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Poaching is directly and indirectly driving the decline of South Africa's large population of white rhinos

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Short title: Direct and indirect poaching effects drive rhino declines.

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Abstract

Large herbivores, particularly in water limited systems, are vulnerable to the impacts of poaching (illegal hunting) and human induced climate changes. However, we have little understanding of how these processes can reshape their populations. With some rapidly declining populations there is a need to understand the effects of these stressors on populations of vulnerable large herbivores like the white rhino (*Ceratotherium simum simum*). We developed age-structured models for the rhino population in Kruger National Park, home to 49% of South Africa’s rhinos. We wanted to determine the relative influence of poaching and climate on the current and future population size and demographics, examine the potential of a *dependency effect* (the loss of calves from poached females) and quantify the *compound effect* (loss of future young). Our results indicated that population declines were largely driven by poaching and included a *dependency effect*. Rainfall had a measurable but smaller influence on rhino populations and had an additive effect; reduced rainfall exacerbated poaching losses. Current poaching levels have resulted in a reduction to the lifetime reproductive output per cow from approximately 6 to 0.7 calves: a compound effect of 5.3 future offspring. Under current levels of poaching, we project a 35% decline in the Kruger rhino population in the next 10 years. However, if poaching intensity is cut in half, we project a doubling of the current population over the same time frame. Overall, our models showed little sensitivity to demographic and environmental parameters, except for adult survival. Our results suggest that maintaining and improving the lifetime reproductive output of rhino cows should thus be the highest management priority and that new management targets should consider both the dependency and compound effects associated with poaching on rhino cows.

Keywords: compound effect, dependency effect, poaching, rainfall, age-structured model, white rhino, population decline, herbivores

Introduction

55 Poaching (illegal hunting) coupled with habitat changes have left many traditionally hunted
56 species at risk of extinction (Koch and Barnosky, 2006; Rizzolo, Ratsimbazafy and Rajaonson, 2017).
57 Poaching threatens biodiversity, deprives protected areas of revenue, and undermines their viability
58 (Gavin, Solomon and Blank, 2010; Rizzolo *et al.*, 2017). Globally, more than 300 mammals are in danger
59 of extinction from poaching and other forms of exploitation (Rosser and Mainka, 2002; IUCN, 2019). A
60 disproportionate number of these endangered mammals are large terrestrial herbivores (e.g. African
61 elephant [*Loxodonta Africana*] and hippopotamus [*Hippopotamus amphibious*]), which face threats from
62 habitat loss and degradation as well as poaching (Milner, Nilsen and Andreassen, 2007; Ripple *et al.*,
63 2015).

64 These overexploited large herbivore populations are also increasingly stressed by human induced
65 climate changes (Parmesan, 2006). Large herbivore populations, particularly in water limited systems like
66 savannas, are often shaped by rainfall (Forchhammer *et al.*, 1998; Ogutu and Owen-Smith, 2003; Owen-
67 Smith, Mason, Ogutu, 2005). Specifically, rainfall during the dry season appears to have the greatest
68 influence on population dynamics because it maintains vegetation quality when resources are limited
69 (Illius and O'Connor, 2000). Still, the influence of rainfall on large herbivores varies with age. For
70 example, drought appears to reduce birth rates (Ferreira *et al.*, 2019), and juveniles may be more sensitive
71 to harsh climatic conditions (e.g. drought, heat) because of the influence of food availability on lactation
72 (Foley, Pettorelli and Foley, 2008; Ogutu and Owen-Smith, 2003; Ryan, Knechtel and Getz, 2007).

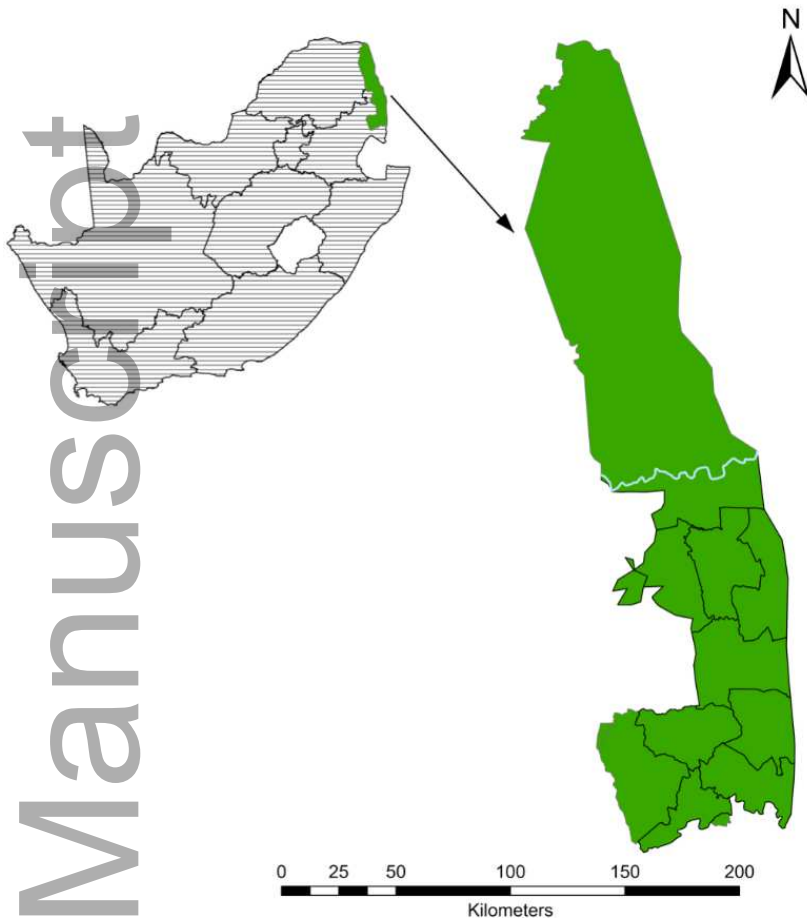
73 While we understand how both poaching and rainfall can alter large herbivore populations, we
74 have less understanding of how their combined effects may alter demography (Milner *et al.*, 2007). There
75 is some evidence, at least for elephants, that competition with humans for limited resources (i.e. water,
76 suitable habitat), which will become increasingly limited due to climate change, may lead to increased
77 poaching losses (Ngcobo *et al.*, 2018). Our understanding of the combined effects of poaching and
78 rainfall, however, is minimal, likely due to large herbivores' longevity, and the time lags in demographic
79 responses (Milner *et al.*, 2007). In the face of elevated levels of poaching (Burn, Underwood and Blacc,
80 2011; Challender and MacMillan, 2014; Duffy *et al.*, 2014) and predictions of an increasingly variable
81 climate (Van Wilgen *et al.*, 2016) there is a need to understand the effects of these processes on
82 vulnerable species like the white rhino (*Ceratotherium simum simum*). While white rhino (hereafter rhino)
83 populations respond to stochastic environmental variation and increased densities of conspecifics (Braude
84 and Templeton, 2009; Rachlow and Berger, 1998; Shrader and Ogutu, 2006), we know less about how
85 their populations respond to poaching and climate stress. It is unclear if rhino poaching causes the indirect
86 loss of dependent calves when an adult female is poached (the *dependency effect*; Wittemyer, Daballen
87 and Douglas-Hamilton, 2013). Research suggests that long-lived species with longer periods of juvenile

