

1 **Running title: Herbivore Population Dynamics in Ngorongoro Crater, Tanzania**

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3 **Title: Long-Term historical and Projected Herbivore Population Dynamics in Ngorongoro**
4 **Crater, Tanzania**

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30 data, drafting the article or revising it critically for important intellectual content. All authors
31 read and approved the manuscript.

32

33 **Abstract**

34

35 The Ngorongoro Crater is an intact caldera with an area of approximately 310 km². Long term
36 records on herbivore populations, vegetation and rainfall made it possible to analyze historic and
37 project future herbivore population dynamics. In 1974 there was a perturbation in that resident
38 Maasai and their livestock were removed from the Crater. Vegetation structure changed in 1967
39 from predominately short grassland to mid and tall grasses dominating in 1995. Even with a
40 change in grassland structure, total herbivore biomass remained relatively stable from 1963 to
41 2012, implying that the crater has a stable multi-herbivore community. However, in 1974,
42 Maasai pastoralists were removed from the Ngorongoro Crater and there were significant
43 changes in population trends for some herbivore species. Buffalo, elephant and ostrich numbers
44 increased significantly during 1974-2012. The zebra population was stable from 1963 to 2012
45 whereas numbers of other eight species declined substantially between 1974 and 2012 relative to
46 their peak numbers during 1974-1976. Numbers of Grant's and Thomson's gazelles, eland,

47 kongoni, waterbuck (wet season only) declined significantly in the Crater in both seasons after
48 1974. Wildebeest numbers decreased in the Crater between 1974 and 2012 but this decrease was
49 not statistically significant. In addition, some herbivore species were consistently more abundant
50 inside the Crater during the wet than the dry season. This pattern was most evident for the large
51 herbivore species requiring bulk forage, comprising buffalo, eland, and elephant. Analyses of
52 rainfall indicated that there was a persistent annual cycle of 4.83 years. Herbivore population size
53 was correlated with rainfall in both the wet and dry seasons. The relationships established
54 between the time series of historic animal counts in the wet and dry seasons and lagged wet and
55 dry season rainfall series were used to forecast the likely future trajectories of the wet and dry
56 season population size for each species under three alternative climate change scenarios.

57
58 **Key words:** Wildlife; ungulates; wildlife conservation; population trends; population dynamics;
59 population status; Population modelling; climate change and variability; Climate change
60 Scenarios; RCP 2.6; RCP 4.5; RCP 8.5; rainfall; temperature; protected areas, Ngorongoro
61 Crater, Ngorongoro Conservation Area, Serengeti-Ngorongoro Ecosystem; African savannas

62 63 **Introduction**

64 The Ngorongoro Crater, Tanzania is known world-wide for the abundance and diversity of its
65 wildlife. It is situated in the Crater Highlands and is linked both to this area and the Serengeti
66 Plains by the seasonal migration of several herbivores [1,2] and the emigration and immigration
67 of large carnivores [4-8].

68

69 Since 1963, the herbivore population of Ngorongoro Crater has been monitored by the
70 Ngorongoro Conservation Area Authority (NCAA), The College of African Wildlife
71 Management and research scientists [1-3,9-12]. Since 1978, the Ngorongoro Ecological
72 Monitoring Program has been responsible for conducting the wet and dry season censuses. The
73 complete data set covers a period of 50 years (1963-2012). This data set makes it possible to
74 assess long-term population trends and the stability of this multi-species wild herbivore
75 community.

76
77 Earlier analyses indicated that the eviction of Maasai, the removal of their livestock and changes
78 in rangeland management correlated with complex changes in vegetation composition and
79 structure and wild herbivore populations. Previous papers have hypothesized that the removal of
80 the Maasai pastoralists was a key factor in changes observed in herbivore populations. Pastoral
81 pasture management may have affected vegetation structure and species composition [12,13].

82
83 This paper further examines the hypothesis that the removal of the Maasai and their livestock
84 from the Crater in 1974 affected the plant structure in the crater and the population dynamics of
85 the resident wild herbivore species depending on their life-history traits (body size, gut
86 morphology) and life-history strategies (feeding style, foraging style, and movement patterns).

87
88 In addition we examine the hypothesis that rainfall variation influences the herbivore population
89 dynamics and density, differentiated by life-history traits and strategies. Extreme rainfall in the
90 Crater, which waterlogs large parts of the Crater should adversely affect wildlife, just like
91 droughts, if large parts of the Crater become waterlogged. Additionally, high rainfall promotes

92 excessive grass growth and dilutes plant nutrients, hence reducing vegetation quality for
93 herbivores.

94

95 Relationships established between historic population abundance and historic rainfall are used to
96 project the impacts of three different future rainfall scenarios on wild herbivore population
97 dynamics to 2100.

98

99 **Methods**

100 **Study Area**

101 Ngorongoro Crater, Tanzania is known world-wide for the abundance and diversity of its
102 wildlife. The crater (3°10' S, 35° 35' E) is a large intact caldera with an area of approximately
103 310 km². The floor of the crater is about 250 km² (1,700 m above sea level) and the sides rise
104 steeply 500 meters to the rim. The geology, soils and vegetation of the crater were described by
105 Herlocker and Dirschl [14] and Anderson and Herlocker [15]. The crater has the largest
106 catchment basin in the Ngorongoro Highlands [16] and receives water from Lalratati and Edeani
107 streams and Lerai spring from Oldeani Mountain to the south. Seneto spring provides water to
108 Seneto swamp and Lake Magadi from the southwest. Olmoti Crater provides runoff to Laawanay
109 and Lemunga rivers in the north, which supply Mandusi swamp and Lake Magadi. Ljoro Nyuki
110 river, in the northeast provides water to Gorigor swamp. Ngaitokitok spring in the eastern part of
111 the crater also supplies Gorigor swamp and Lake Magadi. Soil characteristics and drainage affect
112 vegetation species and during the dry season soil moisture is dependent on the crater's catchment
113 system (Fig. 1). The wildlife of Ngorongoro Crater has had a protected status since 1921. In
114 1974, resident Maasai pastoralists, their bomas and livestock were removed from the crater

115 [10,17]. The area has been administered by the Ngorongoro Conservation Unit since 1959 and by
116 the Ngorongoro Conservation Area Authority since 1975 as part of a protected multiple land use
117 area (8,292 km²).

118

119 **Wild herbivore populations**

120 Long term data sets were available for eleven mammalian herbivores, i.e. Wildebeest
121 (*Connochaetes taurinus*), Plains Zebra (*Equus quagga*), Cape Buffalo (*Syncerus caffer*),
122 Thomson's gazelle (*Eudorcas thomsonii*), Grant's gazelle (*Nanger granti*), Eland (*Tragelaphus*
123 *oryx*), Kongoni (*Alcelaphus buselaphus*), Waterbuck (*Kobus ellipsiprymnus*), Warthog
124 (*Phacochoerus aethiopicus*), Elephant (*Loxodonta africana*) and Black Rhino (*Diceros bicornis*)
125 and one bird, the Ostrich (*Struthio camelus*).

126

127 Zebra are mid-sized herbivores, but they are non-ruminants. Hence they are not limited by a
128 four-chambered stomach system and can opt to consume larger amounts of higher fiber (lower
129 quality) grasses to meet their nutritional requirements [18].

130

131 Buffalo are large bodied ruminants and although they require a larger amount of food per
132 individual, the quality can be lower and they can tolerate a higher proportion of fiber in their diet
133 [18,19]. Buffalo prefer longer grass and select for a high ratio of leaf to stem [20].

134

135 The herbivores were classified into functional categories, i.e., grazers (Thomson's gazelle,
136 kongoni, wildebeest, eland, buffalo, and zebra) and mixed browsers/grazers (Grant's gazelle,

137 waterbuck, black rhino and elephant) [21-27]. The ostrich is primarily a herbivore, but will also
138 eat invertebrates and occasionally rodents [28].

139

140 **Herbivore Total Counts**

141 Since 1963, the herbivore population of Ngorongoro Crater has been monitored by the
142 Ngorongoro Conservation Area Authority (NCAA), The College of African Wildlife
143 Management and research scientists [1-3,9-12]. Since 1987, the Ngorongoro Ecological
144 Monitoring Program has been responsible for conducting the wet and dry season censuses. This
145 data set makes it possible to assess long-term population trends and the stability of this multi-
146 species wild herbivore community. Here, we consider the data set covering a period of 50 years
147 (1963-2012).

148

149 Total counts of large mammals in the wet and dry seasons have been done in the crater since the
150 1963. The floor of the crater was divided into six blocks (Fig 1) that cover the entire area except
151 for inaccessible areas, i.e., Lake Magadi, Lerai Forest and the Mandusi and Gorigor swamps. The
152 ground censuses are done by one team per block composed of one driver, one observer and one
153 recorder in a four-wheel drive vehicle driving along line transects that are one kilometer apart.
154 Since 1987 each of the six teams has been supplied with a 1:50,000 map marked with the
155 transects, a compass, binoculars and a mechanical counter. Each block takes six to eight hours to
156 complete and all blocks are censused simultaneously [12, 29-34]. Unpublished records of NCAA
157 and NEMP 1963 - 2012 provide most of the seasonal data on animal numbers.

158

159 From 1981 to 1985 there were no censuses. In 1986 the total counts were resumed and strip
160 counts were used for counting gazelles and warthog and analyzed with Jolly's method 2 [35].
161 Strip counts were discontinued after 1989 because of unacceptably large confidence limits and
162 the difficulty of maintaining absolutely straight transects in the wet season. Data from strip
163 counts were not used in the analyses. However, 'transects' are still used to ensure complete
164 coverage of each block. Total aerial counts were conducted in 1964, 1965, 1966, 1977, 1978 and
165 1988 [12]. A systematic reconnaissance flight count was done in 1980 which included warthogs
166 for the first time [36]. Total counts of warthogs started in 1986 [12]. The count totals for the 12
167 most common large herbivore species for the Ngorongoro Crater during 1963-2012 are provided
168 in S1 Data. The same data set with the missing counts imputed using a state space model is
169 provided in S2 Data.

170
171 Total biomass for the wet and dry seasons for each year were calculated using unit weights in
172 Coe et al. [37]. Biomass was calculated separately for each species and season. The fact that
173 black rhinos, elephants and warthogs move into the forest at the edge of the crater and into Lerai
174 forest make them more difficult to count and may affect their contribution to biomass.

175
176 **Vegetation**

177 Changes in vegetation composition and structure were measured by digitizing and comparing
178 vegetation maps that were done in 1966-67 and 1995 [14,38]. Maps were digitized in ArcGIS 9.1
179 (ESRI, Redlands, California) and projected to UTM Zone 36, WGS 1984 datum. Attributes on
180 the maps were digitized, and in both maps the plant height for primary and secondary canopy
181 species was used to determine the presence of short, mid, mid-tall and tall grass structure.

182

183 Fires were suppressed from 1974, when the Maasai were removed, until 2001 [39]. Prescribed
184 burning started in 2001. Transects were used to measure canopy height and biomass in kg/ha
185 estimated by linear regression. Starting in 2001, areas with more than 4000 kg/ha were burned
186 every year at the end of the dry season (September/October). It was recommended that 10-20%
187 of the crater floor was burned on a rotational basis. Highest tick density occurred in the peak dry
188 season (September/October) in the longest grass. Twenty-seven months after the start of
189 prescribed burning, there was a significant decrease in tick density in burned areas. Short grass
190 (<10 cm) areas with a fuel load of less than 4000 kg/ha appear to correlate with limited tick
191 survival [39]. From 2002 to 2011 there was prescribed burning but no records were maintained.
192 From 2012 to 2017 approximately 10 to 15 km² were burned each year in different areas. In
193 2012-2015 burning was done in the northern and northeastern portion of the crater. In 2016 and
194 2017 burning was conducted in the eastern and then the east central portion of the crater (Pers
195 comm NCAA 2018).

196

197 **Rainfall**

198 Long-term rainfall data was not available for the crater floor. We therefore used monthly rainfall
199 measured from 1964 to 2014 at Ngorongoro Headquarters on the southern rim of the crater. The
200 rainfall recorded at the Ngorongoro Conservation Area Authority (NCAA) headquarters during
201 1963-2014 is provided in S3 Data.

202

203 **Projection of rainfall and temperature**

204 Total monthly rainfall and average monthly minimum and maximum temperatures for
205 Ngorongoro Crater were projected over the period 2013-2100 based on regional downscaled
206 climate model data sets from the Coordinated Regional Climate Downscaling Experiment
207 (CORDEX). Downscaling is done using multiple regional climate models as well as statistical
208 downscaling techniques. Three climate scenarios defined in terms of Representative
209 Concentration Pathways (RCPs) were used to project rainfall and temperatures for the
210 Ngorongoro Crater. The three RCPs are RCP2.6, RCP4.5 and RCP8.5 in which the numeric
211 suffixes denote radiative forcings (global energy imbalances), measured in watts/m², by the year
212 2100. The RCP2.6 emission pathway (best case scenario) is representative for scenarios leading
213 to very low greenhouse gas concentration levels [40]. RCP4.5 (intermediate scenario) is a
214 stabilization scenario for which the total radiative forcing is stabilized before 2100 by
215 employment of a range of technologies and strategies for reducing greenhouse gas emissions
216 [41]. RCP8.5 (worst case scenario) is characterized by increasing greenhouse gas emission over
217 time representative for scenarios leading to high greenhouse gas concentration levels [42].
218 Rainfall, minimum and maximum temperature projections were made for a 50 × 50 km box
219 defined by longitudes (34.97, 35.7) and latitudes (-3.38, -2.787).

220

221 **Ethics Statement**

222 All the animal counts in the Ngorongoro Crater were carried out as part of a long-term
223 monitoring Program under the auspices of the Ngorongoro Conservation Area Authority
224 (NCAA).

225

226 **Statistical modeling and analysis**

227 **Modeling trends in animal population size and biomass**

228 Time trends in count totals for all the 12 most common large herbivore species were modeled
229 simultaneously using a multivariate semiparametric generalized linear mixed model assuming a
230 negative binomial error distribution and a log-link function. The variance of the negative
231 binomial distribution model $\text{var}(y)$ was specified as a quadratic function of the mean (μ),
232 $\text{var}(y) = \mu(1 + \mu/k)$, where k is the scale parameter. The semi-parametric model is highly
233 flexible and able to accommodate irregularly spaced, non-normal and overdispersed count data
234 with many zeroes or missing values. The parametric part of the model contains only the main
235 effect of animal species to allow direct estimation of the average population sizes for the
236 different species in each season. The non-parametric part of the model contains two continuous
237 random effects, each of which specifies a penalized spline variance-covariance structure. The
238 first random spline effect fits a penalized cubic B-spline (P-spline, [43]) with a third-order
239 difference penalty to random spline coefficients common to all the 12 species and therefore
240 models the temporal trend shared by all the species. The second random spline effect fits a
241 penalized cubic B-spline with random spline coefficients specific to each species and thus
242 models the temporal trend unique to each species. Each random spline effect had 20 equally
243 spaced interior knots placed on the running date of the surveys (1963, ..., 2012) plus three evenly
244 spaced exterior knots placed at both the start date (1963) and end date (2012) of the surveys. De
245 Boor [44] describes the precise computational and mathematical properties of B-splines. The
246 specific smoothers we used derive from the automatic smoothers described in Ruppert, Wand
247 and Carrol [45].

248

249 The full model contains three variance components to be estimated, corresponding to the random
250 spline time trend common to all species, random spline effects for the time trend specific to each
251 species and the scale parameter for the negative binomial distribution. The full trend model was
252 fitted by the residual penalized quasi-likelihood (pseudo-likelihood) method [46] in the SAS
253 GLIMMIX procedure [47]. More elaborate details on this approach to modelling animal
254 population trends can be found in Ogutu et al. [48]. Separate trend models were fit to the wet and
255 dry season count totals for simplicity. The denominator degrees of freedom for Wald-type F-tests
256 were approximated using the method of Kenward and Roger [49]. Temporal trends in total
257 biomass calculated using unit weights in Coe et al. [37] were similarly modeled, separately for
258 each season.

