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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 α_j and β_j and α_a and β_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

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

133
 134

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

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:

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

$$140 \quad p_a(t) = P_a \times g_a(t) \quad (2b)$$

141
142 where P_j and P_a are parameters defining the maximum survival rates for juveniles and adults
143 respectively (see Table 1 for all default values of model parameters), and g_j and g_a are scaling functions
144 allowing to account for density- and resource-dependence in survival. These scaling functions
145 (bounded between 0 and 1) are those used by Wilmers et al. (2007b) and follow:

$$146 \quad g(N(t)) = \frac{\gamma^\delta}{\gamma^\delta + \frac{N(t)}{R}} \quad (3)$$

147
148 where R is the annual rainfall of the site. R varied from 300mm to 900mm by 100 mm increment,
149 which are coherent values for annual rainfall in African savannas (Sankaran et al., 2005; Chamailé-
150 Jammes & Fritz, 2009). We assumed that rainfall determined directly and linearly prey resource
151 availability (Rutherford, 1980). We thus considered rainfall as a proxy of the resource availability and
152 the ratio $N(t)/R$ as a number of individuals sharing the amount of available resource for year t . The
153 half-saturation parameter γ determined the per capita resource availability at which the maximum
154 survival rate was reduced by half. Finally, δ was a shape parameter setting the beginning and the
155 strength of the density-dependence (as in Wilmers et al., 2007b).

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

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

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

$$171 \quad P_f(p_{ai}(t)) = \frac{1}{1 + f_{low} \times e^{-f_{growth} \times p_{ai}(t)}} \quad (4)$$

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

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:

$$214 \quad H(R) = h_{min} + \frac{h_{max} - h_{min}}{1 + e^{B(R-V)}} \quad (5)$$

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

222 For the functional response, we assumed that the number of prey killed and consumed by one predator
 223 during a given year t followed a type II Beddington-DeAngelis functional response. This equation
 224 allows the integration of interference between predators when searching for and capturing prey and is
 225 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, μ a parameter defining the encounter rate between predators and their prey, h the parameter defining the handling time and τ 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 , λ_{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 λ_{max} values, which is a central
 330 parameter of the predator numerical response. Finally, we carried out a sensitivity analysis for the δ
 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>.

533 **11 Literature cited**

- 534 Abrams, P. A., and Ginzburg, L. R. (2000). The nature of predation: prey dependent, ratio dependent or
535 neither? *Trends Ecol. Evol.* 15, 337–341. doi:10.1016/S0169-5347(00)01908-X.
- 536 Atwood, T. C., Gese, E. M., and Kunkel, K. E. (2007). Comparative patterns of predation by cougars and
537 recolonizing wolves in Montana’s Madison Range. *J. Wildl. Manage.* 71, 1098–1106.
538 doi:10.2193/2006-102.
- 539 Bastille-Rousseau, G., Schaefer, J. A., Peers, M. J. L., Ellington, E. H., Mumma, M. A., Rayl, N. D., et
540 al. (2018). Climate change can alter predator-prey dynamics and population viability of prey.
541 *Oecologia* 186, 141–150. doi:10.1007/s00442-017-4017-y.
- 542 Bayliss, P., and Choquenot, D. (2002). The numerical response: rate of increase and food limitation in
543 herbivores and predators. *Philos. Trans. R. Soc. B Biol. Sci.* 357, 1233–1248.
544 doi:10.1098/rstb.2002.1124.
- 545 Bender, L. C., Lomas, L. A., and Browning, J. (2007). Condition, survival, and cause-specific mortality
546 of adult female Mule deer in North-Central New Mexico. *J. Wildl. Manage.* 71, 1118–1124.
547 doi:10.2193/2006-226.
- 548 Bonenfant, C., Gaillard, J. M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., et al. (2009).
549 “Empirical Evidence of Density-Dependence in Populations of Large Herbivores,” in *Advances*
550 *in Ecological Research*, 313–357. doi:10.1016/S0065-2504(09)00405-X.
- 551 Bourgarel, M., Fritz, H., Gaillard, J. M., De Garine-Wichatitsky, M., and Maudet, F. (2002). Effects of
552 annual rainfall and habitat types on the body mass of impala (*Aepyceros melampus*) in the Zambezi
553 Valley, Zimbabwe. *Afr. J. Ecol.* 40, 186–193. doi:10.1046/j.1365-2028.2002.00377.x.
- 554 Candolin, U., and Wong, B. B. M. (2012). *Behavioural Responses to a Changing World*. First. Oxford:
555 Oxford University Press.
- 556 Carbone, C., and Gittleman, J. L. (2002). A Common Rule for the Scaling of Carnivore Density. *Science*
557 . 295, 2273–2276. doi:10.1126/science.1067994.
- 558 Caswell, H. (2001). *Matrix population models: construction, analysis, and interpretation*. Second edi.
559 Sunderland, Massachusetts: Sinauer Associates.
- 560 Chamaillé-Jammes, S., and Fritz, H. (2009). Precipitation-NDVI relationships in eastern and southern
561 African savannas vary along a precipitation gradient. *Int. J. Remote Sens.* 30, 3409–3422. doi:
562 10.1080/01431160802562206.
- 563 Cook, J. G., Johnson, B. K., Cook, R. C., Riggs, R. A., Delcurto, T., Bryant, L. D., et al. (2004). Effects
564 of Summer-Autumn Nutrition and Parturition Date on Reproduction and Survival of Elk. *Wildl.*
565 *Monogr.* 155, 1–61. doi:10.2193/0084-0173(2004)155[1:EOSNAP]2.0.CO;2.
- 566 Cooper, S. M. (1990). The hunting behaviour of spotted hyaenas (*Crocuta crocuta*) in a region containing
567 both sedentary and migratory populations of herbivores. *Afr. J. Ecol.* 28, 131–141.
568 doi:10.1111/j.1365-2028.1990.tb01145.x.
- 569 East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. *Afr. J. Ecol.*
570 22, 245–270. doi:10.1111/j.1365-2028.1984.tb00700.x.
- 571 Eberhardt, L. L. (1977). Optimal policies for conservation of large mammals, with special reference to
572 marine ecosystems. *Environ. Conserv.* 4, 205–212. doi:10.1017/S0376892900025819.
- 573 Elbroch, L. M., Lendrum, P. E., Newby, J., Quigley, H., and Craighead, D. (2013). Seasonal foraging
574 ecology of non-migratory cougars in a system with migrating prey. *PLoS One* 8, 1–14.
575 doi:10.1371/journal.pone.0083375.
- 576 Elliott, J. P., Cowan, I. M., and Holling, C. S. (1977). Prey capture by the African lion. *Can. J. Zool.* 55,
577 1811–1828. doi:10.1139/z77-235.
- 578 Estes, R. (1991). *The behavior guide to African mammals: including hoofed mammals, carnivores,*
579 *primates*. University of California Press.
- 580 Fitzgibbon, C. D., and Fanshawe, J. H. (1989). The condition and age of Thomson’s gazelles killed by
581 cheetas and wild dogs. *J. Zool.* 218, 99–107. doi:10.1111/j.1469-7998.1989.tb02528.x.

- 582 Foley, C., Pettorelli, N., and Foley, L. (2008). Severe drought and calf survival in elephants. *Biol. Lett.*
583 4, 541–544. doi:10.1098/rsbl.2008.0370.
- 584 Forchhammer, M. C., Stenseth, N. C., Post, E., and Langvatn, R. (1998). Population dynamics of
585 Norwegian red deer: density-dependence and climatic variation. *Proc. R. Soc. B Biol. Sci.* 265,
586 341–350. doi:10.1098/rspb.1998.0301.
- 587 Funston, P. J., Mills, M. G. L., and Biggs, H. C. (2001). Factors affecting the hunting success of male and
588 female lions in the Kruger National Park. *J. Zool.* 253, 419–431.
589 doi:10.1017/S0952836901000395.
- 590 Grange, S., Barnier, F., Duncan, P., Gaillard, J. M., Valeix, M., Ncube, H., et al. (2015). Demography of
591 plains zebras (*Equus quagga*) under heavy predation. *Popul. Ecol.* 57, 201–214.
592 doi:10.1007/s10144-014-0469-7.
- 593 Holling, C. S. (1959). The Components of Predation as Revealed by a Study of Small-Mammal Predation
594 of the European Pine Sawfly. *Can. Entomol.* 91, 293–320. doi:10.4039/Ent91293-5.
- 595 Holt, R. D. (2008). Theoretical perspectives on resource pulses. *Ecology* 89, 671–681. doi:10.1890/07-
596 0348.1.
- 597 Hopcraft, Grant, J. C., Sinclair, A. R. E., and Packer, C. (2005). Planning for success: Serengeti lions seek
598 prey accessibility rather than abundance. *J. Anim. Ecol.* 74, 559–566. doi:10.1111/j.1365-
599 2656.2005.00955.x.
- 600 Husseman, J. S., Murray, D. L., Power, G., Mack, C., Wenger, C. R., and Quigley, H. (2003). Assessing
601 differential prey selection patterns between two sympatric large carnivores. *Oikos* 101, 591–601.
602 doi:10.1034/j.1600-0706.2003.12230.x.
- 603 Inouye, D. W., Barr, B., Armitage, K. B., and Inouye, B. D. (2000). Climate change is affecting altitudinal
604 migrants and hibernating species. *Proc. Natl. Acad. Sci.* 97, 1630–1633.
605 doi:10.1073/pnas.97.4.1630.
- 606 IPCC. (2014a). Summary for Policymakers. Geneva, Switzerland: IPCC
607 doi:10.1017/CBO9781107415324.
- 608 IPCC. (2014b). “Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects.
609 Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel
610 on Climate Change,” in (Cambridge: Cambridge University Press), 688.
- 611 Lone, K., Loe, L. E., Gobakken, T., Linnell, J. D. C., Odden, J., Remmen, J., et al. (2014). Living and
612 dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of
613 predation risk imposed by lynx and humans. *Oikos* 123, 641–651. doi:10.1111/j.1600-
614 0706.2013.00938.x.
- 615 Loveridge, A. J., Hunt, J. E., Murindagomo, F., and Macdonald, D. W. (2006). Influence of drought on
616 predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded
617 savannah. *J. Zool.* 270, 523–530. doi:10.1111/j.1469-7998.2006.00181.x.
- 618 Maclean, I. M. D., and Wilson, R. J. (2011). Recent ecological responses to climate change support
619 predictions of high extinction risk. *Proc. Natl. Acad. Sci.* 108, 12337–12342.
620 doi:10.1073/pnas.1017352108.
- 621 Martay, B., Brewer, M. J., Elston, D. A., Bell, J. R., Harrington, R., Brereton, T. M., et al. (2017). Impacts
622 of climate change on national biodiversity population trends. *Ecography (Cop.)*. 40, 1139–1151.
623 doi:10.1111/ecog.02411.
- 624 Mduma, S. A. R., Sinclair, A. R. E., and Hilborn, R. (1999). Food regulates the Serengeti wildebeest: A
625 40-year record. *J. Anim. Ecol.* 68, 1101–1122. doi:10.1046/j.1365-2656.1999.00352.x.
- 626 Mech, D. L., Smith, D. W., Murphy, K. M., and MacNulty, D. R. (2001). Winter severity and wolf
627 predation on a formerly wolf-free elk herd. *J. Wildl. Manage.* 65, 998–1003.
628 doi:10.2307/3803048.
- 629 Mech, L. D., Frenzel, D. J., and Karns, P., D. (1971). “The effect of snow conditions on the vulnerability
630 of white-tailed deer to wolf predation,” in *Ecological studies of the timber wolf in northeastern*