88 development might be particularly vulnerable to the loss of their mother (Stanton *et al.*, 2020). For
89 example, Asian elephants (*Elephas maximus maximus*) calves are 10 times likely to die if their mother is
90 killed before they turn 4 (Lahdenpera *et al.*, 2016; Perera *et al.*, 2018). As such we have reason to believe
91 the loss of a long-lived rhino female may reduce future population sizes, as the potential for future young
92 are lost (the *compound effect*). Since most large mammals can only produce one offspring a year,
93 longevity has a strong influence on overall reproductive success (Zedrosser *et al.*, 2013). However, we
94 have little understanding of the magnitude of the *compound effect* on a poached population and the
95 potential for climate influences to exacerbate losses. Broadly, we do not understand how variation in
96 climate and different poaching intensities will shape the size of future rhino populations. Variation in
97 population sizes will in turn be driven by variation and elasticity in demographic processes (e.g.
98 recruitment, juvenile and adult survival), which respond differently to climate conditions (Gaillard *et al.*,
99 2000). Thus, it is important to identify the most important and sensitive demographic processes that are
100 likely to influence future rhino population sizes. Filling these important gaps will allow us to effectively
101 identify and propose effective management actions.

102 Accordingly, our goal for this study was to understand the current and the future response of the
103 rhino population to poaching and climate variation. We predicted that modeling the loss of calves
104 associated with the loss of a poached mother (i.e. *dependency effect*) would help explain rhino population
105 declines. We expected that projections of constantly high poaching and dry conditions would lead to
106 population declines, as dry conditions often lead to delayed reproductive activity (Ferreira, Le Roex and
107 Greaver, 2019), exacerbating any poaching related losses. Finally, we predicted adult (especially female)
108 survival will have the most influence on population size (Eberhardt, 2002), because low adult female
109 survival results in a reduction in reproductive output. As such, our objectives were to 1) determine the
110 relative influence of poaching and climate on rhino population size, 2) estimate the current rhino
111 population size if there had been no poaching in the past, 3) determine if a *dependency effect* explains
112 reductions in the rhino population size, 4) predict future rhino population sizes and quantify the
113 *compound effect* under different climatic conditions and poaching pressures and 5) identify how variation
114 in different demographic processes will alter future rhino population sizes.

115 **Study Site**

116 Our study was conducted in Kruger National Park (19 485 km², hereafter Kruger), located in the
117 Mpumalanga and Limpopo provinces of South Africa (Fig. 1). In 2015 Kruger was home to
118 approximately 49% of South Africa's rhino population (Ferreira *et al.*, 2018). Rhinos generally occur in
119 the central and southern parts of the park (Fig. 1), although nothing impedes their movement to the
120 northern parts (Pienaar, Bothma and Theron, 1993).



122

123 Figure 1. Map of Kruger National Park in South Africa with sections south of the Olifants River
 124 where white rhinos surveys were conducted from 1998-2019. The light blue line indicates the Olifants
 125 River and the polygons represent the sections where rhinos from this study were located.

126 The central and southern parts of the park are within the lowveld bushveld climate zone and
 127 receive 500-700mm annual rainfall between October and March (Venter, Scholes and Echaradt, 2003). The
 128 rainfall in Kruger occurs in 5 year cycles of wet (high rainfall) and dry (low rainfall), which match La
 129 Niña and El-Niño years (MacFadyen *et al.*, 2018). The El-Niño in 2015 brought hot and dry conditions to
 130 South Africa which resulted in a major drought taking place during the 2015/2016 wet season (Malherbe
 131 *et al.*, 2020).

132 The underlying geology consists of granite and gneiss soils in the western parts, nutrient rich
 133 basalts in the eastern parts and Karoo sediments in the parts where the granite and basalts soils join
 134 (Venter *et al.*, 2003). Vegetation in the south consists of i) savanna woodlands on granite soils where

135 *Combretum spp.* trees dominate and ii) open grassy woodlands on the basalts dominated by *Sclerocarya*
136 *caffra* and *Senegalia nigrescens* (Venter et al., 2003).

137 **Methods**

138 To estimate the relative influence of demographic parameters, rainfall, direct poaching,
139 dependence-based poaching losses, and compound effects of poaching on rhino population size, we
140 developed an age-structured model using a generalized difference equation (Hilborn and Mangel, 1997).
141 Age-structured models are often used to analyze incomplete data in dynamic systems by combining
142 multiple sources of observed data (Hilborn and Mangel, 1997). These models allowed us to focus on
143 uncertainty in one parameter estimate while accounting for uncertainty in the estimate of another
144 parameter; thus improving use of the data and improving the models. Due to the lack of data we assumed
145 no uncertainty in the birthing interval, proportion giving birth at each class and sex ratio. As such, we
146 could not obtain uncertainty around reproductive rates.

147 *Model parameters*

148 *Population size*

149 We used population estimates from the South African National Parks (SANParks) data repository
150 generated from two different methodologies: distance sampling and block surveys, described in detail
151 below. Distance sampling data was available from 1998 to 2017 (except 2009, 2011, 2013 and 2015 when
152 surveys were not done). In 2016 and 2017 estimates of population size were obtained through distance
153 and block surveys and population estimates from both methods were used in these years. After 2017 only
154 block survey methods were available.

