full  
58 picture of the impacts of climate changes.

59 Climate changes have the potential to modify predator-prey interactions, which are central in the  
60 functioning of populations, communities and ultimately ecosystems (Bastille-Rousseau et al., 2018).  
61 First, by altering primary production quality and quantity, climatic conditions influence the body  
62 condition of large mammalian herbivores (rainfall: Bourgarel et al., 2002; Owen-Smith, 2002, NAO:  
63 Mysterud et al., 2001; snow: Saether & Gravem, 1988). Herbivore body condition, in turn, influences  
64 demographic parameters, such as survival (Bender et al., 2007) or fecundity (Cook et al., 2004), which  
65 ultimately affect herbivore population abundance. As a result, climate indirectly influences prey  
66 abundance through density-dependent processes (Forchhammer et al., 1998; Saether, 1997). For  
67 example, several studies linked rainfall to herbivore abundance in savanna ecosystems (East, 1984;  
68 Ogotu et al., 2008), or showed the influence of climatic variations on the dynamics of several  
69 populations of Northern ungulates (Forchhammer et al., 1998; Post & Stenseth, 1999). Extreme  
70 climatic conditions also affect herbivore demographic parameters and ultimately population  
71 abundances (e.g. drought: Foley et al., 2008; Mduma et al., 1999). These changes in herbivore  
72 abundance originating from climate fluctuations will affect predator populations, as the maintenance  
73 of predator populations largely depends on prey abundance (East, 1984; Carbone & Gittleman, 2002).  
74 Prey body condition is thus a first pathway through which climate changes may alter predator-prey  
75 interactions and such climate-driven impact on prey demography has already been taken into account  
76 in pioneering predator-prey modelling works (e.g. Wilmers et al., 2007a; blue arrows in Fig. 1).

77 Predator-prey relationships are also influenced by prey vulnerability, which may arise from  
78 intrinsic (inherent to the prey) or extrinsic (arising from the environment) sources. Prey body condition  
79 is typically an intrinsic factor that can determine prey vulnerability to predators. Indeed, several studies  
80 pointed out that predators tend to select the weakest individuals among prey, and that prey in poorer  
81 body condition are more likely to be preyed upon (in savanna ecosystems: FitzGibbon & Fanshawe,  
82 1989; Pole et al., 2004; in temperate ecosystems: Atwood et al., 2007; Husseman et al., 2003). On the  
83 other hand, habitat characteristics are extrinsic factors that can modulate prey vulnerability to their  
84 predators and that can be influenced by climatic conditions. Several studies stressed out the importance  
85 of vegetation structure and cover, which interact with the predator hunting technique and the prey  
86 escape technique to ultimately affect the hunting outcome. This was shown in savanna (Funston et al.,  
87 2001; Hopcraft et al., 2005) and temperate ecosystems (Husseman et al., 2003, Lone et al., 2014). Other  
88 habitat characteristics can interfere with the predator hunting success. For example, prey were either  
89 more vulnerable to predators with increasing amount of snow (Mech et al., 1971; Post et al., 1999) or  
90 less vulnerable to predators as snow hardness decreased (Stenseth et al., 2004).

91 Hence, the true prey availability to predators results from the interplay between prey abundance  
92 and prey vulnerability, which is characterized by different sources of vulnerability (red arrows in Fig.

93 1). Little is known on the relative importance of climate-induced changes on the different components  
 94 of prey availability to predators, and particularly on the different sources of prey vulnerability. Here,  
 95 we integrate both prey abundance and vulnerability effects (Fig. 1) in a theoretical study investigating  
 96 the immediate response of predator populations to a year of a specific climatic condition, as well as the  
 97 long-term response of predator populations to changes in average climatic conditions. This study aims  
 98 at providing general insights on the interplay between climate-induced changes in prey abundance and  
 99 prey vulnerability. The model is, on purpose, not designed for a specific predator-prey system, so that  
 100 people studying predator-prey interactions worldwide can adapt the model to fit the system there are  
 101 interested in. However, we designed our study with large mammalian herbivores and carnivores of  
 102 African savannas in mind so that the parameters and the functional relationships used are easy to relate  
 103 to a real world. Annual rainfall is expected to decrease in southern Africa and increase in eastern Africa,  
 104 and generally to become more variable (IPCC, 2014b). We therefore specifically focused on the  
 105 influence of rainfall conditions on predator-prey interactions in African savanna ecosystems. We  
 106 modelled the population dynamics of a predator preying on a density-dependent age-structured prey  
 107 population following the model described in Wilmers et al. (2007a, b), but we further and originally  
 108 accounted for prey body condition and environmental effects on prey vulnerability to predation (Fig.  
 109 1).

### 110 3 Materials and methods

#### 111 3.1 The predator-prey model

##### 112 3.1.1 The prey population model without predation

113 We considered a female-only prey population (Caswell, 2001) which, in any year  $t$ , had a total  
 114 population size of  $N(t)$  made of  $J(t)$  juveniles and  $A(t)$  adults. Fluctuations from year to year were  
 115 driven by survival and reproduction of individuals, which are now described.

116 Body condition is a critical individual characteristic, as it links environmental conditions to  
 117 demography. For simplicity, we assumed a linear relationship between body condition and survival,  
 118 and thus only modelled the latter. We modelled the effect of body condition on reproduction using a  
 119 relationship between the probability to reproduce and the probability of survival. Each year, individual  
 120 survival probabilities  $p_{ji}(t)$  and  $p_{ai}(t)$ , for juveniles and adults respectively, were drawn from Beta  
 121 distributions with shape parameters  $\alpha_j$  and  $\beta_j$  and  $\alpha_a$  and  $\beta_a$  for juvenile and adult prey respectively, and  
 122 differed from one individual to another, allowing to integrate individual heterogeneity. However, new  
 123 probabilities were drawn each year and were not preserved through the individual's life, and thus varied  
 124 randomly within individuals from year to year. The method-of-moments gives:

$$125 \alpha_j = p_j \left( \frac{p_j(1-p_j)}{Sd_{p_j}^2} - 1 \right) \quad (1a)$$

$$126 \beta_j = (1 - p_j) \left( \frac{p_j(1-p_j)}{Sd_{p_j}^2} - 1 \right) \quad (1b)$$

127  
 128  
 129  
 130  
 131 for juvenile prey, and

$$132 \alpha_a = p_a \left( \frac{p_a(1-p_a)}{Sd_{p_a}^2} - 1 \right) \quad (1c)$$

134

$$135 \quad \beta_a = (1 - p_a) \left( \frac{p_a(1-p_a)}{Sd_{pa}^2} - 1 \right) \quad (1d)$$

136  
 137 for adult prey, where  $p_j$  and  $p_a$  are mean survival rates and  $Sd_{pj}$  and  $Sd_{pa}$  are standard deviations for  
 138 juvenile and adult prey population respectively. In any year  $t$ , mean survival rates  $p_j$  and  $p_a$  were:

$$139 \quad p_j(t) = P_j \times g_j(t) \quad (2a)$$

$$141 \quad p_a(t) = P_a \times g_a(t) \quad (2b)$$

142  
 143 where  $P_j$  and  $P_a$  are parameters defining the maximum survival rates for juveniles and adults  
 144 respectively (see Table 1 for all default values of model parameters), and  $g_j$  and  $g_a$  are scaling functions  
 145 allowing to account for density- and resource-dependence in survival. These scaling functions  
 146 (bounded between 0 and 1) are those used by Wilmers et al. (2007b) and follow:

$$147 \quad g(N(t)) = \frac{\gamma^\delta}{\gamma^\delta + \frac{N(t)}{R}} \quad (3)$$

148  
 149 where  $R$  is the annual rainfall of the site.  $R$  varied from 300mm to 900mm by 100 mm increment,  
 150 which are coherent values for annual rainfall in African savannas (Sankaran et al., 2005; Chamailé-  
 151 Jammes & Fritz, 2009). We assumed that rainfall determined directly and linearly prey resource  
 152 availability (Rutherford, 1980). We thus considered rainfall as a proxy of the resource availability and  
 153 the ratio  $N(t)/R$  as a number of individuals sharing the amount of available resource for year  $t$ . The  
 154 half-saturation parameter  $\gamma$  determined the per capita resource availability at which the maximum  
 155 survival rate was reduced by half. Finally,  $\delta$  was a shape parameter setting the beginning and the  
 156 strength of the density-dependence (as in Wilmers et al., 2007b).

157 Juvenile survival is expected to be the first demographic parameter affected by increasing density,  
 158 followed by age at first reproduction, reproductive success and finally adult survival (Eberhardt, 1977).  
 159 This hypothesis has found support in large ungulate studies (Bonenfant et al., 2009). As our model was  
 160 conceptualized for large mammals (as for the one of Wilmers et al., 2007b), we assumed a greater  
 161 sensitivity of juvenile survival to increasing density by assuming that  $\gamma_j$  was lower than  $\gamma_a$ .

162 In summary, both rainfall  $R$  and population size  $N$  determined  $g$  and ultimately the average survival  
 163 rates  $p_j$  and  $p_a$  in the population (Fig. 2A). Once mean survival probability had been computed, we  
 164 determined the fate of each individual by randomly drawing a value from a uniform distribution on the  
 165 [0-1] interval, and comparing it to the individual's survival probability. If the value was lower than the  
 166 survival probability, the individual survived; if not, it died.

167 We assumed that juveniles became adults in one year (a realistic assumption for some herbivore  
 168 species; Estes, 1991) and only adults were able to reproduce. Therefore, the number of juveniles at the  
 169 beginning of a given year depended only on the fecundity of adults the year before. We also considered  
 170 that, for each adult, the probability of reproducing ( $P_f$ ) was a function of its survival probability  $p_{ai}(t)$ ,  
 171 and the link between  $P_f$  and  $p_{ai}(t)$  was as follows:

$$172 \quad P_f(p_{ai}(t)) = \frac{1}{1 + f_{low} \times e^{-f_{growth} \times p_{ai}(t)}} \quad (4)$$

173  
 174 where  $f_{low}$  is a parameter determining the probability of reproduction  $P_f$  of individuals whose survival  
 175 probability is close to 0 and  $f_{growth}$  a parameter defining the speed at which  $P_f$  reaches the value of 1  
 176 with increasing  $p_{ai}$  (Fig. 2B). We compared, for each individual, values drawn randomly from a uniform  
 177

180 distribution on the [0-1] interval with their reproduction probability. If the value was lower than the  
 181 reproduction probability, the individual produced one offspring; if not, it did not reproduce.

### 183 3.1.2 Integrating predation into the prey model

184 We modelled an unstructured predator population (similarly to Wilmers et al., 2007a), which, in any  
 185 year  $t$ , had a total population size of  $Y(t)$ . Predator population dynamics resulted from the combination  
 186 of a functional response, which describes how the intake rate of a predator varies with prey abundance  
 187 (Abrams & Ginzburg, 2000; Holling, 1959), and a numerical response, which relates predator intake  
 188 to changes in its abundance (Bayliss & Choquenot, 2002).

189 We integrated the influence of prey body condition by accounting for the fact that only adult prey in  
 190 poor condition, i.e. with a low survival probability, were vulnerable to predators, whereas all juvenile  
 191 prey were vulnerable to predators, irrespectively of their body condition. To do so, we defined a  
 192 threshold of survival probability  $Th$ . Any adult prey with an individual survival probability  $p_{ai}(t)$  below  
 193 this threshold was integrated to the pool of adult prey vulnerable to predators  $A_{vuln}$ . Rainfall and prey  
 194 density both affected  $g_a(t)$  and thus  $p_a(t)$ , the mean survival probability within the population.  
 195 Consequently, they played a crucial role in determining the proportion of adult prey in poor body  
 196 condition. As  $p_a(t)$  decreased, there were more adult prey with low individual survival probabilities,  
 197 and therefore more adult prey with a survival probability under the vulnerability threshold and exposed  
 198 to predation.

200 We integrated the influence of habitat characteristics that could affect prey vulnerability through the  
 201 manipulation of the handling time  $h$ , which is classically defined as the time needed by a predator to  
 202 subdue and consume a prey and during which the predator cannot capture another prey (Abrams &  
 203 Ginzburg, 2000). In our model, this time to subdue one prey corresponded to all predation attempts  
 204 (with one predation attempt being a predation sequence: search, encounter, and attack) leading to a  
 205 successful prey capture. For African savannas, we assumed that an increase in annual rainfall leads to  
 206 a greater vegetation cover (taller grass, more leaves in bushes and trees) and hence better concealment  
 207 opportunities for predators to approach their prey undetected (Hopcraft et al., 2005). Hence, we  
 208 considered that an increase in the climatic variable  $R$  would increase prey vulnerability, and  
 209 consequently decrease the number of attempts leading to a successful attack, i.e. lead to lower handling  
 210 time  $h$  values (an alternate situation were handling time increases with rainfall is presented in the  
 211 Appendix A of the Supplementary material). Therefore,  $h$  varied with rainfall according to the  
 212 following equation:

$$213 \quad H(R) = h_{min} + \frac{h_{max} - h_{min}}{1 + e^{B(R-V)}} \quad (5)$$

214 with  $H(R)$  the value of handling time for a given year  $t$  and the rainfall value  $R$ ,  $h_{min}$  is the lowest value  
 215 of  $h$ ,  $h_{max}$  is the maximum value of  $h$ ,  $B$  is the maximum rate of change,  $V$  is the rainfall value at which  
 216 the rate of change of  $h$  is maximum (or inflexion point). This equation allowed the handling time to  
 217 vary non-linearly and negatively with rainfall (Fig. 2C). One value of  $h$  was calculated for each rainfall  
 218 value and was then incorporated into the functional response  $I(t)$ .

