Does timing of birth affect juvenile and mare survival in wild plains zebra?

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Abstract

In large herbivores, the timing of births is mainly driven by the seasonal availability of their food resource. Population dynamics is strongly influenced by juvenile survival and recruitment, which highly depend on whether individuals are born during a favourable period or not. If births often occur during the most suitable season in northern cyclical environments for many large herbivore species, zebra give birth year-round at Hwange National Park, Zimbabwe, a tropical bushland characterized by the succession of a favourable wet season and a less favourable dry season. We used capture-recapture models for analysing long term observation data collected between 2008 and 2019 in this zebra population. We investigated the effect of the season (as a categorical variable) and the time spent in dry season on three categories of juveniles (younger foals of less than six months old, older foals between six and twelve months old, and yearlings between one and two years old) and mares survival, according to their reproductive state. The season had no effect on any survival. Younger foals annual survival was not affected by the time spent in dry season, whereas older foals and yearlings annual survival decreased with an increasing exposure to the dry season. Mares annual survival also decreased with an increasing time spent in dry season, whatever the reproductive status, but to a large extend when non-reproducing. The timing of birth, by determining the external conditions experienced by the offspring and their mothers during critical phases of their life cycle, plays a determinant role in their survival. As climate change is expected to lead to more frequent droughts, longer and harsher dry seasons in tropical ecosystems, we hypothesize a detrimental effect on zebra population dynamics in the future.

Keywords: capture-mark-recapture, environmental seasonality, Equus quagga, Hwange National Park, reproduction, tropical ecosystem.

Introduction

The timing of births, determined by environmental, biotic and internal factors, is a major life history trait of the organisms, involved in the determination of individual fitness and survival (Plard *et al.* 2015). Although the demographic role of the phenology of reproduction, *i.e.* the distribution of a reproductive event such as births across the year in a given population, has been illustrated theoretically (*e.g.* Calabrese and Fagan 2004 in plants and insects), its empirical support is less clear (*e.g.* Franks *et al.* 2018 in birds). This is particularly true for large herbivores (Plard *et al.* 2014), where it has been only marginally explored because of various limitations (*e.g.* need for detailed long-term individual-based datasets, Clutton-Brock and Sheldon 2010).

The timing of birth and the following months are associated with a critical period for the newborn and its mother in terms of energetic demand: early growth for the former and lactation for the latter (Bronson 1989). In large herbivores, juvenile survival is regulated by various factors such as population size *via* density-dependent effects (Gaillard *et al.* 1998) and predation (Severud *et al.* 2019), but above all, environmental conditions. Juvenile survival depend on the environmental seasonality (*sensu* Heldstab *et al.* 2018), *i.e.* the succession of the seasons defined by an ensemble of environmental and climatic characteristics, with a reduced survival during the harshest season. For instance, calves survival is lower during the dry season than during the wet season in Serengeti wildebeest *Connochaetes taurinus* (Mduma *et al.* 1999). Hence, by determining the environmental conditions experienced by the new individual during its first months of life, the timing of birth has indirect consequences on newborn survival, through the modification of its growth rate for instance (*e.g.* Feder *et al.* 2008).

Thus, the phenology of birth is generally supposed to be adjusted to maximize offspring survival. In large herbivores, this mainly goes through the synchronization of parturition with food resource availability and quality (Post *et al.* 2003). Bighorn sheep *Ovis canadensis* for

instance, give birth during a restricted period of time, just before the forage quality peak, to provide sufficient milk and high-quality vegetation access to their growing lambs (Festa-Bianchet 1988). Nevertheless, numerous species are characterized by highly variable dates of birth inside their population, even when living in seasonal environments (*e.g.* Sinclair *et al.* 2000). Why such a variability, and what are the demographic consequences of this variability? Still few studies have explored the consequences of the timing of birth on early life-stages survival in tropical ungulates, and most of them did not correct for imperfect detection (Gaillard *et al.* 2000, Grange *et al.* 2015), leading to less reliable conclusions. Thus, this field of research remains poorly known and needs further explorations (Lee *et al.* 2017).

In addition, the period around parturition is also critical for reproductive females themselves, as they endure their offspring needs in addition to their own. Lactation costs are particularly high in mammals (Clutton-Brock *et al.* 1989), and could turn reproductive females more susceptible to environmental conditions. Therefore, lactating females have to adjust their foraging behaviour to meet the extra energetic requirements. In zebra *Equus burchellii*, lactating mares do not increase their feeding time to keep matching the activity budget of the rest of their harem, but increase their bite frequency when feeding (Neuhaus and Ruckstuhl 2002). They also lead their harem more frequently than non-lactating mares to initiate movements to waterholes due to their increased water demand (Fischhoff *et al.* 2007). However, if a higher mortality rate could have been observed in females undergoing nursing energetic costs than in those who did not raise an offspring during the same year (Clutton-Brock *et al.* 1983), this does not appear to be the rule. A large literature, mainly based on northern hemisphere species, found no or positive correlation between the reproductive state and survival in mammal females, depending on their age class, social status or overall quality for instance (*e.g.* Weladji *et al.* 2008, Descamps *et al.* 2009, Morano *et al.* 2013). The absence of clear pattern and the low representation of species from the southern hemisphere spurs further investigations.