155 *Distance sampling*

156 We used data from 1998 to 2017 collected via fixed wing aircrafts flown ≈ 76 m above ground
157 level at speeds of 167 – 185 km/hour (Kruger, Reilly and Whyte, 2008). Two observers on each side of
158 the aircraft recorded the number of animals seen and the distance at which they were first seen using a
159 frame attached to the outside of each window that had strip wires denoting four distance categories (0–50
160 m, 50–100 m, 100–200 m, 200–400 m). This provided a transect width of 800 m (400 m on each side of
161 the aircraft) (Kruger *et al.*, 2008). For the 1998 to 2000 surveys we sampled 15% of the park, flying 64
162 transect lines placed 5.6 km apart in an east-west orientation (Appendix 1a; Kruger *et al.*, 2008). We
163 increased the survey effort to cover 22% of the park from 2001 to 2017 by flying 96 transect lines placed
164 3.7 km apart (Appendix 1b). We generated estimates using a distance sampling approach and DISTANCE
165 ver. 4.0 software (Thomas *et al.* 2010). Following Buckland *et al.* (1993), we first examined initial

166 histograms of count frequencies at different distances to determine truncation of observations. Next, we
167 combined 0-50 m and 50-100 m distance categories to improve model fit. Finally, we fit different
168 detection functions (uniform, half-normal and hazard rate and simple polynomial adjustments) with up to
169 3 cosine adjustment terms and selected the most parsimonious function using Akaike Information
170 Criterion (AIC; Burnham and Anderson 2002) (Appendix 2). We evaluated each year separately and
171 generated abundance estimates by multiplying density estimates by the total area of the central and
172 southern region of the Kruger.

173 *Block survey*

174 We used block-based survey methods (Ferreira *et al.*, 2015) for the final 4 years of our models.
175 Observers counted all rhinos within 878 3x3 km blocks from a helicopter flown at 45 m above ground at
176 speeds of 120.38 km/hour (Ferreira *et al.*, 2015). The blocks were randomly distributed throughout the
177 park and covered the 35 landscape types found in Kruger (Appendix 3; (Gertenbach, 1983) with more
178 blocks occurring in the south region where rhinos were more prevalent (Appendix 4; (Ferreira *et al.*,
179 2015). We estimated rhino abundances separately for each landscape type in the sampled blocks and
180 extrapolated to unsampled blocks focusing on the central and southern region of the Kruger. We
181 estimated and corrected for observer bias (the probability of an observer not seeing a rhino when present),
182 using a double observer methodology on 33 randomly selected blocks and increased our raw counts by
183 the estimated probability of missed rhinos (Ferreira *et al.*, 2015). Additionally, we estimated and
184 corrected for availability (obstructed by vegetation or other feature) by monitoring the visibility of 15
185 focal rhinos (i.e. rhino selected for extended observations) for 10 minutes (Ferreira, Greaver and
186 Knight, 2011). Both the observer and availability bias estimates were obtained during the 2013 census.

187 *Demographic estimates*

188 We used data from the SANParks data repository and internal unpublished reports to determine the
189 demographic makeup of the rhino population. The standing age distribution for each year was determined
190 using helicopter-based flights (100 m above ground, \approx 100 km/hr) to assign ages and sexes to at least 100
191 individuals in each of the 9 management zones (Appendix 5; Ferreira, Botha and Emmett, 2012). These
192 are management zones that were designated by SANParks management from where rhinos for live sales
193 were historically removed. We used the body size and height (Appendix 6a) as well as the size and shape
194 of the horns (Appendix 6b) of an individual to estimate its age (Hillman *et al.* 1986; Emslie, Adcock and
195 Hansen, 1995). We estimated the standing age class distribution using surveys in 2010 – 2017 and
196 defined 3 age classes: juveniles (A, B & C age classes 0-24 months old), sub-adults (C & D classes, 2.5 –

197 7 years) and adults (F class – older than 7 years). We assumed between 20 – 50% of sub-adults and adults
198 could reproduce (Rachlow and Berger, 1998).

199 *Rainfall, poaching and management data*

200 We obtained rainfall data for 20 years (1998-2019) by averaging the monthly rainfall from the 12
201 weather stations in our study area (Appendix 7). We used both wet (October – March) and dry season
202 (April – September) rainfall for our models. To quantify poaching, we used records of the annual number
203 of poached rhino carcass found by rangers from 2007 – 2019 (Ferreira et al., 2015). While vultures and
204 scavenging activity facilitates the detection of rhino carcass, we accounted for undetected carcasses to
205 reduce the probability of undercounting poached rhinos. Specifically, we had two observers conduct
206 intensive aerial surveys of 10 (3x3 km) blocks via helicopter and record the GPS location of carcasses.
207 Then we compared the number of carcasses seen by the two observers to those found by rangers on the
208 same 10 blocks. Using a double observer methodology (Cochran, 1977) we estimate that rangers missed
209 11.5% of the carcasses (SANParks, internal report) and used this estimate to correct the annual number of
210 carcasses counted by rangers. In addition to estimates of poaching, we used data on management
211 removals - the numbers of rhinos removed for management purposes from 1998 – 2019. Removals were
212 conducted to provide revenue for conservation objectives or used to establish new populations elsewhere
213 (Ferreira *et al.*, 2012). Historically, management removals targeted sub-adult individuals, particularly
214 females (Ferreira *et al.*, 2012), however, recent increases in poaching have reduced management removals
215 by as much as 80% (Ferreira *et al.*, 2012).

216 **Demographic analysis**

217 We used age-structured models using a generalized difference equation (Hilborn and Mangel,
218 1997) to predict numbers of individuals in different age classes over time (1998 - 2019). We used the
219 models to account for variation in juvenile production, survival potential as a function of rain dependent
220 food availability, management removals, poaching losses, and the potential impact of poaching losses of
221 mature females on associated juveniles (Pascual, Kareiva and Hilborn, 1997). We predicted the numbers
222 (N) of individuals at different ages (a) over time (t) using a balance model (Equation 1) that accounted for
223 age specific natural survival (S_a), the proportion of individuals in an age susceptible to management
224 removals (v_a^r), the proportion of individuals in an age susceptible to poaching (v_a^p), the removal rate (U_t^r)
225 of fully susceptible individuals, and the poaching rate (U_t^p) of individuals fully susceptible to poaching
226 removed.

$$227 N_{a+1,t+1} = N_{a,t} S_a * (1 - v_a^r U_t^r) (1 - v_a^p U_t^p) \quad (\text{Equation 1: individuals at different age classes})$$

228

229 The management removal (U_t^r) and poaching (U_t^p) rates (Equation 2) were conditioned on estimates of
230 the total population size vulnerable to each removal type. This approach ensures that the actual observed
231 removals (R) or individuals poached (P) are removed each time step but allows the removal rate to be
232 constrained to <1 to prevent numerical instability. These rates are then used in Equation 1.