219 For the functional response, we assumed that the number of prey killed and consumed by one predator  
 220 during a given year  $t$  followed a type II Beddington-DeAngelis functional response. This equation  
 221 allows the integration of interference between predators when searching for and capturing prey and is  
 222 formulated as follows:

226

$$I(P(t), Y(t)) = \frac{\mu P(t)}{1 + \tau Y(t) + \mu h P(t)} \quad (6)$$

where  $P(t)$  is the number of vulnerable prey,  $Y(t)$  the number of predators,  $\mu$  a parameter defining the encounter rate between predators and their prey,  $h$  the parameter defining the handling time and  $\tau$  the interference between predators (Abrams & Ginzburg, 2000). Finally, this type of functional response allows both prey and predator densities to impact predators' intake and therefore the regulation of predator populations.

Predation occurs all year around. Consequently, to account for the depletion of prey that occurred throughout the year and could affect the estimation of the number of prey actually captured, we recursively applied the functional response presented in (6) over daily time steps, adjusting prey number at each time step. We named  $M(t)$  the total number of prey killed by predators and calculated it as follows:

$$M(t) = P(t) - \sum_{d=1}^{365} I(P(d)Y(t)) \quad (7)$$

where  $P(t)$  is the number of vulnerable prey to predation,  $P(d)$  the pool of prey vulnerable to predation at the beginning of day  $d$  and  $Y(t)$  the number of predators at the beginning of year  $t$ .

The numbers of juvenile and adult prey killed by a given predator during a year are given by:

$$M_j(t) = M(t) \times \frac{J(t)}{P(t)} \quad (8)$$

$$M_a(t) = M(t) - M_j(t) \quad (9)$$

The  $M_j(t)$  juveniles killed in year  $t$  were randomly removed from the  $J(t)$  juveniles present at the beginning of the year  $t$ . Similarly, the  $M_a(t)$  adults killed in year  $t$  were randomly removed from the pool of vulnerable adults  $A_{vuln}$ , i.e. individuals whose survival probabilities were below the threshold of survival probability  $Th$ . For simplification, we assumed that adult and juvenile prey were equally profitable to predators. Similar assumption can be found in other modelling studies (e.g. Wilmers et al. 2007a).

Finally, the predator numerical response was given by:

$$Y(t + 1) = \lambda_{max} \times P_{rel}(t) \times Y(t) \quad (10)$$

where  $Y(t)$  is the number of predators present in year  $t$ ,  $\lambda_{max}$  is the maximum growth rate of the predator population and  $P_{rel}(t)$  was calculated as follows:

$$P_{rel}(M(t), Y(t)) = \frac{M(t)}{\frac{1}{h_{min}} \times 365 \times Y(t)} \quad (11)$$

with  $h_{min}$  the smallest value possible for the handling time.  $P_{rel}$  was therefore bounded between 0 and 1 and quantified predators hunting efficiency over a year by expressing the amount of prey actually eaten in year  $t$  as a proportion of the maximum amount of prey that predators could have eaten.

### 3.2 Simulations

To study how climatic conditions may impact predator populations through their influence on prey body condition or habitat characteristics, we designed 4 scenarios:

271 *Scenario 1:* climatic conditions influence prey availability through their effect on prey body condition  
 272 and ultimately on prey abundance. Prey vulnerability to predators did not vary with prey body condition  
 273 (all prey were vulnerable to predators) nor with habitat characteristics. Climatic conditions therefore  
 274 influenced predator-prey interactions only through their impacts on prey survival and fecundity, i.e.  
 275 through prey abundance only (blue arrows in Fig. 1). This demographic effect of climate is present in  
 276 all scenarios.

277 *Scenario 2:* prey vulnerability was affected by climatic conditions through their influence on prey body  
 278 condition (red arrows in Fig. 1). The poorer a prey body condition, the more vulnerable to predators  
 279 the prey was. Therefore, climatic conditions influence prey availability through their effect on prey  
 280 body condition affecting both abundance and prey vulnerability to predation.

281 *Scenario 3:* prey vulnerability was affected by climatic conditions through climate-driven changes in  
 282 habitat characteristics (e.g. vegetation) (red arrows in Fig. 1). Therefore, climatic conditions influence  
 283 prey availability through their effect on prey body condition affecting prey abundance and on habitat  
 284 characteristics affecting prey vulnerability to predation

285 *Scenario 4:* prey vulnerability was affected by both prey body condition and climate-driven changes  
 286 in habitat characteristics. In this scenario combining scenarios 2 and 3, climatic conditions influence  
 287 prey availability through their effect on prey body condition and habitat characteristic and, ultimately,  
 288 prey abundance and vulnerability to predation.

289 While in scenarios 1 and 3 predators could capture any prey individual, in scenarios 2 and 4  
 290 predators could capture any juvenile, but could only subdue adult prey that were in poor body  
 291 condition. These differences between scenarios were modelled by setting the value of the threshold of  
 292 survival probability  $Th$  at 1 in scenario 1 and 3, and at 0.5 in scenario 2 and 4 (Table 1). As vulnerability  
 293 to predators was independent from habitat characteristics in scenarios 1 and 2, the handling time was  
 294 set constant and equal to  $h = 5$  in these scenarios. In scenarios 3 and 4, prey vulnerability to predators  
 295 was dependent on habitat characteristics and handling time  $h$  varied with climatic conditions following  
 296 equation 5 (for a summary of the model functioning see Fig. 3).

297 We focused on these 4 scenarios only, as the goal of this study was to assess how the addition  
 298 of prey vulnerability to traditional predator-prey models that considered prey abundance only would  
 299 change the expectations in terms of responses of predator populations to climatic changes.

300  
 301 For simulations, parameters were given default values considered realistic for African large mammals.  
 302 These default values and initial values for state variables are presented Table 1. The sensitivity of the  
 303 main results to some of these parameter values was investigated by sensitivity analyses (see section  
 304 below). As we were mostly interested in how the link between climatic conditions and prey  
 305 vulnerability could affect predator dynamics, predators were characterized by identical parameter  
 306 values in the different scenarios, but for the threshold  $Th$  and handling time  $h$  values. Therefore, in our  
 307 work, all differences in predator dynamics between scenarios emerged from differences in these two  
 308 parameters.

### 309 **3.2.1 Immediate response of predator populations to specific rainfall conditions**

310 We assessed, for each scenario, the immediate response of the predator population to specific rainfall  
 311 conditions. We simulated over 198 years the dynamics of the predator population under the long-term  
 312 annual rainfall 600 mm, then imposed a predefined rainfall in year 199 (different values were tested:  
 313 from 300mm to 900mm, by 100mm increments), and calculated the predator population growth rate  
 314 over that year (calculated as  $\lambda = Y_{t+1}/Y_t$ ). To obtain robust estimates of predator population growth  
 315 rates and account for within-simulation variability in prey demographic rates, each simulation,  
 316 characterized by a long-term annual rainfall value of 600mm and one predefined rainfall for the last  
 317 year, was replicated 1000 times.

### 318 **3.2.2 Long-term response of predator populations to changes in mean annual rainfall**

319 We assessed, for each scenario, how a change in mean annual rainfall may affect predator populations  
 320 on the long run. We compared the average predator population size (over the last twenty-one years of  
 321 a 200-year simulation) across simulations run under different long-term rainfall averages. The mean  
 322 annual rainfall values varied from 300mm to 900mm, by 100mm increments. For each value,  
 323 simulations were replicated 1000 times, allowing again to account for within simulation variability in  
 324 prey demographic rates.

### 325 **3.2.3 Sensitivity analyses**

326 Because model outcomes can be sensitive to the choice of parameter values, we conducted sensitivity  
 327 analyses for some model parameters. We first investigated the effect of changes in parameter  $h_{min}$  and  
 328  $Th$ , which are of importance because differences between scenarios originate from these two  
 329 parameters. In addition, we also tested for the influence of changes in  $\lambda_{max}$  values, which is a central  
 330 parameter of the predator numerical response. Finally, we carried out a sensitivity analysis for the  $\delta$   
 331 parameter, which describes the shape of density dependence and determines the magnitude of the prey  
 332 population response, the number of individuals per resource units, and ultimately prey dynamics. We  
 333 always varied this parameter simultaneously for adult and juvenile, ensuring that juvenile survival  
 334 never exceeded adult survival (see Fig. 2A). Sensitivity analyses were conducted by increasing or  
 335 decreasing each of these parameters, one at a time, by 20 percent around its default value. For each  
 336 parameter value, simulations were replicated 500 times. Results of the sensitivity analyses are  
 337 presented in the Appendix B of the Supplementary Material.

338 An example of the behaviour of the model for one run showing fluctuations of rainfall, prey and  
 339 predator population size over 200 years is presented in Fig. S7 (Appendix C of the Supplementary  
 340 Material) and a summary of the key steps of the modelling process and of the different scenarios can  
 341 be found in Fig. 3. All simulations were conducted in R 4.0.2 (R Core Team, 2020).

## 342 **4 Results**

### 343 **4.1 Immediate response of predator populations to specific rainfall conditions**

344 In scenario 1, i.e. when climatic conditions influenced prey abundance only (through survival and  
 345 fecundity) and not prey vulnerability, the population growth rate of predators was not influenced by  
 346 the specific climatic condition of the year (Fig. 4A). This result was not surprising as according to the  
 347 model design, the demographic consequences of climate are expected to be visible in prey population  
 348 the following year ( $t+1$ ) and, therefore, would only impact predator growth rate calculated over the  
 349 year  $t+1$  and  $t+2$ . In contrast, in the three other scenarios, i.e. when climatic conditions influenced prey  
 350 vulnerability, either through changes in prey body condition (scenario 2) or through changes in habitat  
 351 characteristics (scenario 3) or both (scenario 4), the population growth rate of predators one year was  
 352 influenced by the specific climatic condition of the year. Population growth rates in scenarios 2 and 3  
 353 showed opposite patterns (Fig. 4A). Predators from scenario 2 benefited from below-average rainfall  
 354 (600mm) and their populations increased, as shown by the growth rate being greater than 1, but there  
 355 was a negative effect of above-average rainfall (Fig. 4A). In scenario 3, there was a negative effect of  
 356 below-average rainfall and a positive effect of above-average rainfall on predator growth rate (Fig.  
 357 4A). Because scenario 4 is a combination of scenarios 2 and 3, the population growth rate of predators  
 358 from scenario 4 was intermediate between those of scenarios 2 and 3 (Fig. 4A).

### 359 **4.2 Long-term response of predator populations to changes in mean annual rainfall**

360 Our results showed an effect of mean annual rainfall on the size of predator populations for all  
 361 scenarios, but the shape of the relationships varied. In scenario 1 (when climatic conditions influenced  
 362 prey abundance only), the size of predator populations increased near-linearly with rainfall (Fig. 4B).  
 363 As expected because all individuals were vulnerable to predation, the size of predator populations in  
 364 this scenario was always greater than the one observed in other scenarios. The size of predator  
 365 populations in scenario 2 (when climatic conditions influenced prey vulnerability through changes in  
 366 prey body condition only) also increased near-linearly with mean annual rainfall. It was consistently  
 367 lower than the size of the predator population in scenario 1 because only a fraction of the prey  
 368 population is vulnerable to predation in scenario 2. However, the effect of climatic conditions on  
 369 predator population sizes was weaker in scenario 2 than in scenario 1: as the amount of rainfall  
 370 increased, the difference between scenarios 1 and 2 in the size of predator populations increased (Fig.  
 371 4B). Conversely, the size of predator populations varied non-linearly with increasing rainfall in  
 372 scenario 3, when climatic conditions influenced prey vulnerability through changes in habitat  
 373 characteristics only, and in scenario 4, when climatic conditions influenced prey vulnerability through  
 374 both changes in prey body condition and habitat characteristics. More specifically, the size of predator  
 375 populations in scenario 3 were smaller than those from scenario 2 up until mean annual rainfall reached  
 376 values around 600mm, but were greater for values above (Fig. 4B). In addition, for mean annual rainfall  
 377 of 900mm, the size of predator populations in scenario 1 and 3 were almost equal. In scenario 4,  
 378 changes in the size of predator populations with increasing mean annual rainfall generally followed a  
 379 similar pattern than those observed from the scenario 3. However, the difference in the size of predator  
 380 populations between scenario 4 and 3 increased with increasing rainfall (Fig. 4B). Conversely, the size  
 381 of predator populations were virtually identical between scenario 4 and 2 at the wettest end of the  
 382 rainfall gradient (Fig. 4B). In all cases, the size of predator populations in scenario 4 was always equal  
 383 or lower than in the other scenarios (Fig. 4B).

## 384 5 Discussion

385 Our work shows how predator populations could respond differently to changing climatic conditions  
 386 depending on how climate influences prey vulnerability (habitat characteristics vs. body condition).  
 387 For example, in a context of aridification, a predator-prey system where prey vulnerability depends  
 388 mainly on prey body condition (scenario 2) would be characterized by larger predator populations than  
 389 a system where prey vulnerability is mainly affected by the habitat (scenario 3) (see section 5.1 for the  
 390 role of species traits). It thus highlights the importance of having a good understanding of the processes  
 391 determining vulnerability at play within the predator-prey pair studied, as integrating climate influence  
 392 on prey vulnerability, in addition to resource-mediated climate effects on prey abundance, leads to  
 393 different responses of predator populations (on the short- and the long-term) to changes in climatic  
 394 conditions.