- 631 Minnesota, eds. L. D. Mech and D. J. Frenzel (North Central Forest Experimental Station, St.
632 Paul, Minnesota: USDA Forest Service Research Paper NC-52), 51–59.
- 633 Mech, L. D., Smith, D. W. and MacNulty, D. R. (2015). “Introduction The Wolf as a Killing Machine,”
634 in *Wolves on the hunt the behavior of wolves hunting wild prey*, eds. D. R. Mech, L. D., Smith,
635 D. W. and MacNulty (Chicago: The University of Chicago Press), 1–9.
- 636 Melis, C., Jędrzejewska, B., Apollonio, M., Bartoń, K. A., Jędrzejewski, W., Linnell, J. D. C., et al.
637 (2009). Predation has a greater impact in less productive environments: Variation in roe deer,
638 *Capreolus capreolus*, population density across Europe. *Glob. Ecol. Biogeogr.* 18, 724–734.
639 doi:10.1111/j.1466-8238.2009.00480.x.
- 640 Metz, M. C., Smith, D. W., Vucetich, J. A., Stahler, D. R., and Peterson, R. O. (2012). Seasonal patterns
641 of predation for gray wolves in the multi-prey system of Yellowstone National Park. *J. Anim.
642 Ecol.* 81, 553–563. doi:10.1111/j.1365-2656.2011.01945.x.
- 643 Mills, M. G. L. (1995). Notes on wild dog *Lycaon pictus* and lion *Panthera leo* population trends during
644 a drought in the Kruger National Park. *Koedoe* 38, 95–99. doi:10.4102/koedoe.v38i1.309.
- 645 Moyes, K., Nussey, D. H., Clements, M. N., Guinness, F. E., Morris, A., Morris, S., et al. (2011).
646 Advancing breeding phenology in response to environmental change in a wild red deer population.
647 *Glob. Chang. Biol.* 17, 2455–2469. doi:10.1111/j.1365-2486.2010.02382.x.
- 648 Mysterud, A., Stenseth, N. C., Yoccoz, N. G., Langvatn, R., and Steinheim, G. (2001). Nonlinear effects
649 of large-scale climatic variability on wild and domestic herbivores. *Nature* 410, 1096–1099.
650 doi:10.1038/35074099.
- 651 Ogutu, J. O., Piepho, H.-P., Dublin, H. T., Bhola, N., and Reid, R. S. (2008). Rainfall influences on
652 ungulate population abundance in the Mara-Serengeti ecosystem. *J. Anim. Ecol.* 77, 814–829.
653 doi:10.1111/j.1365-2656.2008.01392.x.
- 654 Owen-smith, N. (1990). Demography of a large herbivore, the greater kudu *tragelaphus strepsiceros*, in
655 relation to rainfall. *J. Anim. Ecol.* 59, 893–829. doi:10.2307/5021.
- 656 Owen-smith, N. (2008). Changing vulnerability to predation related to season and sex in an African
657 ungulate assemblage. *Oikos* 117, 602–610. doi: 10.1111/j.0030-1299.2008.16309.x.
- 658 Owen-Smith, N. (2002). Adaptive herbivore ecology from resources to populations in variable
659 environments. Cambridge: Cambridge University Press doi:10.1017/CBO9780511525605.
- 660 Owen-Smith, N., and Mills, M. G. L. (2008a). Predator-prey size relationships in an African large-
661 mammal food web. *J. Anim. Ecol.* 77, 173–183. doi:10.1111/j.1365-2656.2007.01314.x.
- 662 Owen-Smith, N., and Mills, M. G. L. (2008b). Shifting prey selection generates contrasting herbivore
663 dynamics within a large-mammal predator-prey web. *Ecology* 89, 1120–1133. doi:10.1890/07-
664 0970.1.
- 665 Pacifici, M., Visconti, P., Butchart, S. H. M., Watson, J. E. M., Cassola, F. M., and Rondinini, C. (2017).
666 Species’ traits influenced their response to recent climate change. *Nat. Clim. Chang.* 7, 205–208.
667 doi:10.1038/nclimate3223.
- 668 Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., et al. (1999).
669 Poleward shifts in geographical ranges of butterfly species associated with regional warming.
670 *Nature* 399, 579–583. doi:10.1038/21181.
- 671 Pole, A., Gordon, I. J., Gorman, M. L., and MacAskill, M. (2004). Prey selection by African wild dogs
672 (*Lycaon pictus*) in southern Zimbabwe. *J. Zool.* 262, 207–215. doi:10.1017/S0952836903004576.
- 673 Post, E., Peterson, R. O., Stenseth, N. C., and McLaren, B. E. (1999). Ecosystem consequences of wolf
674 behavioural response to climate. *Nature* 401, 905–907. doi:10.1038/44814.
- 675 Post, E., and Stenseth, N. C. (1999). Climatic Variability, Plant Phenology, and Northern ungulates.
676 *Ecology* 80, 1322–1339. doi: 10.1890/0012-9658(1999)080[1322:CVPPAN]2.0.CO;2.
- 677 Radloff, F. G. T., and Du Toit, J. T. (2004). Large predators and their prey in a southern African savanna:
678 a predator’s size determines its prey size range. *J. Anim. Ecol.* 73, 410–423. doi:10.1111/j.0021-
679 8790.2004.00817.x.

- 680 R Core Team (2020). R: A language and environment for statistical computing. R Foundation for
 681 Statistical Computing, Vienna, Austria.
- 682 Rutherford, M. C. (1980). Annual plant production precipitation relations in Arid and Semi-arid regions.
 683 S. Afr. J. Sci. 76, 53–57.
- 684 Saether, B.-E. (1997). Environmental stochasticity and population dynamics of large herbivores: a search
 685 for mechanisms. Trends Ecol. Evol. 12, 143–149. doi:10.1016/S0169-5347(96)10068-9.
- 686 Saether, B.-E., and Gravem, A. J. (1988). Annual variation in winter body condition of Norwegian moose
 687 calves. J. Wildl. Manage. 52, 333–336. doi:10.2307/3801245.
- 688 Salnicki, J., Teichmann, M., Wilson, V., and J. and Murindagomo, F. (2001). Spotted hyaenas *Crocuta*
 689 *crocuta* prey on new-born elephant calves in Hwange National Park, Zimbabwe. Koedoe 44, 79–
 690 83. doi: 10.4102/koedoe.v44i2.177.
- 691 Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., et al. (2005).
 692 Determinants of woody cover in African savannas. Nature 438, 846–849.
 693 doi:10.1038/nature04070.
- 694 Schaller, G. B. (1972). The Serengeti Lion A study of Predator-Prey Relations. First. Chicago: The
 695 University of Chicago Press.
- 696 Stenseth, N. C., Shabbar, A., Chan, K., Boutin, S., Rueness, E. K., Ehrich, D., et al. (2004). Snow
 697 conditions may create an invisible barrier for lynx. Proc. Natl. Acad. Sci. 101, 10632–10634.
 698 doi:10.1073/pnas.0308674101.
- 699 Visser, M. E., Holleman, L. J. M., and Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to
 700 climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147,
 701 164–172. doi:10.1007/s00442-005-0299-6.
- 702 Wilmers, C. C., Post, E., and Hastings, A. (2007a). The anatomy of predator-prey dynamics in a changing
 703 climate. J. Anim. Ecol. 76, 1037–1044. doi:10.1111/j.1365-2656.2007.01289.x.
- 704 Wilmers, C. C., Post, E., and Hastings, A. (2007b). A perfect storm: The combined effects on population
 705 fluctuations of autocorrelated environmental noise, age structure, and density dependence. Am.
 706 Nat. 169, 673–683. doi:10.1086/513484.
- 707 Yang, L. H., Bastow, J. L., Spence, K. O., and Wright, A. N. (2008). What can we learn from resource
 708 pulses? Ecology 89, 621–634. doi:10.1890/07-0175.1.
- 709

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
α_a	First shape parameter of the Beta distribution from which are drawn adult prey individual survival rate	Calculated at each time step
α_j	First shape parameter for Beta distribution from which are drawn juvenile prey individual survival rate	Calculated at each time step
β_a	Second shape parameter for Beta distribution from which are drawn adult prey individual survival rate	Calculated at each time step
β_j	Second shape parameter for Beta distribution from which are drawn juvenile prey individual survival rate	Calculated at each time step
P_a	Maximum adult prey survival probability	0.95
P_j	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	$p_j = P_j \times g_j$
γ_{Pa}	Adult half-saturation, point at which adult prey survival is lowered by half	30
γ_{Pj}	Juvenile half-saturation, point at which juvenile prey survival is lowered by half	20
δ_{Pa}	Shape parameter, defines the onset of density-dependence for adult prey	2
δ_{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
μ	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
τ	Interference between predators in the predator functional response	0.3
λ_{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.