233
$$U_t^r = R_t / \sum_a v_a^r N_{a,t} \text{ or } U_t^p = P_t / \sum_a v_a^p N_{a,t} \quad (\text{Equation 2: removal and poaching rates})$$

234 We estimated age specific survival as a constant maximum rate (S_a') for each age or as a hyperbolic
235 function of per capita available resources (F_t) where γ_a determines the per capita food level at which
236 survival drops to half the maximum value (Equation 3). Note that when γ_a is set to 0 the maximum age
237 survival rate is used each year. Per capita food availability was modeled as a scaled function of rainfall (
238 RF_t).

239
$$S_a = S_a' \frac{F_t}{\gamma_a + F_t} \text{ where } F_t = \frac{1.25RF_t}{\sum_a N_{a,t}} \quad (\text{Equation 3: age-specific survival rates})$$

240 Since grass growth depends on the amount and distribution of rainfall, we calculated a food effect by
241 using an established relationship between dry seasoning rainfall and fresh grass growth (Mduma, Sinclair
242 and Hilborn, 1999). Studies have shown that food supply is usually inadequate during the dry season
243 which can lead to mortalities (Dudley *et al.*, 2001; Knight, 1995). Following (Hilborn and Mangel, 1997),
244 we used a regression equation for grass growth on monthly dry season rainfall with the slope of 1.25
245 (Mduma, Sinclair and Hilborn 1999). A similar equation was used to mediate birthrate (Equation 4)
246 where br_a is the age specific birth rate and γ_{br} is the per capita food availability where the age specific
247 birth rate drops to half the maximum value br_a' .

248
$$br_a = br_a' \frac{F_t}{\gamma_{br} + F_t} \text{ where } F_t = \frac{1.25RF_t}{\sum_a N_{a,t}} \quad (\text{Equation 4: food effect on birth rates})$$

249 We used the best available estimates to determine rhino's demographic parameters: birth frequency in
250 rhino, population sex ratio, and senescence age (Table 1) and assumed these were constant over time.
251 When available, we used published and unpublished demographic estimates from the Kruger rhino
252 population. If these estimates were not available, we used estimates from other populations (Table 1). We
253 assumed the population size at time 0 ($N_0 = 1998$) to be known. We used the model to estimate the
254 influence of rainfall on food availability as well as the effect of combined removals through poaching and
255 management removals (Appendix 8) on rhino birthrates, age specific survival and population growth rate.
256 We estimated these dynamic parameters by maximum likelihood (Pascual *et al.*, 1997) assuming

257 Gaussian error structure and the estimated uncertainty for each population estimate (Hilborn and Mangel,
258 1997; Pascual *et al.*, 1997). Note that in 2016 and 2017 population estimates from distance and block
259 surveys were used since there was no reason to assume one method was superior to the other. To
260 understand the relative influence of climate and poaching on rhino population growth and examine the
261 potential for a *dependency effect*, we evaluated three scenarios.

262 *Scenario 1*

263 In the first scenario, we assumed changes in population were influenced by changes in rainfall
264 and the resulting changes in survival due to food effects. We used this scenario to determine the relative
265 influence of rainfall in the absence of poaching.

266 *Scenario 2*

267 In the second scenario, we assumed changes were a result of rainfall plus poaching, where
268 poaching removals were assumed to come from the sub-adult and adult populations. This scenario
269 allowed us to determine if patterns of rhino population demography could be explained by the poaching
270 of sub-adult and adult individuals.

271 *Scenario 3*

272 Finally, for scenario 3, we made the same assumptions as scenario 2 plus an additional
273 assumption that there were indirect mortalities of calves from the loss of their mothers. For scenario 3, the
274 calves (i.e. up to 2 years) of all poached adults and a portion of sub-adults died. Not knowing the
275 proportion of sub-adults in the poached population, we trialled different biologically reasonable values (5
276 – 50%). Based on model performance, 20% was a good fit for scenarios 2 and 3.

277 To compare our three scenarios, we assessed model fit based on a visual inspection of model fit to
278 observed estimates and likelihood ratio tests. Likelihood ratio test are based on Wilks's theorem (Wilks
279 1938) where 2 times the difference between loglikelihoods can be approximated with a χ^2 -distribution
280 with degrees of freedom equal to the dimensionality difference between the models. For models with
281 similar dimensionality, a likelihood difference of 2 would result in a p-value of slightly less than 0.05.
282 Next, we generated likelihood profiles to produce confidence intervals for calf, sub-adult and adult
283 survival, food effect on juveniles, adults and birthrates following the theoretical statistics described by
284 Kendall and Stewart (1979). This allowed us to investigate how the variation in each parameter
285 influenced demographic responses and population growth using Markov chain Monte Carlo (MCMC)
286 simulations where parameter values were drawn randomly assuming a normal distribution defined by the
287 95% confidence intervals (Gaillard *et al.*, 1998; Gaillard and Yoccoz, 2003). To quantify the potential for

288 future direct and indirect impacts of poaching we assumed constant rainfall, survival and poaching and
289 projected the models into the future, from 2020 to 2030. We also projected future population estimates
290 using the best fitting model, modified to evaluate different poaching and climate scenarios and the
291 sensitivity of model parameters.

292 *Variable rainfall and poaching models*

293 We developed two modified models to understand the sensitivity and influence of food effects
294 and survival parameters on future populations. First, we set juvenile, sub-adult, adult survival to their
295 upper limits and food parameters to their lower limits (based on the likelihood profiles from the best
296 fitting model). Second, we set survival parameters to their lower limits and food effects to their upper
297 limits. We developed two additional modifications to understand the influence and sensitivity of our
298 model to weather. We set rainfall to 1) high and 2) variable (high and low) rainfall conditions. Under the
299 variable model rainfall fluctuated every 5 years, to correspond with the cyclical regional weather patterns
300 (MacFadyen *et al.*, 2018).