### 395 5.1 How species traits influence the relative importance of the different sources of 396 vulnerability

397 Ultimately, whether the predator-prey pair studied will respond according to one scenario or another  
 398 will depend upon the traits of the species involved. Here, we will illustrate the importance of the  
 399 predator hunting mode and the prey escape tactics, as well as the importance of the relative size of the  
 400 predator and the prey. Predator hunting mode (cursorial or ambush) and prey escape tactics (fleeing,  
 401 fighting or freezing) are key behavioural traits involved in predator-prey interactions that can affect  
 402 how climatic conditions contribute, indirectly *via* forage resources or vegetation cover, to determine  
 403 the vulnerability of prey to predation. For example, cursorial predators, such as spotted hyaenas  
 404 *Crocuta crocuta* (Cooper, 1990) and wild dogs *Lycaon pictus* (Pole et al., 2004) in African savannas,

405 or wolves in temperate ecosystems (Mech et al., 2015), are active predators, i.e. they can chase down  
 406 their prey over long distances and are more likely to kill individuals in poor body condition. They  
 407 therefore exemplify predators from scenario 2 (climatic conditions influence prey vulnerability through  
 408 changes in prey body condition only), as prey in poorer condition because of a shortage of food will  
 409 be particularly more vulnerable to predation from these predators (Atwood et al., 2007; Mills, 1995;  
 410 Pole et al., 2004). Conversely, ambush predators, such as African lions *Panthera leo* and leopards  
 411 *Panthera pardus* in African savannas, or cougars *Puma concolor* and lynx *Lynx lynx* in temperate  
 412 ecosystems, stalk their prey before attacking them by surprise when they come within short distance  
 413 (Elliott et al., 1977; Husseman et al., 2003). As such, they rely less on prey body condition. However,  
 414 to approach their prey undetected, ambush predators need concealment. Therefore, their hunting  
 415 success is prone to be influenced by vegetation (Funston et al., 2001; Lone et al., 2014), and negatively  
 416 affected by an increased aridity and a subsequent decrease in vegetation density (scenario 3, climatic  
 417 conditions influence prey vulnerability through changes in habitat characteristics only). Whereas prey  
 418 escape tactics might not be that crucial for the outcome of an encounter with an ambush predator, a  
 419 climate-driven decrease in prey body condition will negatively influence prey fleeing capacity leading  
 420 to an overall disadvantage against cursorial predators (scenario 2).

421 Predator body size influences the prey body size targeted by the predator (Owen-Smith & Mills,  
 422 2008a; Radloff & du Toit, 2004) and climate-driven changes in prey body condition can interfere with  
 423 the chance of successfully subduing an adult prey depending on the relative size of the predator and  
 424 the prey considered (Mech et al., 2001; Metz et al., 2012). For example, for lion-impala interactions, it  
 425 is very likely that climatic conditions will not affect the likelihood of lions to capture an adult impala  
 426 *Aepyceros melampus*, while in the case of lion-buffalo *Syncerus caffer* interactions, lions are expected  
 427 to successfully hunt adult buffaloes, which are dangerous prey for them, in dry conditions only  
 428 (scenario 2, Owen-Smith, 2008). This is also true at the interspecific level: prey species that are usually  
 429 inaccessible because they are too difficult to be captured under normal climatic conditions may become  
 430 vulnerable due to unfavourable conditions, allowing predators to kill young individuals of larger  
 431 species (e.g. with elephants: Loveridge et al., 2006; Salnicki et al., 2001).

432

## 433 5.2 Importance of integrating climate-driven changes in prey vulnerability

434 Our results show how predator population responses to changes in climatic conditions differ when we  
 435 take into account climate-driven changes in prey vulnerability in addition to climate-driven changes in  
 436 prey abundance (existing work take into account climate-driven changes in prey abundance only – Fig.  
 437 1). For example, while the overall trend depicted in all 4 scenarios on the long-term is that there are  
 438 more predators when rainfall increases, because of an overall increase in prey population abundance,  
 439 the originality of our study is to illustrate how prey vulnerability and its drivers influence the link  
 440 between predator populations and climate.

441 When changes in climatic conditions influence prey vulnerability through changes in prey body  
 442 condition (scenario 2), a below average rainfall event leads to poorer herbivore body condition, and  
 443 hence results in an increase in the pool of adult prey vulnerable to predators (Fig. S8A). Unsurprisingly,  
 444 this, in turn, favours the immediate growth rate of the predator population. This result is in accordance  
 445 with field observations, which reported a positive effect of drought conditions over the short-term on  
 446 large carnivore populations (Mills, 1995). These dry-condition increases in prey vulnerability can be  
 447 assimilated to “resource pulses” for the predators and to be beneficial to them (Holt, 2008; Yang et al.,  
 448 2008). Contrarily, above average rainfall events negatively affects the population growth rate of  
 449 predators, as very few prey adults are vulnerable in years characterized by high levels of resources  
 450 (Fig. S8A). Over the long term, predator populations benefit from the overall increase in prey  
 451 populations associated with increasing rainfall (Fig. S9). However, predators in scenario 2 can only

452 subdue a portion of adult prey and have a smaller pool of available prey than predators in scenario 1.  
 453 They are therefore maintained at smaller population size. In addition, the proportion of vulnerable adult  
 454 prey decreases with increasing rainfall (Fig. S8B), which leads to the observed increase in the  
 455 difference between the size of predator populations in scenario 1 and 2.

456 When changes in climatic conditions influence prey vulnerability through changes in habitat  
 457 characteristics and habitat-driven hunting success increases with rainfall (scenario 3), predator growth  
 458 rates are negatively impacted by below average rainfall and positively influenced by above average  
 459 rainfall. This is typically the case in African savannas where grass height is related to rainfall  
 460 (Rutherford, 1980) and lions are hunters that are more successful in tall grass (Funston et al., 2001).  
 461 Over the long term, predator populations benefit from the combined linear increase of prey abundance  
 462 (Fig. S9) and non-linear increase of hunting success (i.e. decrease of handling time, Fig. 2C), leading  
 463 to an overall non-linear increase as rainfall increases.

464 Finally, when changes in climatic conditions influence prey vulnerability through changes in  
 465 both prey body condition and habitat characteristics (scenario 4), the growth rate of predator  
 466 populations combines the effects of both sources of vulnerability and predators are affected by opposite  
 467 effects of different sources of vulnerability. For below average rainfall, predators benefit from the  
 468 positive effect of lower prey body conditions, which buffers the negative effect of a lower hunting  
 469 success due to habitat characteristics, and inversely for above rainfall level, leading to the observed  
 470 intermediate pattern of predator growth rate (Fig. 4A, Fig. 2C, Fig. S8A). Over the long term, predator  
 471 populations of scenario 4 follow the same patterns as the populations in scenario 3 with the exception  
 472 that they can only subdue a proportion of adult prey. They subsequently remain at a smaller population  
 473 size.

### 474 **5.3 Contrasting predator responses to short- and long-term climate fluctuations**

475 Our study highlights the importance of the temporal scale considered as the patterns observed differed  
 476 whether we considered the short- or long-term temporal scale. While a sudden arid event can be  
 477 beneficial to predator population, increasing aridity over time leads to an overall decrease in predator  
 478 population size. The explanation of such differences lies in the fact that a predator response over the  
 479 long term integrates the predator responses over the short-term, along with the long-term response of  
 480 prey, which declines with increasing aridity (Fig. S9). Therefore, our results illustrate that the long-  
 481 term response of predator populations to changes in mean annual rainfall cannot be predicted only from  
 482 the immediate response of predator populations to specific rainfall conditions.

### 484 **5.4 Considerations on the model**

485 Modelling studies are difficult exercises where one walk on a thin line between complexity/realism  
 486 and simplification that is required for conceptualization, i.e. building some theoretical understanding.  
 487 We have tried to do this successfully but we want to underline here a few simplifications made in this  
 488 study (and already made in classical models of predator-prey interactions – e.g. Wilmers *et al.*, 2007a,  
 489 b). It is noteworthy that the code of the model is available ([https://github.com/aissamorin/climate-prey-  
 490 vulnerability-and-predators](https://github.com/aissamorin/climate-prey-vulnerability-and-predators)) so that one can parametrize it for a specific system and add the complexity  
 491 that would be considered critical. First, in our model, juvenile prey contribute as much energy as adult  
 492 prey. Second, the predator population is not age-structured. Third, the predator-prey system modelled  
 493 here involves one prey and one predator only, yet multi-species assemblages often characterize both  
 494 prey and predator communities. Predators often prey on several prey species, with primary and  
 495 secondary prey and display prey switching depending on prey availability and catchability (Owen-  
 496 Smith & Mills 2008b, Elbroch et al. 2013). The presence of an alternative prey could influence model

497 outcomes for scenarios 2, 3 and 4: when the vulnerability of the primary prey decreases, if the predator  
498 can switch to an alternate prey species available and more vulnerable, the decrease in predator  
499 population growth rate or over the long term may be weaker or not observed. In contrast, the presence  
500 of competitors preying on the same prey could intensify the decrease in the number of vulnerable prey  
501 available to each predator owing to additive effects (Melis et al. 2009), and negatively influence  
502 predator population size.

## 503 **5.5 Conclusion**

504 Despite its general simplicity, this theoretical study highlights the importance of understanding, and  
505 accounting for, the vulnerability factors in predator-prey relationships, and sheds light on the  
506 complexity of predicting predator-prey relationships in a changing climate. We believe it is a  
507 prospective study that suggests interesting future research directions. Based on our work, we advise  
508 that future theoretical and empirical works should integrate climate-driven changes in prey  
509 vulnerability if we want to grasp the full picture of the impacts of climate changes on predator-prey  
510 interactions.

## 511 **6 Conflict of Interest**

512 The authors declare that the research was conducted in the absence of any commercial or financial  
513 relationships that could be construed as a potential conflict of interest.

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## 519 **8 Author contributions**

520 MV and SC conceived the ideas; AM and SC designed the model. All authors analysed the results,  
521 wrote the manuscript, and gave approval for publication.

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529

## 530 **10 Data availability statement**

531 The code used for the model and the simulations is available from a GitHub repository:  
532 <https://github.com/aissamorin/climate-prey-vulnerability-and-predators>.

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711 **Table 1:** Definitions and values of the state variables and parameters for prey and predators used in the model.

Variables	Definition/description	Values
$N(t)$	Prey population size at the beginning of year t	$N_1=10000$
$J(t)$	Number of juvenile prey at the beginning of year t	$J_1=2500$
$A(t)$	Number of adult prey at the beginning of year t	$A_1=7500$
$Y(t)$	Predator population size at the beginning of year t	$Y_1=10$
$P(t)$	Pool of prey vulnerable to predation for year t	Calculated at each time step
$M(t)$	Pool of prey consumed at the end of year t	Calculated at each time step
$\alpha_a$	First shape parameter of the Beta distribution from which are drawn adult prey individual survival rate	Calculated at each time step
$\alpha_j$	First shape parameter for Beta distribution from which are drawn juvenile prey individual survival rate	Calculated at each time step
$\beta_a$	Second shape parameter for Beta distribution from which are drawn adult prey individual survival rate	Calculated at each time step
$\beta_j$	Second shape parameter for Beta distribution from which are drawn juvenile prey individual survival rate	Calculated at each time step
$Pa$	Maximum adult prey survival probability	0.95
$Pj$	Maximum juvenile prey survival probability	0.8
$Sd_{pa}$	Standard deviation, variation of adult prey survival	0.05
$Sd_{pj}$	Standard deviation, variation of juvenile prey survival	0.05
$g_a$	Effect of increased population density on adult survival	$g(N(t)) = \frac{\gamma_{Pa}^{\delta_{Pa}}}{\gamma_{Pa}^{\delta_{Pa}} + \frac{N(t)}{R}}$
$g_j$	Effect of increased population density on juvenile survival	$g(N(t)) = \frac{\gamma_{Pj}^{\delta_{Pj}}}{\gamma_{Pj}^{\delta_{Pj}} + \frac{N(t)}{R}}$
$p_a$	Mean adult prey survival probability	$p_a = P_a \times g_a$

$p_j$	Mean juvenile prey survival probability	$p_j = P_j \times g_j$
$\gamma_{Pa}$	Adult half-saturation, point at which adult prey survival is lowered by half	30
$\gamma_{Pj}$	Juvenile half-saturation, point at which juvenile prey survival is lowered by half	20
$\delta_{Pa}$	Shape parameter, defines the onset of density-dependence for adult prey	2
$\delta_{Pj}$	Shape parameter, defines the onset of density-dependence for juvenile prey	2
$R$	Annual level of rainfall	Varies between 300 & 900mm, by 100mm increment
$F_{low}$	Value determining fecundity value when adult survival is close to 0	100
$F_{growth}$	Rate at which fecundity value reaches 1	15
$Th$	Prey threshold of survival probability below which predators can catch and consume the prey.	$Th = 1$ for scenarios 1 & 3; $Th = 0.5$ for scenarios 2 & 4
$H_{min}$	Lowest value that can be taken by the handling time across all scenarios	5
$H_{max}$	Highest value that can be taken by the handling time across all scenarios	8
$B$	Maximum rate of change of the handling time	0.015
$V$	Rainfall value for which the rate of change of the handling time is maximum (or inflexion point)	600
$\mu$	Encounter rate in the predator functional response	0.0002
$h$	Predator handling time for one prey in the predator functional response	$h = 5$ , for scenarios 1 & 2; $h$ defined by $H = h_{min} + \frac{h_{max}-h_{min}}{1+e^{+B(R-V)}}$ , for scenarios 3 & 4
$\tau$	Interference between predators in the predator functional response	0.3
$\lambda_{max}$	Predator maximum growth rate	1.8

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For herbivore demographic parameters, we chose values that were consistent with values reported in the literature on African large herbivores (e.g. Owen-Smith et al., 1990; Grange et al., 2015). For large carnivore parameters, we chose values that were either consistent with the published literature (e.g. Schaller, 1972), or consistent with our field knowledge of lion and hyaena ecology, or, for parameters that have never been estimated, we adjusted them to allow the model to run and give realistic outcomes.