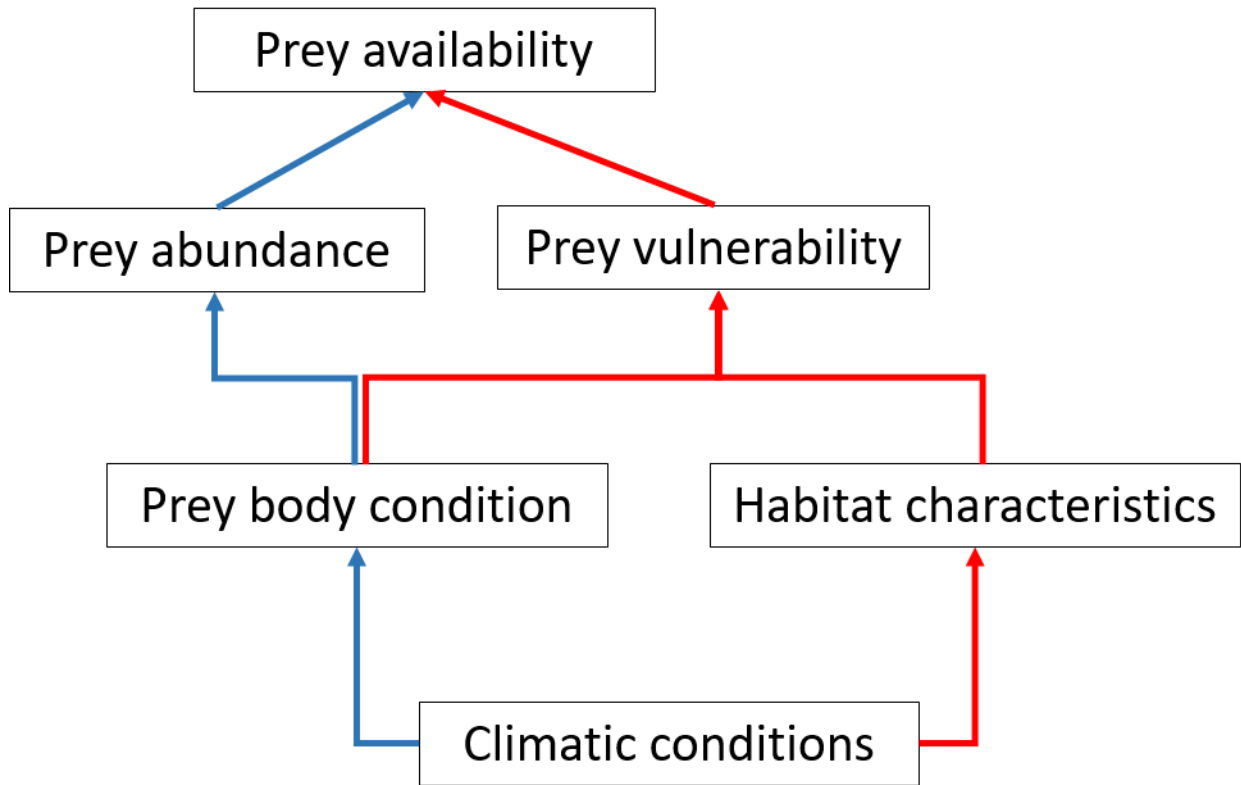
717 **13 Figure captions**

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).

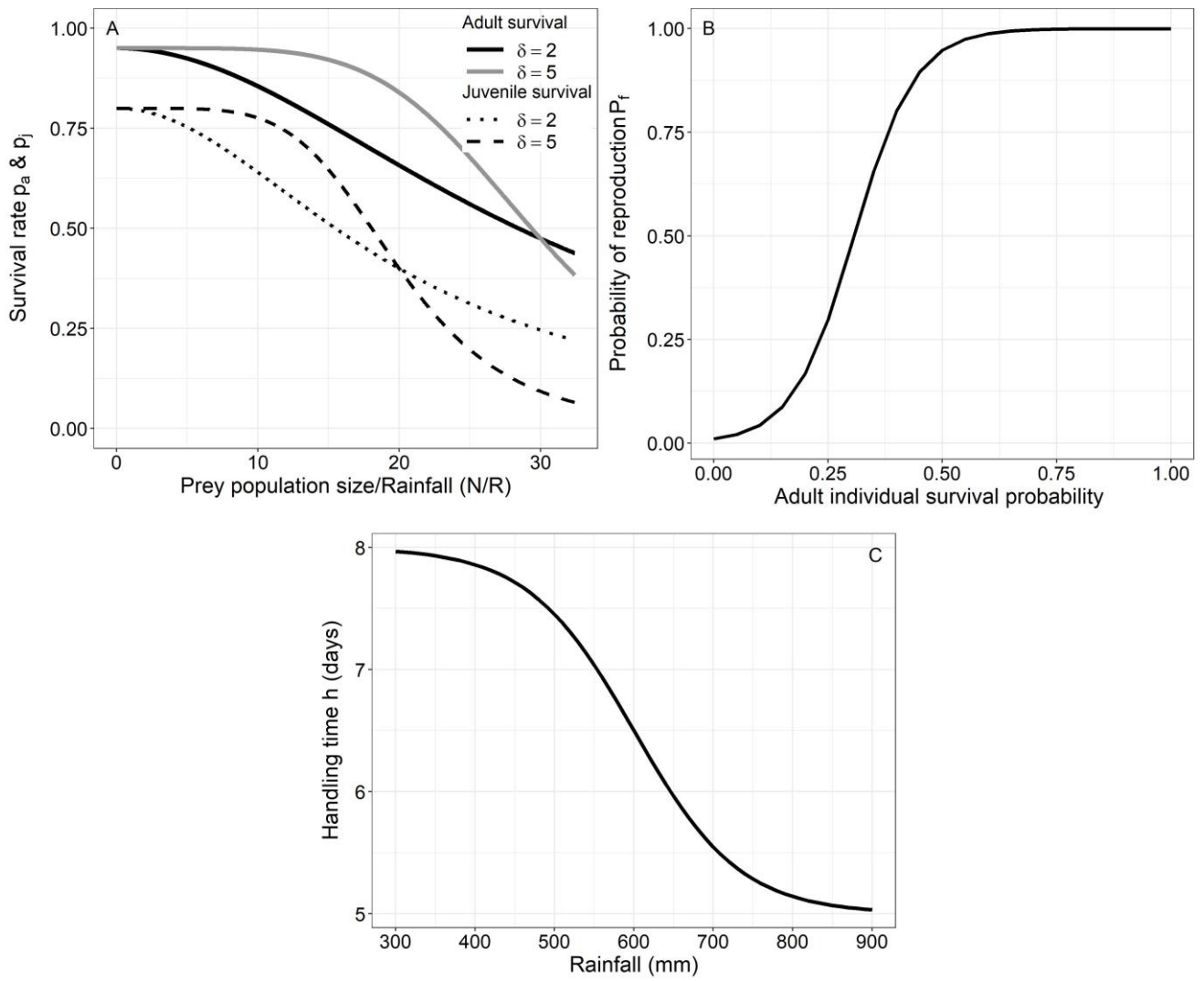
721
722 **Figure 2:** Summary of the functional relationships underlying the model. (A) Effect of increased
723 number of individuals per resource unit (approximated by rainfall) on mean juvenile and adult prey
724 survival rates adapted from Wilmers et al. (2007b). Mean adult and juvenile prey survival rates have
725 been represented for two values of δ 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.

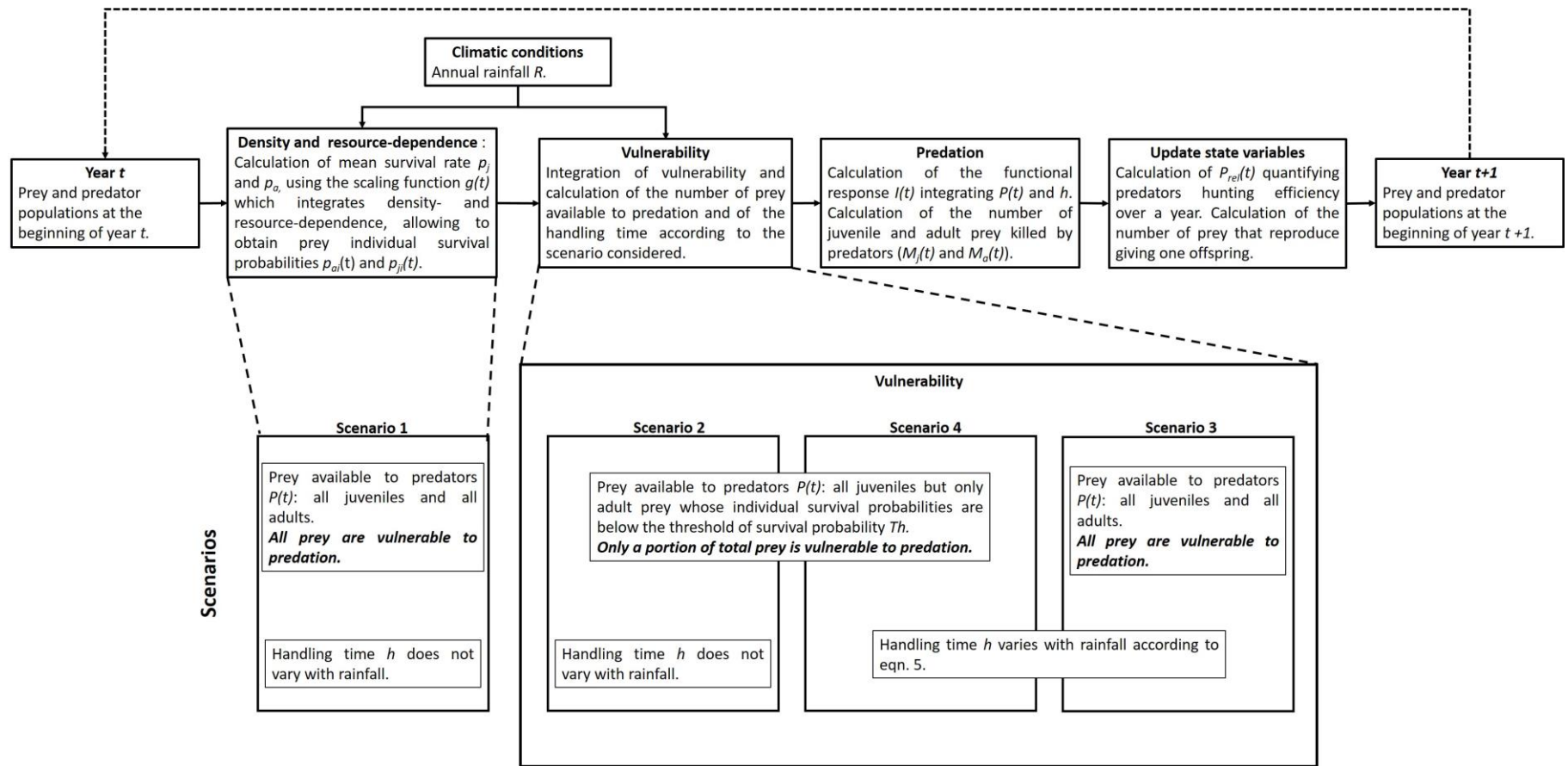
735
736 **Figure 4:** (A) Immediate response of predator populations to a specific rainfall condition. Relationship
737 between the growth rate of predator populations and a specific annual rainfall in a system characterized
738 by a long-term mean annual rainfall of 600 mm. (B) Long-term response of 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**