259
260 We used constructed spline effects to estimate and contrast population sizes for each species
261 between 1964 versus 1974 when the Maasai and their livestock were evicted from the Crater and
262 1974 versus 2012. The constructed spline effects consisted of a cubic B-spline basis with three
263 equally spaced interior knots. A constructed regression spline effect expands the original time
264 series of animal survey dates into a larger number of new variables (seven in this specific case).
265 Each of the new variables is a univariate spline transformation. The constructed spline effects are
266 special model effects, in contrast to classical classification or continuous effects, and can be
267 constructed using various other basis functions, including the truncated power function basis.
268 These special model effects allowed estimation of the expected counts of each animal species at
269 specified values of time (1964, 1974 and 2012). Because of the two comparisons made for each
270 species, a multiplicity correction was made to control the familywise Type I error rate. We thus
271 computed simulation-based step-down-adjusted p -values [50].

272

273 **Modeling temporal variation in rainfall**

274 The time series of rainfall was analyzed by using the unobserved components model (UCM),
275 which is a special case of the linear Gaussian state space or structural time series model, to
276 decompose the annual, wet season and dry season rainfall time series (r_t) into their trend (μ_t),
277 cyclical (φ_t), seasonal (δ_t) and irregular (ϵ_t) components

278

$$279 \quad r_t = \mu_t + \varphi_t + \delta_t + \partial_t + \sum_{i=1}^p \theta_i r_{t-i} + \sum_{j=1}^m \beta_j x_{jt} + \epsilon_t; \quad t = 1, 2, \dots, n \quad (1)$$

280

281 in which ∂_t is the autoregressive component, $\sum_{i=1}^p \theta_i r_{t-i}$ is the autoregressive regression terms,
282 β_j are the explanatory regression coefficients, x_{jt} are regression variables treated as fixed effects
283 and (ϵ_t) are independent and identically (*i.i.d.*) normally distributed errors or disturbances having
284 zero mean and variance σ_ϵ^2 . This is equivalent to assuming that ϵ_t is a Gaussian white noise
285 process. The different model components are assumed to be statistically independent of each
286 other.

287

288 We first assume a random walk (RW) model for the time trend, or equivalently that the trend (μ_t)
289 remains approximately constant through time. The RW trend model can be specified as

290

$$291 \quad \mu_t = \mu_{t-1} + \eta_t \quad (2)$$

292

293 where $\eta_t \sim i.i.d. N(0, \sigma_\eta^2)$. Note that $\sigma_\eta^2 = 0$ implies that $\mu_t = a \text{ constant}$.

294

295 Additionally, we assume a stochastic cycle (φ_t) with a fixed period ($p > 2$), a damping factor (ρ)
 296) and a time-varying amplitude and phase given by

$$298 \begin{bmatrix} \varphi_t \\ \varphi_t^* \end{bmatrix} = \rho \begin{bmatrix} \cos\omega & \sin\omega \\ -\sin\omega & \cos\omega \end{bmatrix} \begin{bmatrix} \varphi_{t-1} \\ \varphi_{t-1}^* \end{bmatrix} + \begin{bmatrix} v_t \\ v_t^* \end{bmatrix} \quad (3)$$

299
 300 where $0 < \rho \leq 1$, $\omega = 2 \times \pi/p$ is the angular frequency of the cycle, v_t and v_t^* are independent
 301 Gaussian disturbances with zero mean and variance σ_v^2 and $0 < \omega < \pi$. Values of ρ , p and σ_v^2 are
 302 estimated from the data alongside the other model parameters. The damping factor ρ governs the
 303 stationarity properties of the random sequence φ_t such that φ_t has a stationary distribution with
 304 mean zero and variance $\sigma_v^2/(1 - \rho^2)$ if $\rho < 1$ but is nonstationary if $\rho = 1$. We specified and
 305 tested for significance of up to three cycles in the annual, wet season and dry season rainfall
 306 components.

307
 308 Besides the random walk model (2), we modelled the trend component using a locally linear time
 309 trend incorporating the level and slope components and specified by

$$311 \mu_t = \mu_{t-1} + \beta_{t-1} + \eta_t, \quad \eta_t \sim i.i.d. (0, \sigma_\eta^2) \quad (4)$$

$$312 \beta_t = \beta_{t-1} + \xi_t, \quad \xi_t \sim i.i.d. (0, \sigma_\xi^2),$$

313
 314 where the disturbance variances σ_η^2 and σ_ξ^2 are assumed to be independent. The UCM models (1)
 315 and (4), without the seasonal and regression components, were fitted by the diffuse Kalman
 316 filtering and smoothing algorithm [51] in the SAS UCM procedure [47].

317
318 We grouped years with the annual rainfall falling within the 0–10, 11–25, 26–40, 41–75, 76–90,
319 91–95 and 96–100th percentiles of the frequency distribution of the annual rainfall as extreme,
320 severe or moderate drought years, normal, wet, very wet or extremely wet years, respectively.
321 The dry (June to October) and wet (November to May) seasons were similarly grouped [52].
322 These percentiles allowed us to quantify the degree of rainfall deficit or surfeit and represent the
323 expected broad transitions in rainfall influences on vegetation production and quality in each
324 year and season.

325

326 **Relating animal population size to rainfall**

327 Rainfall primarily governs vegetation production and quality in savannas [53-55], and therefore
328 also the aggregate and species-specific biomass levels of large African savanna ungulates [37,56-
329 58]. Population size was related to moving averages of the annual, wet season and dry season
330 rainfall components each computed over 1, 2, ..., 6 years for a total of six different moving
331 averages per rainfall component. The maximum of 6-year window was chosen to match the
332 approximately 5-year dominant periodicity or quasi-cyclical pattern estimated for the time series
333 of the wet season and annual rainfall components (Fig S3), based on the UCM model and
334 spectral functions evaluated by the finite Fourier transform method. Spectral densities were
335 obtained by smoothing the raw spectra or periodograms using moving average smoothing with
336 weights derived from the Parzen kernel [47].

337

338 The moving rainfall averages index changing habitat suitability for ungulates associated with
339 carry-over effects of prior rainfall on vegetation conditions. Population sizes was related to each

340 of the 18 moving averages using a generalized linear model assuming a negative binomial error
341 distribution and a log link function. The following six different functional forms were used for
342 each of the 18 moving averages [58]:

343 $\mu = \exp(\alpha r)$ (5)

344

345 $\mu = \exp(\alpha r + \beta r^2)$ (6)

346

347 $\mu = \exp(\alpha \ln(r))$ (7)

348

349 $\mu = \exp(\alpha r + \beta \ln(r))$ (8)

350

351 $\mu = \exp(\alpha r + \beta r^2 + \gamma \ln(r))$ (9)

352

353 $\mu = \exp(\alpha r + \beta \ln(r) + \gamma \ln(r))$ (10)

354

355 These models were selected to represent (1) a linear increase or decrease in animal population
356 size with increasing rainfall, (2) an increase in animal abundance with increasing rainfall up to
357 some asymptote, or (3) an increase in animal abundance with increasing rainfall up to a peak at
358 some intermediate levels of rainfall, followed by decline with further increase in rainfall [58].

359 The most strongly supported rainfall component, specific moving average and functional form
360 were then selected using the corrected Akaike Information Criterion (AICc, [59] Tables S13-
361 S14).

362

363 **Forecasting animal population dynamics using projected future climate**

364 The relationships established between the time series of historic animal counts in the wet and dry
365 seasons and lagged wet and dry season rainfall series were used to forecast the likely future
366 trajectories of the wet and dry season population size for each species under three alternative
367 climate change scenarios. We used the (Vector Autoregressive Moving Average Processes)
368 VARMAX model to model the dynamic relationships between the wet and dry season counts of
369 each species and the lagged wet and dry season rainfall and to forecast the seasonal animal
370 counts. The model is very general and highly flexible and allows for the following among other
371 features. 1) Modelling several time series of animal counts simultaneously. 2) Accounting for
372 relationships among the individual animal count component series with current and past values
373 of the other series. 3) Feedback and cross-correlated explanatory series. 4) Cointegration of the
374 component animal series to achieve stationarity. 5) Seasonality in the animal count series. 6)
375 Autoregressive errors. 7) Moving average errors. 8) Mixed autoregressive and moving average
376 errors. 9) Distributed lags in the explanatory variable series. 10). Unequal or heteroscedastic
377 covariances for the residuals.

378 The VARMAX model incorporating an autoregressive process of order p , moving average
379 process of order q and in which the number of lags of exogenous (independent) predictor
380 variables s is denoted as VARMAX(p,q,s). Since some animals move seasonally between the
381 Ngorongoro Crater and the surrounding multiple use areas, the wet and dry season counts do not
382 estimate the same underlying population size. We therefore treat the wet and dry season counts
383 as two separate but possibly correlated variables and use a bivariate VARMAX(p,q,s) model. We
384 allow variation in herbivore numbers in the wet and dry season to depend on the total wet and
385 dry season rainfall in the current year (t) and in the preceding five years ($t-1, \dots, t-5$). The model

386 thus allows the current wet and dry season rainfall components and their lagged values up to five
387 years prior to the current count year to influence the population size of herbivores in the current
388 wet and dry season. The model can also therefore be viewed as a multiple (or distributed) lag
389 regression model. The VARMAX (p,q,s), model we used to forecast the future population
390 dynamics of the five most abundant herbivore species can thus be cast as:

$$391 \quad \mathbf{N}_t = \sum_{j=1}^p \Phi_j \mathbf{N}_{t-j} + \sum_{j=0}^s \Omega_j^* \mathbf{x}_{t-j} + \boldsymbol{\epsilon}_t - \sum_{j=1}^q \Omega_j \boldsymbol{\epsilon}_{t-j} \quad (11)$$

392
393 where $\mathbf{N}_t = (N_{wet,t}, N_{dry,t})^T$ are the population sizes of the same species in the wet and dry
394 seasons at time t , $\mathbf{x}_t = (wet_{t-0}, \dots, wet_{t-5}, dry_{t-0}, \dots, dry_{t-5})^T$ are the wet and dry season
395 rainfall components divided by their long-term means and lagged over 0 to 5 years. $\boldsymbol{\epsilon}_t =$
396 $(\epsilon_{wet,t}, \epsilon_{dry,t})^T$ are a two-dimensional vector white noise process. It is assumed that $E(\boldsymbol{\epsilon}_t) = \mathbf{0}$, E
397 $(\boldsymbol{\epsilon}_t \boldsymbol{\epsilon}_t^T) = \boldsymbol{\Sigma}$ and $E(\boldsymbol{\epsilon}_t \boldsymbol{\epsilon}_u^T) = \mathbf{0}$ for $t \neq u$. We further assume that p and q are each equal to either 1 or 2
398 whereas s is set equal to 5. Accordingly, the model can be denoted symbolically as a VARMAX
399 (2,2,5) model. In other words, in order to project the population dynamics of the Ngorongoro
400 large herbivores, we built a model relating the population size of each herbivore species in the
401 current year (t) to the population size in the past one to two years (year $t-1$ and $t-2$; i.e.,
402 autoregressive process of order $p = 1$ or 2). The model also allows residuals for the current year
403 to depend on the residuals for the previous one to two years (i.e. a moving average process of
404 order $q = 1$ or 2). Since herbivore numbers are counted once in the wet season and once in the dry
405 season of each year we did not allow for seasonal variation in the counts.

407

408 The VARMAX (p,q,s) model can be represented in various forms, including in state space and
409 dynamic simultaneous equation or dynamic structural equations forms. We used bivariate
410 autoregressive moving average models with the wet and dry season rainfall as the explanatory
411 variables. We tested and allowed for various lags in rainfall so that the models can be
412 characterised as autoregressive and moving-average regression with distributed lags. We also
413 used dead-start models that do not allow for present (current) values of the explanatory variables.
414 We tested for heteroscedasticity in residuals and tested the appropriateness of GARCH-type
415 (generalized autoregressive conditional heteroscedasticity) conditional heteroscedasticity of
416 residuals. We used several information-theoretic model selection criteria as aids to determine the
417 autoregressive (AR) and moving average (MA) orders of the models. The specific criteria we
418 used were the Akaike information criterion (AIC), the corrected AIC (AICc) and the final
419 prediction error (FPE). As additional AR order identification aids, we used partial cross-
420 correlations for the response variable, Yule-Walker estimates, partial autoregressive coefficients
421 and partial canonical correlations. Parameters of the selected full models were estimated using
422 the maximum likelihood (ML) method. Roots of the characteristic functions for both the AR and
423 MA parts (eigenvalues) were evaluated for the proximity of the roots to the unit circle to infer
424 evidence for stationarity of the AR process and inevitability of MA process in the response
425 series.

426

427 The adequacy of the selected models was assessed using various diagnostic tools. The specific
428 diagnostic tools we used are the following. 1) Durbin-Watson (DW) test for first-order
429 autocorrelation in the residuals. 2) Jarque-Bera normality test for determining whether the model
430 residuals represent a white noise process by testing the null hypothesis that the residuals are

431 normally distributed. 3) F tests for autoregressive conditional heteroscedastic (ARCH)
432 disturbances in the residuals. This F statistic tests the null hypothesis that the residuals have
433 equal covariances. 4) F tests for AR disturbance computed from the residuals of the univariate
434 AR(1), AR(1,2), AR(1,2,3) and AR(1,2,3,4) models to test the null hypothesis that the residuals
435 are uncorrelated. 5) Portmanteau test for cross correlations of residuals at various lags. Final
436 forecasts and their 95% confidence intervals were then produced for the animal population size
437 series for each of the five most common species in each season for lead times running from 2013
438 up to 2100.

439
440 In the table of the parameter estimates for the bivariate VARMAX (2,2,5) model fitted to the two
441 time series of herbivore population size in the wet and dry seasons (Table S1), the five lagged
442 dry and wet season rainfall components (rightmost column labelled variable) for the current year
443 (year t) up to five years prior to the current year (years $t-1, \dots, t-5$) are denoted by dry (t), ..., dry
444 ($t-5$) and wet (t), ..., wet ($t-5$), respectively. Analogously, for the dry season counts, the
445 autoregressive process of order 2 is denoted by, e.g., wildebeest_dry_ $(t-1)$ and wildebeest_dry (t
446 -2) while the moving average process of order 2 by e1($t-1$) and e2 ($t-2$). A parallel notation is
447 used for the wet season counts. The estimated regression coefficients (estimate) for the
448 parameters associated with each of these variables plus the intercept (Const1), the standard
449 errors of the estimates and a t -test (t -value) of the null hypothesis that each coefficient is not
450 significantly different from zero ($\text{Pr } > |t|$) are also provided in Table S1. Furthermore, the
451 estimated roots of the autoregressive (Table S2) and moving average (Table S3) processes are
452 provided. It is important to note that the population of each herbivore species in the wet season
453 of the current year depends not only on its lagged values in the preceding one to two years and

454 on the current and past values of rainfall but also on the population of the same herbivore species
455 in the dry season lagged over the past one to two years. The same applies to the population of
456 each herbivore species in the current dry season. This interdependence of the two series on each
457 other is made possible because of the bivariate nature of the VARMAX (p,q,s) model. This
458 model was fitted to the population counts of the herbivores for the wet and dry seasons for the
459 period 1964-2012 based on historic station rainfall data for 1963 to 2012. Note that the historic
460 total wet season rainfall component was divided by its mean for use in the model. The same was
461 done for the total dry season rainfall component. Future forecasts were then produced by
462 supplying the projected wet and dry season rainfall values, each divided by its mean, for
463 Ngorongoro for 2013 to 2100.

464 Several univariate model diagnostics were used to extensively assess how well the selected
465 bivariate VARMAX (p,q,s) model fitted the count data (Tables S4-S7). The first model
466 diagnostic tool, the Portmanteau Test for Cross Correlations of Residuals (Table S4) was
467 significant, considering only up to lag 5 residuals. This test of whether the residuals are white
468 noise residuals (i.e. uncorrelated) based on the cross correlations of the residuals, suggests that
469 the residuals were apparently correlated, when only up to lag 5 residuals are considered. Even so,
470 results of the univariate model ANOVA diagnostics suggest that the models for both the dry and
471 wet season counts were highly significant and had high predictive power (r^2 , Table S5). Results
472 of the Univariate Model White Noise Diagnostics (Table S6) suggest that the residuals are
473 normally distributed (Jarque-Bera normality test) and have equal covariances (ARCH (1)
474 disturbances test). The Univariate AR Model Diagnostics indicate that the residuals are
475 uncorrelated, contrary to the finding of the multivariate Portmanteau test (Table S7). The
476 modulus of the roots (eigenvalues) of the AR characteristic polynomial are less than 1 suggesting

477 that the series are stationary. These tests suggests that the fitted models are reasonable. The log-
478 transformed animal count totals, rainfall deviates, projected rainfall and forecast animal count
479 totals (log scale) are provided in S4 Data. The SAS program codes used to analyze the rainfall
480 data are provided in S1 Text while the code for analyzing the animal counts is provided in S2
481 Text.