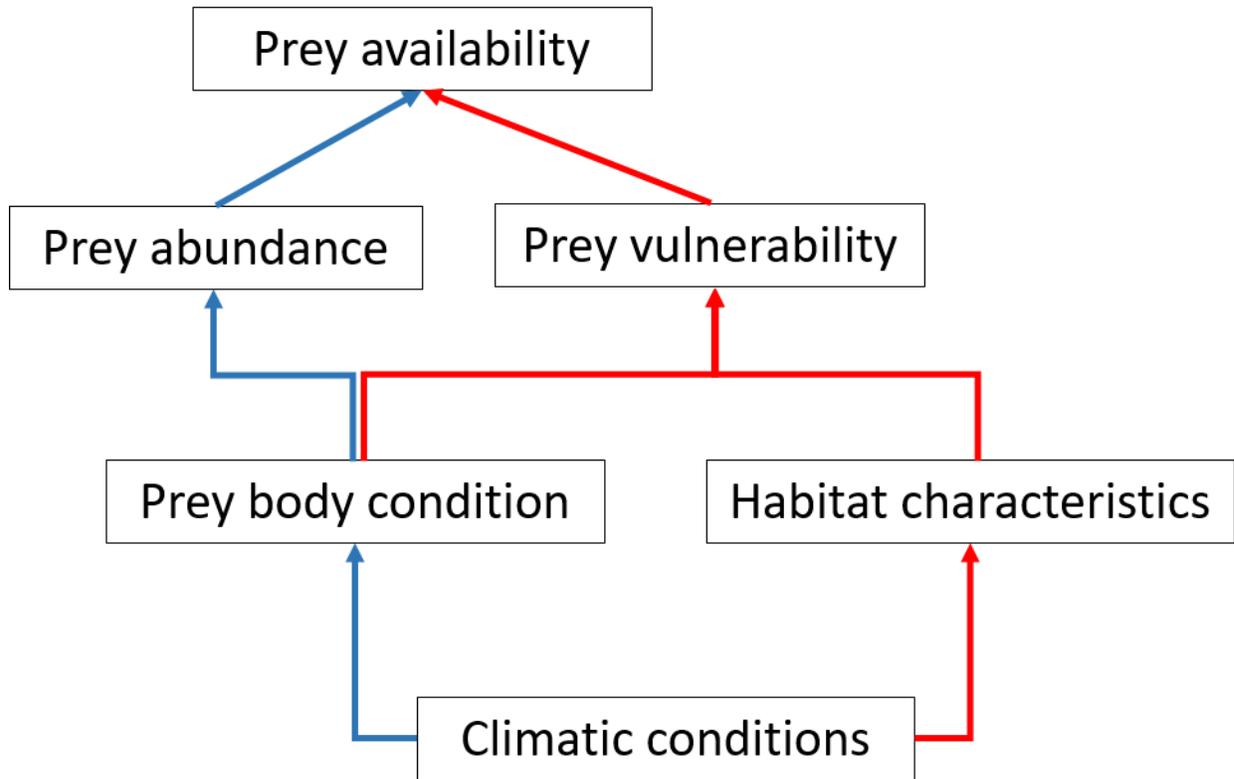
717 **13 Figure captions**

718 **Figure 1:** The potential pathways by which climatic conditions can affect prey availability for predators  
719 The blue arrows represent the links classically modelled in existing models (scenario 1 in this study).  
720 The red arrows represent the links originally modelled in this work (through scenarios 2 to 4).

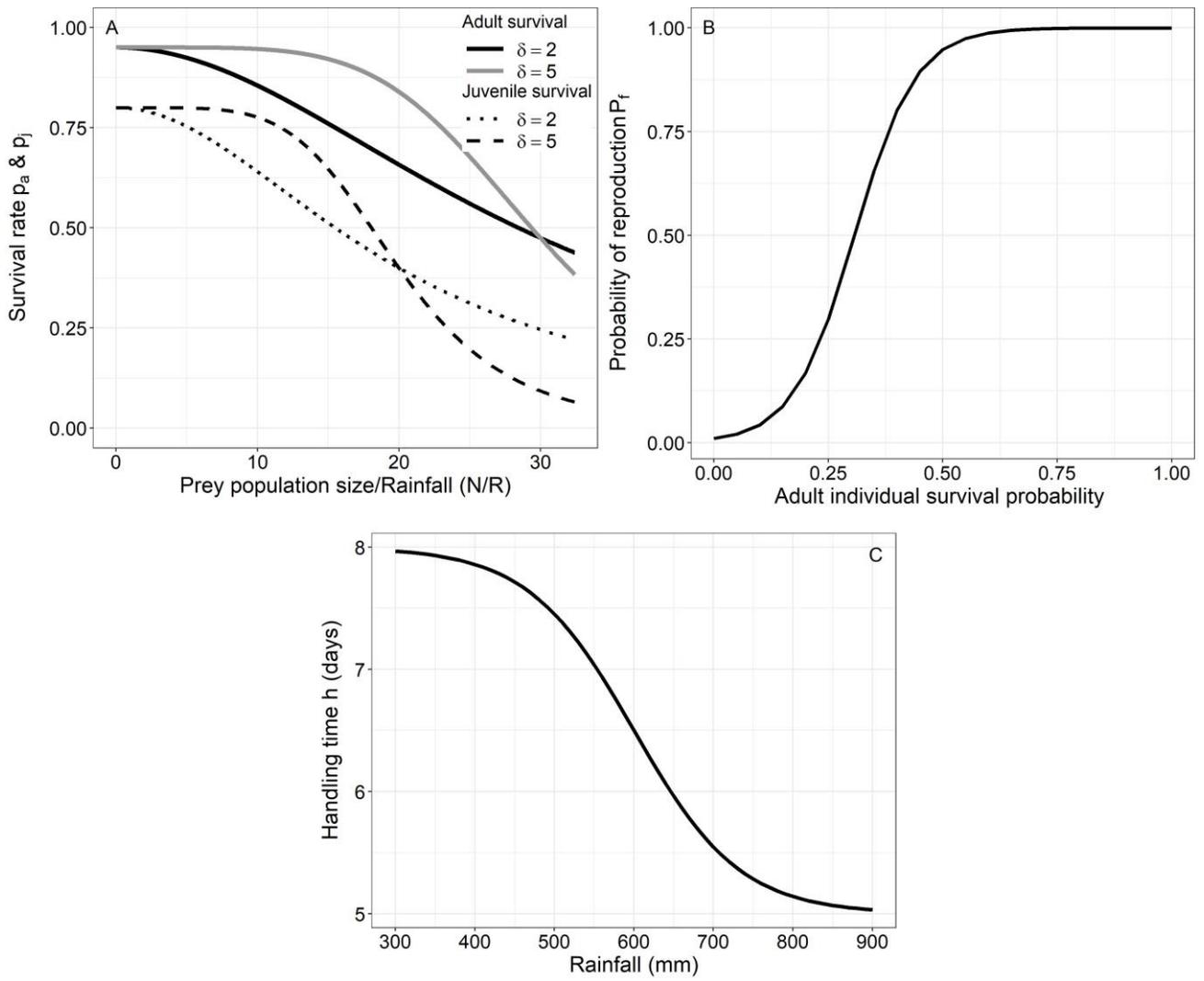
721  
722 **Figure 2:** Summary of the functional relationships underlying the model. (A) Effect of increased  
723 number of individuals per resource unit (approximated by rainfall) on mean juvenile and adult prey  
724 survival rates adapted from Wilmers et al. (2007b). Mean adult and juvenile prey survival rates have  
725 been represented for two values of  $\delta$  parameter, which controls the onset and the strength of the density  
726 dependence. Juvenile prey survival rate has been set to be the first impacted by increasing density. (B)  
727 Probability of reproduction as a function of survival probability  $p_{ai}(t)$ . (C) Functional relationship  
728 between rainfall and predator handling time  $h$  as defined by eqn. 5 for parameters given in Table 1.  
729 The hunting success varies inversely with the handling time.

730  
731 **Figure 3:** Model summary with the key model steps. The dashed line arrow symbolizes the next time  
732 step. As scenario 1 is independent from vulnerability sources, it is presented aside from the other  
733 scenarios. Conversely, details of the processes defining vulnerability related to either body condition  
734 or habitat characteristics are presented in scenarios 2, 3 and 4.

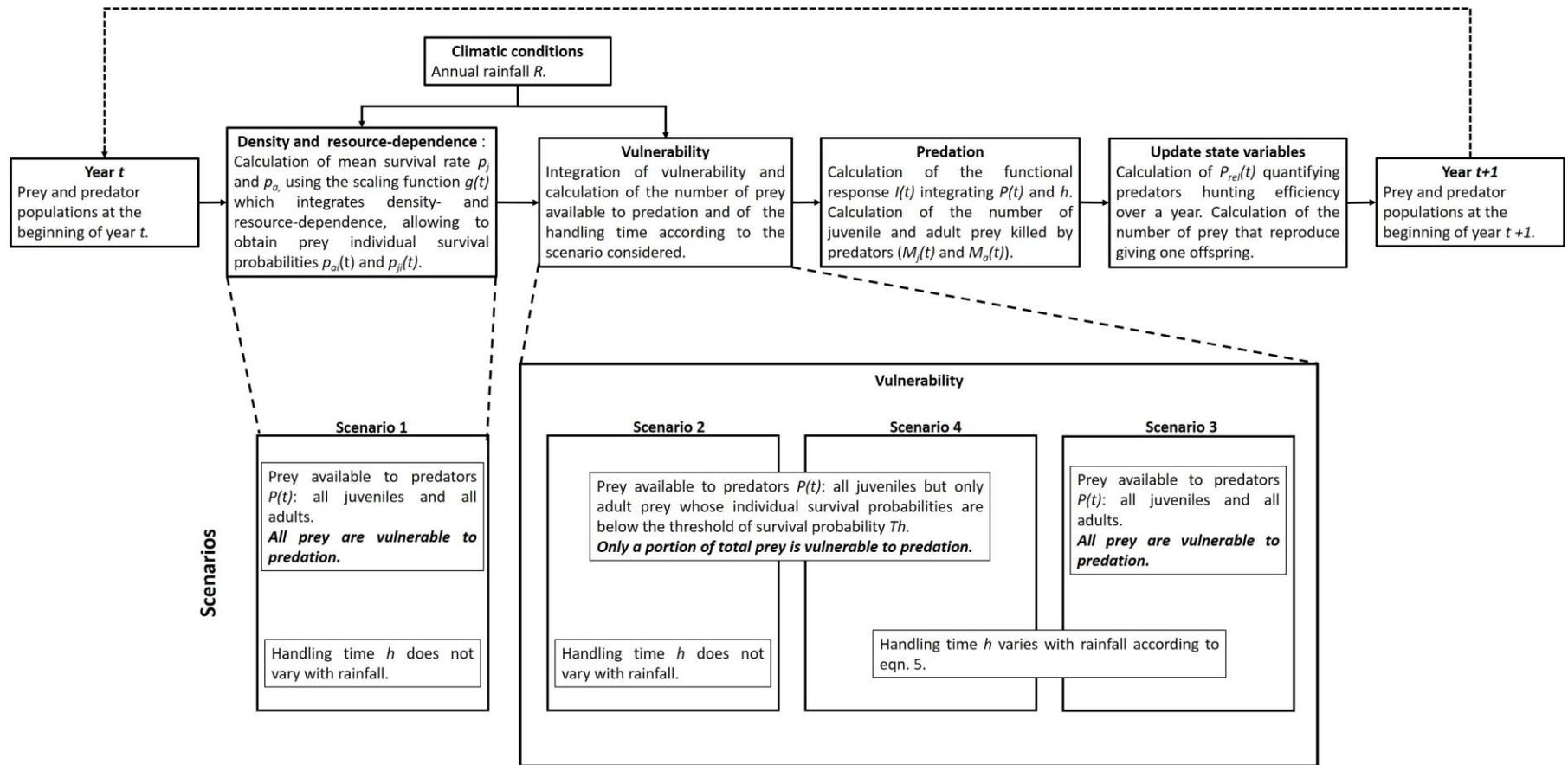
735  
736 **Figure 4:** (A) Immediate response of predator populations to a specific rainfall condition. Relationship  
737 between the growth rate of predator populations and a specific annual rainfall in a system characterized  
738 by a long-term mean annual rainfall of 600 mm. (B) Long-term response of predator populations to  
739 changes in mean annual rainfall. Relationship between the size of predator populations and long-term  
740 mean annual rainfall. While in scenario 1, prey vulnerability to predators did not vary with climatic  
741 conditions, in scenario 2, 3 and 4 climatic conditions affected prey vulnerability through, respectively,  
742 changes in prey body condition, in habitat characteristics or both. Light-coloured envelopes include  
743 minimum and maximum values of predator growth rates (A) or mean predator population sizes (B).