Here we investigated the effect of the phenology of births on juvenile and mother annual survival in relation to environmental conditions in wild plains zebra *Equus quagga*. We explored the impact of the time spent in dry season, defined by the timing of birth and the duration of the associated dry season, on the survival of two juvenile stages, yearlings and adult females. We took advantage of a population of individually known animals living in Hwange National Park (HNP), Zimbabwe and followed since 2004. Even if their environment is seasonal (*i.e.* characterized by the succession of a wet and a dry season, Chamaillé-Jammes *et al.* 2006), zebras breed year round in this study site. Coupled with a high inter-annual variability in the starting date of the seasons, this constitutes the adequate framework to study the impact of variable environmental conditions related to seasonality on juveniles and females survival during the reproductive period, in a tropical herbivore.

As a large-bodied species living in a seasonal environment, the plains zebra is supposed to belong to the capital end of the capital-income breeder continuum (Jonsson 1997, Ogutu *et al.* 2014). Once the mother is engaged in reproduction, she will provide the energetic effort to bring her foal to weaning age mainly using previously stored resources. Moreover, newborn almost exclusively rely on its mother for food provisioning through lactation and nursing (Jackson *et al.* 2021), and is not exposed to thermo-regulation issues in our tropical study site. Thus, we hypothesized foals survival should not be sensitive to environmental conditions until weaning (*i.e.* during the first six months of life) (i). Then, the foal becoming progressively independent from its mother during the following six months (*i.e.* between six and 12 months of age, Smuts 1976), it should experience a subsequent decrease in its survival probability (ii). We expected a similar trend in yearling (*i.e.* between one and two years old) survival (Gaillard *et al.* 2000) because at this stage, it is fully independent from its mother but not fully grown yet (iii). To the contrary, the period immediately following parturition should be critical for the mother, which could experience lower survival than a non-breeding female (iv-1) and a stronger

negative response to harsh environmental conditions (v-1). Besides, regarding the variability in the findings associated with the literature focusing on reproductive females survival and the possible confounding effect of mares quality, we also considered the alternative hypothesis that a reproductive female could instead experience higher survival than a non-reproductive one (iv-2) and show less sensitivity to harsh environmental conditions (v-2).

Materials and methods

1. Context of the study

1.1. Study site

Hwange National Park (19°00' S, 26°30' E), Zimbabwe, covers 14,651 km^2 of bushlands, woodlands and scrublands interspersed with grassland (Arraut *et al.* 2018), at between 900 and 1,100 m a.s.l.. Average annual rainfall is c. 600 mm, with high inter-annual variations (Chamaillé-Jammes *et al.* 2006). Most, if not all, rainfall events occur during the wet season from October to April. The start of the wet season is characterised by a high inter-annual variability, leading to variable duration of the dry season. The study took place in the north-east of the park where artificial waterholes retain water year round and where areas > 8 km from a waterhole are rare, even in the dry season (Chamaillé-Jammes *et al.* 2007). There is no hunting in the park, but the densities of the two main zebra predators, lion *Panthera leo*, and spotted hyena *Crocuta crocuta* are high (Loveridge *et al.* 2007, Drouet-Hoguet 2007).

1.2. Study species

Plains zebras live in harems composed of a stallion, several mares and their foals under two years old (Klingel 1969). They give birth year-round in most of their range, including Zimbabwe (Dasmann and Mossman 1962), even if a births peak can be observed around January to March in this area. Foals are weaned around 11 months of age (Smuts 1976), and

are considered as "followers" on the hider-follower gradient (Lent 1974), as they stand and follow their mother soon after birth (Sinclair *et al.* 2000). Zebras are grazers, feeding virtually only on grasses. Their food resource is thus mainly driven by rainfall (DuPlessis 2001). In HNP, the population of zebras is mostly resident (unpublished GPS data).

1.3. Zebra demographic data

Following the protocol presented in Grange *et al.* (2015), we recorded the presence of individually identified zebras between 2008 and 2019 using visual identification of their unique stripe pattern. Censuses were conducted twice a year, around March and August, during field sessions (hereafter called "sessions") at the transition between wet and dry seasons (n = 24 sessions, *mean session duration* = 45 ± 25 days, *range* = 13 - 88 days). When first sighted, individuals were classified according to three age classes: foal (from birth to 12 months old), yearling (12 to 24 months old) and adults (more than 24 months old). When possible, the precise age of foals and yearlings was determined using the criteria of Smuts 1975 and Penzhorn 1984, and photographs of individuals of known age (see details in Grange *et al.* 2015). For those individuals, we estimated a date of birth and its accuracy.