482 **Results**

483 **Rainfall**

484 Rainfall can be subdivided into the dry and wet season components. The dry season occurs from
485 June to October whereas the wet season occurs from November to May. The wet season rainfall
486 component is strongly bimodal, with the two modes corresponding to peaks in the long rains and
487 the short rains. The major peak in rainfall occurs in April during the long rains (January-May)
488 whereas the minor peak occurs in December during the short rains (November-December, Fig
489 2a). The total monthly rainfall averaged 78.3 ± 84.2 mm and was highly variable (%CV =
490 107.5%) during 1963-2014 (Fig 2a). The total annual rainfall averaged 937.5 ± 300.7 mm during
491 1963-2014 (Fig. 2b) out of which the wet season rainfall (851.7 ± 297.3 mm) contributed 90.9%
492 (Fig 2c) and the dry season rainfall (85.5 ± 65.2 mm) a mere 10.1% (Fig 2d). There were also
493 considerable interannual variations in the annual, wet and dry season rainfall components (Figs
494 2b-d). Smoothing of the time series of the total monthly rainfall exposed substantial variation
495 with periods of below-average rainfall centered around 1966, 1975, 1980 and 1999 (Fig S1).

496
497 Analysis of the annual rainfall showed that extreme droughts occurred in 1966, 1980, 1993,
498 1995, 1999 and 2000 while severe droughts were recorded in 1974-1976, 1981, 1991, 2004 and
499 2014. Further, the extremely wet years were 1983 and 2007 whereas very wet years were 1964,

500 1997 and 1998. Analysis of the wet season rainfall identified the same extreme and severe
501 droughts and very wet years as the annual rainfall did (Table S8, Fig S2). In addition, the wet
502 season of 1969 experienced an extreme drought while the 1982 wet season was a severe drought.
503 The dry seasons of 1968, 1985, 1987, 1990, 1992 and 1993 were extremely dry and the dry
504 seasons of 1970, 1973, 1995, 1996, 1999, 2001 and 2010 were severe droughts. By contrast the
505 dry seasons of 1967, 1969, 1982, 1989 and 2011 were either extremely wet or very wet (Table
506 S8, Fig S2).

507
508 There were significant quasi-cyclic oscillations in the three rainfall components with
509 approximate cycle periods of 4.64, 4.64 and 2.47 years for the annual, wet season and dry season
510 rainfall components, respectively, based on spectral analysis (Table S9, Fig S3). Based on the
511 unobserved components model (UCM), the oscillations in the annual, wet season and dry season
512 rainfall components had dominant cycle periods of 4.83, 3.82 and 2.45 years, respectively (Table
513 S10, Fig S4). In addition, there were secondary cycles in the wet and dry season rainfall
514 components with approximate cycle periods of 2.2 years for the wet season component and 11.3
515 years for the dry season component (Table S10, Figs S4). The estimated damping factors for the
516 cycles were all less than 1 except for the cycle for the annual rainfall component with a period of
517 4.83 years and the cycle with a period of 2.2 years for the wet season rainfall component both of
518 which had damping factors equal to 1 (Table S10, Fig S4). The two cycles with damping factors
519 equal to 1 are persistent whilst the remaining cycles with damping factors smaller than 1 are
520 transient.

521

522 The disturbance variances for the irregular components for the wet and dry season rainfall, but
523 not for the annual rainfall, were close to zero and statistically insignificant. This implies that the
524 irregular components for the two seasonal rainfall components were deterministic whereas the
525 irregular component for the annual rainfall was stochastic. Moreover, the estimated disturbance
526 (error) variances for the cyclical components were significant for the 3.83-year cycle for the wet
527 season and for both cycles for the dry season but not for the 4.83-year cycle for the annual
528 rainfall (Table S10, Figs S4). These features jointly imply that the 4.83-year cycle identified for
529 the annual rainfall is persistent and deterministic whereas the cycles identified for both the wet
530 and dry season rainfall are stochastic and transient (Table S10, Figs S4). Even so, significance
531 analysis of the disturbance (error) variances of the cyclical components in the model at the end of
532 the estimation span indicate that the disturbance variances for the cycle in the annual rainfall
533 component and both cycles in the wet season rainfall component were significant but those for
534 the two cycles in the dry season rainfall component were insignificant (Table S11). Since the
535 4.83-cycle in the annual rainfall component is deterministic the additional significant test result
536 means that the annual cycle is indeed significant. The significant disturbance variances for the
537 two stochastic cycles in the wet season rainfall component (Table S11) applies only to the part of
538 the time series of wet season rainfall near the end of the estimation span.

539

540 The disturbance terms for the level component for all the three rainfall components were
541 significant only for the wet season but not for the annual or dry season rainfall. As well, the slope
542 component was significant only for the wet season rainfall (Table S11, Fig S4). This implies that,
543 of the three rainfall components, only the wet season rainfall increased systematically over time
544 in Ngorongoro (Table S11, Fig S4). The smoothed rainfall cycles in the three rainfall

545 components further reinforce the conclusion that the oscillation in annual rainfall is persistent
546 and deterministic whereas the oscillations in the wet and dry season rainfall are transient and
547 stochastic (Fig S4).

548

549 **Projected rainfall and temperatures**

550 The projected annual rainfall showed no evident systematic trend under all the three scenarios.
551 However, the general average rainfall level is consistently and substantially higher under the
552 RCP2.6 than the RCP4.5 and 8.5 scenarios. The RCP4.5 and 8.5 scenarios have comparable
553 average levels but RCP4.5 is expected to receive somewhat more rainfall. Notably, rainfall
554 shows marked inter-annual variation characterized by sustained quasi-cyclic oscillations during
555 2006-2100 regardless of scenario (Fig S5).

556

557 The minimum and maximum temperatures are expected to rise during 2006-2100, on average, by
558 1, 2 and 6 °C under the RCP2.6, 4.5 and 8.5 scenarios, respectively. Consequently, the average
559 maximum temperature is expected to increase during 2006-2100 from 23 to 24 °C under
560 RCP2.6, 24 to 26 °C under RCP4.5 and 23 to 29 °C under RCP8.5. The average minimum
561 temperature is similarly anticipated to rise during 2006-2100 from 14 to 15 °C under RCP2.6, 14
562 to 16 °C under RCP4.5 and 14 to 20 °C under RCP8.5 (Fig S5).

563

564 **Changes in vegetation composition and structure**

565 From 1966/67 [14] to 1995 [38] there have been significant changes in the structure of the major
566 and secondary herbaceous species. In 1966/67 the Crater floor was dominated by short grass

567 herbaceous species. By 1995, most of the short grasslands had been replaced by mid to tall plant
568 species.

569

570 **Table 1. Changes in vegetation structure from 1966/67 to 1995.**

Major Herbaceous Species (ha)		
	Herlocker	Chuwa
Short	20868	10626
Mid	2110	9540
Mid-tall	5794	4506
Tall	1377	4227
Secondary Herbaceous Species (ha)		
Short	18584	4794
Mid	2812	3905
Mid-tall	2004	9096
Tall	1317	2258

571

572 **Historic herbivore population dynamics**

573 The population size of wildebeest, zebra, Thomson's gazelle, Grant's gazelle, kongoni (Coke's
574 hartebeest), and black rhino increased from 1964 to a peak around 1974-1976 and then declined
575 thereafter in both the wet and dry seasons. Eland and waterbuck had a general downward trend
576 from the early 1970's. Zebra numbers increased again from 1995 to 2012 whereas Grant's
577 gazelle and kongoni numbers in the dry season increased again from 1995 to 2000 before
578 declining further (Fig 3). In stark contrast to the other species, numbers of buffalo increased
579 markedly following the removal of Maasai livestock from the Crater in 1974. Elephant and
580 ostrich numbers have similarly increased in the Crater, with substantial increase apparent in

581 ostrich numbers following the extreme 1993 dry season drought (Fig 3). Buffalo, eland, elephant
582 and black rhino were more abundant in the Crater in the wet than the dry season. There were far
583 more eland and black rhino in the Crater in the wet season compared to the dry season in the
584 1970s than in the 2000s. Conversely, there were far more buffalo and elephants in the Crater in
585 the wet season compared to the dry season in the 2000s than there were in the 1970s (Fig 3).
586 Zebra were the only species to have maintained similar population sizes from 1964 to 2012.
587
588 Comparisons of the expected population sizes between 1964 and 1974 as well as between 1974
589 and 2012 based on constructed spline effects showed that while some species increased
590 significantly over time, others did not, or even declined. Species that increased but not
591 significantly between 1964 and 1974 in the wet season were wildebeest, Grant's gazelle,
592 waterbuck and ostrich (Table S12, Fig 3). Only buffalo, Thomson's gazelle and kongoni
593 numbers increased significantly between 1964 and 1974 in the wet season. Species that
594 decreased in numbers but not significantly between 1964 and 1974 in the wet season were zebra,
595 eland, elephant and black rhino. Between 1974 and 2012, the numbers of Thomson's gazelle,
596 Grant's gazelle, black rhino, eland, kongoni and waterbuck decreased significantly in the wet
597 season. In the same season and period, the numbers of buffalo and elephant increased
598 significantly. Zebra, wildebeest, and ostrich had no significant change (Table S12, Fig 3). In the
599 dry season, by contrast, numbers of some species either increased significantly between 1964
600 and 1974 (buffalo, elephant, eland, kongoni), increased but not significantly (waterbuck) or
601 decreased but not significantly (wildebeest, zebra, Thomson's gazelle, Grant's gazelle, ostrich).
602 However, between 1974 and 2012 in the dry season, numbers of some species either increased
603 significantly (buffalo, ostrich), increased but not significantly (waterbuck), decreased

604 significantly (Thomson's gazelle, Grant's gazelle, black rhino, eland, kongoni), or decreased but
605 not significantly (wildebeest, zebra, elephant, Table S12, Fig 3).

606

607 **Herbivore biomass dynamics**

608 Herbivore biomass in the wet season was initially dominated by wildebeest, followed by zebra.

609 Following the eviction of the Maasai and their livestock from the Crater in 1974, buffalo biomass

610 increased relative to wildebeest and zebra to a peak during 1999-2000. After the 1999-2000

611 drought, the biomass of buffalo and the other herbivore species declined to the pre-drought

612 levels. Nevertheless, wildebeest still makes a smaller contribution to the total biomass currently

613 than they did before cattle left the Crater and buffalo numbers were still low (Fig 4a). The

614 relative increase of buffalo biomass compared to wildebeest and zebra was also apparent in the

615 dry season biomass (Fig 4b).

616

617 The total herbivore biomass trends in the Crater have been dynamic and relatively stable. During

618 the dry season from 1964 to 1974 there was no significant change and this trend was also non-

619 significant for the dry season from 1974 to 2011 (Table 2). This scenario of a non-significant

620 trend from 1964 to 1974 and again from 1974 to 2011 was also consistent for the wet season

621 (Table 2).

622 **Table 2. The expected aggregate biomass in the wet and dry seasons of 1964, 1974 and 2011 and the difference between the**
 623 **1964 vs 1974 and 1974 vs 2011 estimates and test of significance of their difference based on constructed penalized cubic B-**
 624 **splines.**

Statement Number	Label	Estimate	Standard Error	DF	t Value	Pr > t	Adjustment	Adj P
1	Dry Season at time=1964	-63.3804	265.19	2.326	-0.24	0.8306		.
2	Dry Season at time=1974	-41.5788	146.46	2.349	-0.28	0.7996		.
3	Dry Season at time=2011	8.0933	0.1129	47.44	71.67	<0.0001		.
5	Wet Season at time=1964	-64.2763	265.14	2.326	-0.24	0.8282		.
6	Wet Season at time=1974	-41.5482	146.46	2.349	-0.28	0.7998		.
7	Wet Season at time=2011	8.4434	0.1336	50.95	63.2	<0.0001		.
4	Diff for Dry Season at time= 1964 vs time= 1974	21.8017	123.24	2.309	0.18	0.8739	Simulated	0.9479
4	Diff for Dry Season at time= 1974 vs time= 2011	49.6721	146.46	2.349	0.34	0.7625	Simulated	0.8474
8	Diff for Wet Season at time= 1964 vs time= 1974	22.7281	123.16	2.309	0.18	0.8686	Simulated	0.9447
8	Diff for Wet Season at time= 1974 vs time= 2011	49.9916	146.46	2.348	0.34	0.761	Simulated	0.8463

625

626 **Relationship between herbivore population size and rainfall**

627 Herbivore population size was correlated with rainfall in both the wet and dry seasons. The
628 particular rainfall component most strongly correlated with population size as well the specific
629 functional form of the relationship both varied with species and season (Figs 5 and 6, Tables
630 S13-S14). In the wet season, population size was most tightly correlated with 1) 6-year moving
631 averages of the wet season rainfall (wildebeest, zebra, buffalo, eland, kongoni, waterbuck,
632 ostrich, elephant, black rhino), 2) 6-year moving average of the annual rainfall (Thomson's and
633 Grant's gazelles), or 3) the current annual rainfall (warthog). In the dry season, population size
634 had the strongest correlation with 1) 6-year moving average of the wet season rainfall
635 (Thomson's and Grant's gazelle, buffalo, waterbuck, ostrich), 2) 5-6-year moving average of the
636 dry season rainfall (wildebeest, zebra, warthog), 3) 6-year moving average of the annual rainfall
637 (eland, kongoni), or 4) 3-4-year moving average of dry season rainfall (elephant, black rhino,
638 Figs 5 and 6, Tables S13-S14). The dependence of population size on rainfall followed three
639 general patterns. The first pattern is characterized by a decline in population size with increasing
640 rainfall and is shown by wildebeest, eland, kongoni, waterbuck and black rhino in the wet
641 season, and Thomson's gazelle, Grant's gazelle and waterbuck in the dry season. The second
642 pattern consists of an increase in population size with increasing rainfall and is shown by zebra,
643 buffalo, ostrich and elephant in the wet season and wildebeest, zebra, buffalo, ostrich and
644 warthog in the dry season. The third and last pattern is characterized by a humped relationship
645 between population size and rainfall in which population size peaks at intermediate levels of
646 rainfall and is shown by Thomson's and Grant's gazelles and warthog in the wet season and
647 eland, kongoni, elephant and black rhino in the dry season (Figs 5 and 6, Tables S13-S14).
648

649 **Projected herbivore population dynamics**

650 The projected ungulate population dynamics should mirror the pronounced and sustained
651 oscillations in the projected rainfall. Further, large-sized herbivores dependent on bulk, low-
652 quality forage should prosper under the wet and cooler conditions expected under RCP2.6.
653 Likewise, small-sized herbivores requiring high-quality forage should thrive under the relatively
654 low rainfall and warmer conditions anticipated under RCP4.5 and 8.5. The warmer temperatures
655 expected under RCP8.5 than under RCP4.5 imply that conditions should be most arid under this
656 scenario.

657 The projected population trajectories suggest that under the RCP2.6 scenario, buffalo numbers
658 will likely continue to increase after 2012, albeit at a decelerating rate, towards 7000-11000
659 animals by 2100 (Fig 7). But the Crater buffalo population is likely approaching its upper bound
660 of about 4000 animals and will likely fluctuate about this number (4000) till 2100 under the
661 RCP4.5 and 8.5 scenarios regardless of season (Fig 7). As expected, the population of this large-
662 sized bulk grazer is projected to be highest on average under RCP2.6, least under RCP8.5 and
663 intermediate under RCP4.5 for both the wet and dry seasons (Fig 7).