744  
745 **Figure 1**

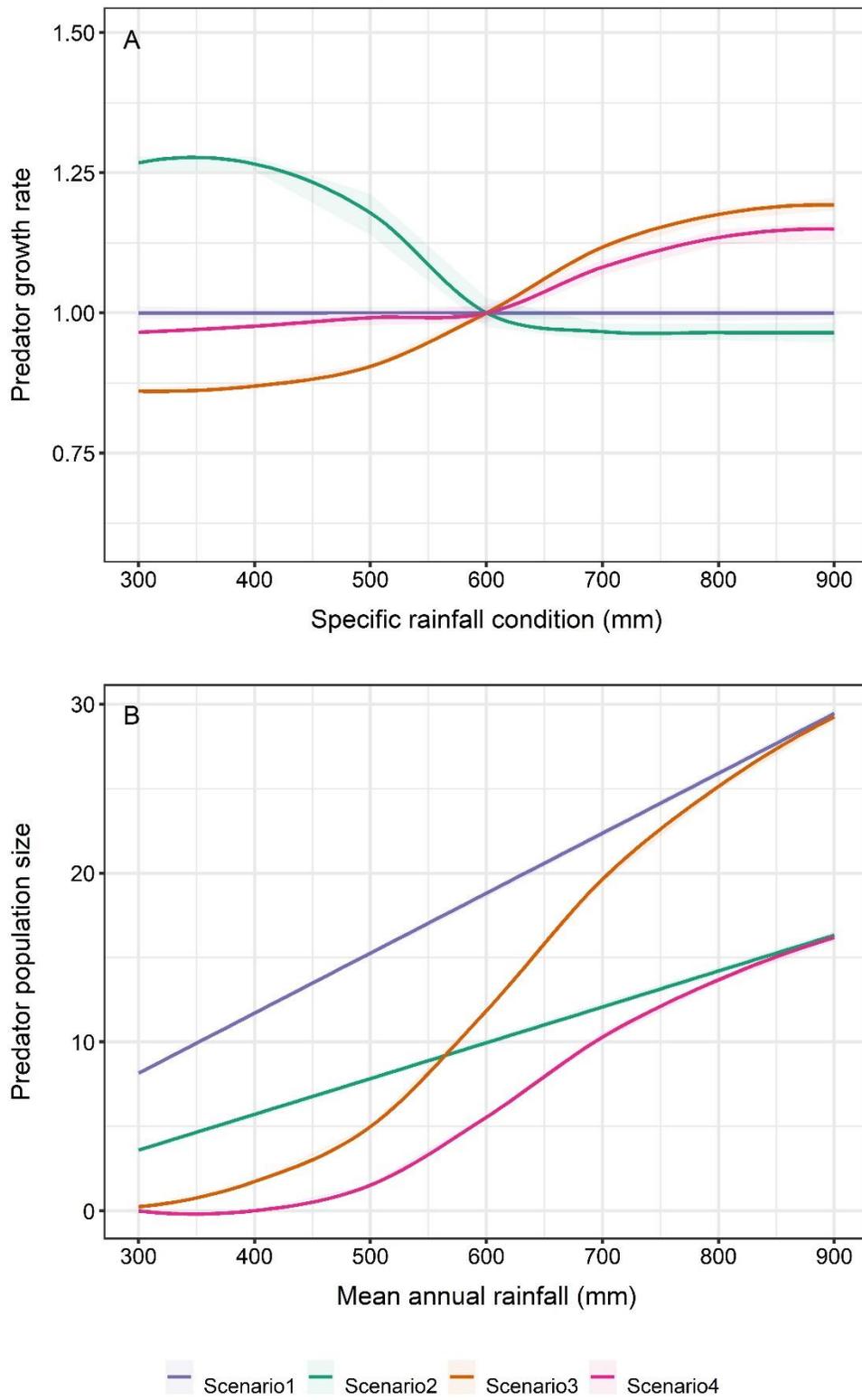


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747 **Figure 2**



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Figure 3



*Supplementary Material*

# 1 Appendix A: Responses of predator populations to an increase in rainfall when habitat driven hunting success decreases with rainfall

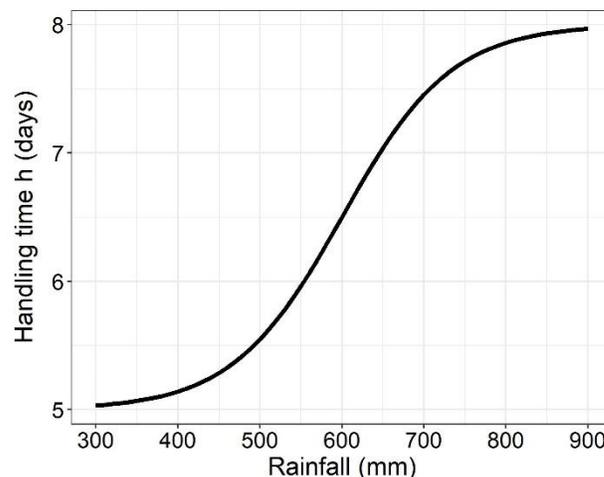
## 1.1 Context

The results presented in the main manuscript only accounted for a positive relationship between predator hunting success and rainfall which is expected in semi-arid ecosystems such as savanna. Hereafter, we present the methods, results and sensitivity analyses for systems characterized by the alternate relationship with hunting success decreasing as rainfall increases.

## 1.2 Materials and methods

The predator-prey model is the same as the one presented in the main manuscript. In this alternate situation, we again integrated the influence of habitat characteristics that could affect prey vulnerability through the manipulation of the handling time  $h$ . However, here we assumed that handling time  $h$  would increase with rainfall and that higher rainfall levels would correspond to higher  $h$  values and consequently longer times to subdue one prey, i.e. decreased hunting efficiency and success than at lower rainfall levels (Fig. S1). Therefore,  $h$  varies with rainfall according to the following equation:

$$H(R) = h_{min} + \frac{h_{max} - h_{min}}{1 + e^{-B(R-V)}} \quad (1)$$



**Figure S1:** Functional relationship between rainfall and predator handling time  $h$  as defined by (1). The hunting success varies inversely with the handling time. For parameters see Table 1 of the main manuscript.

## 1.3 Results

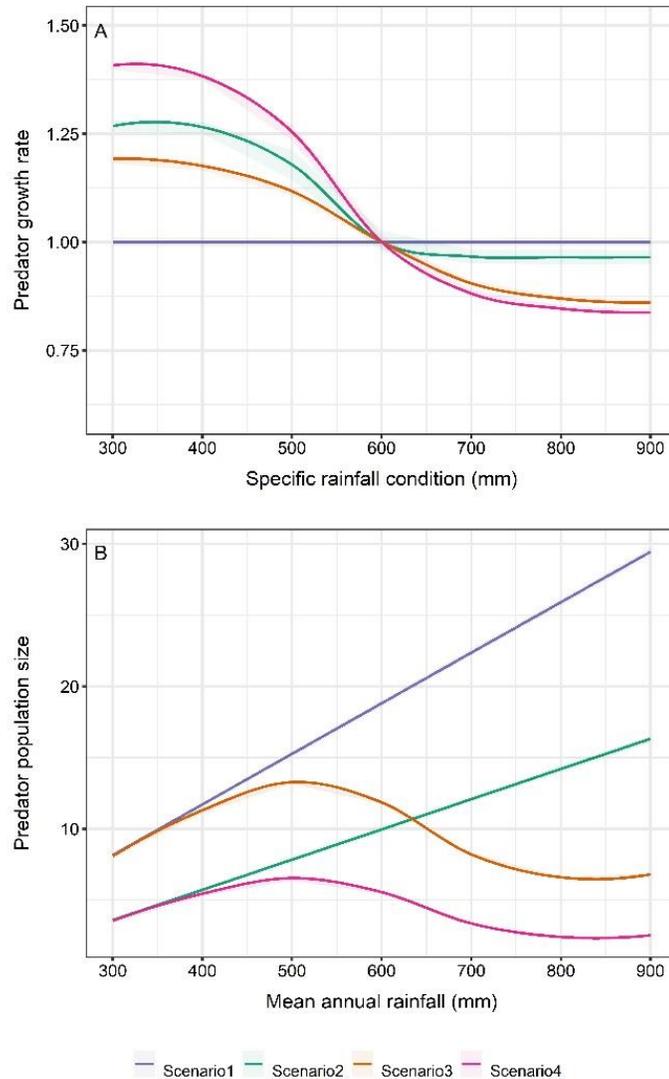
### 1.3.1 Immediate response of predator populations to specific rainfall conditions

When climatic conditions influenced prey abundance only (scenario 1), the population growth rate of predators was not influenced by the specific climatic condition of the year (Fig. S2A). In contrast, in the three other scenarios, the population growth rate of predators in one year was influenced by the specific climatic condition of the year. Predators from the three scenarios, benefited from below-

average rainfall (600mm) and their populations increased, but were negatively impacted by increasing rainfall (Fig. S2A). Finally, unlike the results presented in the main manuscript, the combination of vulnerability effects in scenario 4 made this scenario the one with the most extreme responses, and predator growth rates were negative at above-average rainfall and positive at below-average rainfall (Fig. S2A).

### **1.3.2 Long-term response of predator populations to changes in mean annual rainfall**

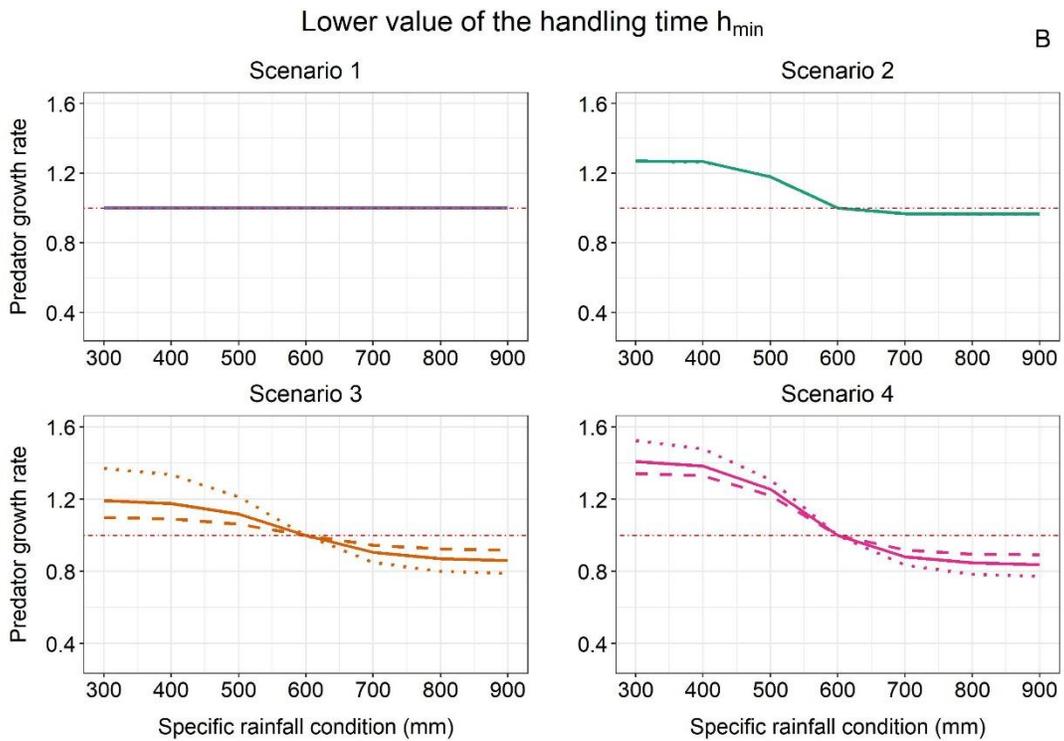
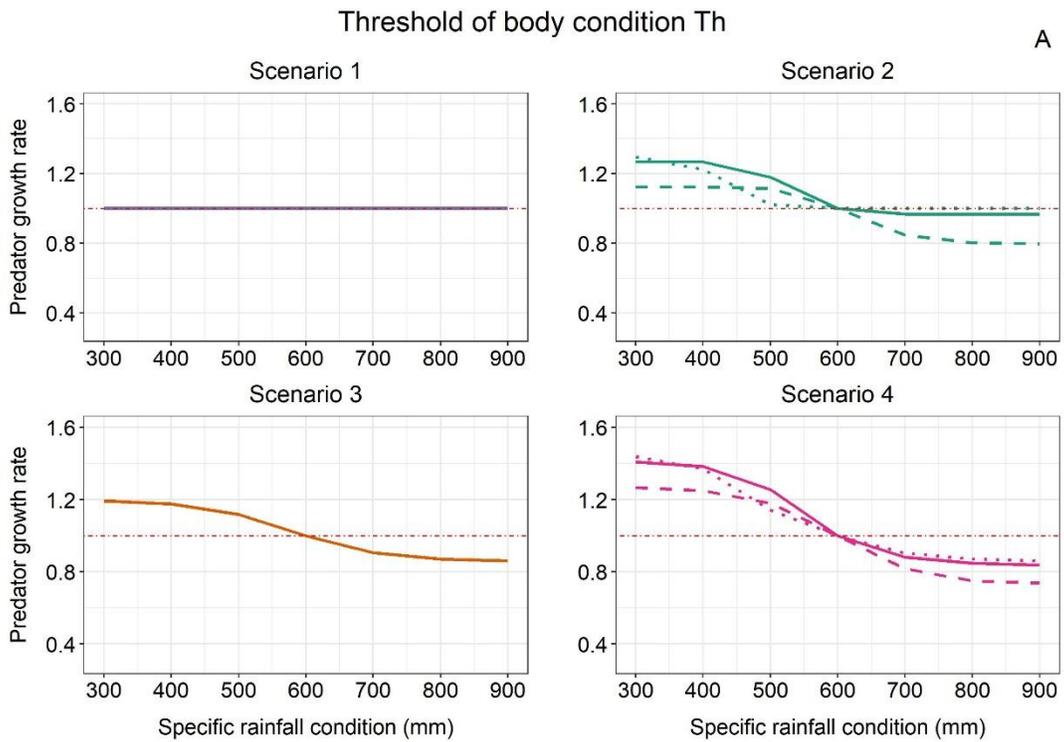
Over the long term, our results show here again an effect of mean annual rainfall on the size of predator populations for all scenarios. Scenario 1 and 2 show similar patterns as those presented in the main results, as the size of predator populations increased near-linearly with rainfall for both scenarios and scenario 2 being characterized by lower predator population size than scenario 1. The size of predator populations in scenario 3 and 4 also varies non linearly, displaying a unimodal response to increasing rainfall. In scenario 3, the size of predator population first increased with increasing mean annual rainfall, before decreasing (Fig. S2B). The size of predator populations in scenario 3 were greater than those from scenario 2 up until mean annual rainfall reached values around 600mm, but were smaller for values above (Fig. S2B). The size of predator populations from scenario 4 varied virtually identically as in scenario 3 with rainfall but with lower values of predator population sizes (Fig. S2B).