1.4. Season delineation

For each year, we identified the transition date between wet and dry season using 500 m resolution bi-monthly Normalized Difference Vegetation Index (NDVI) records from the NASA website (MOD13A1 product, https://modis.gsfc.nasa.gov) and daily rainfall records from the Climate Hazards Center website (Rainfall Estimates from Rain Gauge and Satellite Observations, https://www.chc.ucsb.edu)(Supporting information 1). During the study period and according to our estimations, the wet season in HNP started between the 1st of November

and the 19th of December, and the dry season started between the 9th of May and the 29th of July.

2. Statistical analysis

2.1. General purpose

We ran Capture-Mark-Recapture (CMR) analyses (Lebreton *et al.* 1992) on two distinct datasets: a first one for individual of known date of birth with an accuracy ranging from 0 to ± 90 days (n = 310) to estimate the annual probability of survival of the two foal age classes (*i.e.* "younger foals" of less than six months old and "older foals" between six and 12 months old) and yearling (*i.e.* between one and two years old). We used a second dataset composed of adult females (n = 205) to estimate the annual probability of survival of mares according to their reproductive state using multi-states models (Lebreton *et al.* 2009). We tested the effect of the time spent in dry season since births for younger foals and mothers, and the subsequent time spent in dry season between two successive seasons for older foals, yearlings and non-reproductive mares (detailed below). We performed CMR analyses using the program MARK (www.phidot.org/software/mark) and R (R statistical software, www.r-project.org), with the R package *RMark* (Laake 2013). The Goodness Of Fit tests (GOF) were assessed using the R package *R2ucare* (Gimenez *et al.* 2017).

For both datasets, we considered each session as punctual, summarized by its starting date. As it was variable, we accounted for the time interval between two successive sessions in the model specification. We calculated the proportion of time elapsed between two successive sessions pertaining a year as follows: $\Delta t_{s2\text{-}s1} = (Start\ date_{s2} - Start\ date_{s1}) / 365$.

188 *2.2. Juvenile survival*

189 As in previous works of demographic analyses performed on these data (Grange *et al.* 2015,
190 Vitet *et al.* 2020, Vitet *et al.* 2021), we ran the analyses on individuals observed at least once
191 in the field ($n = 290$), but also on individuals which were never observed but whose mother was
192 detected to be pregnant thanks to opportunistic faecal sampling and subsequent hormone (20-
193 oxopregnanes and oestrogens, Ncube *et al.* 2011) dosage ($n = 20$, Supporting information 2).
194 We recorded those foals as being identified at birth only and never seen again. For both
195 categories (*i.e.* seen and unseen individuals), we retained individuals whose date of birth was
196 estimated ($n = 310$). We attributed a session and a season of birth to each individual based on
197 the date of birth nearest session. So, all the foals born during the same session constituted a
198 cohort, experimenting similar environmental conditions. We defined three age classes:
199 "younger foals" of less than six months old, "older foals" between six and 12 months old and
200 "yearlings" between one and two years old. Individuals remained in the dataset even after
201 becoming adults (*i.e.* > 2 years old) to get better estimations of yearling survival, but adult
202 survival was not considered in this analysis. We estimated the time spent in dry season between
203 two successive sessions. The variable *tids* was defined as the proportion of days of dry season
204 between the first day of the session s and the first day of the following session $s+1$. We used
205 the scaled value of *tids* in the models to ease model convergence. We summarized observations
206 data in a life history dataset, with one observation per known individual per session: 0
207 corresponding to "no sighting of the individual during the session s", and 1 corresponding to
208 "at least one sighting of the individual during the session s".

209 The GOF tests of the fully time-dependent model (Gimenez *et al.* 2018) denoted
210 problems of overdispersion (Test 2.CL: $\chi^2 = 40.79$, $df = 16$, $P < 0.01$; Test 3.Sm: $\chi^2 = 11.05$, df
211 $= 19$, $P = 0.92$), trap-dependence ($\chi^2 = 139.35$, $df = 17$, $P < 0.01$) and transience ($\chi^2 = 70.47$, df
212 $= 22$, $P < 0.01$). After examination of Test 2.CL, we noticed that overdispersion was mainly