664 For wildebeest, the projected trajectories suggest strong and sustained oscillations in population
665 size under all the three scenarios and both seasons, reflecting the strong projected rainfall
666 oscillations (Fig 8). The oscillatory population dynamics in both the wet and dry seasons
667 exhibited by wildebeest reveal extended periods of population increase followed by prolonged
668 periods of persistent population declines. Nevertheless, there are also discernible differences in
669 the projected population trajectories under the three climate change scenarios. The projected
670 wildebeest population trajectories suggest that the population will continue to fluctuate widely
671 between 5000 and 15000 animals in all the scenarios and seasons. It is only under the RCP2.6

672 scenario that the dry season population shoots beyond 20000 animals around 2070 and 2090 (Fig
673 8). In the wet season, the projected average wildebeest abundance is highest under RCP4.5,
674 intermediate under RCP8.5 and lowest under RCP2.6. In the dry season, however, wildebeest
675 abundance is highest on average under RCP2.6, intermediate under RCP4.5 and lowest under
676 RCP8.5 (Fig 8).

677 The zebra population trajectories also reveal striking oscillations in population size under all the
678 three scenarios, a general increase in population size under RCP2.6 scenario in both seasons and
679 a decrease and then increase in the RCP8.5 scenario in the wet season (Fig 9). The zebra
680 population size is projected to decline in the long term under the RCP4.5 scenario in both
681 seasons and the RCP8.5 scenario in the dry season (Fig 9). In general, zebra will perform the best
682 under RCP2.6 and the worst under RCP8.5. The performance of zebra under RCP4.5 will be
683 intermediate between RCP2.6 and 8.5 from 2006 to around 2070 after which it will drop below
684 that expected under RCP8.5 (Fig 9).

685 The decline observed in historic Thomson's gazelle numbers is projected to be persistent and to
686 remain below the peak attained historically around 1974 under all scenarios and both seasons
687 (Fig 10). Besides the general decline, Thomson's gazelle numbers are projected to show
688 persistent and marked oscillations irrespective of scenario or season. As predicted by their small
689 body size and selective grazing, Thomson gazelles will likely perform the best under RCP8.5
690 with the least rainfall, intermediately under RCP4.5, and the worst under RCP2.6 (Fig 10).

691 As with Thomson's gazelles, the projected population trajectories for Grant's gazelle show
692 marked and sustained oscillations (Fig 11). Despite these persistent oscillations, Grant's gazelle
693 numbers will likely remain lower than the historically attained peak numbers around 1974-1976.

694 Moreover, the declining trend in Grant's gazelle numbers is projected to be replaced by an
695 increasing trend after some time under the RCP4.5 and 8.5 scenarios for both seasons. Even, so
696 Grant's gazelle numbers, are less likely to increase up to the highest historically recorded
697 numbers around 1974-1976 (Fig 11). Consistent with their small body size and selective grazing,
698 Grant's gazelles will also likely flourish the best under RCP8.5 with the least rainfall,
699 intermediately under RCP4.5, and the worst under RCP2.6 (Fig 11).

700

701 **Discussion**

702 **Rainfall**

703 Drought is a recurrent feature of the Ngorongoro Conservation Area. The annual rainfall shows
704 evident persistent and deterministic quasi-periodic oscillation with a cycle period of about 5
705 years. Oscillations in the wet and dry season rainfall were stochastic and transient. The quasi-
706 cyclic oscillations in annual, wet and dry season rainfall were statistically significant. The
707 oscillations are associated with recurrent severe droughts that cause food scarcity and hence
708 nutritional stress for the large herbivores. The wet season rainfall increased systematically in
709 Ngorongoro between 1964 and 2014 but the annual or dry season rainfall did not increase. The
710 oscillations in rainfall imply that the large herbivores are exposed to above average food supply
711 for about 2.5 years and to below average food supply for the subsequent 2.5 years. The rainfall
712 patterns also imply that portions of the Crater may be waterlogged or flooded during the high
713 rainfall years. High rainfall supports above-average production of plant biomass. But the forage
714 produced during high rainfall years is likely to be of low quality due to the dilution of plant
715 nutrients. Predation risk for herbivores is also likely to rise due to poor visibility associated with
716 tall grass growth during periods of high rainfall [60].

717

718 **Long-term Vegetation Trends**

719 Vegetation maps from before and after the removal of pastoralists and their livestock indicate
720 that major changes in vegetation structure occurred. Maasai pastoralists manage their grazing
721 areas with movement of livestock and fire [16, 61,62]. This type of range management selects for
722 shorter grasses and more palatable species [63,64]. The 1995 vegetation map shows that there
723 was a significant change in the vegetation structure of the Crater floor, such that there was a
724 decrease in the availability of short grasses and an increase in medium and tall grassland.

725

726 **Historic herbivore population dynamics**

727 Temporal variation in herbivore numbers in the Crater followed four general patterns. First,
728 buffalo, elephant and ostrich numbers increased significantly in the Crater from 1974-2012. The
729 transition of the Crater grasslands to a majority of the area being mid to tall-grass would have
730 favored Cape buffalo reproduction and survivorship. The increase in ostrich and elephant
731 numbers in both seasons became more marked after the severe 1993 drought. Second, the overall
732 average number of zebra in the Crater appeared stable whereas numbers of the other eight
733 species declined substantially between 1974 and 2012 relative to their peak numbers during
734 1974-1976. Third, numbers of both gazelles, eland, kongoni, waterbuck (wet season only) and
735 black rhino declined significantly in the Crater in both seasons following the removal of the
736 Maasai and their cattle from the Crater in 1974. The decline in black rhino is mainly attributed to
737 poaching in the 1970's and 1980's which reduced the population to 10 individuals [65]. Fourth,
738 wildebeest numbers decreased in the Crater between 1974 and 2012 but this decrease was not
739 statistically significant. In addition, some herbivore species were consistently more abundant

740 inside the Crater during the wet than the dry season. This pattern was most evident for the large
741 herbivore species requiring bulk forage, comprising buffalo, eland, elephant and black rhino. The
742 latter may spend less time in the swamps and the forest during the wet season and may be easier
743 to count.

744

745 **Herbivore biomass**

746 Despite the significant changes in the population sizes of individual species in the Crater, the
747 total herbivore biomass remained relatively stable from 1963 to 1974 and from 1974-2012,
748 implying that the Crater has a stable multi-herbivore community. There is a tendency towards a
749 higher biomass during the wet season, but it is not significant. Total wild herbivore biomass has
750 not been significantly affected by the removal of the pastoralists and their livestock. The change
751 in the grassland structure from mainly short grasses to mid to tall grasses after the removal of the
752 Maasai and their livestock may have enhanced the forage availability for Cape buffalo, a large-
753 bodied ruminant. The biomass of buffalo had the most dramatic increase post 1974 to become a
754 major constituent of the total large herbivore biomass after the elimination of cattle from the
755 Crater in 1974. A similar increase in buffalo numbers at the expense of small and medium
756 herbivores has also been documented for Nairobi and Lake Nakuru National Parks in Kenya
757 [66,67].

758

759 **Relationship between herbivore population size and rainfall**

760 Rainfall significantly influenced herbivore abundance in Ngorongoro Crater and this influence
761 varied with species and season and partly reflect functional distinctions between the species
762 based on their life-history traits (body size, gut morphology) or life-history strategies (feeding

763 and foraging styles). Herbivores responded to rainfall variation in three different ways in both
764 seasons. In the wet season, numbers of herbivore species either decreased (wildebeest, eland,
765 kongoni, waterbuck and rhino), increased (zebra, buffalo, ostrich and elephant) or increased up
766 to intermediate levels of rainfall and then decreased with further increase in rainfall (both
767 gazelles and warthog). Similarly, in the dry season the numbers of the herbivore species either
768 decreased (both gazelles and waterbuck), increased (wildebeest, zebra, buffalo, ostrich and
769 warthog) or increased up to intermediate levels of rainfall and then decreased with further
770 increase in rainfall (eland, kongoni, elephant and rhino).

771

772 **Forecasted herbivore population dynamics**

773 The projected population trends suggest strong interspecific contrasts regarding the scenario
774 under which each species will likely perform best but broad similarities exist between seasons
775 for each scenario. Except for buffalo whose numbers appear to approach asymptotes, population
776 trajectories for wildebeest, zebra and both gazelles exhibit pronounced and sustained oscillatory
777 dynamics, reflecting rainfall oscillations. The projected population trajectories for buffalo and
778 zebra suggest that both species will be most abundant in the Crater under the RCP2.6 scenario,
779 intermediate under RCP4.5 and least abundant under RCP8.5 in both seasons. This is expected
780 since buffalo is a large-sized bulk grazer and zebra is a large-sized non-ruminant able to process
781 large quantities of low quality forage expected to be most abundant under the wetter and cooler
782 conditions anticipated under RCP2.6 relative to RCP4.5 and 8.5. Moreover, for both buffalo and
783 zebra, the projected trajectories are generally similar between the RCP4.5 and 8.5 scenarios for
784 both seasons.

785

786 By contrast, the wildebeest that requires short, green grass is anticipated to be more abundant
787 under the RCP4.5 and 8.5 scenarios than under the RCP2.6 scenario with wetter conditions in the
788 wet season. In the more arid dry season conditions, wildebeest should however thrive better
789 under the more moist RCP2.6 scenario than under RCPs 4.5 and 8.5.

790
791 Trajectories for both gazelles suggest that both species will be most abundant under RCP8.5 with
792 the lowest average rainfall, intermediate under RCP4.5 with intermediate rainfall and least
793 abundant under RCP2.6 with the highest rainfall. This is consistent with the preference of both
794 species for high-quality, short grasses and forbs. For both gazelles numbers will likely increase
795 from about 2050-2060 to 2100 under RCP4.5. Also, for both gazelles, the projections suggest
796 persistent and similar population oscillations between both seasons under each of the three
797 scenarios. The oscillations suggest extended periods of population decline followed by increase
798 for both gazelles in both seasons. We reiterate that these projections are based solely on rainfall
799 influences on large herbivore population dynamics, yet the dynamics of large herbivores are
800 often influenced by a multitude of other factors.

801

802 **Predation**

803 The major predators in Ngorongoro Crater are lions and spotted hyenas. These species, their
804 population dynamics and feeding ecology have been studied since the 1960's [4-8, 68-70].

805

806 In the 1960's the Ngorongoro Crater had a population of approximately 298 spotted hyenas [4].
807 When Höner et al [70] started their research in 1996 the population was about 117 hyenas and
808 the recruitment rate was higher and the mortality was lower than during Kruuk's study period in

809 the 1960's. Herbivore census data indicates that there had been a decline in the spotted hyena
810 prey populations, i.e. wildebeest, zebra, Thomson's gazelle, and Grant's gazelle by 1996. From
811 1996 to 2002, there was an increase in the hyena population to 333 individuals. From 1996 to
812 2002 there was an increase in the abundance of these prey species with an average prey density
813 of 139 ± 76 prey animals per km^2 . Höner et al [70] attribute the decline in the hyena population
814 from the 1960's to 1996 to the decline in their prey populations. However, from 1996 to 2002,
815 the major predictor for the spotted hyena population increase was the increase in their prey
816 population. Subsequently there was a reduction and then recovery of the population during an
817 outbreak of *Streptococcus equi ruminatorum* in 2001 to 2003. Mortality was higher in adult
818 males and yearlings in territories where prey densities were low. In the short term the bacterial
819 infection had a top-down impact on sex and age classes that had relatively poor nutrition. In the
820 longer-term after the disease perturbation, the reduced population growth was due to lower
821 juvenile survival. By 2008 the population had recovered and was approximately 450 [71] and in
822 2012 the population was estimated at 508 of which 364 were adults (pers com Höner 2018).

823
824 From 1970 to 1972, Elliot and McTaggart Cowan [68] studied lions in the Crater and estimated a
825 resident population of 65 lions in four prides. They estimated that lions annually killed or
826 scavenged approximately 7% of the wildebeest, 4.3% of the zebra and 6.2% of the Thomson's
827 gazelle. Adapted from Kruuk [4] they estimated that hyenas took at least 7.6% of the wildebeest
828 population, 6.5% of the zebra population and 1.6% of the Thomson's gazelle population. Thus
829 the estimated annual percentage of wildebeest killed or scavenged by lions and hyena was
830 approximately 14.6%, roughly equal to the wildebeest recruitment rate [4]. The predation and
831 scavenging rate on zebra was approximately 10.7%.

832
833 Long term research on lions in the Ngorongoro Crater [7,8,69]() indicates that the lion
834 population may not be food limited but that weather extremes (high rainfall/drought) correlate
835 with disease outbreaks and pest infestations (Canine distemper virus and biting *Stomoxys* flies).
836 The resulting mortality is exacerbated by pride takeovers and infanticide. A severe infestation of
837 *Stomoxys* flies in 1962 reduced the lion population to 10 lions that were joined by seven
838 immigrating males in 1975. This severe population reduction may have been a ‘bottleneck’ and
839 the current population may be based on 15 founders [7]. The population rose to a high of 124
840 lions in 1983, but by 1991 there were 75 to 100 lions, and numbers dropped to 29 in 1998 [7,8].
841 The lion population may be density dependent since it has had positive reproductive performance
842 when the population has been less than 60 individuals and has had negative reproductive
843 performance when the population was more than 60 individuals. From 1994 to 2004, the
844 population had not had reduced reproductive performance. Kissui and Packer [8] attribute the
845 declines in the lion population to disease outbreaks that correlated with extreme weather events
846 that occurred in 1962, 1994, 1997, and 2001. During 2000/2001 there was a decrease in the lion
847 population due to death (*Stomoxys* flies) and emigration [70].

848

849 **Poaching**

850 The black rhino declining trend from the 1970’s to mid 1980’s was due to poaching [72]. Since
851 the early 1990’s there has been limited poaching and the population is slowly recovering.
852 Conservative population projections in 1995 [65] predicted that with the best scenario, i.e. no
853 poaching, the population should be approximately 35 to 40 individuals by 2017. The current
854 Black rhino population is 59 individuals (Pers comm, M. Musuha, 2018, NCAA,).

855

856 **Disease**

857 Before the 1960's, rinderpest was a source of significant mortality to buffalo, wildebeest and
858 eland in the Crater Highlands and there was a serious outbreak affecting yearling buffalo
859 adjacent to the Ngorongoro Crater in 1961 [73]. The NCAA started an inoculation campaign
860 against rinderpest in the 1950's and eradicated the disease by the 1960's [73]. Inoculations
861 against rinderpest for cattle continued. Subsequently there was an outbreak in 1982 that affected
862 buffalo, eland and giraffe, but not cattle [32]. Despite the losses from rinderpest during 1982, the
863 buffalo population increased steadily from 1980 and had doubled by 1987.

864

865 Rinderpest was also a significant source of mortality in the adjacent Serengeti ecosystem and the
866 inoculation campaigns appear to have reduced mortality in both wildebeest populations. From
867 1963 to 1974 the Serengeti migratory wildebeest population tripled in size [74]. During the same
868 time the more sedentary population in Ngorongoro Crater increased from roughly 7,600
869 wildebeest to about 14,000.

870

871 In 2000 and 2001 there was significant mortality in buffalo (1500), wildebeest (250) and zebra
872 (100) apparently due to nutritional stress resulting from the severe drought in the dry season in
873 2000 [2, 39,75] .

874

875 In 2001, five black rhinos died in January and five lions during February [62]. The reports
876 indicated that three of the black rhinos died from *Babesiosis* [75]. Nijhof et al [75] analysed
877 samples from Ngorongoro (Bahati and Maggie) and a dead black rhino (Benji) from Addo

878 Elephant National Park. Sequence analyses of the sample from Bahati's brain revealed a novel
879 species that was named *Babesia bicornis* ap.nov. Subsequent analyses showed that both Maggie
880 and Benji were positive for *Babesia bicornis* ap.nov. Hence, *Babesia bicornis* ap.nov. may be a
881 species new to the Ngorongoro Crater and the Serengeti ecosystem. Two black rhino were
882 translocated from Addo Elephant National Park to Ngorongoro Crater in 1997. The translocation
883 that was done to enhance the Ngorongoro black rhino population may have had negative
884 repercussions by introducing a new tick borne disease. The impact of the novel parasite, *Babesia*
885 *bicornis* ap.nov., may have been exacerbated by drought and high tick densities. The literature
886 indicates that *Babesia bicornis* can cause fatal babesiosis [75]. The remaining 10 black rhinos
887 were treated with a curative babesicidal drug and survived [39].