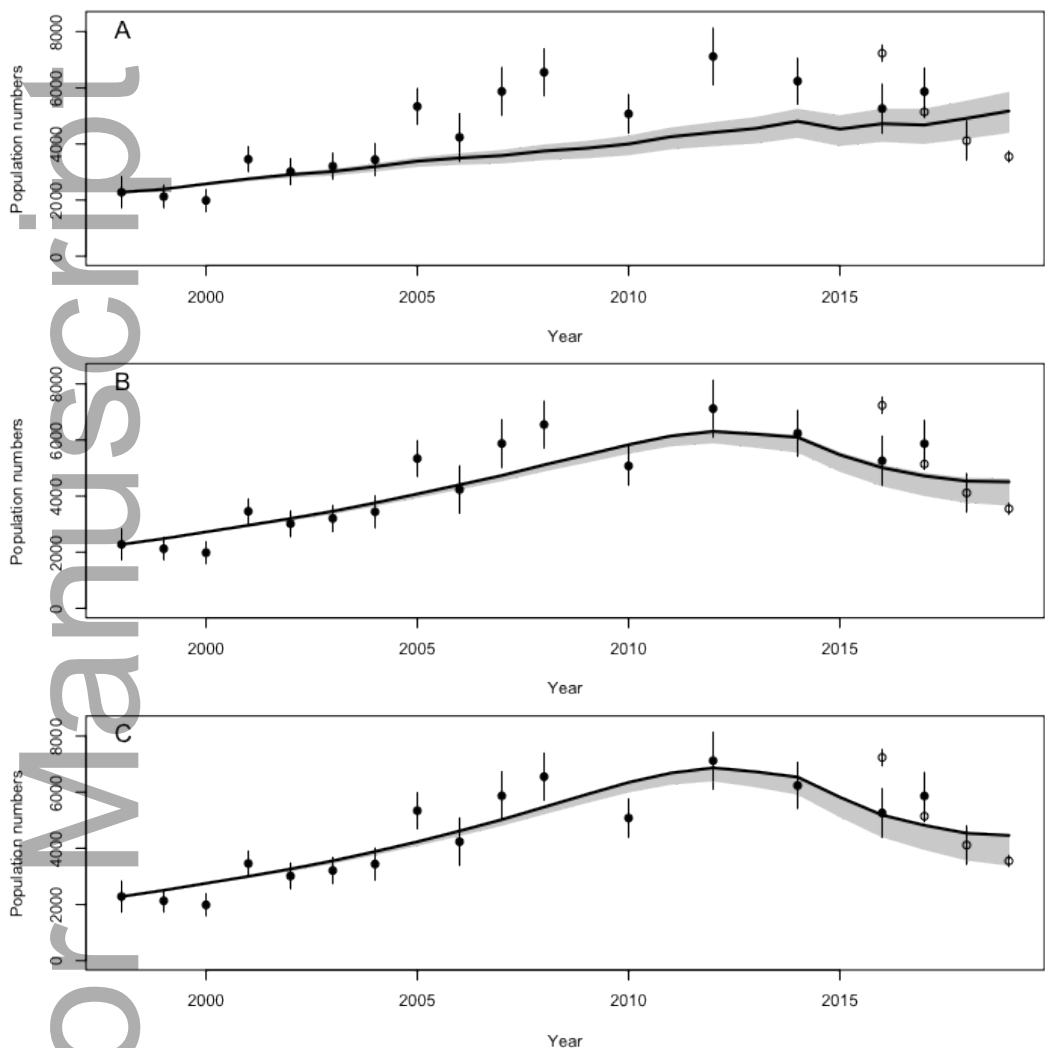
301 To understand how variation in poaching might influence future rhino populations, we projected
302 the baseline model and the modified models based on different poaching pressures. We examined future
303 populations under current (i.e. 2019) poaching levels and levels that were a 50% and 80% reduction of the
304 current level. This allowed us to understand how reductions in poaching could alter future rhino
305 population sizes. Then we used the baseline model and modifications to understand the magnitude of a
306 *compound effect* under different conditions. We calculated the compound effect as lifetime reproductive
307 success by determining the number of potential calves a female would produce if there was 1) no
308 poaching, 2) poaching but no calf losses and 3) poaching plus calf losses. We then linked different
309 poaching levels to the potential calf numbers under poaching with no calf loss and poaching with calf loss
310 to determine the number of calves that a female would produce under different poaching pressures.

311 **Results**

312 *Climate, poaching and dependency effects scenarios*

313 In general, the pattern observed from census data was that of a steadily declining rhino population
314 following the increase in poaching rates around 2007/2008. Evaluating our models, we found scenario 1
315 (rainfall only) with a log likelihood of 229.52 ($\Delta L = 39.04$; $p < 0.0001$; ΔL is the delta loglikelihood
316 change between model 1 and model 2) did not fit the observed data well (Fig. 2A). Scenario 2 (rainfall
317 and direct poaching) had a log likelihood of 190.48 ($\Delta L = 3.65$; $p = 0.0069$) and was a better fit than
318 scenario 1 (Fig. 2B). However, scenario 3 (rainfall, direct and indirect poaching) with a log likelihood of