213 caused by three sessions in the dataset. So, we considered it as marginal and ignored
214 overdispersion in the analyses. We took into account trap-dependence by adding a default trap-
215 dependence (*td*) effect in each recapture model tested. Transience was likely due to the age
216 structure as young individuals often have low survival in large herbivores (Gaillard *et al.* 2000).
217 Thus, we fitted all survival models tested with a default age class effect. We explored the effect
218 of the season and *tids* on recapture and survival probabilities, for the two age classes of foals
219 and the yearlings, and on several groupings of those age classes (Supporting information 3).
220 We also fitted the null models and models including solely a time effect. We conducted a similar
221 analysis on the two foal age classes using a Generalized Linear Model (GLM) approach,
222 presented in Supporting information 4.
223
224 *2.3. Mare survival*
225 We ran the analyses on all the adult females observed at least once during the sessions (n =
226 322). The season and *tids* variables were defined in the same way than for juveniles (see above).
227 We summarized observations data in a life history dataset, with one observation per known
228 individual per session: 0 corresponding to "no sighting of the mare during the session *s*", 1
229 corresponding to "at least one sighting of the mare alone during the session *s*" and 2
230 corresponding to "at least one sighting of the mare with a dependent foal during the session *s*".
231 We considered a dependent foal as an individual that is still suckled, so under 6 months of age.
232 Even if weaning generally occurs around 11 months of age in zebras, foals can survive without
233 their mother from 9 months old upwards (Smut 1976). We chose 6 months to exclude such
234 possibility and match our sessions frequency.
235 As there were too few repetitions to conduct the GOF tests of the multi-states model,
236 we conducted the GOF tests on the one-state model instead. The tests denoted overdispersion
237 (Test 2.CL: χ^2 = 49.02, df = 19, P < 0.01; Test 3.Sm: χ^2 = 72.10, df = 20, P < 0.01), trap-

238 dependence ($\chi^2 = 112.13$, $df = 21$, $P < 0.01$) and transience ($\chi^2 = 62.23$, $df = 21$, $P < 0.01$). After
239 examination of Test 2.CL and 3.Sm, we noticed that overdispersion was mainly caused by five
240 and three sessions in the dataset respectively. So overdispersion could be ignored because
241 considered as marginal. We took into account trap-dependence by adding a default trap-
242 dependence effect in each recapture model tested. To take into account transience, we added a
243 categorical covariable *sight* in all survival models to differentiate between mares captured for
244 the first time during the survey and mares already captured at least once during the survey,
245 following the method described by Pradel *et al.* 1997. We evaluated the effect of the
246 reproductive state (*i.e.* with or without a dependent foal), the season and *tids* on recapture,
247 survival and transition probabilities. Unfortunately, age was not known for a large number of
248 females, so we were not able to include it in the models. We also fitted null models and models
249 including solely a time effect.
250
251 *2.4. Model selection*
252 Because of the huge number of combinations possible between recapture and survival (and
253 transition for mares) models, we conducted a two-step selection model using the lowest Akaike
254 Information Criterion adjusted for small sample sizes (AICc) and the number of parameters
255 (principle of parsimony) (Burnham 2002). We conducted a first model selection step on
256 recapture and survival (and transition for mares) models independently. When proceeding to
257 model selection on a given demographic parameter (*i.e.* recapture, survival or transition), we
258 set the other models to depend exclusively on the covariables related to GOF corrections (*e.g.*
259 *w*hen selecting recapture models in foals, we set survival model as depending on the age class,
260 see Supporting information 3). We considered all the models within ΔAICc < 2 from the best
261 model for the next model selection step. When there was only one competing model emerging
262 from this model selection step for a given demographic parameter, we also included the second

best model in terms of AICc to allow a real model selection for each of the demographic parameters based on at least two different models (see model selection for data on mares in Supporting information 3).

In the second selection step, we ran all the combinations possible between the best recapture and survival (and transition for mares) models resulting from the first model selection step to identify the best complete models. We retained the complete models (recapture and survival, and transition for mares) within ΔAICc < 2 from the best model as competing models, and we retained the models with the lowest number of parameters as the best models. Following Arnold 2010, we set the confidence intervals at 85%, in accordance with our AICc model selection procedure.

Results

Juvenile survival

We found four competing models (*AICc* ∈ [1718.922; 1720.291], *deviance* ∈ [1658.641; 1660.011]) to estimate the survival and recapture of juveniles, three of them correspond to the most parsimonious models (k = 29, see Table 1 and Supporting information 3). In all three models, the probability of recapture included an additive effect of trap-dependence and time, and the probability of survival increased with age and decreased with the proportion of time spent in dry season. The difference between them lied in the effect of *tids*, which was found to act in addition with the age class, or exclusively on older foals, or on older foals and yearlings grouped together in a unique age category. The season was not retained in the competing models.

Table 1: Statistics of the four competing models investigating the relationship between annual survival and the proportion of time spent in dry season according to the age class in plains zebra juveniles (Hwange National Park, Zimbabwe, 2008-2019).