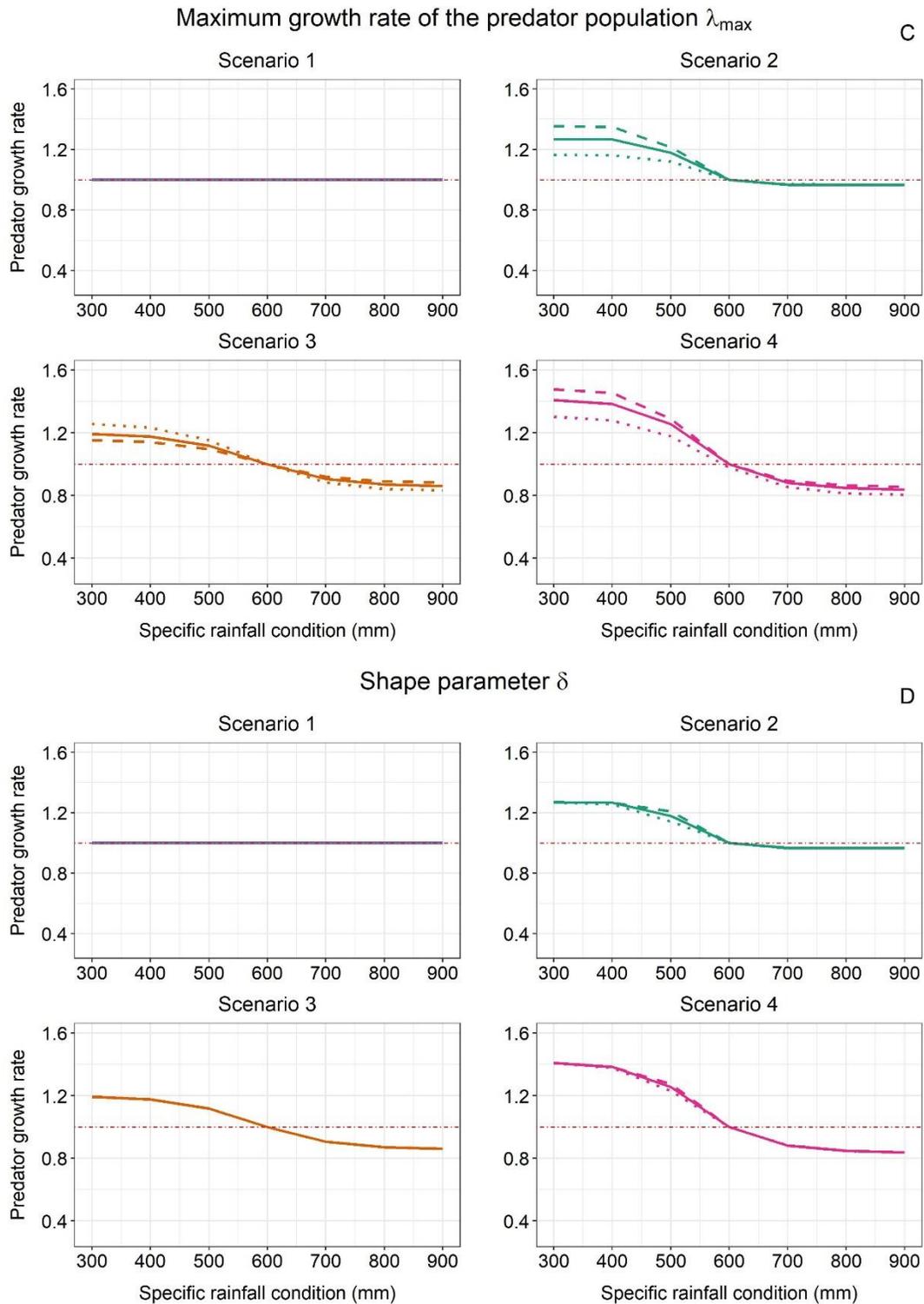


**Figure S2:** (A) Immediate response of predator populations to a specific rainfall condition. Relationship between the growth rate of predator populations and a specific annual rainfall in a system characterized by a long-term mean annual rainfall of 600 mm. (B) Long-term response of predator populations to changes in mean annual rainfall. Relationship between the size of predator populations and long-term mean annual rainfall. Light-coloured envelopes include minimum and maximum values of predator growth rates (A) and mean population size (B).

#### 1.4 Sensitivity analyses

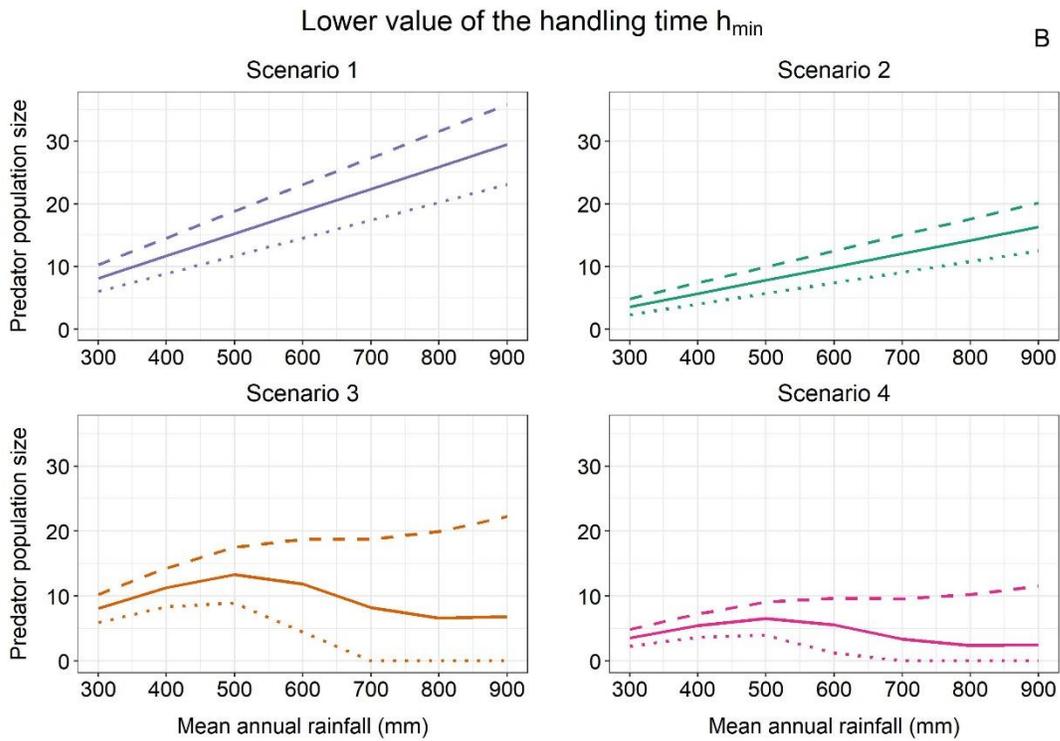
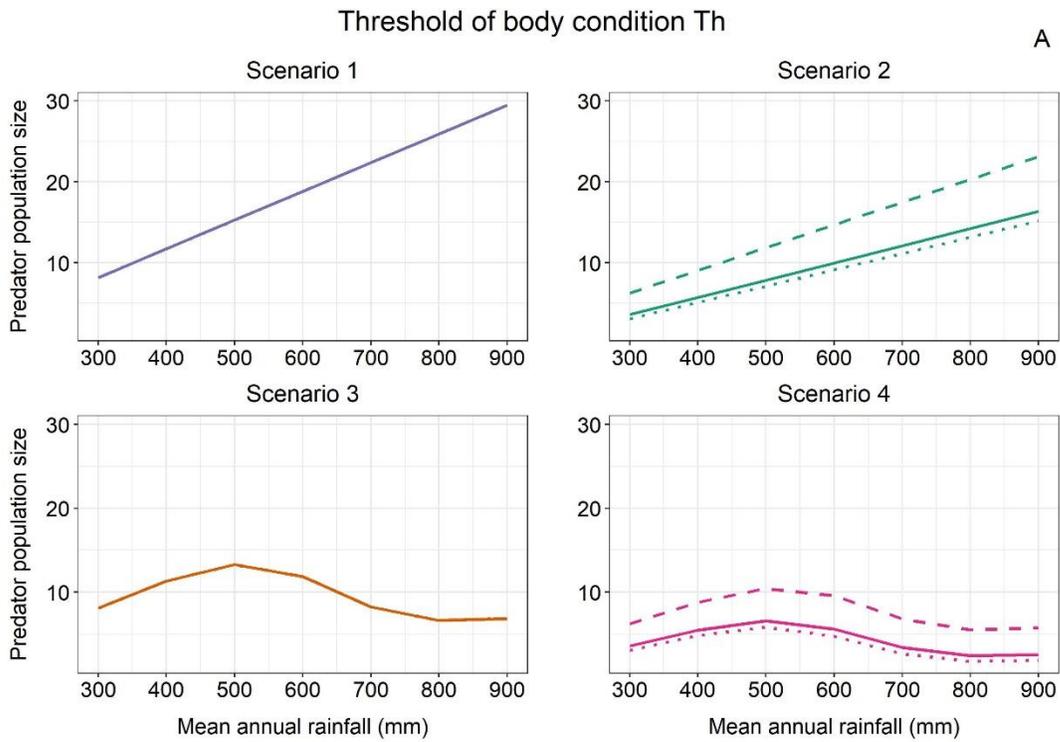
Sensitivity analyses of the immediate response of predator to 20% change in parameters when the habitat-driven hunting success decreases with rainfall.

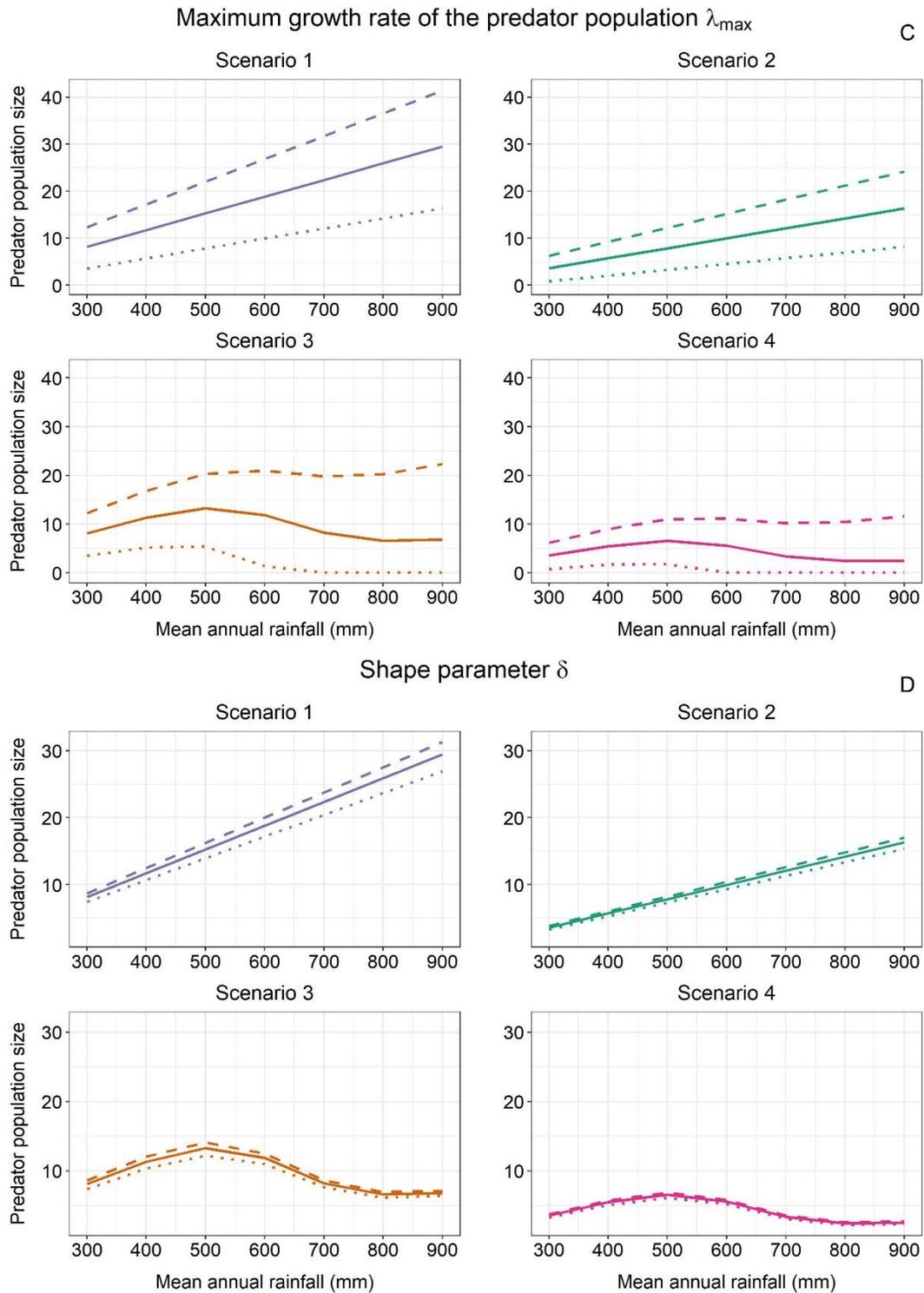




**Figure S3:** Influence of a specific rainfall condition on the growth rate of predators from the four scenarios for three values (default: solid line, + 20%: dashed line, -20%: dotted line) of tested parameters: (A)  $Th$ , (B)  $h_{min}$ , (C)  $\lambda_{\max}$ , (D)  $\delta$ , when the habitat-driven hunting success decreases with rainfall. All other parameters are set to default values. Red dotted lines correspond to a predator growth rate equal to 1.