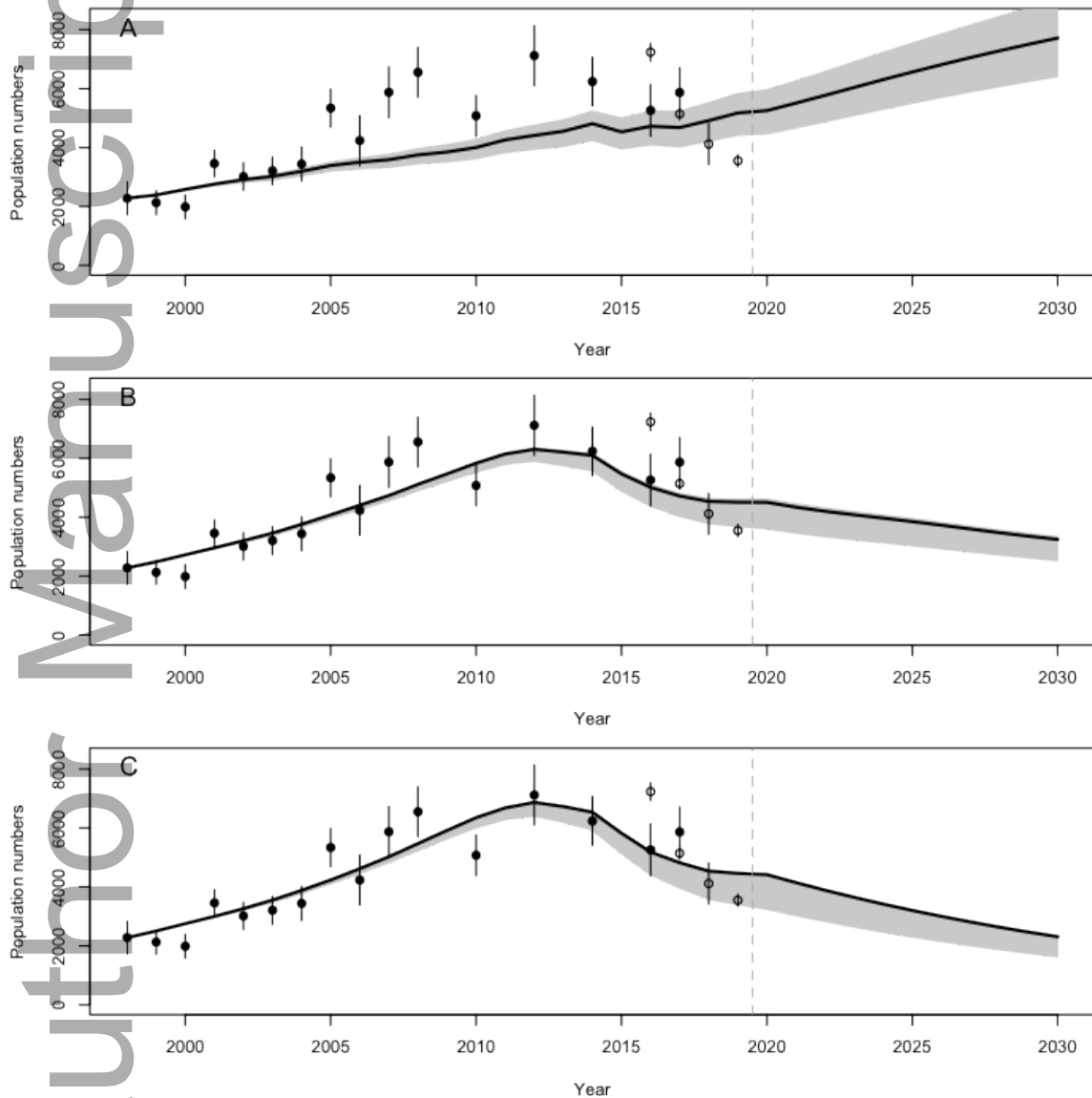
319 186.83, was the best fitting modeling, and supported the prediction that poaching can have direct and
320 indirect effects on the population because of the loss of calves that have not been weaned (Fig. 2C).



321
322 Figure 2. Fit of the age structured population model (black line) to white rhino population
323 estimates (black dots = distance sampling surveys, open dots = block census surveys, with standard error
324 bars) for the Kruger National Park from 1998-2019 under three modeling scenarios A) no poaching model
325 (rainfall affects food availability), B) the direct poaching model (rainfall plus poaching of adults and sub-
326 adults affecting demographic parameters), and C) the combined direct and indirect poaching model
327 (rainfall plus poaching of adults and sub-adults and the indirect mortalities of calves from the loss of their
328 mothers). Light grey polygon depicts the 95% quantile of population trajectory from Markov chain Monte
329 Carlo simulations.

330

331 In the absence of poaching (scenario 1) we estimated a population of 7100 (6410-8994) rhinos in
332 the year 2030 (Fig. 3A). When we projected the model with rainfall and direct poaching (scenario 2) to
333 the year 2030 we estimated 3078 (2528-3334) individuals, a 13.3% decrease from the 2019 estimate (Fig.
334 3B). Projecting the best fitting model (scenario 3), we estimated a population of 2312 (1724-2364)
335 individuals by 2030. This would be a 35 % decline from the 2019 population estimate (Fig. 3C).



336
337 Figure 3. Predicted population trajectory (black line) to the year 2030 for the Kruger National
338 Park white rhino population (black dots = distance sampling population estimates; open dots = block
339 census population estimates, with standard error bars) using age-structured population models under three
340 scenarios A) no poaching model (rainfall affects food availability), B) the direct poaching model (rainfall
341 plus poaching of adults and sub-adults affecting demographic parameters), and C) the combined direct

342 and indirect poaching model (rainfall plus poaching of adults and sub-adults and the indirect mortalities
343 of calves from the loss of their mothers). Light grey polygon depicts the 95% quantile of the population
344 trajectory from Markov chain Monte Carlo simulations. The dashed vertical line indicates the year when
345 forward projections start; projections were done under current (2019) poaching rates and average rainfall.

346 *Variable rainfall and poaching models*

347 Evaluating the model with increase rainfall, we estimated 2345 (1711-2400) rhinos in the year
348 2030, an increase of about 2% from baseline predictions with average rainfall (Table 2). Alternatively, the
349 model with variable rainfall resulted in a 0.6% increase from baseline predictions with 2326 (1707-2377)
350 rhinos predicted for the year 2030. Using the best fitting model (scenario 3), we found that a 50%
351 reduction in poaching would result in a doubling of the population by the year 2030, with a total of 5383
352 (4031-5491) rhinos. Furthermore, an 80% reduction in poaching would result in 8685 (6522-8843) rhinos
353 in the year 2030.

354 *The compound effect*

355 If no further poaching occurred after 2019 and average rainfall conditions prevailed, we would
356 expect a rhino female to produce 5.7 calves. However, the *compound effect* of poaching on rhino resulted
357 in a substantial reduction of this prediction to 0.73 calves per female if direct poaching continues.
358 Accounting for a continuation of both direct and indirect poaching we would expect a female's lifetime
359 reproductive output to be 0.52 calves (Table 2).

360 *Variation in demographic processes*

361 Investigating how the variation of dynamic parameters influenced demographic responses and population
362 growth, we found that besides survival, the initial three models (rainfall, rainfall and direct poaching, and
363 rainfall, direct and indirect poaching) had minimal sensitivity to variation in parameters (age specific
364 survival, food effects on juveniles, adults, and birthrates; Table 3). For scenario 1 we found limited
365 variation in both sub-adult and adult survival (0.97 - 0.99) suggesting that sub-adults and adults were
366 buffered from impacts caused by changes in rainfall. Calf survival varied between 0.91 – 0.99, which
367 suggests that calves were vulnerable to impacts caused by changes in rainfall. We found a weak but
368 measurable (0 – 0.053) food effect on birthrates suggesting changes in rainfall influence reproduction
369 (Table 2). For scenario 2, we again found limited variation in both sub-adult and adult survival (0.97 -
370 0.99) and variable calf survival 0.91 – 0.99. We found a weaker food effect for juvenile survival (0 -
371 0.014), adult survival (0 - 0.003) and on birthrates (0 – 0.025) suggesting that poaching accounted for
372 more variation in population growth than rainfall (Table 3). Finally, for scenario 3 we again found limited

373 variation in both sub-adult and adult survival (0.97 - 0.99). Calf survival was unsurprisingly most variable
374 (0.89 – 0.99), indicating that the combined effects of rainfall and indirect poaching had a sizeable
375 influence on calf survival. We found a weak food effect for juvenile (0 - 0.006) and adult (0 - 0.001)
376 survival and birthrates (0 – 0.012). Survival parameters had the most measurable influence on population
377 size (Table 2). There was a 10% decrease in the population estimate from the best fitting model when we
378 set the survival parameters to their lower limits and the food parameters to their upper limits.