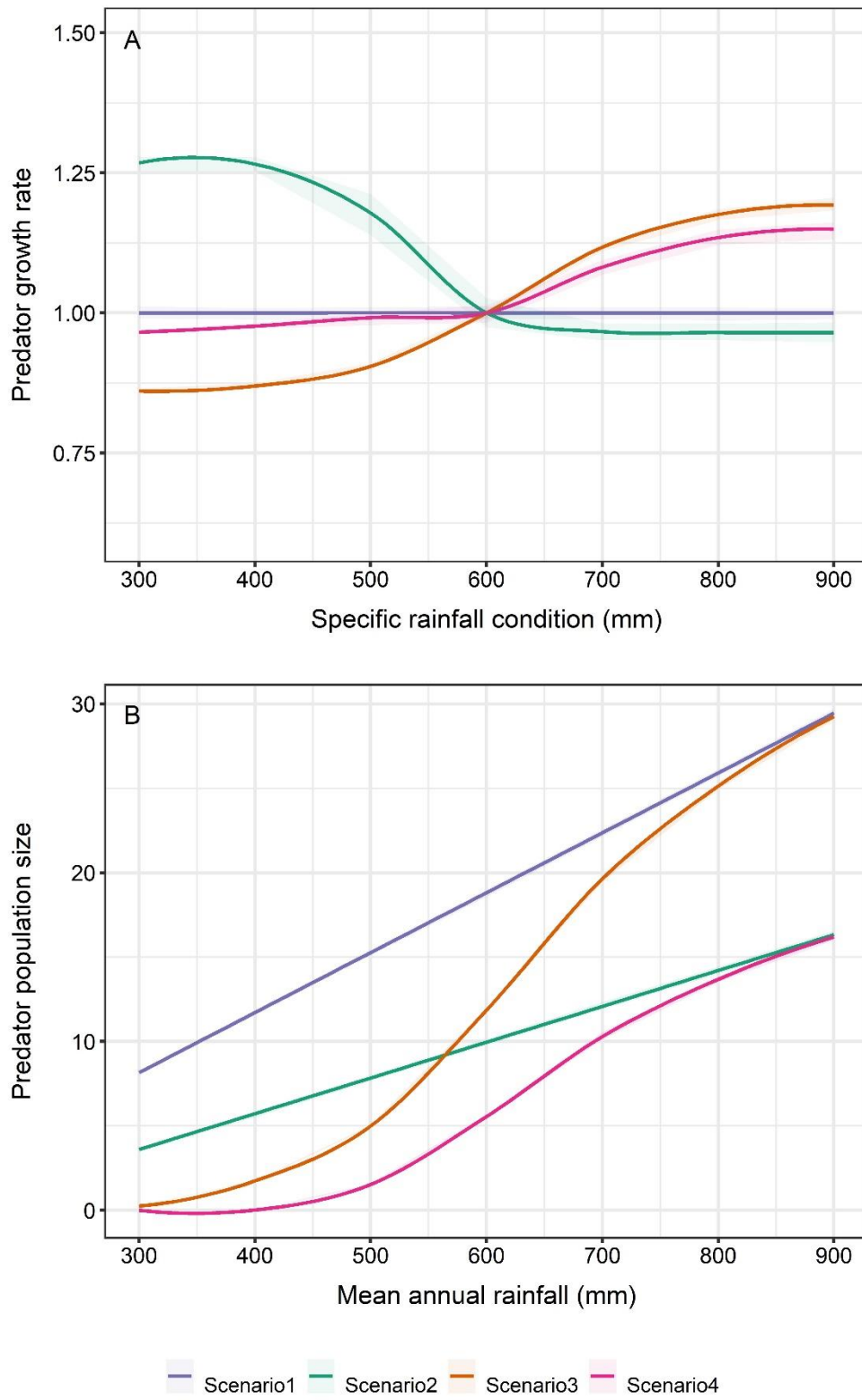


746
747 **Figure 2**



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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:

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

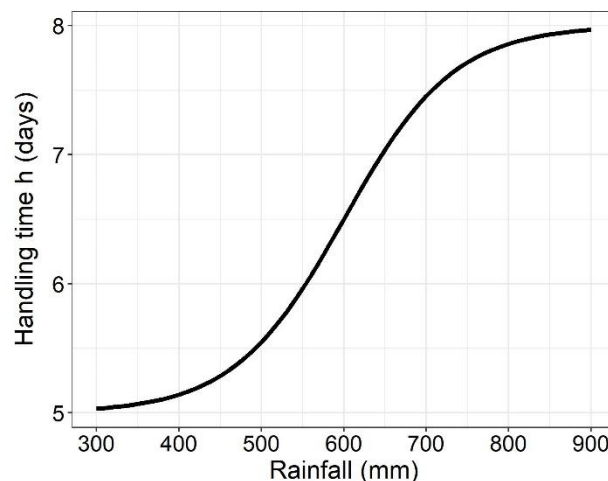


Figure S1: Functional relationship between rainfall and predator handling time h as defined by (1). The hunting success varies inversely with the handling time. For parameters see Table 1 of the main manuscript.

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).

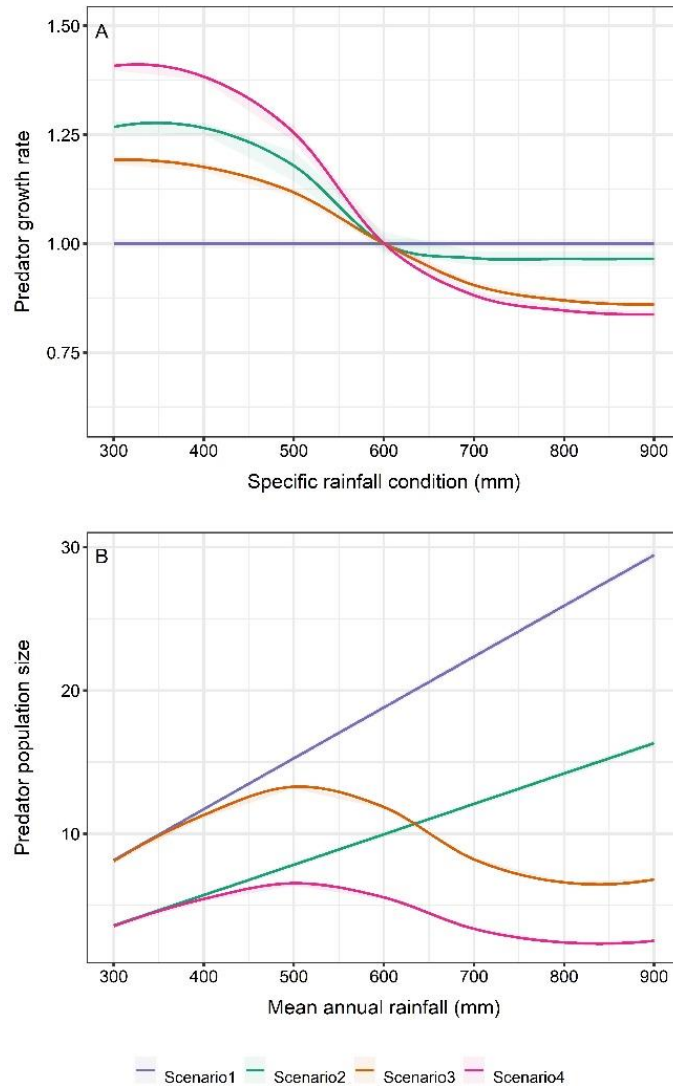
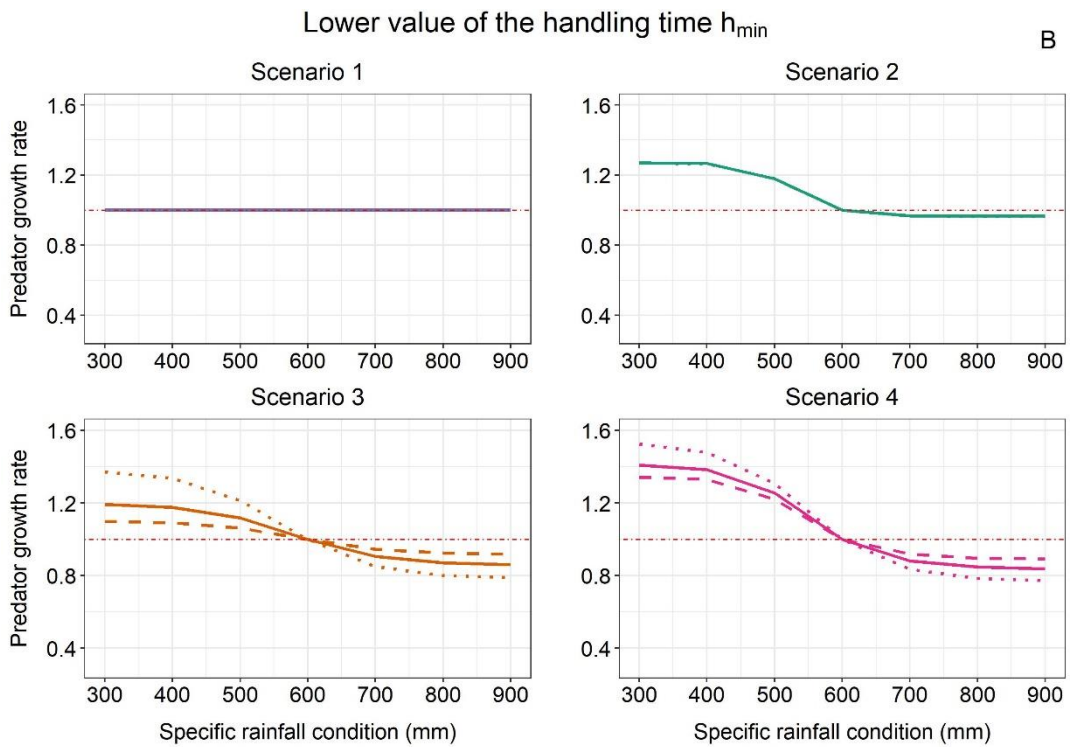
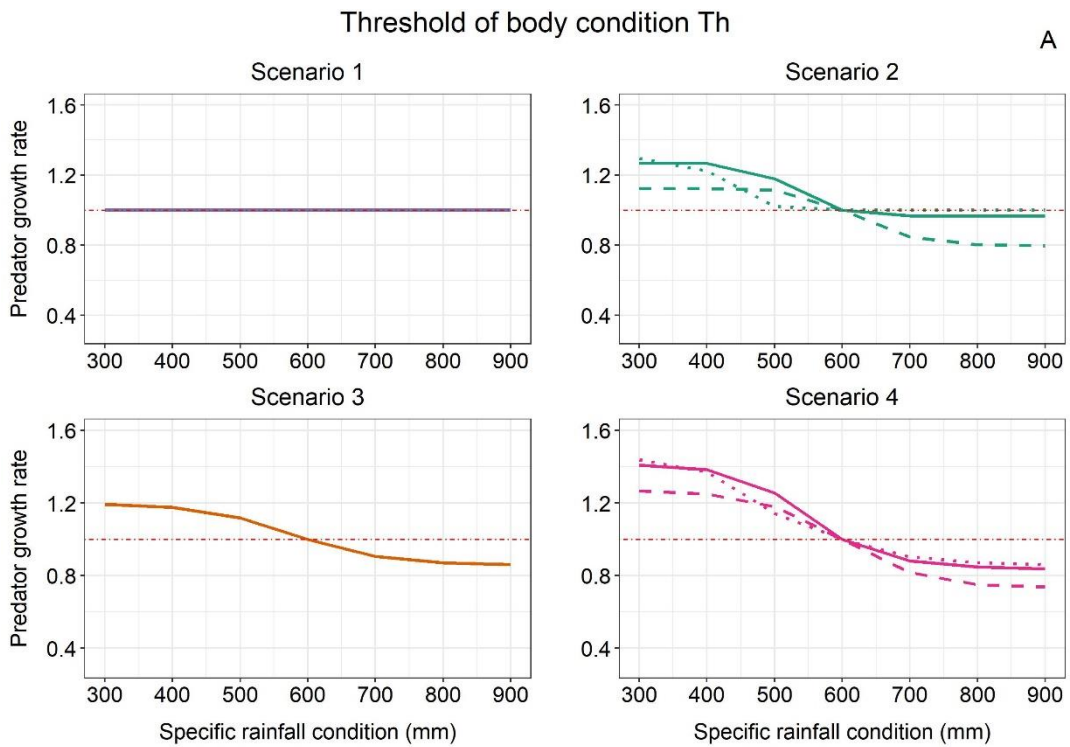