888
889 However, in the case of the buffalo mortalities, high tick burdens and tick borne protozoal
890 diseases may have been contributing factors [75]. A limited survey of the buffalo, wildebeest and
891 lions that died in 2001 did not reveal the presence of *Babesia bicornis* ap.nov. Lion necropsy's
892 revealed the presence of tick borne parasites (*Ehrlichia* spp., *Babesia* and *Theileria* sp) but
893 canine distemper and a plague of *Stomoxys* stinging flies were also implicated and the cause of
894 mortality has not been determined [39].

895
896 Prescribed burning was started in the dry season of 2001 and research was done on tick densities,
897 vegetation structure and tick host preference in adjacent burned and unburned areas [39]. Before
898 burning, most adult ticks were present in the wet season (May to June) and most immature ticks
899 occurred during the dry season (September, October). There were significantly more adult ticks
900 in the tall grass in the wet season and significantly more immature ticks in the less grazed areas

901 in the dry season. In 2001, the mean tick density in tall grass (>50cm) was $57 \pm 6.93/m^2$ (adults,
902 wet season) and in less grazed (>20 cm) areas $961 \pm 146 /m^2$ (immature, dry season). Twenty-
903 seven months (2004) later there was a significant difference between burned and unburned areas,
904 with almost no adult ticks and relatively few immature ticks in the burned areas. However, the
905 unburned areas also had much lower adult tick and immature tick densities than that recorded in
906 2001.

907

908 **Conclusions**

909

910 Ngorongoro Crater has an annual rainfall cycle period of about 5 years. Oscillations in annual,
911 wet and dry season rainfall were statistically significant. The oscillations are associated with
912 recurrent severe droughts that cause food scarcity and hence nutritional stress for the large
913 herbivores. Rainfall oscillations imply that large herbivores are exposed to above average food
914 supply for about 2.5 years and to below average food supply for the subsequent 2.5 years. High
915 rainfall supports above-average production of plant biomass which may be of low quality due to
916 the dilution of plant nutrients.

917

918 In 1974 there was a perturbation in that resident Maasai and their livestock were removed from
919 the Crater. Vegetation maps from before and after the removal of pastoralists and their livestock
920 indicate that major changes in vegetation structure occurred. The 1995 vegetation map shows
921 that there was a significant change in the vegetation structure of the Crater floor, such that there
922 was a decrease in the availability of short grasses and an increase in medium and tall grassland.

923

924 Temporal variation in herbivore numbers in the Crater followed four general patterns. First,
925 buffalo, elephant and ostrich numbers increased significantly in the Crater from 1974-2012.
926 Second, the overall average number of zebra in the Crater appeared stable whereas numbers of
927 the other eight species declined substantially between 1974 and 2012 relative to their peak
928 numbers during 1974-1976. Third, numbers of both gazelles, eland, kongoni, waterbuck (wet
929 season only) and black rhino declined significantly in the Crater in both seasons following the
930 removal of the Maasai and their cattle from the Crater in 1974. The decline in black rhino is
931 mainly attributed to poaching in the 1970's and 1980's. Fourth, wildebeest numbers decreased in
932 the Crater between 1974 and 2012 but this decrease was not statistically significant. In addition,
933 some herbivore species were consistently more abundant inside the Crater during the wet than
934 the dry season. This pattern was most evident for the large herbivore species requiring bulk
935 forage, comprising buffalo, eland, elephant and black rhino. The latter may spend less time in the
936 swamps and the forest during the wet season and may be easier to count. Even with a change in
937 grassland structure, total herbivore biomass remained relatively stable from 1963 to 2012,
938 implying that the Crater has a stable multi-herbivore community.

939

940 Rainfall significantly influenced herbivore abundance in Ngorongoro Crater and this influence
941 varied with species and season. Herbivores responded to rainfall variation in three different ways
942 in both seasons. In the wet season, numbers of herbivore species either decreased (wildebeest,
943 eland, kongoni, waterbuck and rhino), increased (zebra, buffalo, ostrich and elephant) or
944 increased up to intermediate levels of rainfall and then decreased with further increase in rainfall
945 (both gazelles and warthog). Similarly, in the dry season the numbers of the herbivore species
946 either decreased (both gazelles and waterbuck), increased (wildebeest, zebra, buffalo, ostrich and

947 warthog) or increased up to intermediate levels of rainfall and then decreased with further
948 increase in rainfall (eland, kongoni, elephant and rhino).

949
950 The relationships established between the time series of historic animal counts in the wet and dry
951 seasons and lagged wet and dry season rainfall series were used to forecast the likely future
952 trajectories of the wet and dry season population size for each species under three alternative
953 climate change scenarios. They suggest strong interspecific contrasts regarding the scenario
954 under which each species will likely perform best but broad similarities exist between seasons
955 for each scenario.

956
957 There is information on the population trends of the two major predators, i.e. lions and spotted
958 hyenas. It would be useful to correlate predator impact on herbivore populations with rainfall.
959 Disease is an important perturbation in the population trends of lions and spotted hyenas and
960 potentially Black rhino, Cape buffalo and other herbivores. Tick borne diseases can potentially
961 be managed with systematic burning of some grassland areas.

962

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973

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1220

1221 **Figure legends**

1222

1223 **Fig 1. Ngorongoro Crater and Census Blocks [12]).**

1224

1225 **Fig 2. The distribution of a) total monthly rainfall (mean \pm 1sd = 78.3 \pm 84.2 mm) across**

1226 **months in the Ngorongoro Crater National Park averaged over 1963-2014 and the**

1227 **interannaul variation in standardized deviations of the b) annual rainfall (mean \pm 1SD**

1228 **=937.5 \pm 300.7 mm), c) wet season rainfall (mean \pm 1SD =851.7 \pm 297.3 mm), and d) dry**

1229 **season rainfall (mean \pm 1SD =85.5 \pm 65.2 mm) in the Ngorongoro Crater during 1963-2014.**

1230 The vertical needles are the standardized deviates, the solid curves are the 5-year (annual and wet

1231 season) and 2-year (dry season) moving averages and the dashed horizontal lines are percentiles

1232 of the frequency distributions of the rainfall deviates.

1233

1234

1235 **Fig 3. Trends in the population sizes of the 12 most common large herbivore species in the**

1236 **Ngorongoro Crater in the wet and dry seasons from 1964 to 2012.** The vertical needles

1237 denote wet season (solid) and dry season (dashed) count totals. Thick solid and dashed curves

1238 denote the fitted wet season and dry season trend curves. The shaded regions are the 95% point
1239 wise confidence bands.

1240

1241 **Fig 4. Temporal trends in the cumulative total biomass (kg) of the 12 most common large**
1242 **herbivore species in the Ngorongoro Crater during a) the wet season and b) the dry season**
1243 **during 1964 to 2012.** The unit weights (kg) are 1725, 816, 450, 340, 200, 160, 125, 123, 114,
1244 45, 40 and 15 for elephant, rhino, buffalo, eland, zebra, waterbuck, kongoni, wildebeest, ostrich,
1245 warthog, Grant's gazelle and Thomson's gazelle, respectively. Note that wildebeest and zebra
1246 were not counted in the dry season of 1968. In years when multiple surveys were done in the
1247 same season (e.g., the wet season of 1966 or 1970), only the survey with the maximum count
1248 was used to calculate biomass.

1249

1250 **Fig 5. The selected best regression relationships between the wet season and dry season**
1251 **count totals of wildebeest, zebra, Thomson's gazelle, buffalo, Grant's gazelle, and eland**
1252 **and the moving averages of the annual, wet season and dry season rainfall components for**
1253 **the Ngorongoro Crater during 1964-2012.**

1254

1255 **Fig 6. The selected best regression relationships between the wet season and dry season**
1256 **count totals of kongoni, waterbuck, ostrich, elephant, black rhino and warthog and the**
1257 **moving averages of the annual, wet season and dry season rainfall components for the**
1258 **Ngorongoro Crater during 1964-2012.**

1259

1260 **Fig 7. Historic and projected population size of buffalo in the Ngorongoro Crater during**
1261 **the wet and dry seasons based on the three climate change scenarios RCP2.6, RCP4.5 and**
1262 **RCP8.5.**

1263

1264 **Fig 8. Historic and projected population size of wildebeest in the Ngorongoro Crater**
1265 **during the wet and dry seasons based on the three climate change scenarios RCP2.6,**
1266 **RCP4.5 and RCP8.5.**

1267

1268 **Fig 9. Historic and projected population size of zebra in the Ngorongoro Crater during the**
1269 **wet and dry seasons based on the three climate change scenarios RCP2.6, RCP4.5 and**
1270 **RCP8.5.**

1271

1272 **Fig 10. Historic and projected population size of Thomson's gazelle in the Ngorongoro**
1273 **Crater during the wet and dry seasons based on the three climate change scenarios**
1274 **RCP2.6, RCP4.5 and RCP8.5.**

1275

1276 **Fig 11. Historic and projected population size of Grant's gazelle in the Ngorongoro Crater**
1277 **during the wet and dry seasons based on the three climate change scenarios RCP2.6,**
1278 **RCP4.5 and RCP8.5.**

1279

1280 **Supporting Information**

1281 **S1 Data. The count totals for each of the 12 most common large herbivore species counted**
1282 **during the wet and the dry seasons in the Ngorongoro Crater from 1964 to 2012.**

1283

1284 **S2 Data. The count totals for each of the 12 most common large herbivore species counted**

1285 **during the wet and the dry seasons in the Ngorongoro Crater from 1964 to 2012.** The

1286 missing values were imputed using a state space model, separately for each species and season

1287 combination.

1288

1289 **S3 Data. Total monthly rainfall in mm recorded at the Ngorongoro Conservation Area**

1290 **headquarters from 1963 to 2014.**

1291

1292 **S4 Data. The logarithm of the observed and predicted population size for each of the five**

1293 **most common species for the wet and dry season and the 95% pointwise prediction**

1294 **confidence band for 1964 to 2012.** The logarithm of the forecasted population size is also

1295 provided for each of the five most abundant herbivore species for 2013 to 2100.

1296

1297 **Table S1. Parameter estimates for the bivariate VARMAX (2,2,5) model for the five most**

1298 **abundant herbivore species in the dry and wet seasons in the Ngorongoro Crater,**

1299 **Tanzania, during 1963-2012.** Model selection was based on information theory so no effort has

1300 been made to remove insignificant coefficients. By restricting a few of the highly insignificant

1301 coefficients to be zero, many of the apparently insignificant coefficients become significant.

1302

1303 **Table S2. Roots of AR characteristic polynomials for the bivariate model for the five most**

1304 **abundant herbivore species in the dry and wet seasons in the Ngorongoro Crater,**

1305 **Tanzania, during 1963-2012.** The modulus of the roots of its AR polynomial should be less
1306 than 1 for a time series to be stationary.

1307

1308 **Table S3. Roots of the MA characteristic polynomials for the bivariate model for the five**
1309 **most abundant herbivore species in the dry and wet seasons in the Ngorongoro Crater,**
1310 **Tanzania, during 1963-2012.**

1311

1312 **Table S4. Portmanteau Test for Cross Correlations of Residuals from the bivariate**
1313 **VARMAX(2,2,5) model for the five most abundant herbivore species in the dry and wet**
1314 **seasons in the Ngorongoro Crater, Tanzania, during 1963-2012.** The results show tests for
1315 white noise residuals based on the cross correlations of the residuals. Insignificant test results
1316 show that we cannot reject the null hypothesis that the residuals are uncorrelated.

1317

1318 **Table S5. Univariate model ANOVA diagnostics for the five most abundant herbivore**
1319 **species in the dry and wet seasons in the Ngorongoro Crater, Tanzania, during 1963-2012.**
1320 The results show that each model is significant.

1321

1322 **Table S6. Univariate Model White Noise Diagnostics for the five most abundant herbivore**
1323 **species in the dry and wet seasons in the Ngorongoro Crater, Tanzania, during 1963-2012.**

1324 The results show tests of whether the residuals are correlated and heteroscedastic. The Durbin-
1325 Watson test statistics test the null hypothesis that the residuals are uncorrelated. The Jarque-Bera
1326 normality test tests the null hypothesis that the residuals are normally distributed. The F statistics

1327 and their p -values for ARCH(1) disturbances test the null hypothesis that the residuals have
1328 equal covariances.

1329

1330 **Table S7. Univariate AR Model Diagnostics for the five most abundant herbivore species in**
1331 **the dry and wet seasons in the Ngorongoro Crater, Tanzania, during 1963-2012.** The F
1332 statistics and their p -values for AR(1), AR(1,2), AR(1,2,3) and AR(1,2,3,4) models of residuals
1333 test the null hypothesis that the residuals are uncorrelated.

1334

1335 **Table S8. Classification of years and seasons into extreme drought, severe drought,**
1336 **moderate drought, normal, wet, very wet and extremely wet years or seasons using**
1337 **percentiles of the frequency distributions of the total annual, wet season or dry season**
1338 **rainfall recorded at the Ngorongoro Conservation Area headquarters from 1963 to 2014.**

1339

1340 **Table S9. The estimated frequency, period, periodogram, spectral density, co-spectra,**
1341 **quadrature, squared coherence, amplitude and phases of the oscillations in the annual, wet**
1342 **and dry season rainfall components for the Ngorongoro Crater during 1963-2014.**

1343

1344 **Table S10. The estimated variances of the disturbance terms, the variances of the irregular**
1345 **components, damping factor and periods of the cycles in the annual, wet and dry season**
1346 **rainfall components recorded for the Ngorongoro Crater during 1963-2014.**

1347

1348 **Table S11. Significance analysis of components (based on the final state).**

1349

1350 **Table S12. The expected population size of each of the 12 wildlife species in 1964, 1974 and**
1351 **2012 and the difference between the two estimates for 1964 and 1974 and 1974 and 2012**
1352 **and test of significance of their difference based on constructed penalized cubic B-splines.**

1353

1354 **Table S13. Selection of the rainfall component, moving average and functional form of the**
1355 **relationship between population size and the moving average component for each of the 12**
1356 **most common large herbivore species based on the corrected Akaike Information Criterion**
1357 **(AICc). Only models with delta AICc no more than 4 are shown. Model selection was**
1358 **carried out separately for the wet and dry season counts for each species.**

1359

1360 **Table S14. Parameters estimates, their standard errors and *t*-tests of whether the**
1361 **parameters are significantly different from zero for the AICc-selected best models relating**
1362 **population size and moving average rainfall, for the wet and season counts, for the 12 most**
1363 **common large herbivore species in the Ngorongoro Crater.**

1364

1365 **S1 Text. SAS code used to analyze the rainfall data for the Ngorongoro Conservation Area**
1366 **headquarters.**

1367

1368 **S2 Text. SAS code used to model trends in the animal counts, relate the counts to rainfall**
1369 **and project population dynamics to 2013-2100.**

1370

1371 **Fig S1. Temporal variation in the original and smoothed total monthly rainfall in the**
1372 **Ngorongoro Crater from 1963 to 2014.**

1373

1374 **Fig S2. Percentiles of the annual, dry and wet season rainfall components. The percentiles**
1375 **are used to classify years or seasons as extreme, severe or moderate drought years or**
1376 **seasons, normal, wet, very wet or extremely wet years or seasons as described in the text.**

1377

1378 **Fig S3. Spectral density versus period of cycles (in years) for a) annual rainfall, b) wet**
1379 **season rainfall, and c) dry season rainfall based on rainfall recorded for the Ngorongoro**
1380 **Conservation Authority headquarters from 1963 to 2014. A large value of spectral density**
1381 **means that the corresponding period has greater support in the data.**