379 Discussion

380 We present evidence that the dramatic decline in Kruger’s rhino population size was
381 predominantly a function of increased poaching, starting in 2008 (Thomas, 2010). Additionally, we show
382 that the subsequent change in the rhino population size was a function of direct loss of individuals plus
383 the indirect loss of calves from the *dependency effect*. Furthermore, we found support for rainfall having
384 an additive effect on poaching losses, with poached populations further depressed by cyclic rainfall
385 patterns.

386 Our best model for the rhino population in Kruger predicted a further 35 % decline by 2030 (2019
387 = 3549; 2030 = 2296) if current poaching rates continue. Field observations (Maggs, K. SANParks pers.
388 comm.) also support the idea that dependent calves and juveniles die when their mothers are poached.
389 Calves run away from poachers and may die from overheating, dehydration, hunger, and predation
390 (Maggs, K. SANParks pers. comm.). Having found evidence for the indirect effects of poaching on
391 calves, it is likely that calf mortalities have been underreported. This is likely due to their reduced
392 persistence on the landscape relative to adult rhinos (Sanparks, internal. report).

393 One of the reasons that the rhino population in Kruger is likely to continue to decline without an
394 intervention or change in poaching rates is because of the loss of lifetime reproductive potential. Without
395 poaching a female can produce approximately 6 calves, but with current poaching levels, the lifetime
396 reproductive output is reduced to 0.7 calves – a *compound effect* of approximately 5.3 offspring. When
397 we also account for the *dependency effect*, the lifetime reproductive success of a rhino cow is reduced to a
398 dismal 0.5 offspring, not enough to sustain a population (Sodhi, Brook, & Bradswah, 2009). This impact
399 is further compounded because, on average, half of the lost offspring would have been females whose
400 lifetime reproductive output was also lost.

401 A reduction in poaching would allow the population to recover, our models predicted that a 50%
402 reduction in poaching would result in the doubling of the population size by 2030. This result concurs
403 with previous research showing that when rhinos are afforded better protection populations can recover

404 (Amin *et al.*, 2006). Similarly, in another megaherbivore, a poached elephant population in Tanzania
405 rebounded when poaching was stopped (Foley and Faust, 2010).

406 Our models suggest that climate impacts were minimal compared with those of poaching;
407 however, we did see clear linkages between rhino reproduction, population growth and rainfall. Our
408 climate only model predicted the 2020 population size (5097) to be 44% greater than the current 2019
409 population (3549) if the current climate conditions persisted. This is a lower estimate than targeted by the
410 Biodiversity Management Plan (Knight, *et al.*, 2015). However, with the climate predictions for southern
411 Africa, and Kruger specifically, suggesting longer dry seasons and higher temperatures, these targeted
412 population sizes may not be realistic (Van Wilgen *et al.*, 2016). While rhinos do not appear to respond to
413 normal climatic variability (Shrader and Ogutu, 2006), substantial drought can cause reductions in
414 recruitment and increase mortality (Ferreira *et al.*, 2019). Our models highlight the potential for climate
415 induced declines to exacerbate poaching losses by an additional 10% decrease in rhino population over
416 the next decade.

417 Like other studies (Foley *et al.*, 2008; Gaillard *et al.*, 1993, 1998; Ogutu and Owen-Smith, 2003),
418 we found both climate and poaching accounted for the variation in juvenile survival. However, the
419 variability of juvenile survival did not have consequences for population growth. Instead, adult survival
420 had the greatest measurable changes to projected population size estimates. A reduction in adult survival
421 resulted in lower reproductive rates and population growth. Research has shown that for long-lived
422 species proportional changes in juvenile survival have less effect on population growth than proportional
423 change in adult survival (Gaillard *et al.*, 2000; Eberhardt, 2002; Gaillard and Yoccoz, 2003).

424 **Model considerations**

425 We made several assumptions for our models that were likely to influence our results. We
426 assumed all dependent calves and juveniles died when their mothers were poached because dependent
427 calves cannot fend for themselves. We also assumed some demographic parameters to be constant when
428 realistically they would vary over time and this variability would increase the uncertainty in the
429 population trajectories. Additionally, based on model fit we assumed 20% of the poached population was
430 sub-adults. We also assumed that the loss of younger females would have the same effects on the
431 population as the loss of older females. An older female may have already contributed most of her calves
432 per lifetime into the population, whereas a younger female may have not. Modeling this individual level
433 of variation requires high quality data on age-specific survival and other fitness components (Gaillard *et al.*
434 *et al.*, 2000; Richard *et al.*, 2014) not available for our study. Finally, we acknowledge that there would be
435 greater uncertainty in our reproductive estimates if we understood the uncertainties around birthing

436 intervals. It is also important to note that our future predictions do not include the effects of management
437 removals. Kruger removes rhinos as part of range expansion initiatives and to generate revenue (Clements
438 *et al.*, 2020; Ferreira *et al.*, 2012). Our predictions, however, are likely realistic because the complexities
439 of bovine tuberculosis quarantine requirements limit the movement of rhinos (Miller *et al.*, 2018), and
440 current poaching rates do not allow for the removal of rhinos without the potential for further population
441 declines (Ferreira *et al.*, 2012).