Figure S2: (A) Immediate response of predator populations to a specific rainfall condition. Relationship between the growth rate of predator populations and a specific annual rainfall in a system characterized by a long-term mean annual rainfall of 600 mm. (B) Long-term response of predator populations 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.



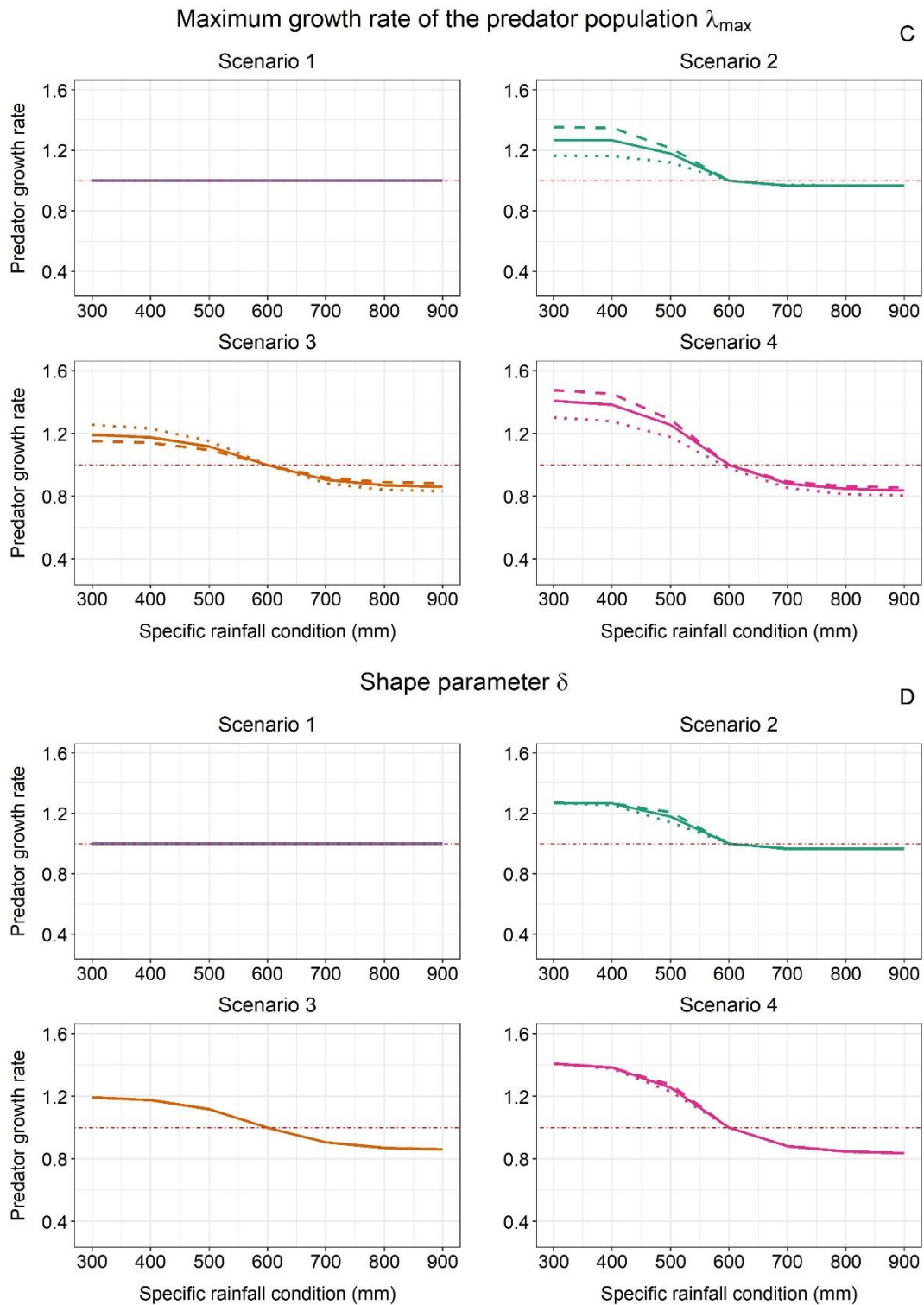
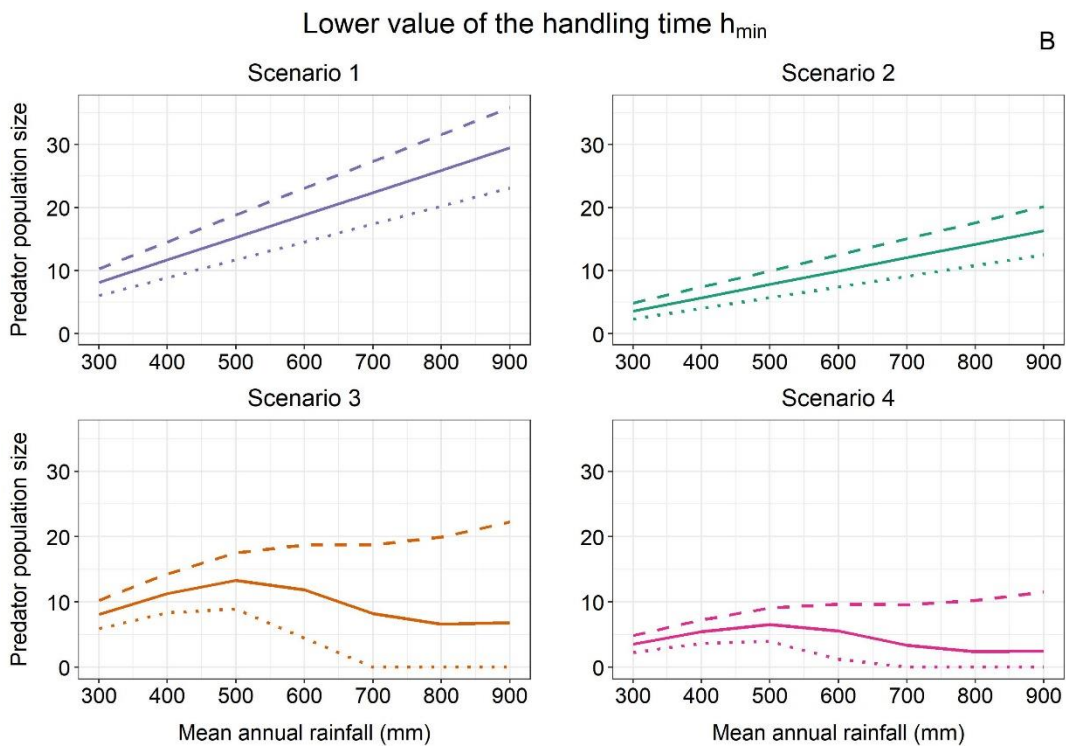
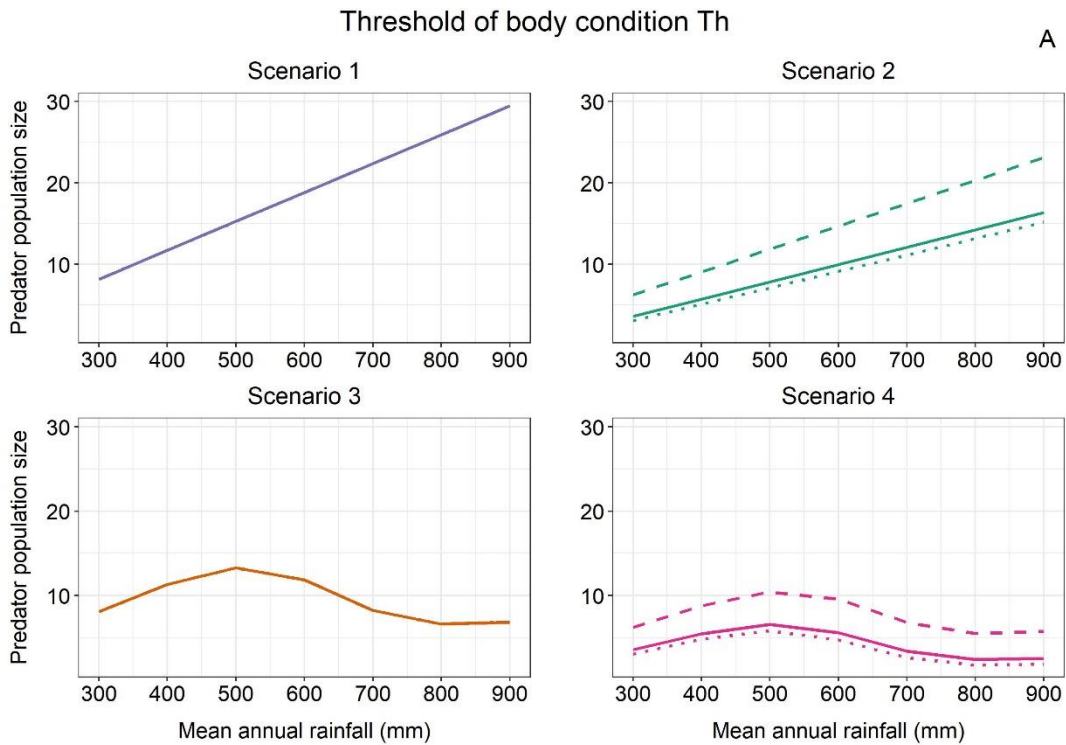