Model	Explanatory variables	Nb. of parameters (k)	AICc	Deviance	ΔAICc
1	Survival ~ foal_old + yearl + adult + tids * fo_ye Recapture ~ td + time	29	1718.922	1658.641	0
2	Survival ~ foal_old + yearl + adult + tids * fo_ye Recapture ~ td + age_class + time	32	1719.827	1653.049	0.906
3	Survival ~ foal_old + yearl + adult + tids * foal_old Recapture ~ td + time	29	1720.134	1659.853	1.212
4	Survival ~ age_class + tids Recapture ~ td + time	29	1720.291	1660.011	1.37

tids = proportion of time spent in dry season; foal_old = older foals; yearl = yearlings; fo_ye = older foals and yearlings gathered.

The following stated results are from Table 1, model 1: the variable *tids* had a significant negative effect on both older foals and yearlings (β = -0.637 ± 0.367 SE, 85% CI [-1.167; -0.108]). The probability of survival of older foals ranged from 0.840 ± 0.108 SE, 85% CI [0.624; 0.944] when the proportion of time spent in dry season was the shortest (*i.e.* 9 % of the time) to 0.378 ± 0.144 SE, 85% CI [0.201; 0.595] when the proportion of time spent in dry season was the longest (*i.e.* 80 % of the time, Fig. 1). Similarly, the probability of survival of yearlings ranged from 0.891 ± 0.085 SE, 85% CI [0.699; 0.967] to 0.486 ± 0.123 SE, 85% CI [0.318; 0.657]. The survival of younger foals was not significantly affected by *tids*, and was of 0.431 ± 0.042 SE, 85% CI [0.371; 0.492] on average. Besides, the supplementary analyses on the two foal age classes using a GLM approach provided similar results (Supporting information 4). Therefore, hypotheses (i) stating that younger foals survival should not be sensitive to environmental conditions, (ii) and (iii) stating that older foals and yearlings *resp.* survival should be lower, were validated by our results. The effect of trap-dependence on the probability of recapture was significant (β = 1.756 ± 0.182 SE, 85% CI [1.494; 2.018]). The

probability of recapture varied from 0.123 ± 0.069 SE, 85% CI [0.053; 0.259] to 0.634 ± 0.151 SE, 85% CI [0.404; 0.815].

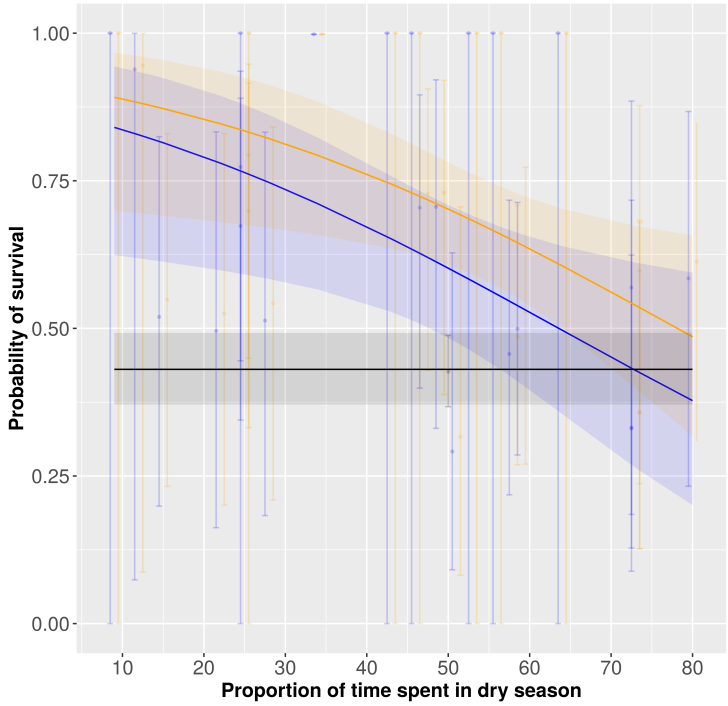

Figure 1: Probability of annual survival of plains zebras juveniles in Hwange Nation Park, Zimbabwe (2008-2019), according to the proportion of time spent in dry season. Black: younger foals (between birth and six months old), blue: older foals (between six and 12 months old), orange: yearlings (between one and two years old). Solid lines represent predicted values from the best model. Shaded areas represent 85% confidence intervals of these predicted values. Dots represent survival predicted by the time model, vertical bars represent 85% confidence intervals. Scaled proportion of time spent in dry season converted back to the proportion of time spent in dry season.