Sensitivity analyses of the long-term response of predators to 20% change in parameters when the habitat-driven hunting success decreases with rainfall.





**Figure S4:** Influence of long-term mean annual rainfall on the size of predator populations from the four scenarios for three values (default: solid line, +20%: dashed line, -20%: dotted line) of tested parameters: (A)  $Th$ , (B)  $h_{\min}$ , (C)  $\lambda_{\max}$ , (D)  $\delta$ , when the habitat-driven hunting success decreases with rainfall. All other parameters are set to default values.

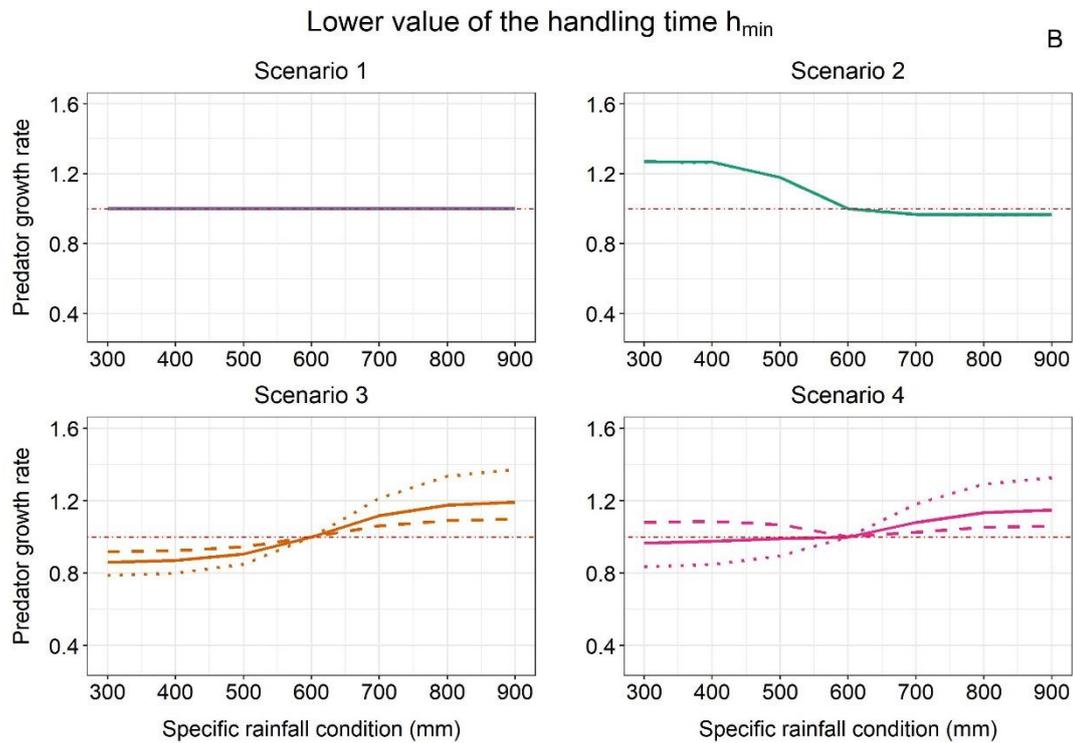
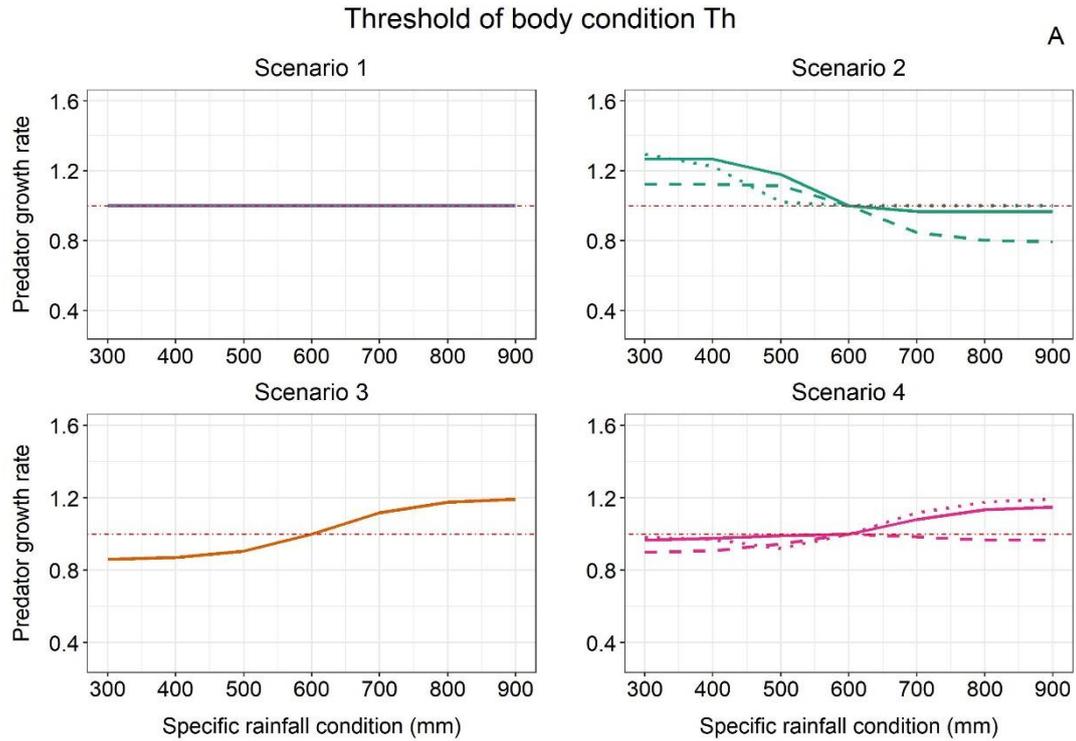
## 2 Appendix B: Sensitivity analyses

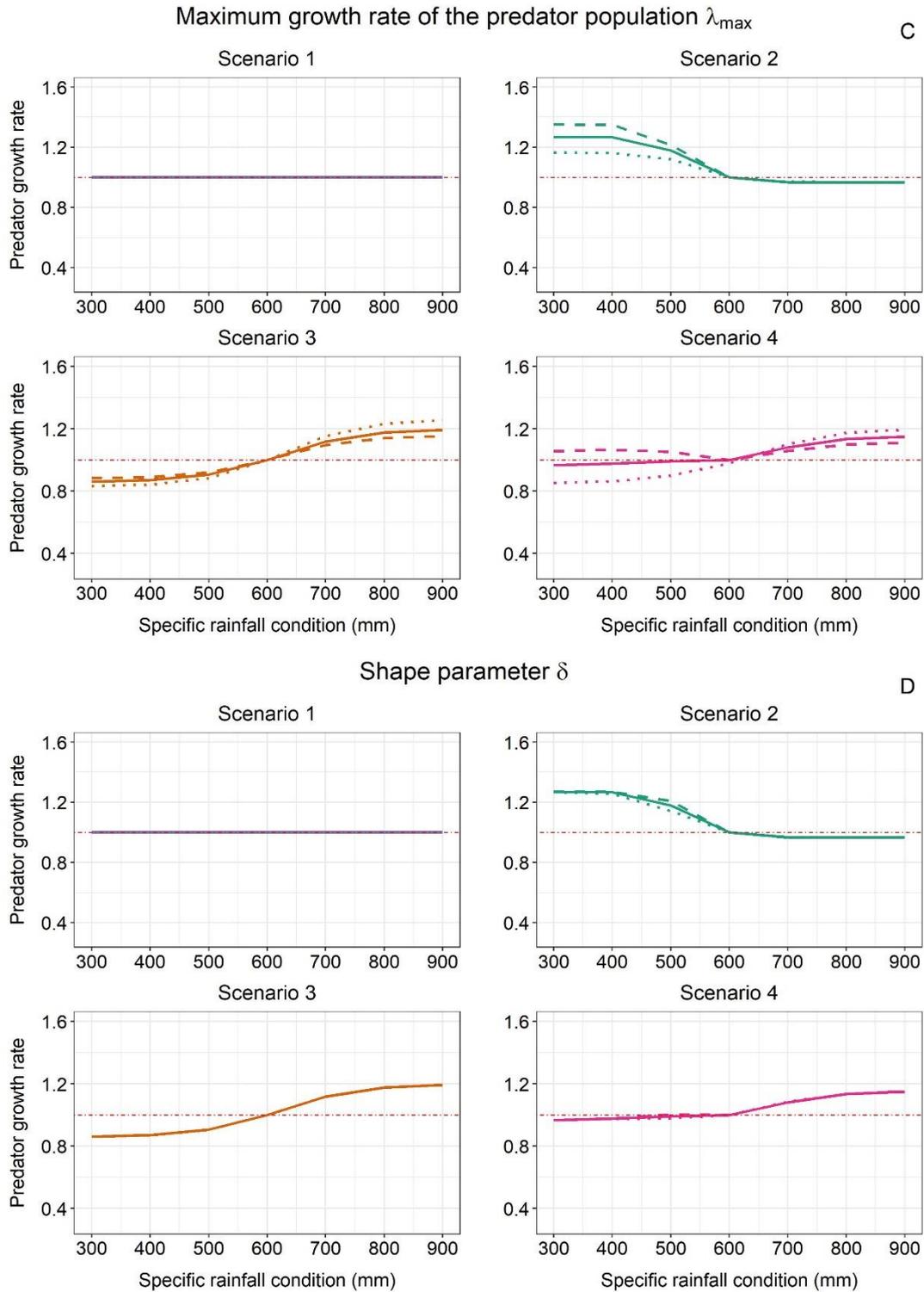
### 2.1 Results of sensitivity analyses

Sensitivity analyses showed that the results observed were robust to changes in the 4 study parameters as decreasing or increasing parameter values by 20% mostly triggered quantitative rather than qualitative changes in the patterns compared to those displayed for default values (Figures S5 and S6). However, we can note that when we increase  $Th$  by 20% for scenario 4 (Figure S5A), the predator population growth rate remains below 1 for high values of rainfall contrary to our expectation. However, it remains greater than the growth rate observed for lower values of rainfall. Additionally, other particular cases arise when we increase  $\lambda_{max}$  and  $h_{min}$  by 20% for scenario 4 (Figures S5B and S5C), for small rainfall values. The explanation probably lies in the fact that  $\lambda_{max}$  and  $P_{rel}$ , which contains  $h_{min}$  in its denominator as shown by *eqn. 11*, are both included in *eqn. 10* but reached values too high for the effect of prey populations on predators to be still detectable in comparison to the rate of increase of predator population. This allowed the rate of increase to remain positive and predator populations to increase.