Figure S3: Influence of a specific rainfall condition on the growth rate of predators from the four scenarios for three values (default: solid line, + 20%: dashed line, -20%: dotted line) of tested parameters: (A) Th , (B) h_{min} , (C) λ_{\max} , (D) δ , when the habitat-driven hunting success decreases 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.



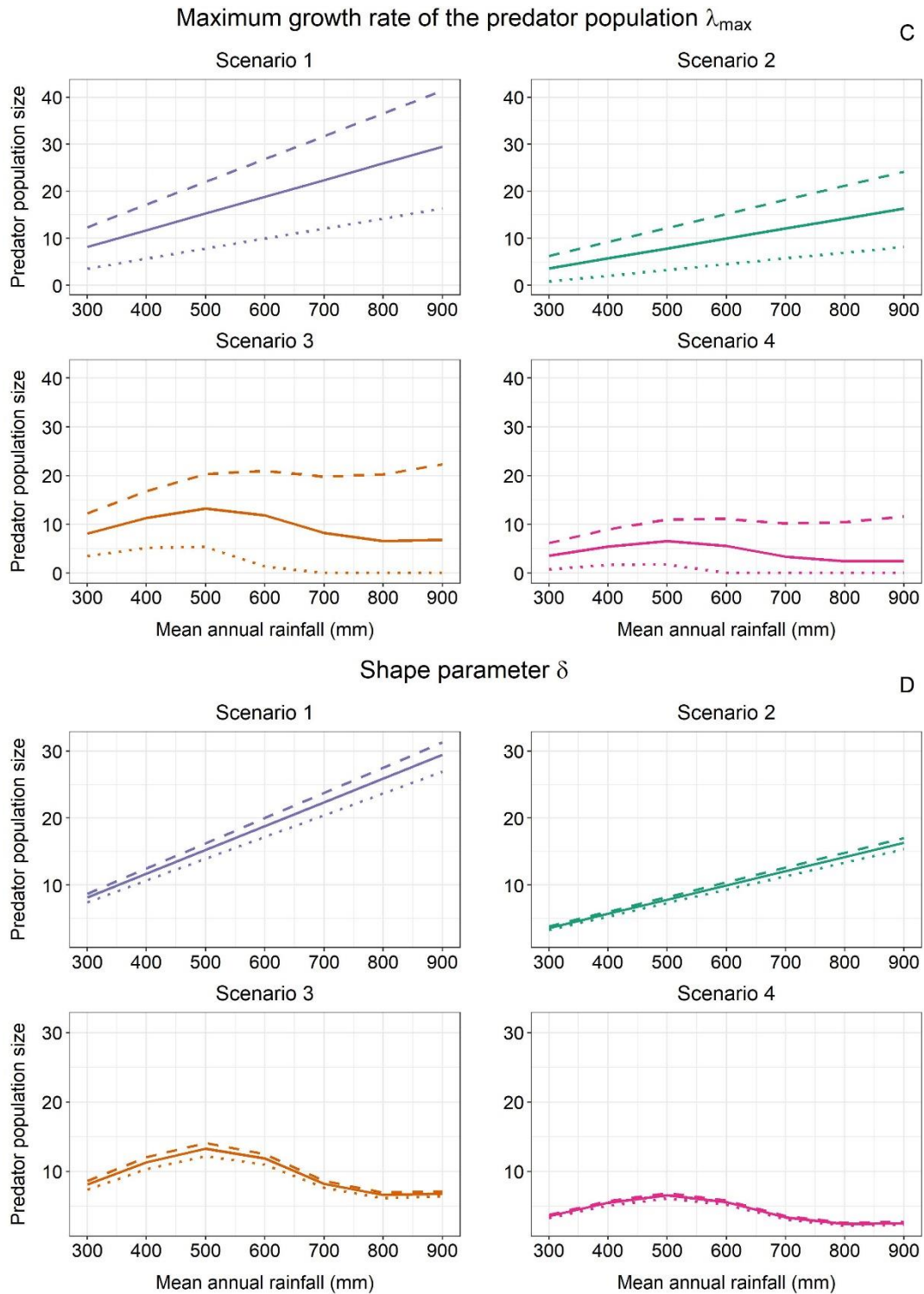


Figure S4: Influence of long-term mean annual rainfall on the size of predator populations from the four scenarios for three values (default: solid line, +20%: dashed line, -20%: dotted line) of tested parameters: (A) Th , (B) h_{\min} , (C) λ_{\max} , (D) δ , when the habitat-driven hunting success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

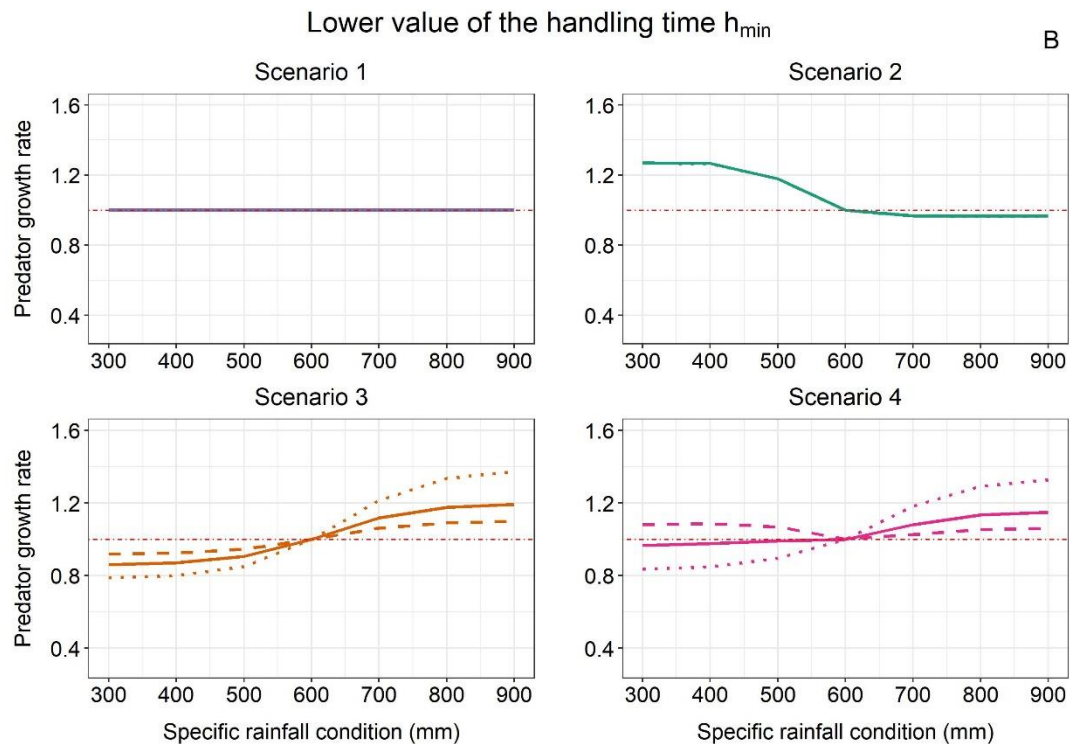
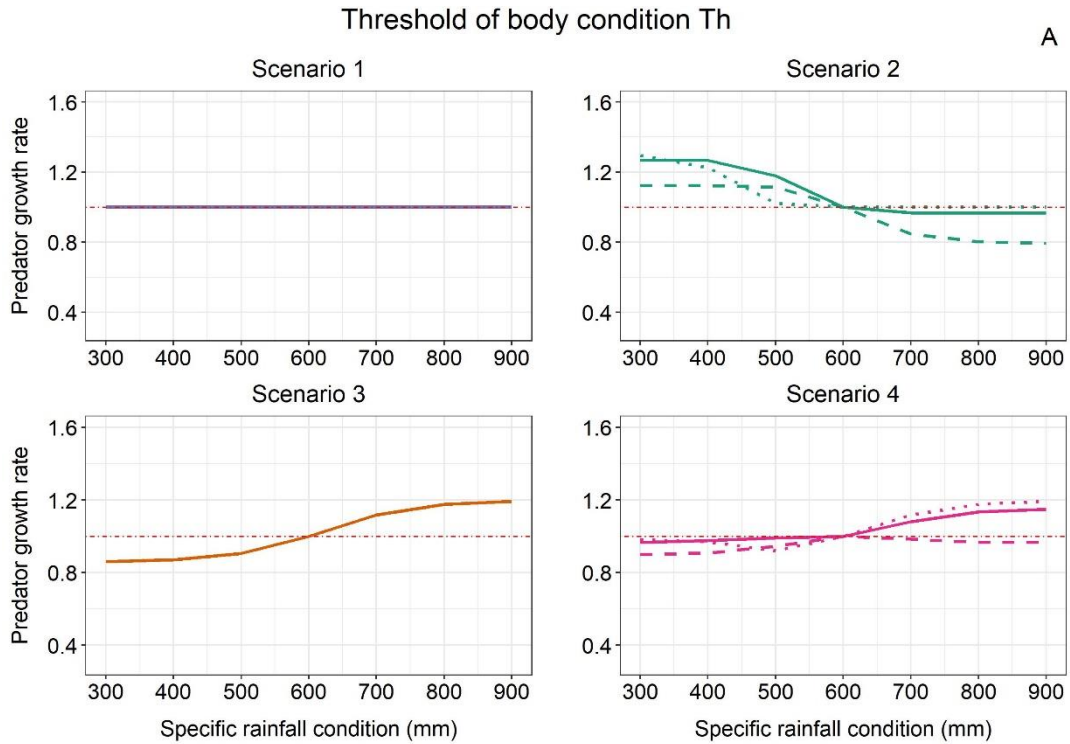
2 Appendix B: Sensitivity analyses