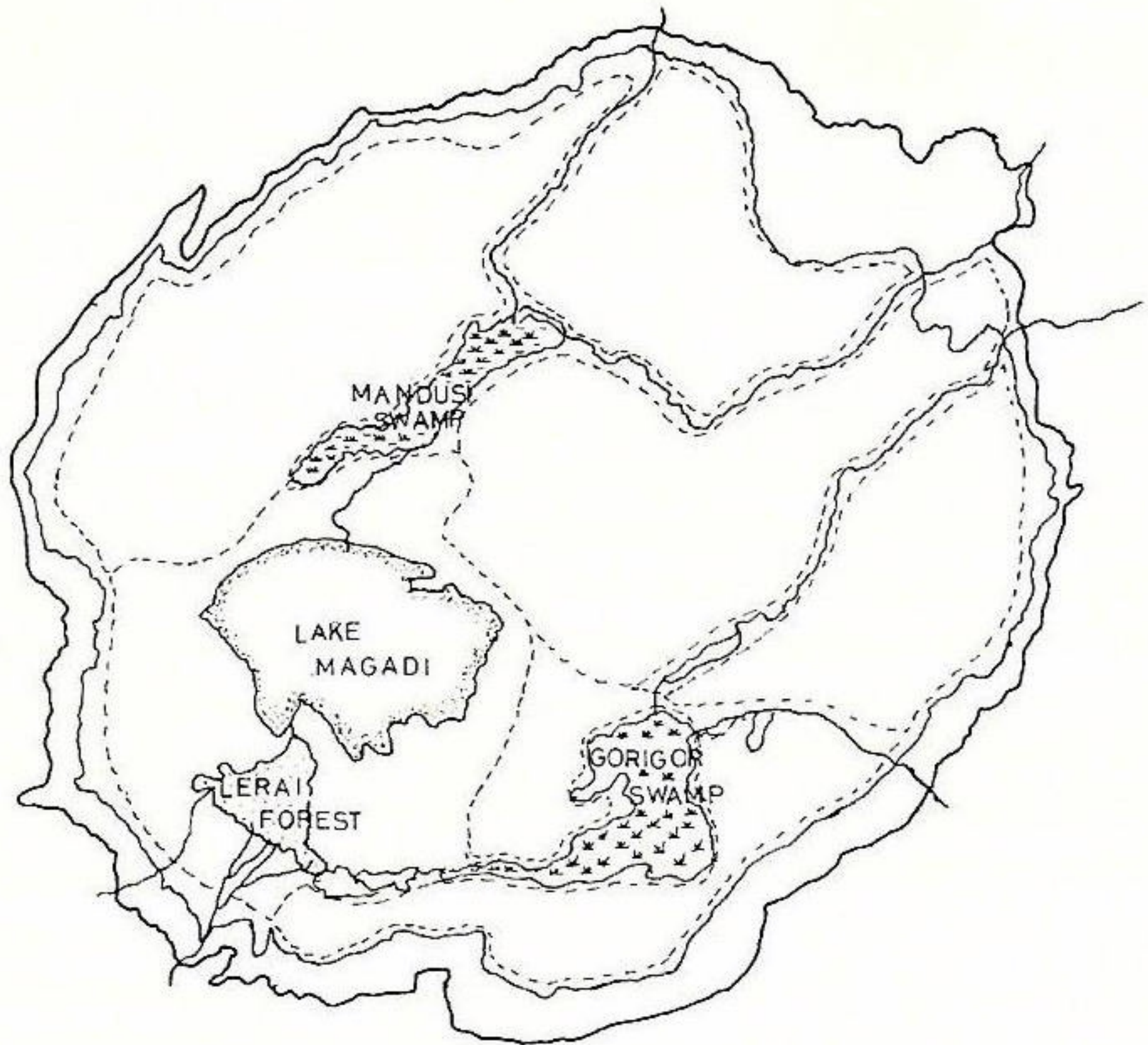
1382

1383 **Fig S4. Smoothed cycles and trends based on the structural time series analysis versus the**
1384 **year of observation for the standardized annual (annualstd), wet season (wetstd) and dry**
1385 **season (drystd) rainfall for the Ngorongoro Crater for 1963-2014.**

1386

1387 **Fig S5. Projected total annual rainfall, average maximum and minimum temperatures for**
1388 **Ngorongoro Crater in Tanzania under three climate scenarios (RCP2.6, RCP4.5 and**
1389 **RCP8.5) for the period 2006-2100.**

1390



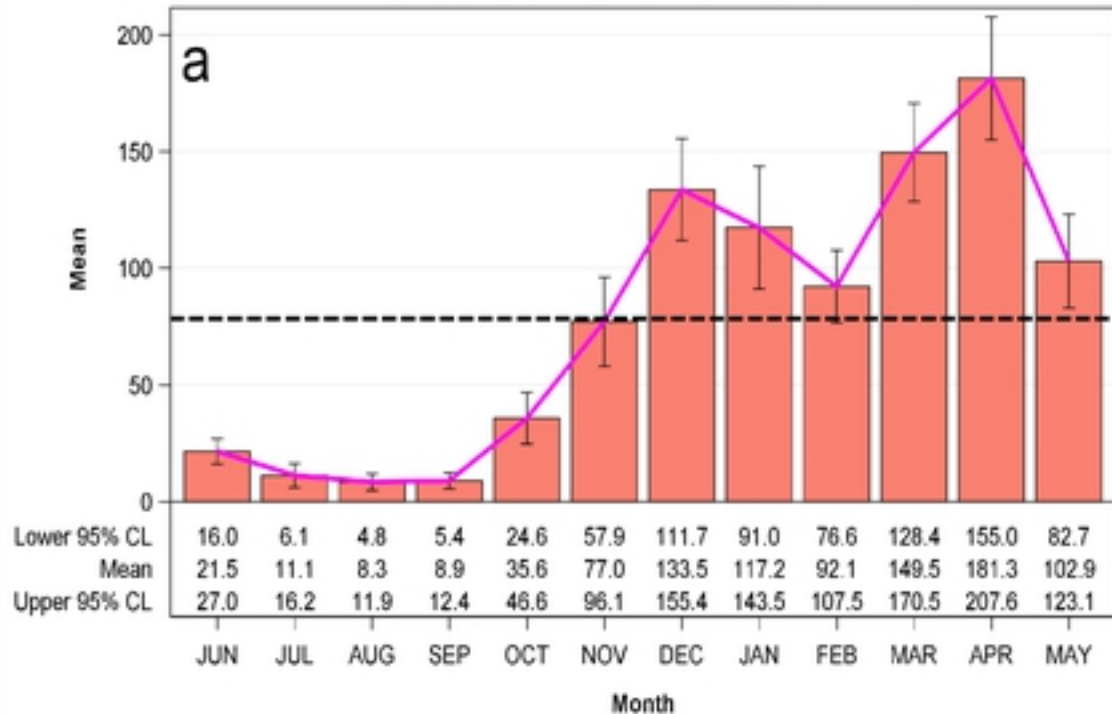
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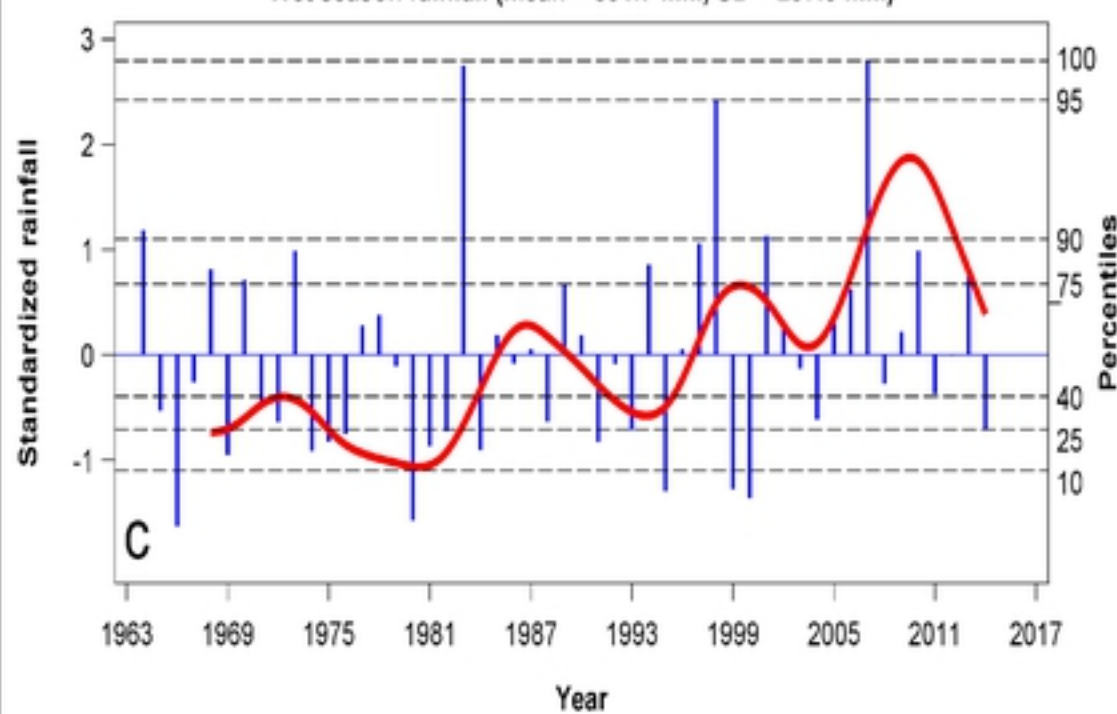
LERAI
FOREST

GORIGOR
SWAMP

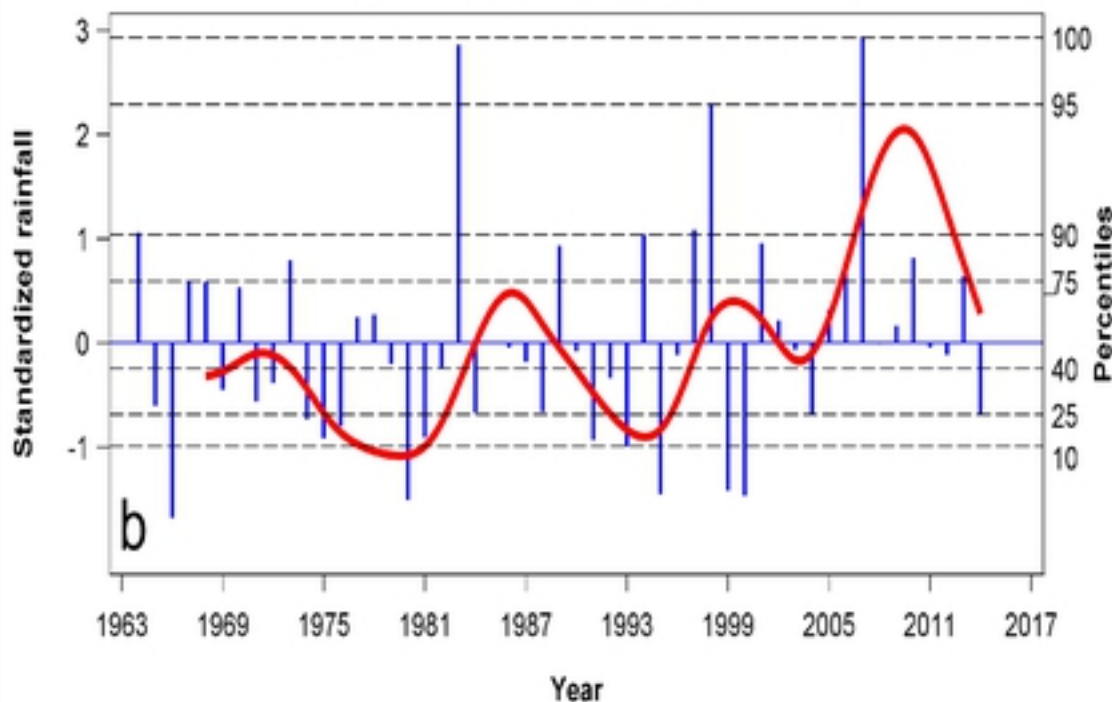
Mean monthly rainfall (mean = 78.3 mm, SD = 84.2 mm)



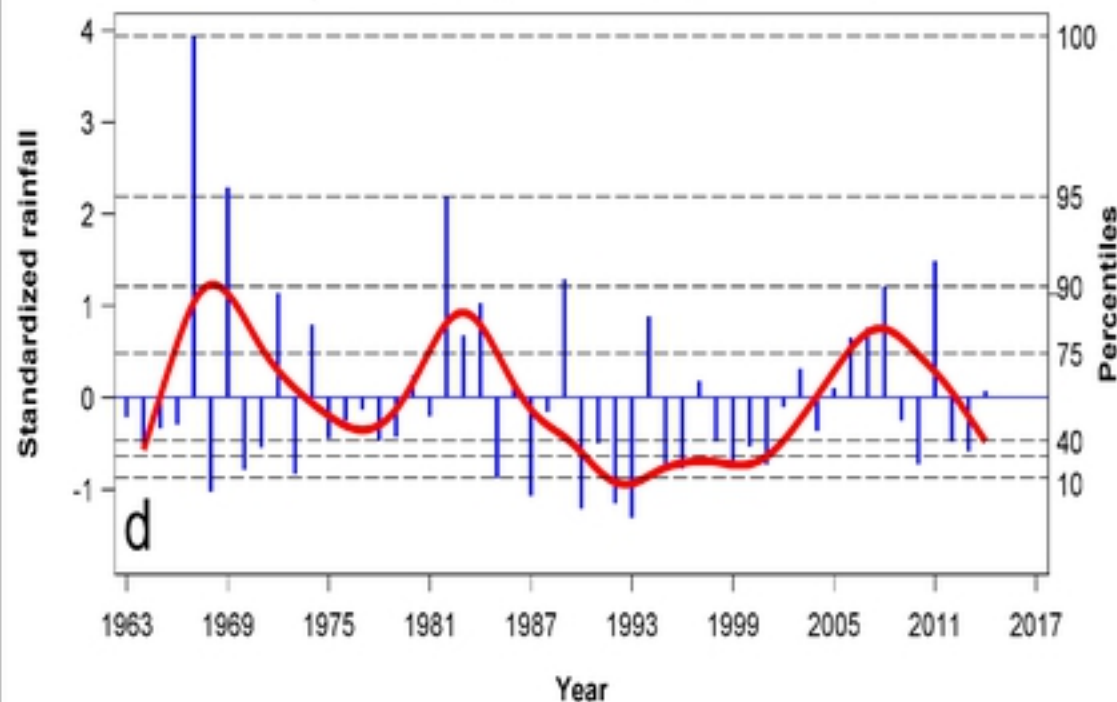
Wet season rainfall (mean = 851.7 mm, SD = 297.3 mm)

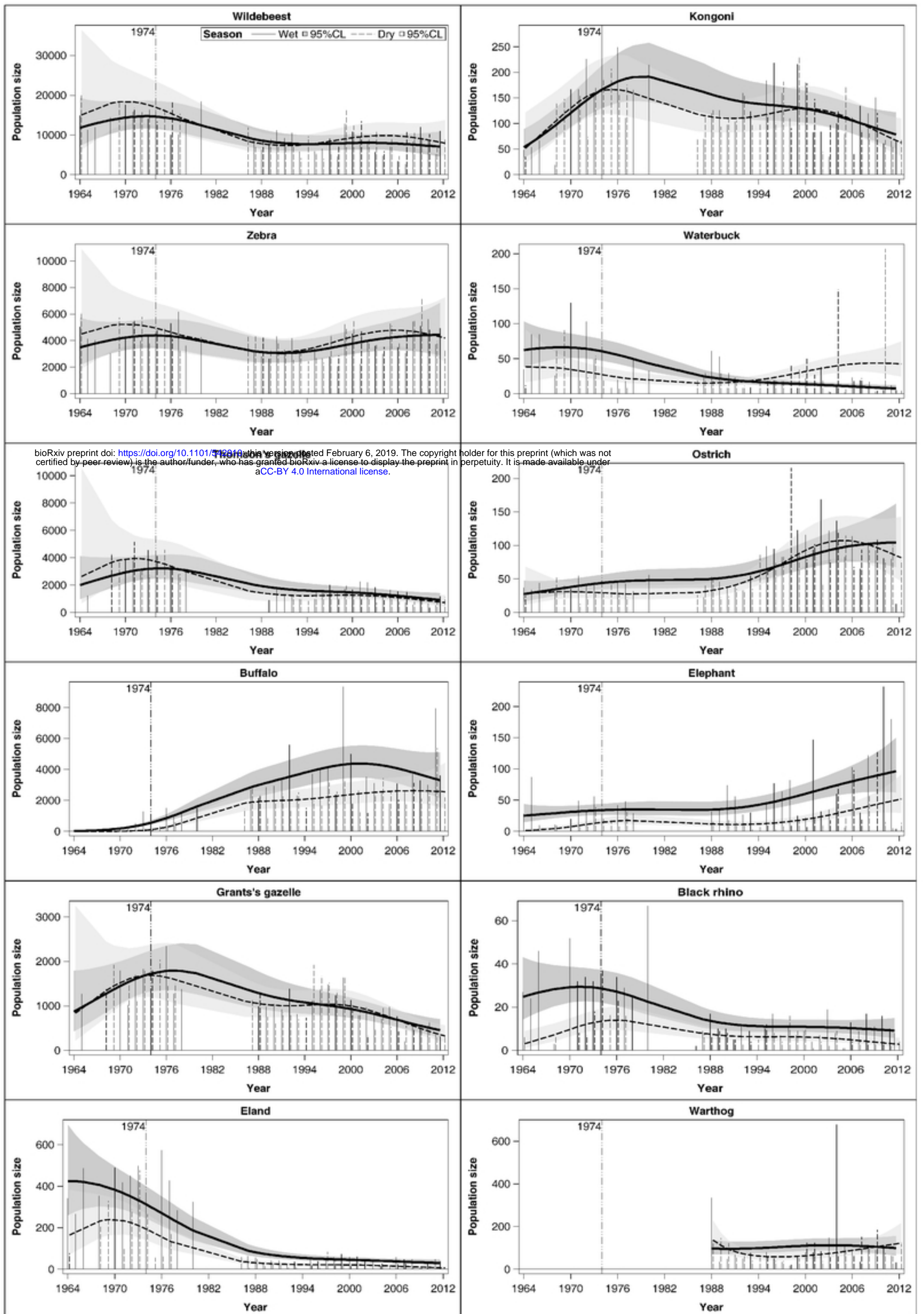


Annual rainfall (mean = 937.5 mm, SD = 300.7 mm)