Mare survival

We found two competing models (*AICc* ∈ [3294.197; 3295.161], *deviance* ∈ [3226.108; 3224.943]) to estimate the survival, transition between reproductive states and recapture of mares, one of them being the most parsimonious model (k = 33, see Table 2 and Supporting information 3). In both models, the probability of recapture included an additive effect of the

trap-dependence, reproductive state and time. The probability of survival was higher for reproductive than for non-reproductive mares, and the proportion of time spent in dry season decreased the probability of survival. The probability of transition between reproductive states varied according to the season (see details below). The only difference between the two models came from the fact that *tids* acted either in addition or in interaction with the reproductive state to predict mares survival.

Table 2 : Statistics of the two competing models investigating the relationship between annual survival and the proportion of time spent in dry season according to the reproductive state in plains zebra mares (Hwange National Park, Zimbabwe, 2008-2019).

Model	**Explanatory variables**	**Nb. of parameters (k)**	**AICc**	**Deviance**	**ΔAICc**
1	Survival ~ sight + repro_status + tids Recpature ~ td + repro_status + time Transition ~ season * from_repro_status * to_repro_status	33	3294.197	3226.108	0
2	Survival ~ sight + repro_status * tids Recapture ~ td + repro_status + time Transition ~ season * from_repro_status * to_repro_status	34	3295.161	3224.943	0.964

tids = proportion of time spent in dry season; sight = first capture or not for a given female; repro_status = reproductive state; from_repro_status = reproductive state of departure for the transition models; to_repro_status = reproductive state of arrival for the transition models; td = trap-dependence.

The best-supported model included a significant effect of *sight* on the survival probability (β = 1.075 ± 0.272 SE, 85% CI [0.683; 1.467]). Here we present results for mares in their second and following observations only, results relying on a single first observation being less informative. The best-supported model also included a significant negative effect of *tids* on both reproductive and non-reproductive females (β = -0.729 ± 0.221 SE, 85% CI [-1.047; -0.410], Fig. 2a). The probability of survival of non-reproductive females varied from 0.963 ± 0.020 SE, 85% CI [0.921; 0.984] when the proportion of time spent in dry season was

340 the shortest to 0.690 ± 0.060 SE, 85% CI [0.600; 0.769] when the proportion of time spent in
341 dry season was the longest. Similarly, the probability of survival of reproductive females varied
342 from 0.989 ± 0.008 SE, 85% CI [0.969; 0.996] to 0.883 ± 0.054 SE, 85% CI [0.779; 0.941].
343 Therefore, hypothesis (iv-1) was not validated by our results in favour of hypothesis (iv-2)
344 stating that mothers could experience higher survival than non-breeding females. Similarly, we
345 did not validate hypothesis (v-1) in favour of hypothesis (v-2) stating that mothers could
346 experience a lower negative response to harsh environmental conditions. The probability for a
347 mare to move from the reproductive to the non-reproductive state was significantly higher (at
348 least 0.713 ± 0.044 SE, 85% CI [0.646; 0.772]) than the probability to stay in the reproductive
349 state (at most 0.287 ± 0.044 SE, 85% CI [0.228; 0.354]) whatever the season (Fig. 2b). The
350 probability to stay in the non-reproductive state was similar to the probability to move from the
351 non-reproductive to the reproductive state in the dry season (0.486 ± 0.039 SE, 85% CI [0.431;
352 0.542] and 0.514 ± 0.039 SE, 85% CI [0.458; 0.569] respectively), but it was significantly
353 higher in the wet season (0.688 ± 0.058 SE, 85% CI [0.600; 0.765] against 0.312 ± 0.058 SE,
354 85% CI [0.235; 0.400] respectively). The effect of trap-dependence on the probability of
355 recapture was significant (β = 1.034 ± 0.174 SE, 85% CI [0.784; 1.284]). The probability of
356 recapture was higher for non-reproductive than for reproductive females. It varied from 0.411
357 ± 0.072 SE, 85% CI [0.313; 0.517] to 0.908 ± 0.049 SE, 85% CI [0.808; 0.959] for non-
358 reproductive females, and from 0.129 ± 0.041 SE, 85% CI [0.080; 0.200] to 0.676 ± 0.106 SE,
359 85% CI [0.511; 0.807] for reproductive females.