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 λ_{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 λ_{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.



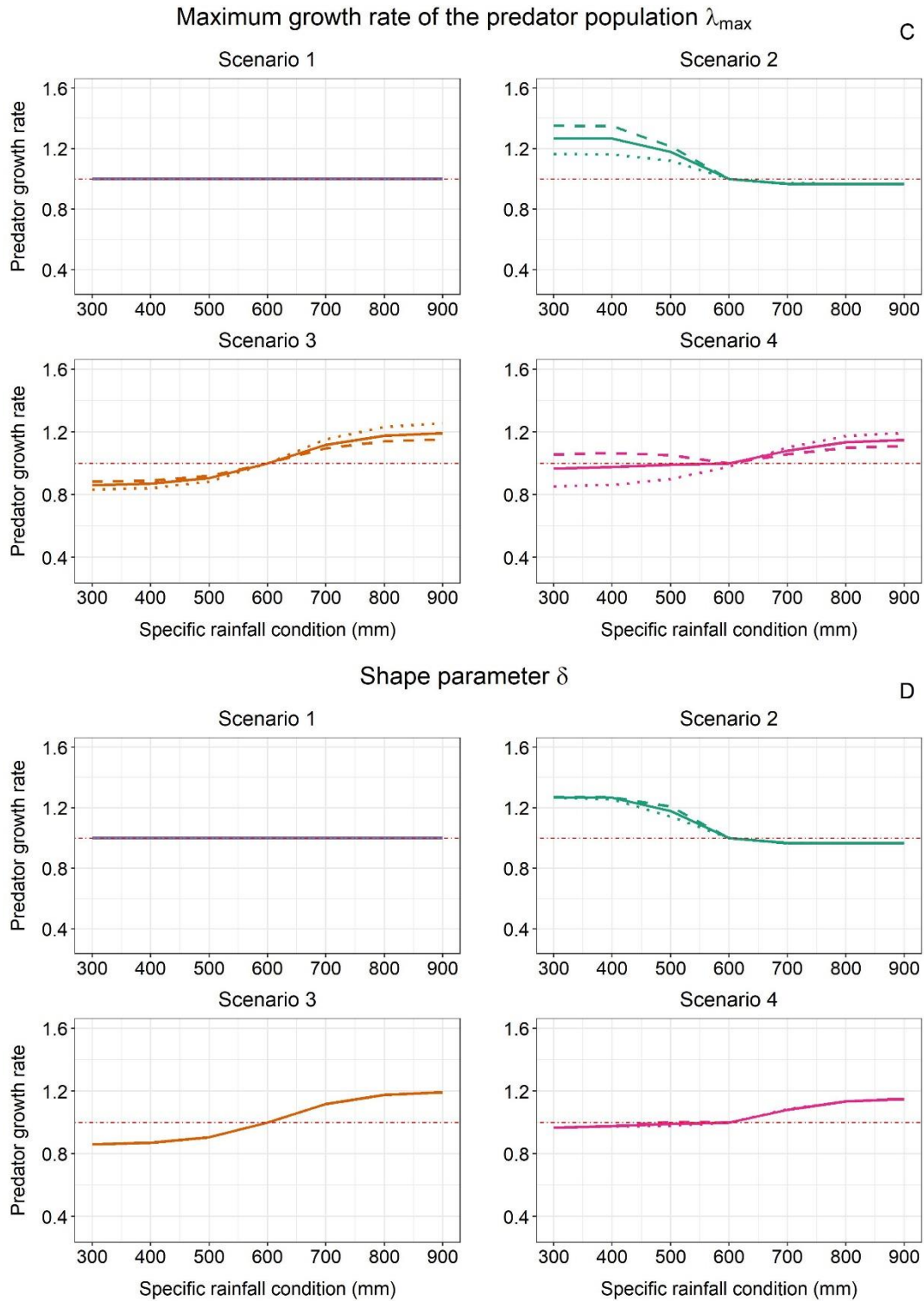
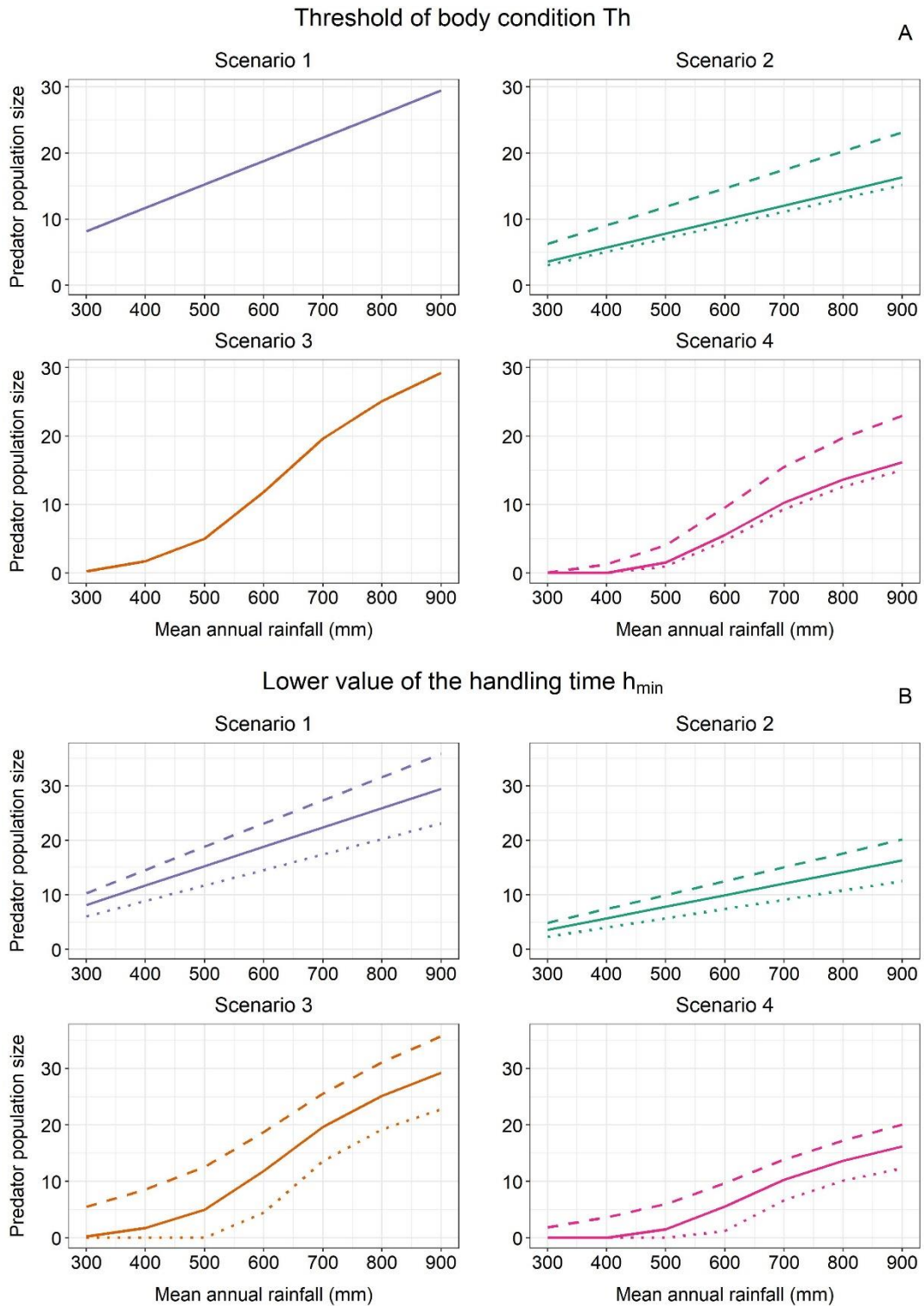


Figure S5: Influence of a specific rainfall condition on the growth rate of predators from the four scenarios for three values (default: solid line, +20%: dashed line, -20%: dotted line) of tested parameters: (A) Th , (B) h_{min} , (C) λ_{max} , (D) δ . All other parameters are set to default values. 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.