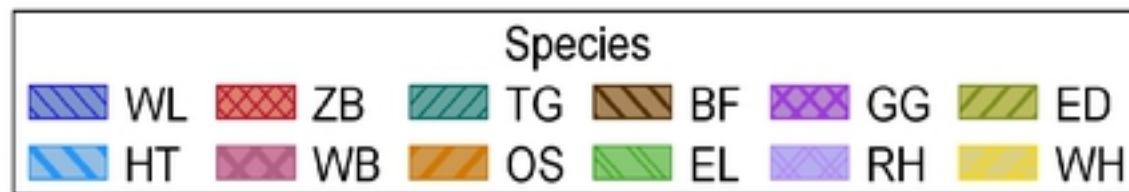
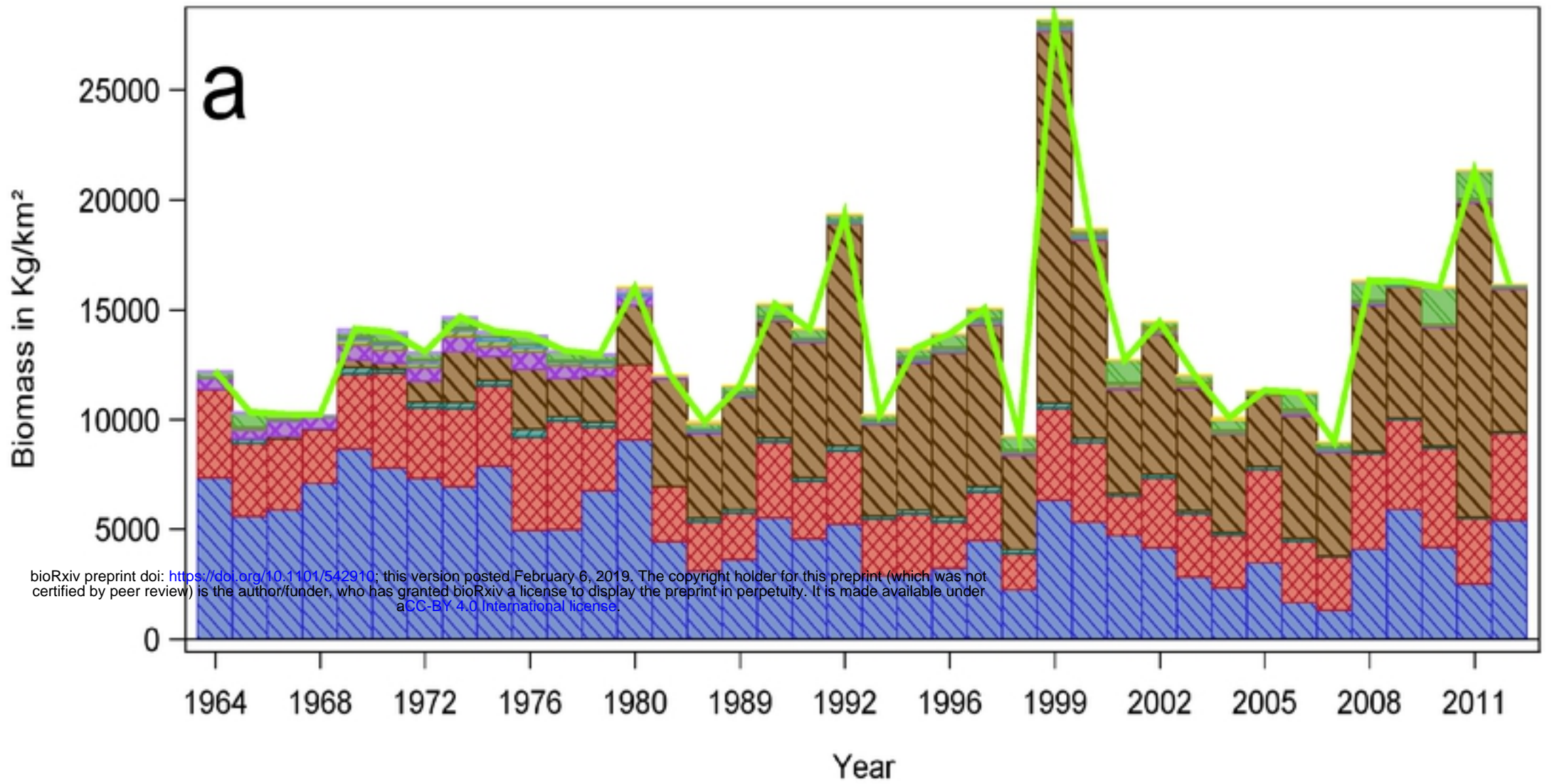


Dry season rainfall (mean = 85.5 mm, SD = 65.2 mm)

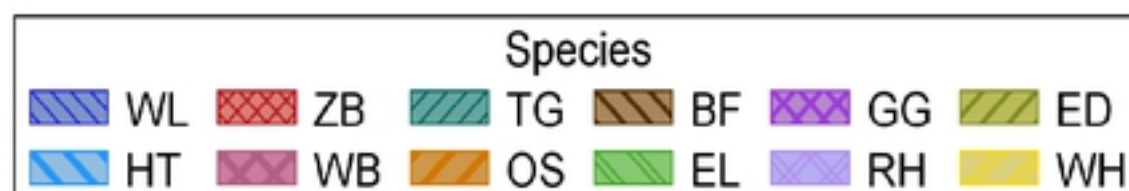
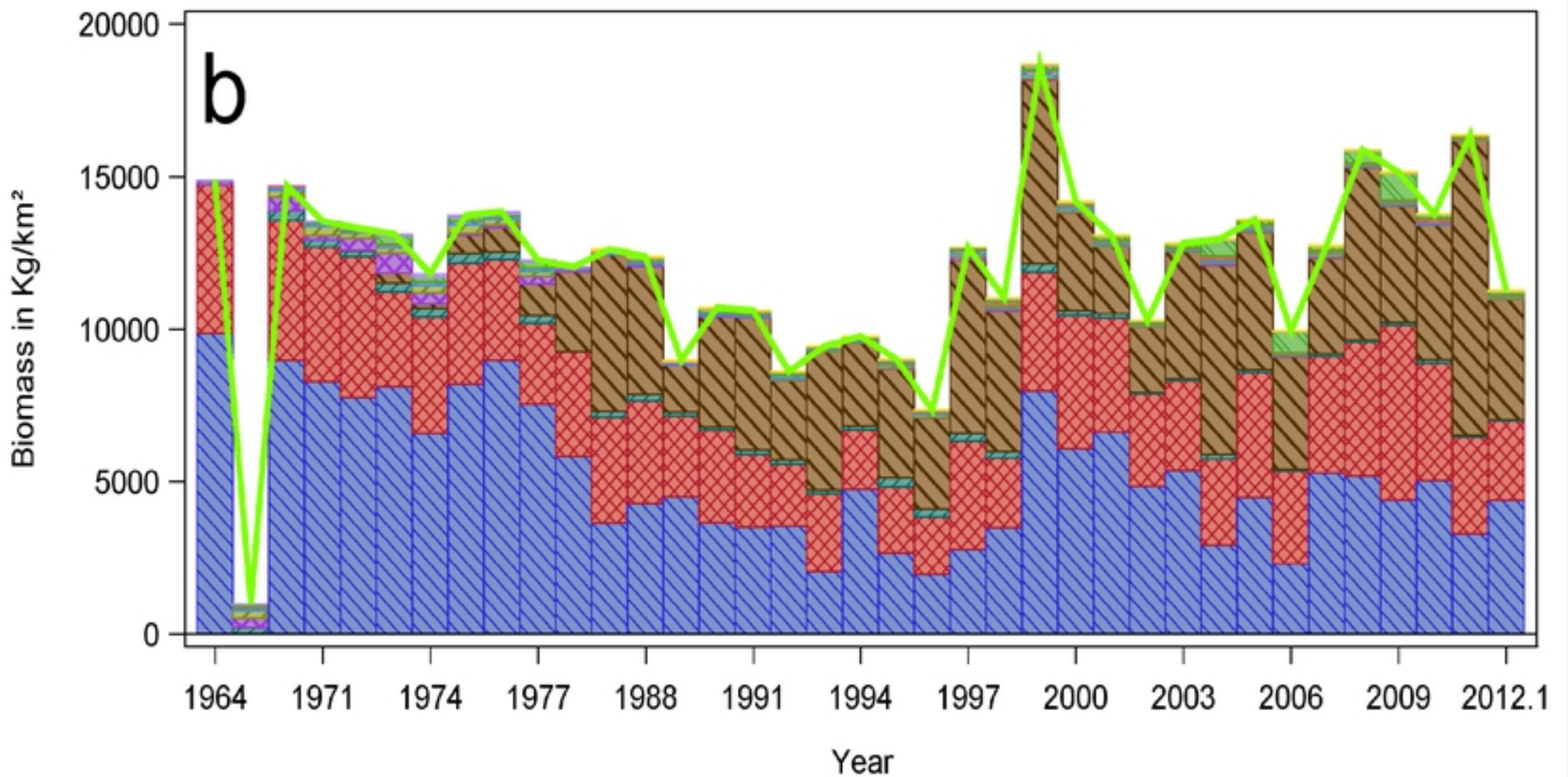


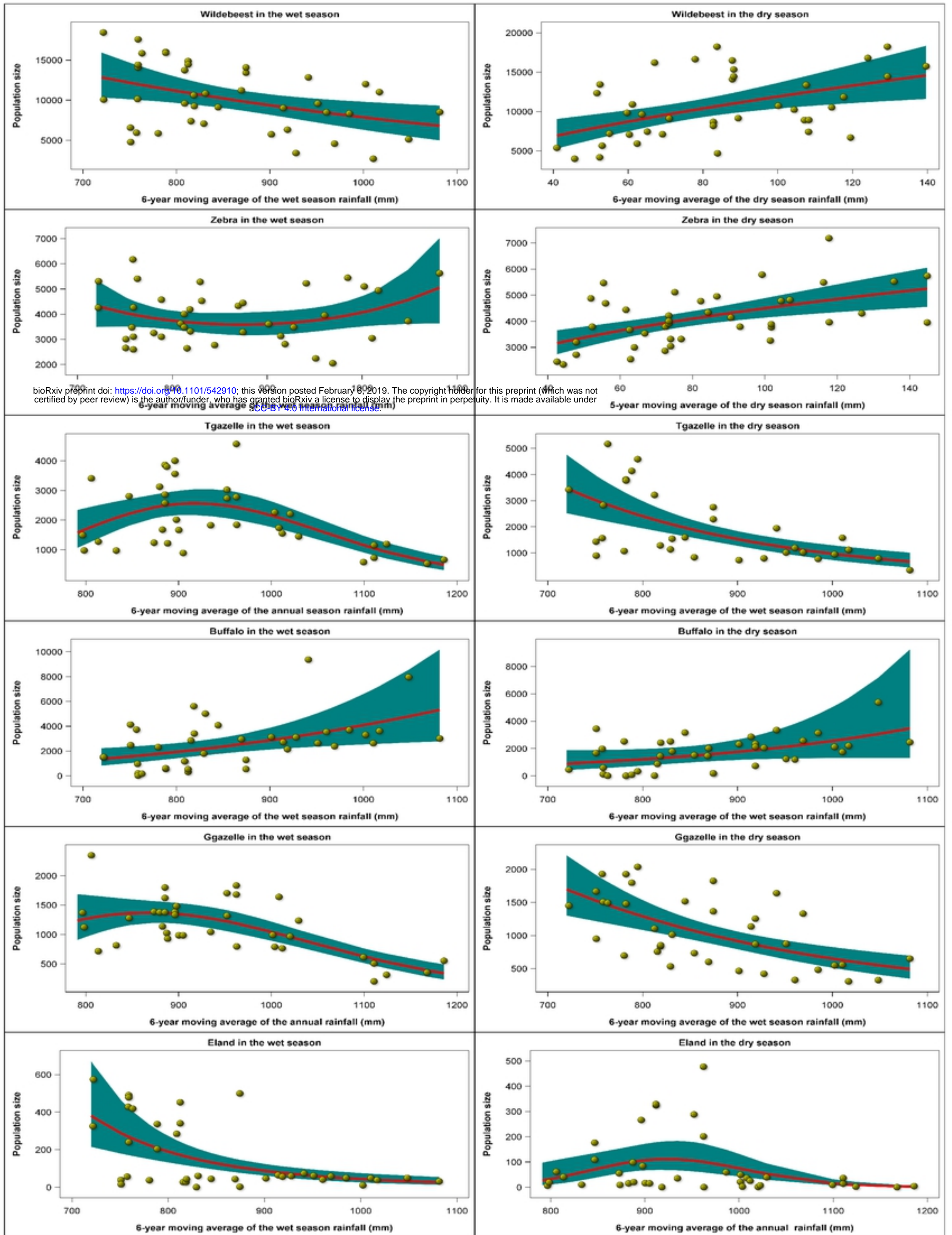


Biomass in the wet season

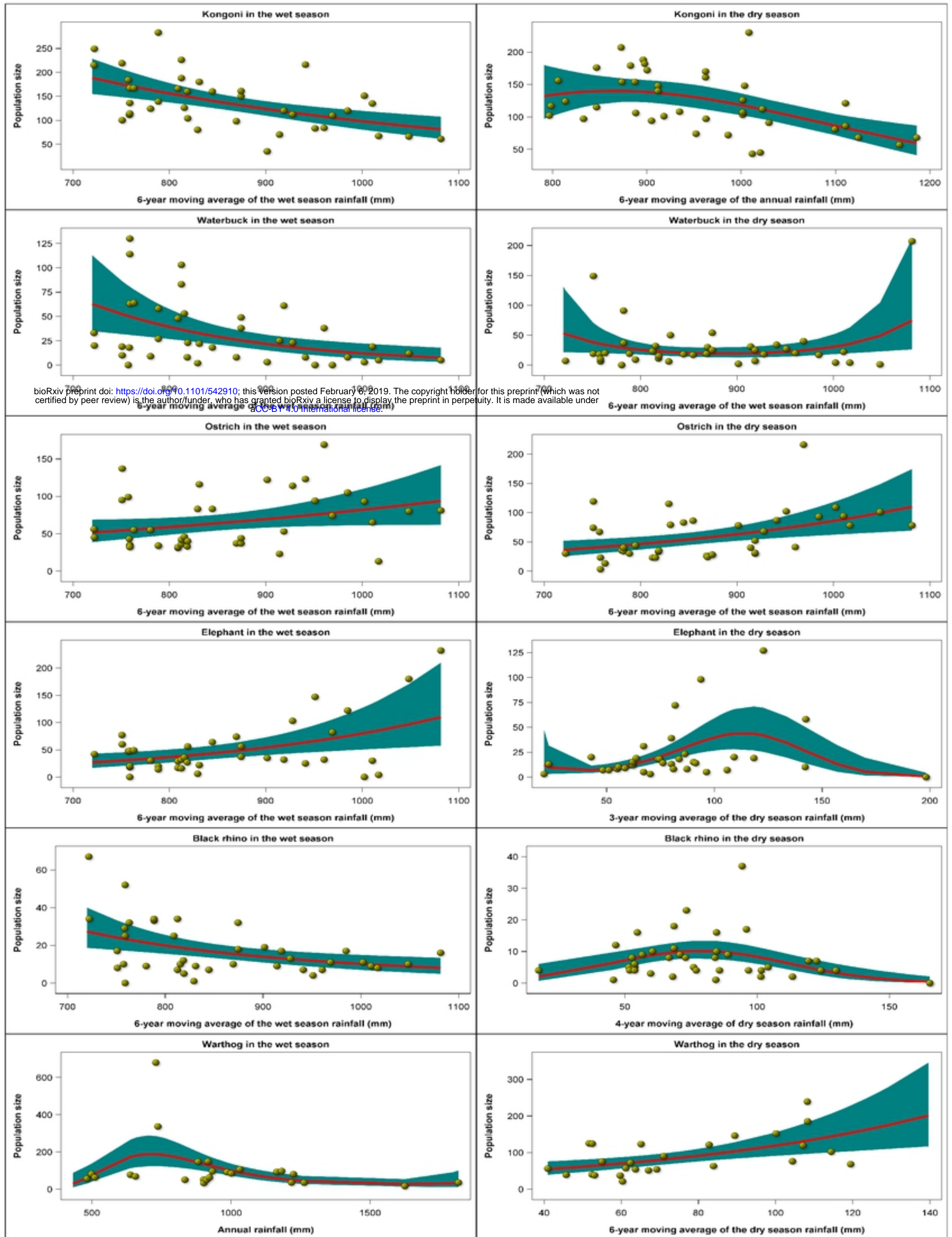


Biomass in the dry season





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Forecasting Buffalo population size in relation to rainfall