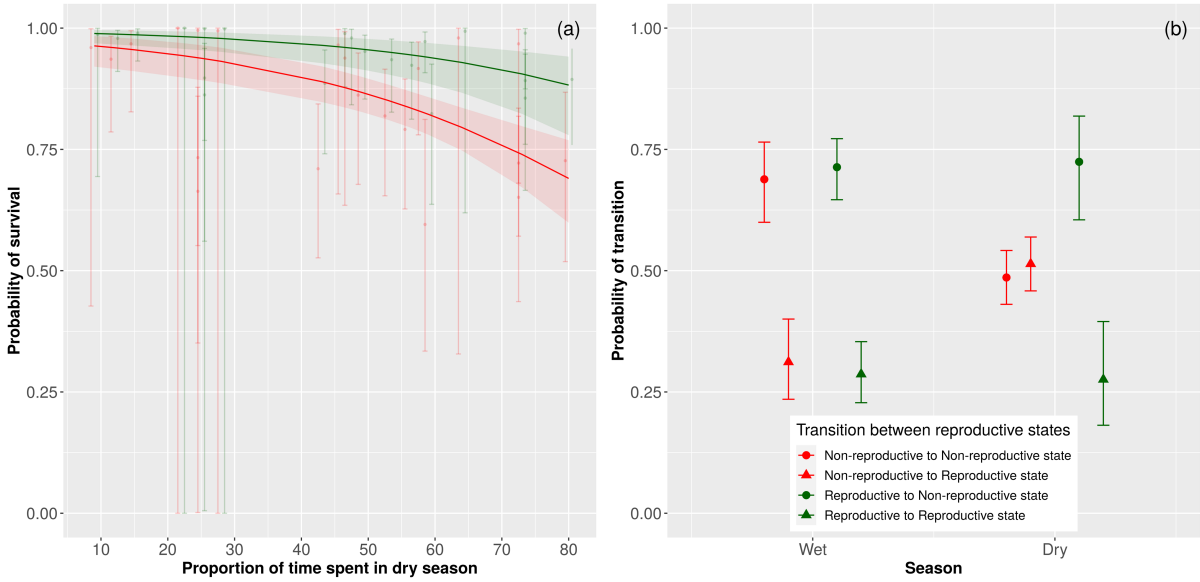

Figure 2: a) Probability of annual survival of plains zebra mares according to the proportion of time spent in dry season and their reproductive state (for mares in their second and subsequent observations only, see text for details). Solid lines represent predicted values from the best model (red: non-reproductive females, green: reproductive females). Shaded areas represent 85% confidence intervals of these predicted values. Dots represent females survival predicted by the time model respectively, vertical bars represent 85% confidence intervals. Scaled proportion of time spent in dry season converted back to the proportion of time spent in dry season. b) Probability of transition between reproductive and non-reproductive states for plains zebra mares according to the season. Dots represent predicted values from the best model. Vertical bars represent 85% confidence intervals of these predicted values. For both graphs: data from Hwange Nation Park, Zimbabwe (2008-2019).

Discussion

The phenology of births, by determining the environmental conditions experienced by newborn at birth and during the following months, has major effects on their survival. Although the annual cohort survival of younger foals (between birth and six months old) is stable around 0.431, the one of older foals (between six and twelve months old) and even yearlings (between one and two years old) significantly decreases with increasing time spent in dry season. The

378 decline observed, from approx. 0.8 to 0.4 for both age classes, is of a factor two between the
379 shortest and the longest exposure to dry season experienced by juveniles in this study. Mares
380 annual survival is also altered by an increasing time spent in dry season weather they are in a
381 reproductive state (*i.e.* with a dependent foal) or not, but in a lower extent. However, this effect
382 is all the more strong for non-reproductive females.

383 The timing of birth is intrinsically related to the timing of conception because of a slight
384 flexibility in the duration of gestation (Kiltie 1982). As the reproductive cycle of zebra mares
385 lasts slightly more than one year (Ncube *et al.* 2011), even if they experience post-partum
386 oestrus (Klingel 1969), one can expect their parturition date should progressively be shifted
387 from the optimal period, unless they delay their reproductive cycle to wait for the next
388 favourable birthing period. But a consequence of this is that their inter-birth interval (mean
389 inter-birth interval of 480 ± 116 days in the study site, Barnier *et al.* 2012) would be
390 significantly increased and their lifetime reproductive success decreased (as observed in giraffe
391 *Giraffa camelopardalis,* Lee *et al.* 2017). In addition, we found only a small negative effect of
392 the time spent in dry season on reproductive mares annual survival and no effect on annual
393 survival of younger foals, demonstrating that the timing of birth seems not to be crucial for
394 them. Moreover, females can engage reproduction only when they reach a certain threshold in
395 body condition (Grimsdell 1973), which can be delayed in case of adverse environmental
396 conditions during the year preceding parturition, such as drought years (Ogutu *et al.* 2014). This
397 is thus a supplementary factor acting as a constraint on the determination of the timing of birth.
398 Altogether, these observations argue in favour of breeding year-round in our zebra population
399 in the interest of the mare fitness, as observed in our population.