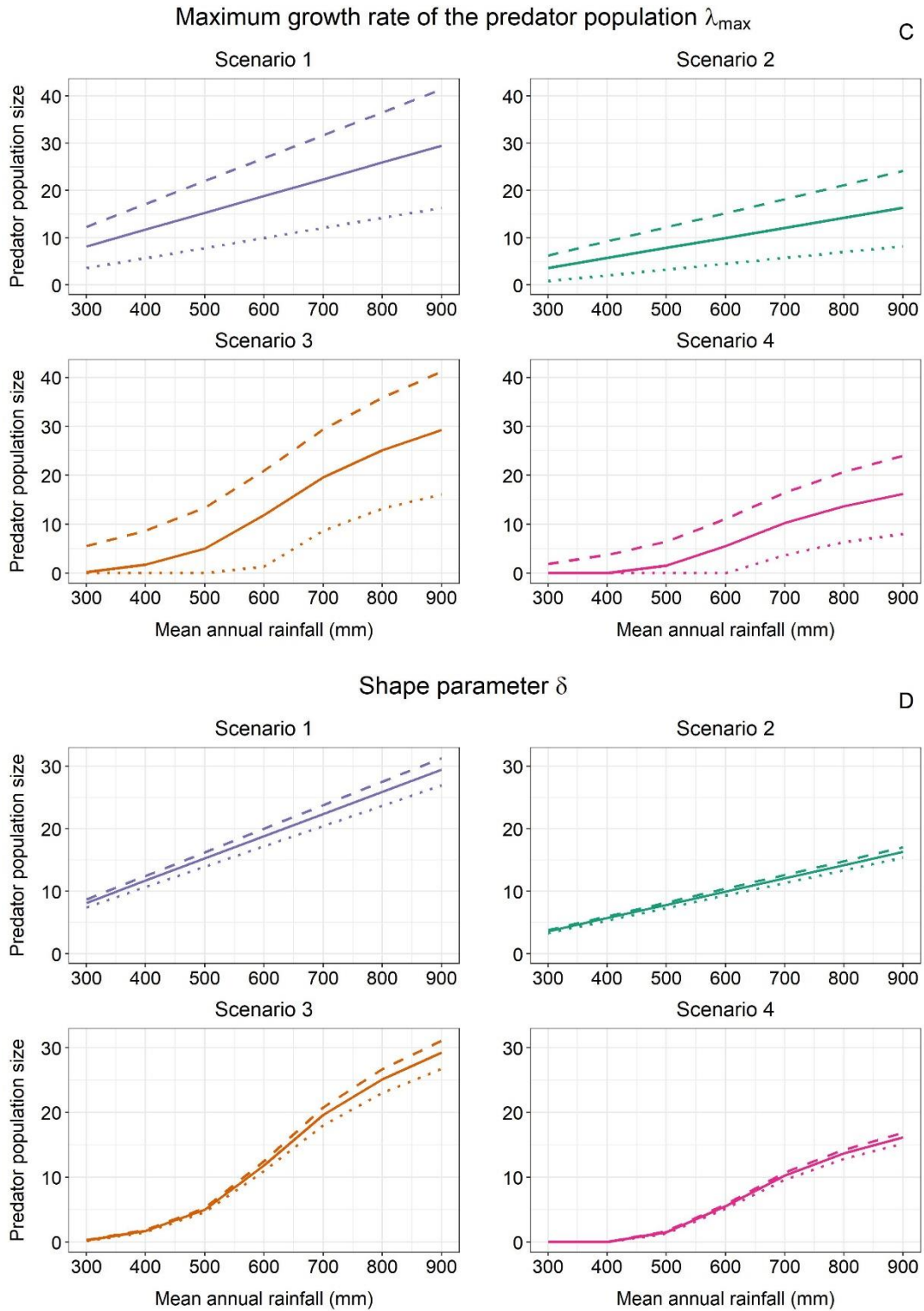


Figure S6: Influence of long-term mean annual rainfall on the size of predator populations from the four scenarios for three values (default: solid line, +20%: dashed line, -20%: dotted line) of tested parameters: (A) Th , (B) h_{\min} , (C) λ_{\max} , (D) δ . All other parameters are set to default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

3 Appendix C: Supplementary figures

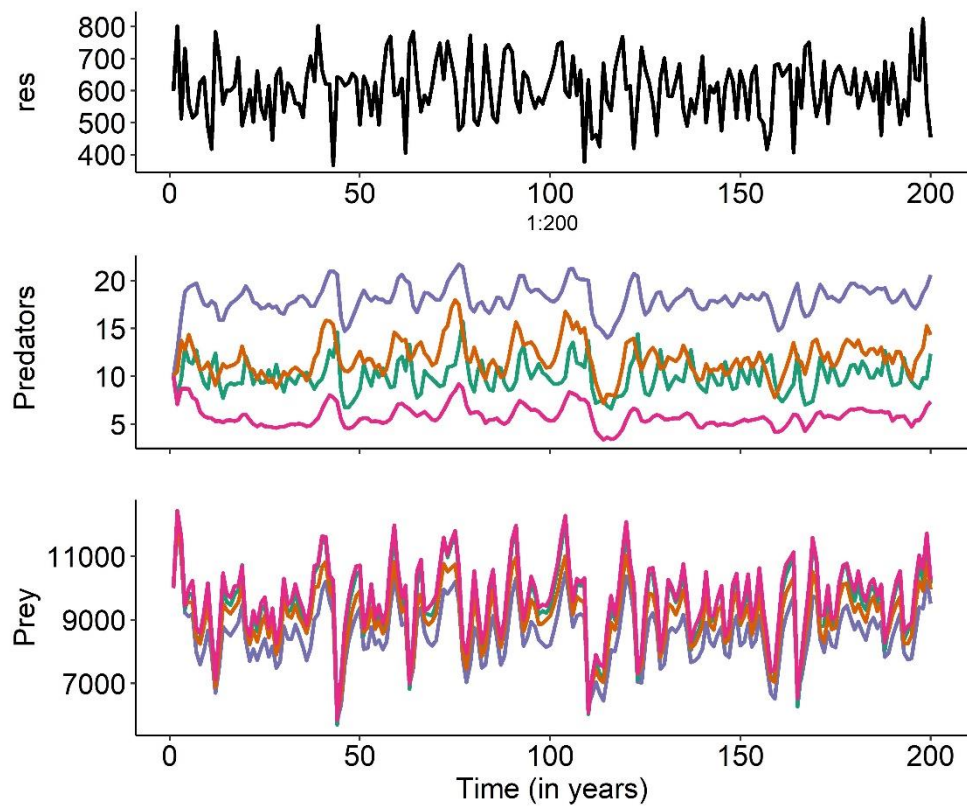


Figure S7: Model behaviour for one run. Rainfall (top), predator (middle) and prey (bottom) population sizes, for a 200-year run. Used parameter values are presented in Table 1.

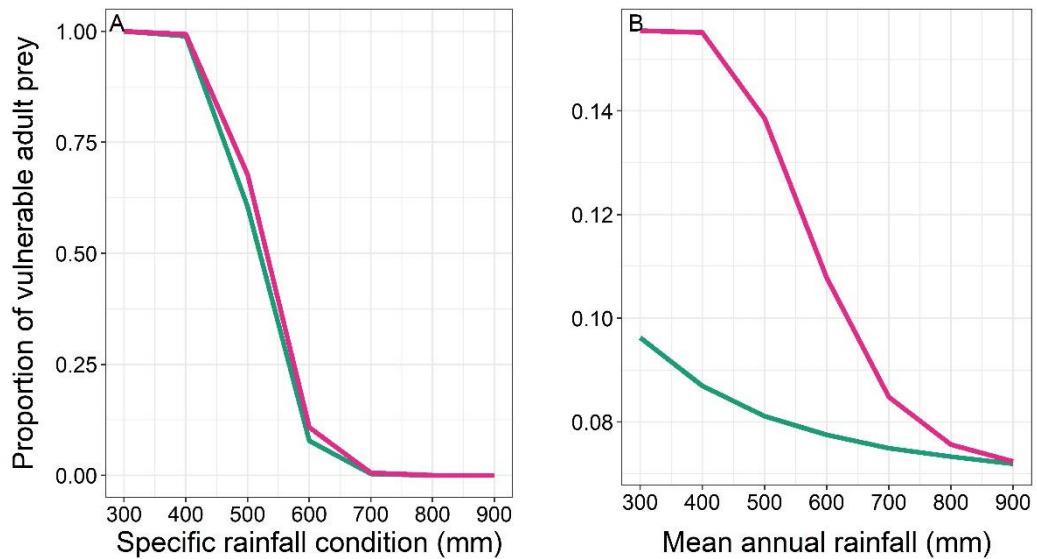


Figure S8: (A) Influence of a specific rainfall condition on the proportion of adult prey vulnerable to predators in scenarios 2 (green) and 4 (pink). (B) Influence of mean annual rainfall on the proportion of adult prey vulnerable to predators in scenarios 2 (green) and 4 (pink). By definition the proportion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

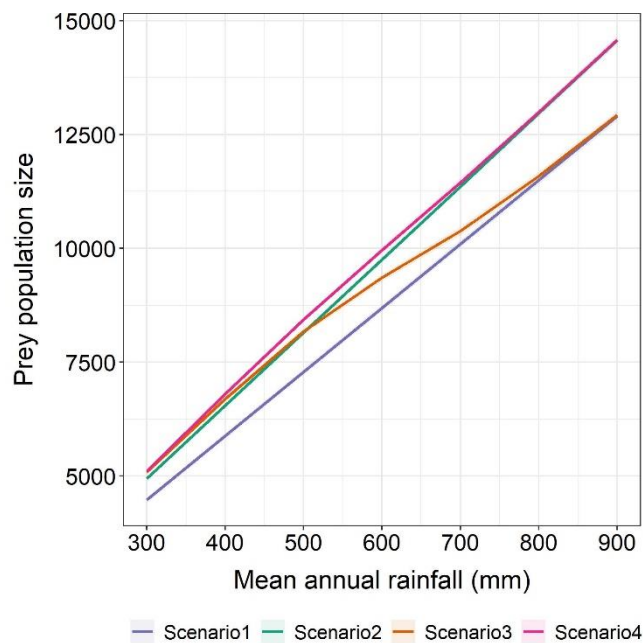


Figure S9: Influence of mean annual rainfall on the size of prey populations, for the four scenarios.