442 **Management implications**

443 Large mammal populations are limited by the number of reproductive females (Gaillard *et al.*,
444 2000; Gosselin *et al.*, 2014). Ensuring and improving the lifetime reproductive output of rhino cows
445 should thus be the highest priority for rhino management as it will result in high population growth rates.
446 Antipoaching initiatives for apprehending poachers must be coupled with an effective legal system that
447 distinguishes and places emphasis on population impacts associated with the poaching of cows over bulls.
448 As deterrents, we recommend those convicted of poaching a rhino cow get harsher sentences. This would
449 likely involve amendments to existing sentencing laws, but it could be achieved by demonstrating the
450 negative impacts associated with poaching cows. Live rhino cows are worth more than bulls, even when
451 you ignore the cost of future calves. In 2016, bulls sold for R270 000 at auction, while a cow plus a heifer
452 calf sold for R500 000 (SANParks intern. Report). This is revenue that was used to fund conservation
453 initiatives, which has been lost since the halting of live rhino auctions due to poaching. We also
454 recommend dehorning female rhinos that reside in high poaching areas to deter poachers. Any short-term
455 stresses detected in rhino's fecal glucocorticoid metabolites from the procedure (Badenhorst *et al.*, 2016)
456 do not appear to impact rhinos physiologically (Penny *et al.*, 2020), nor their reproductive success (Penny
457 *et al.*, 2019). Finally, managers should also consider translocating female rhinos or deterring them away
458 from high poaching areas, potentially by manipulating their perception of predation risk through the
459 introduction of predator cues (e.g. humans and lions; Cromsigt *et al.*, 2013; Clinchy *et al.*, 2016).
460 Harnessing animal's fear has been suggested as a management strategy for deterring animals away from
461 areas with high mortality risk (Cromsigt *et al.*, 2013; Kuijper *et al.*, 2019).

462 With the increasing likelihood of droughts (Cherwin and Knapp, 2012; Craine *et al.*, 2013) and
463 little indication that wildlife poaching will abate (Burn *et al.*, 2011; Challender and MacMillan, 2014;
464 Duffy *et al.*, 2014), large herbivores may be particularly vulnerable to population declines. South Africa
465 has failed to achieve its white rhino targets for 2020 (Knight, *et al.*, 2015). If authorities seek to achieve
466 the population targets in the next 2 decades, poaching levels must be reduced. Additionally, we
467 recommend a revision of population targets (Emslie and Brooks, 1999; Knight, *et al.*, 2015) to account

468 for the effects that a changing climate will have on rhino populations, as well as both the dependency and
469 compound effects associated with the poaching of rhino cows.

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474

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649

650 **Figure Captions**

651 **Figure 1:** Map of Kruger National Park in South Africa with sections south of the Olifants River where
652 white rhinos surveys were conducted from 1998-2019. The light blue line indicates the Olifants River and
653 the polygons represent the sections where rhinos from this study were located.

654 **Figure 2:** Fit of the age structured population model (black line) to white rhino population estimates
655 (black dots = distance sampling surveys, open dots = block census surveys, with standard error bars) for
656 the Kruger National Park from 1998-2019 under three modeling scenarios A) no poaching model (rainfall
657 affects food availability), B) the direct poaching model (rainfall plus poaching of adults and sub-adults
658 affecting demographic parameters), and C) the combined direct and indirect poaching model (rainfall plus
659 poaching of adults and sub-adults and the indirect mortalities of calves from the loss of their mothers).
660 Light grey polygon depicts the 95% quantile of population trajectory from Markov chain Monte Carlo
661 simulations.

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663 **Figure 3:** Predicted population trajectory (black line) to the year 2030 for the Kruger National Park
664 white rhino population (black dots = distance sampling population estimates; open dots = block census
665 population estimates, with standard error bars) using age-structured population models under three
666 scenarios A) no poaching model (rainfall affects food availability), B) the direct poaching model (rainfall
667 plus poaching of adults and sub-adults affecting demographic parameters), and C) the combined direct
668 and indirect poaching model (rainfall plus poaching of adults and sub-adults and the indirect mortalities
669 of calves from the loss of their mothers). Light grey polygon depicts the 95% quantile of the population

670 trajectory from Markov chain Monte Carlo simulations. The dashed vertical line indicates the year when
 671 forward projections start; projections were done under current (2019) poaching rates and average rainfall.

672 **Table 1:** A priori known demographic parameters derived from published and unpublished literature on
 673 the biology of white rhinos.

Description	Origin
Starting population – 2280	SANParks unpublished data
Birth frequency – 2.5 years	(Owen-Smith, 1982, 1988; Bertschinger, 1994)
Senescence age - 30	(Bertschinger, 1994)
Sex ratio – 0.54	SANParks unpublished data

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676 **Table 2:** Population estimates and reproductive success for the Kruger National Park white rhino
 677 population under different poaching levels and model scenarios 1) the combined direct and indirect
 678 poaching model (rainfall plus poaching of adults and sub-adults and the indirect mortalities of calves from
 679 the loss of their mothers), 2) high survival and low food effect, and 3) low survival and high food effect 4)
 680 high rainfall, 5) variable rainfall. Where food effect refers to food availability because of the amount of
 681 dry seasoning rainfall.

Model	2030 estimate under current poaching	50% of current poaching	20% of current poaching	Lifetime reproductive – no poaching	Lifetime reproductive – poaching	Lifetime reproductive – poaching + calf loss
Baseline						
Model	2312	5383	8685	5.70	0.73	0.52

High
Survival,

low food effect	2107	4894	7881	5.93	0.75	0.53
Low survival, high food effect	2072	4811	7745	5.93	0.75	0.53
High rainfall	2345	5443	8825	5.86	0.74	0.53
Variable rainfall	2326	4687	7915	5.93	0.75	0.53

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684 **Table 3:** Maximum likelihood Estimations (MLE) for demographic parameters from the Kruger National
685 Park white rhino population model based on 3 1) no poaching model (rainfall affects food availability), B) the
686 direct poaching model (rainfall plus poaching of adults and sub-adults affecting demographic parameters), and C)
687 the combined direct and indirect poaching model (rainfall plus poaching of adults and sub-adults and the indirect
688 mortalities of calves from the loss of their mothers).

Model	Parameter	MLE (95% CI)
Scenario 1	Calf survival	0.99 (0.94-0.99)
	Sub-adult survival	0.99 (0.98-0.99)
	Adult survival	0.99 (0.99-0.99)
	Food effect on juveniles	0 (0-0.034)
	Food effect on adults	0.015 (0-0.017)
	Food effect on birthrates	0 (0-0.053)

Scenario 2	Calf survival	0.99 (0.91-0.99)
	Sub-adult survival	0.99 (0.96-0.99)
	Adult survival	0.99 (0.98-0.99)
	Food effect on juveniles	0 (0-0.014)
	Food effect on adults	0.002 (0-0.003)
	Food effect on birthrates	0.005 (0-0.025)
Scenario 3	Calf survival	0.99 (0.94-0.99)
	Sub-adult survival	0.99 (0.98-0.99)
	Adult survival	0.99 (0.99-0.99)
	Food effect on juveniles	0 (0-0.006)
	Food effect on adults	0.0006 (0-0.001)
	Food effect on birthrates	0 (0-0.012)

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