### 2.2 Figures

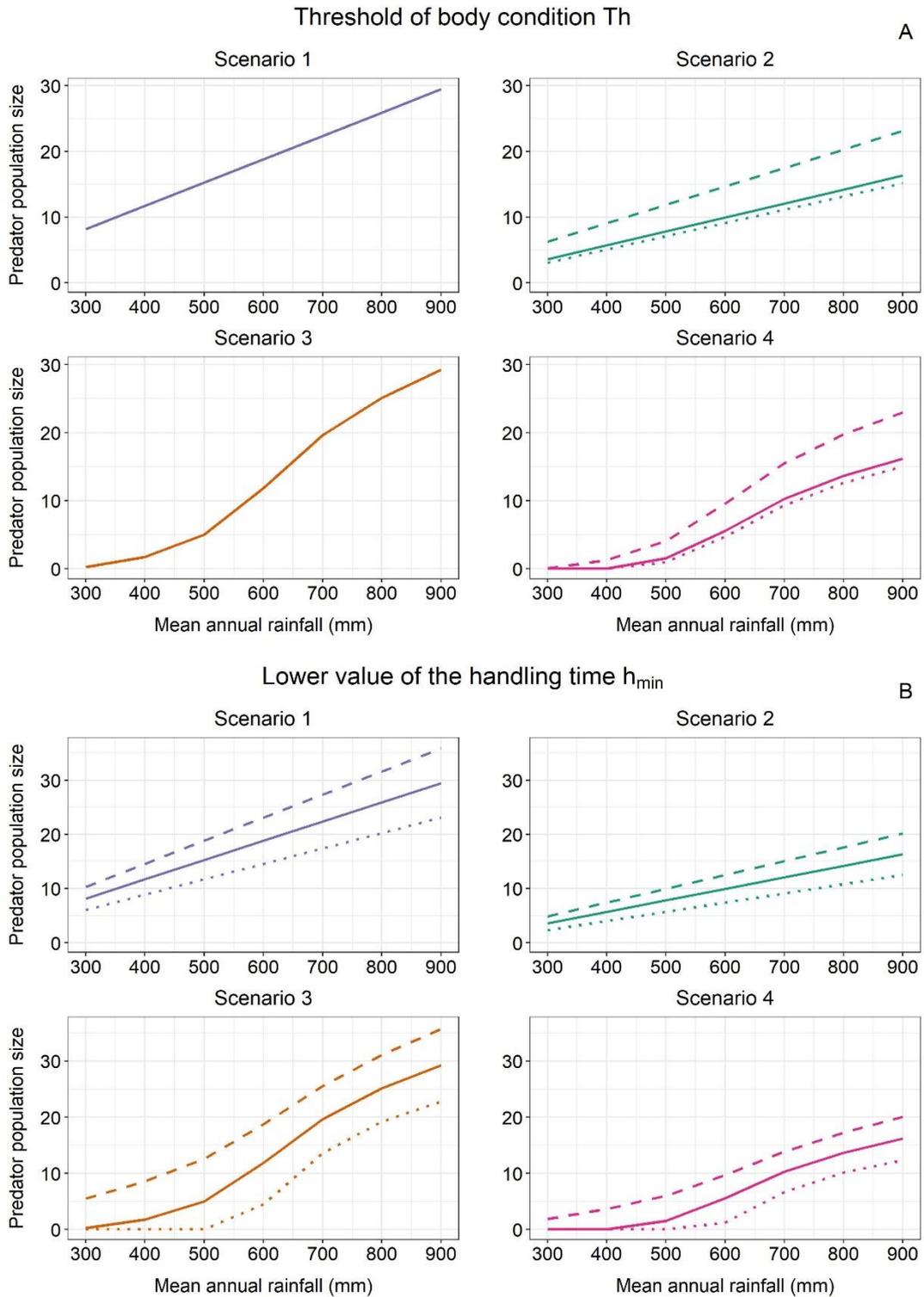
Sensitivity analyses of the immediate response of predators to 20% change in parameters.

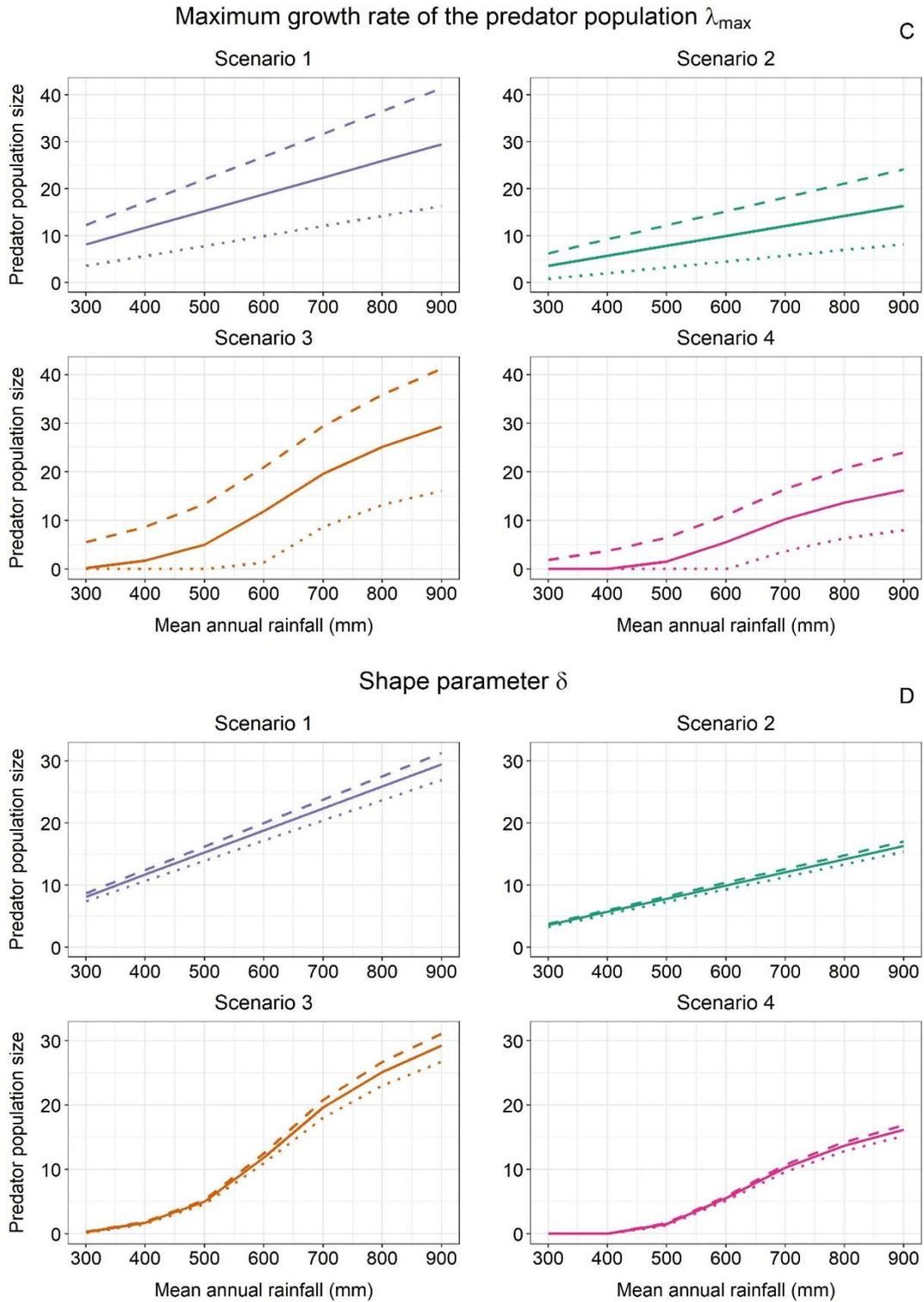




**Figure S5:** Influence of a specific rainfall condition on the growth rate of predators from the four scenarios for three values (default: solid line, + 20%: dashed line, -20%: dotted line) of tested parameters: (A)  $Th$ , (B)  $h_{min}$ , (C)  $\lambda_{max}$ , (D)  $\delta$ . All other parameters are set to default values. Red dotted lines correspond to a predator growth rate equal to 1.

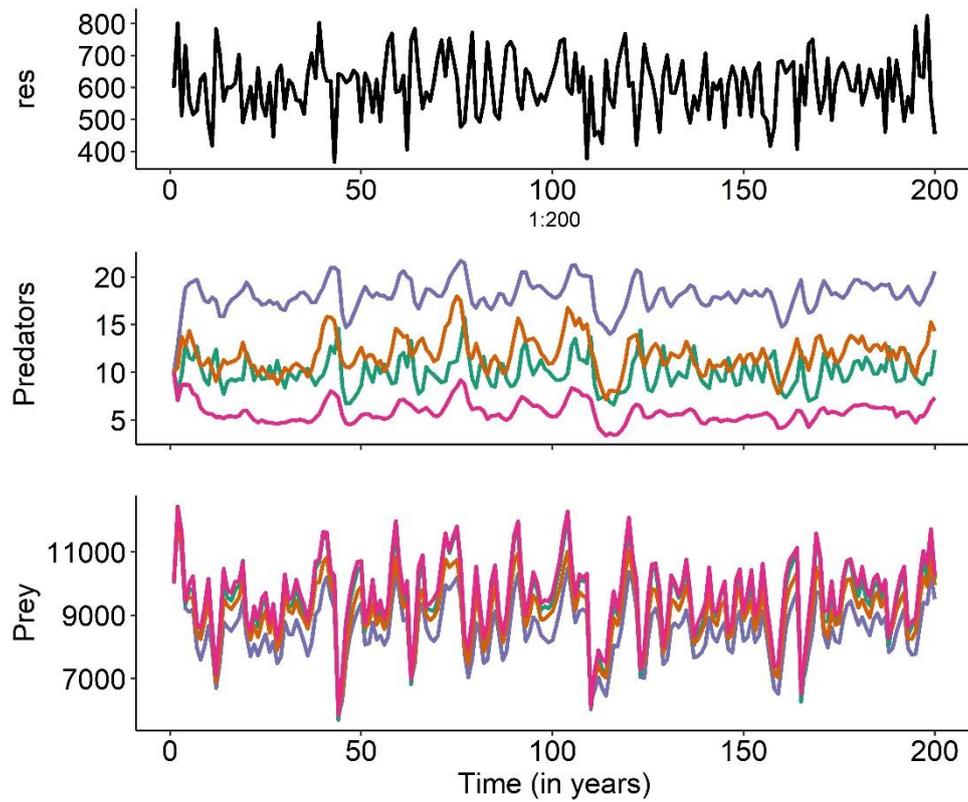
Sensitivity analyses of the long-term response of predators to 20% change in parameters.



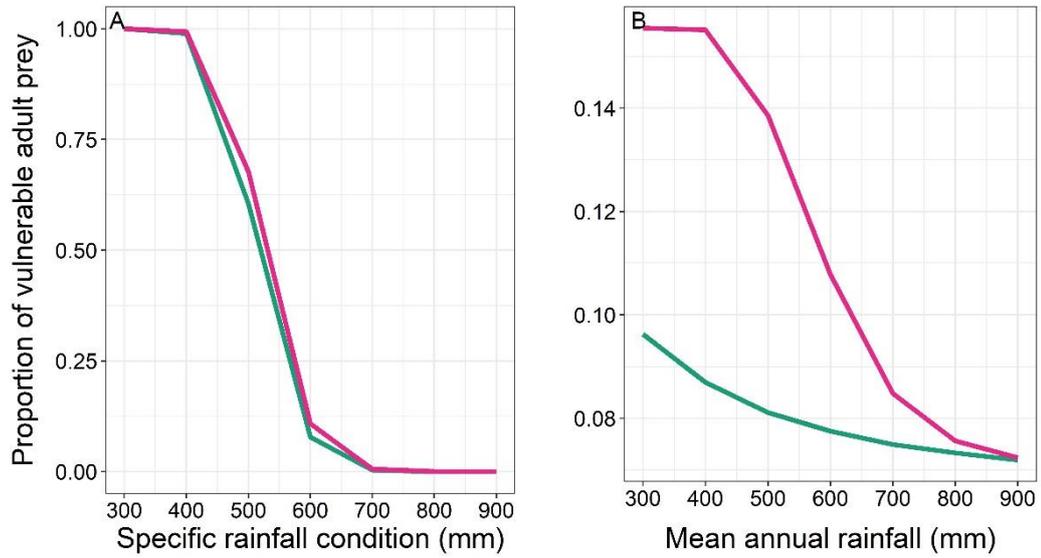


**Figure S6:** Influence of long-term mean annual rainfall on the size of predator populations from the four scenarios for three values (default: solid line, +20%: dashed line, -20%: dotted line) of tested parameters: (A)  $Th$ , (B)  $h_{\min}$ , (C)  $\lambda_{\max}$ , (D)  $\delta$ . All other parameters are set to default values.

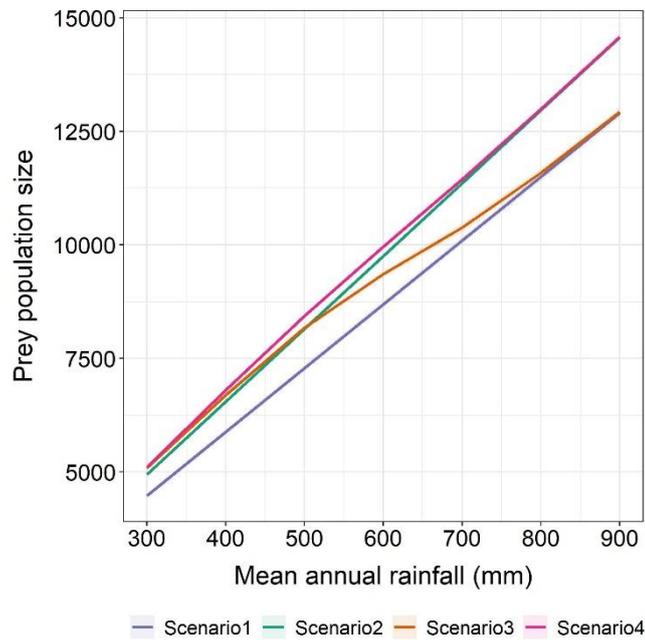
### 3 Appendix C: Supplementary figures



**Figure S7:** Model behaviour for one run. Rainfall (top), predator (middle) and prey (bottom) population sizes, for a 200-year run. Used parameter values are presented in Table 1.



**Figure S8:** (A) Influence of a specific rainfall condition on the proportion of adult prey vulnerable to predators in scenarios 2 (green) and 4 (pink). (B) Influence of mean annual rainfall on the proportion of adult prey vulnerable to predators in scenarios 2 (green) and 4 (pink). By definition the proportion of adult prey for predators from scenarios 1 and 3 is set to 1.



**Figure S9:** Influence of mean annual rainfall on the size of prey populations, for the four scenarios.