400 However, older foals and yearlings annual survival suffered from a date of birth
401 exposing them to a long period of time in dry season while they are gaining independence from
402 their mother. The date of birth can be the result of a trade-off between the mother and the

403 offspring, with the most adequate period being not necessarily the same for the mother than for
404 the offspring (Dezeure *et al.* 2021). In our study, one can hypothesize that the optimal timing
405 of birth for the offspring is situated at the beginning of the dry season: the harsh conditions
406 during early life are buffered by the mother at this time, and the offspring starts to become
407 independent while conditions are improving through the following wet season. Moreover, the
408 foal benefits from higher quality reserves stored by the mother during the previous wet season,
409 as suggested in African large herbivores (Ogutu *et al.* 2014). To the contrary, the optimal timing
410 of parturition for the mare could be more variable, in order to minimize the inter-birth interval
411 as they are only slightly affected by environmental conditions.

412 Although the timing of birth defines the environmental conditions experienced at birth,
413 it also determines susceptibility to predation, which is a major factor of mortality in zebra foals
414 (Mills and Shenk 1992) and probably in adults too (Grange *et al.* 2015). On the one hand, the
415 dry season implies higher water demand (which shall be added to the already increased demand
416 of lactating mares) while its availability is reduced. As water holes are hot spots of predation
417 (zebras use movement strategies to minimize risk such as diel migration, Courbin *et al.* 2018),
418 one can expect a higher predation risk on foals and mares during this season. This could explain
419 their higher mortality as the time spent in dry season increases. On the other hand, they could
420 also benefit from an interaction between environmental conditions and predation during the dry
421 season: the reduced vegetation cover could improve predator detectability and reduce the
422 exposure of zebras to predation (Lee *et al.* 2017). It is necessary to explore the interactive effect
423 of environmental conditions and predation as defined by the timing of birth to understand their
424 concurrent effect on juvenile survival in tropical ecosystems.

425 We did not have information about the quality of the mares of our population, whereas
426 it is known to influence reproductive success in other large herbivore species, as illustrated by
427 a lower offspring survival or a lower probability to breed in lower quality females (Hamel *et al.*

428 2009). These observations are nevertheless indirectly supported by our data too, as non-
429 reproductive females were more sensitive to the time spent in dry season with a survival
430 decreasing more rapidly than reproductive females. This suggests that they were of lower
431 quality or at least in poorer body condition than breeding females, and were unable to engage
432 reproduction or lost their foal at an early stage.

433 Due to data collection happening only every six months, our ability to precisely estimate
434 the age of the foals was variable, depending on the distance between its date of birth and its
435 date of first observation (but the same limitations are often encountered in similar studies
436 conducted *in natura*, Lee *et al.* 2017). Foals born during the field sessions were more likely to
437 be assigned a precise date of birth. This variability in the precision of the estimation of the dates
438 of birth (ranging from ± 0 to 90 days) together with the gathering of foals in discrete periods of
439 births could have limited the robustness of our analyses. However, the same analysis conducted
440 on individuals with a date of birth twice as accurate (*i.e.* ranging from ± 0 to 45 days) provided
441 very similar results, with an analogous negative effect of the time spent in dry season on older
442 foals and yearlings survival (β = -0.571 ± 0.430 SE, 85% CI [-1.191; 0.048], results not shown).
443 In addition, the low detectability of early dead foals limits the ability to spot them in the field.
444 However, the opportunistic faecal samples coupled with the hormone dosage conferred a major
445 strength to this study by allowing the detection of a consistent number of probable early dead
446 foals (n = 20) and their inclusion in the foals survival estimations, even if the cause and age of
447 death remained unknown.

448 In large ungulates, juvenile survival and then recruitment have long term consequences
449 on the population dynamics (Gaillard *et al.* 2000, Raithel *et al.* 2007). The phenology of births,
450 by determining the external conditions experience at birth and then the timing of the first critical
451 phases of the life cycle of the individuals (*e.g.* early growth, age at sexual maturity), plays a
452 determinant role in the quality of the cohort produced (Holmes *et al.* 2021), affecting in turn

the population growth rate. In the southern hemisphere, climate change is expected to lead to an increasing frequency of droughts and of their unpredictability, but also to longer and harsher dry seasons in general (Zhao and Dai 2015, Dunning *et al.* 2018). The latter, associated with a lower survival of older foals and yearlings as the time spent in dry season increases, could affect the population dynamics of zebras. However, as southern species already live in unpredictable environments to a certain extent (Owen-Smith and Ogutu 2013), one could expect phenotypic adjustments in the timing of birth could occur in response to the changing climate, as it is already observed in drought years in topi or warthog (Ogutu *et al.* 2010). Phenotypic adjustments are more likely than evolutionary processes, which seems overall less frequently observed in response to climate change (Hoffmann and Sgrò 2011), in particular in species with a long generation time.

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Authors' contributions: SCJ, CB and LT conceived the ideas and designed methodology; SCJ organised data collection; LT, CB and SCJ analysed the data; LT, SCJ and CB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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