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LN(Buffalo Population Size +1)

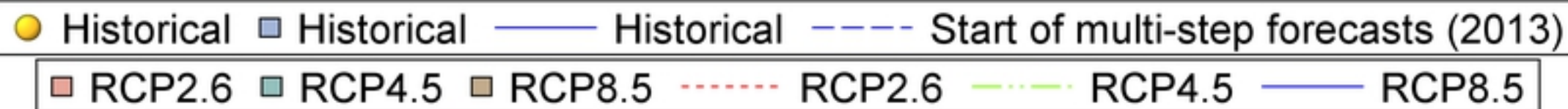
10.0
7.5
5.0
2.5
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10.0
7.5
5.0
2.5
0.0

1975 2000 2025 2050 2075 2100

Year

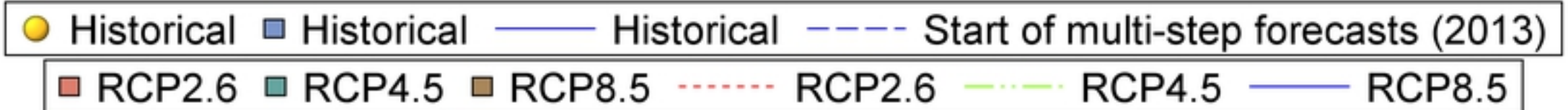
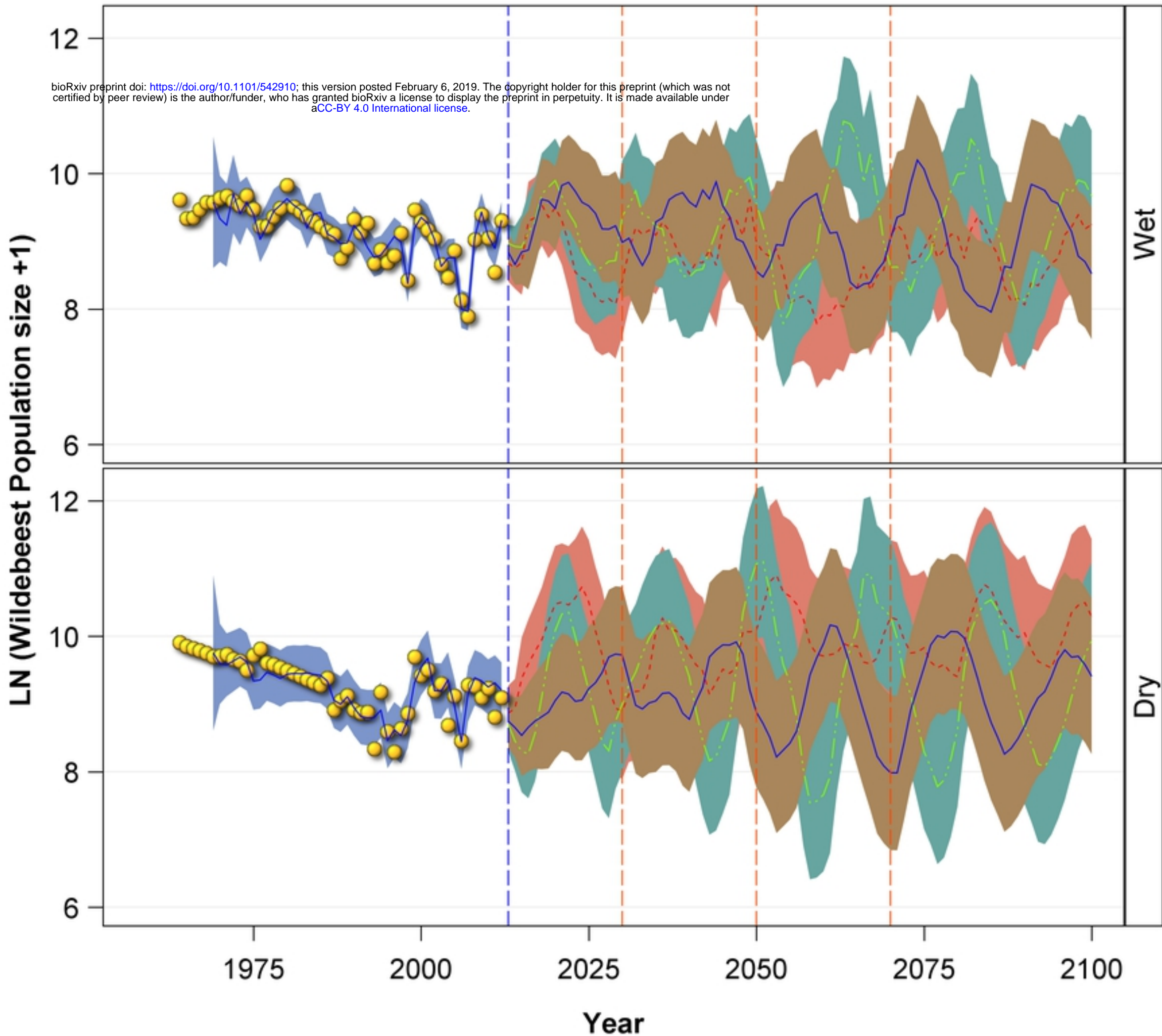
Wet

Dry



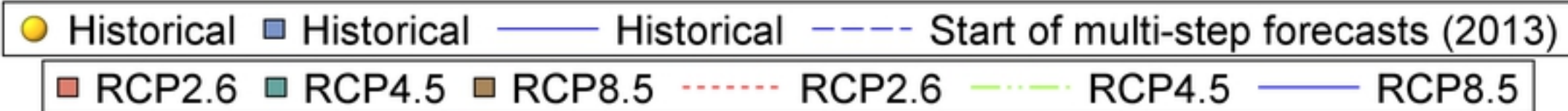
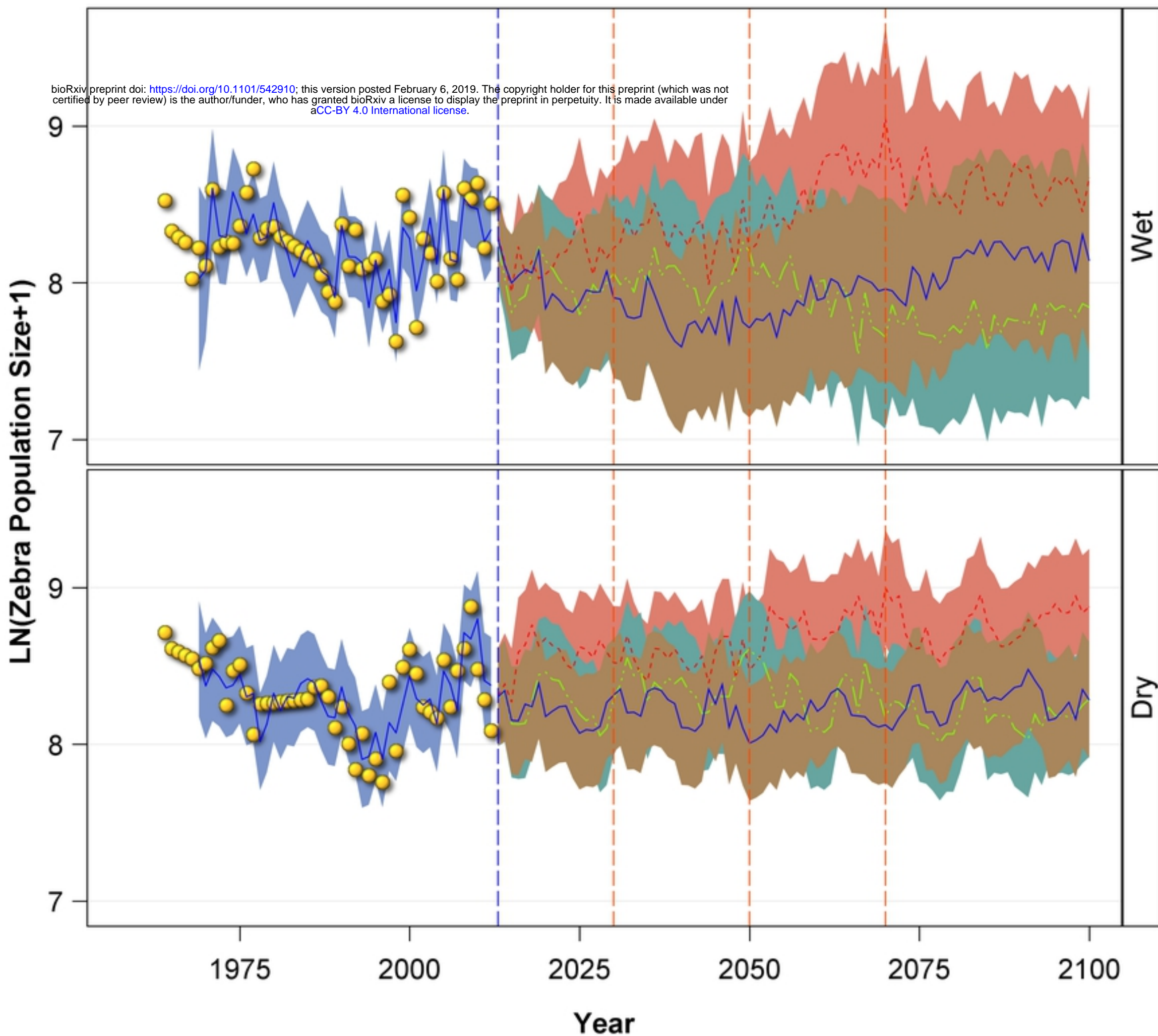
Forecasting wildebeest population size in relation to rainfall

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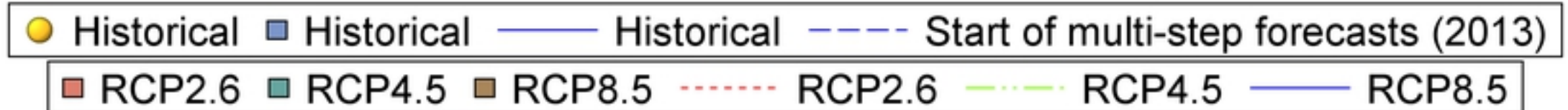
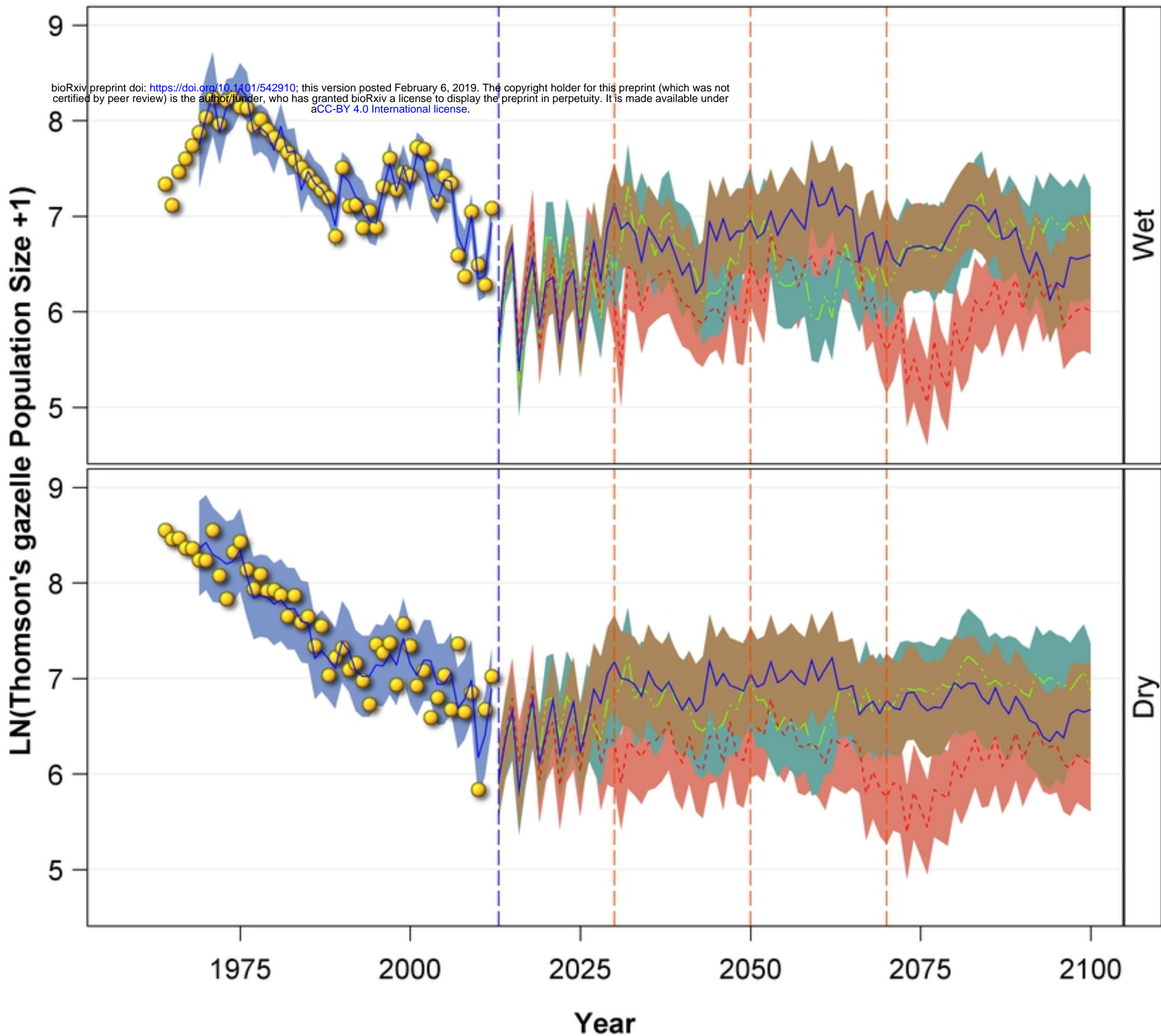
Forecasting Zebra population size in relation to rainfall

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Forecasting Thomson's gazelle population size in relation to rainfall

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Forecasting Grant's gazelle population size in relation to rainfall

