# Good moms: dependent-young and their mothers cope better than others with longer dry season in plains zebras

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1 **Author contributions**: LT, CB and SCJ were involved in the Conceptualization, Investigation, Methodology, Writing, Funding acquisition. CB and SCJ were involved in the Supervision and Validation. LT and CB were involved in the Formal analysis. LT and SCJ were involved in the Data curation. LT was involved in the Visualization. SCJ was involved in the Data collection, Project administration.

## Abstract

In large herbivores, the timing of births often matches the seasonal peak of availability of food resources, likely to improve juvenile survival and reduce reproduction costs. Some species however breed year round, even in seasonal environments. To what extent being born during the lean season reduces juveniles and reproductive females survival remains mostly unknown. This holds particularly true in tropical ecosystems where the demographic processes underlying population dynamics are often poorly studied. We investigate the variability of survival for plains zebras (*Equus quagga*) in Hwange National Park (Zimbabwe), a highly seasonal savanna ecosystem. We used capture-recapture models to analyse long-term demographic data (2008-2019). We investigated the effect of seasonality as a categorical (wet versus dry season) and continuous (duration of the dry season) variable on survival. We found little variability in the survival of younger foals (< 6 m.o.), whereas older foals and yearlings' survival, which was higher on average, decreased with the length of the dry season. Female survival was high but decreased with increasing exposure to the dry season for the non-reproductive ones only. The probability of females becoming reproductive the next year was not affected by the length of the dry season. Together, our results highlight the importance of individual quality in reproductive performance, as reproductive females seem to buffer the effect of environmental variability on their own survival and that of their foal. Timing of birth in this population might be the result of a trade off between minimising mother's reproductive costs and maximising juvenile survival.

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

## Introduction

In long-lived species, the recruitment of juveniles in the population is often the most variable demographic rate, and therefore the major determinant of the variation in population growth rate (Gaillard et al. 1998, Gaillardet al. 2000, Kiffner and Lee 2019). Specifically, in large mammalian herbivores, recruitment depends mostly on juvenile survival (Gaillard et al. 2003), which is affected primarily by environmental conditions experienced by mothers during the last months of gestation and the first year of life of newborns (Sadleir 1982, Lindström 1999, Beckerman et al. 2003, Kiffner and Lee 2019). For instance, a lower fawn survival is observed in red deer (*Cervus elaphus*) when they are exposed to harsher winters (Loison and Langvaten 1998). Environmental conditions also interact with the mothers' condition and their ability to feed their offspring (Pigeon et al. 2022). For capital breeders, female body condition during the previous year or even during the current pregnancy is conditioned by resource availability at this time and can in turn affect the weight of the newborn at birth (Cameron et al. 1993) and its survival to weaning (Jackson et al. 2021). In seasonal environments where food resource availability and quality vary strongly within a year, the timing of developmental stages and of the reproductive cycle is therefore critical for juvenile survival and the mother's reproductive success.

It is well known from studies in temperate and boreal ecosystems that the timing of birth is a major life history trait of organisms, accounting for early-life survival and individual fitness (Plard et al. 2015). By determining the early environmental conditions experienced by newborns during the first months of life, timing of birth contributes directly (*e.g.* through thermal stress which may cause hypothermia; Grovenburg et al. 2012) and also indirectly (*e.g.* through potentially lower food availability reducing growth rate; Feder et al. 2008) to the annual variation of juvenile survival. The season of parturition is critical to reproductive females themselves, as they endure their offspring's needs in addition to their

own. Lactation costs are particularly high in mammals (Sadleir 1982, Clutton-Brock et al. 1989), and could make reproductive females more susceptible to harsh environmental conditions. These selection pressures acting on newborns and mothers are thought to underlie the commonly observed strong seasonality in time-of-birth across ungulates in temperate ecosystems (Bronson 1989). Additionally, the timing of parturition can generate reproductive costs for females by lowering the chances of successfully reproducing the next year (Green and Rothstein 1991). In red deer the later a hind gives birth at any given year, the less likely she is to conceive again during the following breeding season (Clutton-Brock et al. 1983). In short, in temperate and boreal systems, the timing of birth accounts for the variation in juvenile survival and reproductive success of the mother of large herbivores, explaining why births are synchronised with the best period in terms of food resource availability and quality (Post 2003).

Even though less predictable than temperate and boreal ecosystems, arid and semi-arid ecosystems also show a pronounced seasonality, i.e. wet and dry seasons mainly driven by the distribution of rains within the year (Desmukh 1984, Owen-Smith and Ogutu 2013). Although some large herbivores reproduce according to the seasons (e.g. the blue wildebeest (*Connochaetes taurinus*); Sinclair et al. 2000), others have more extended breeding periods (Owen-Smith and Ogutu 2013), or even breed year-round (e.g. the plains zebras (*Equus quagga*); Sinclair et al. 2000). In such species, and even if a peak of birth is often observed during the wet season, some females give birth during the dry season, at a time when food and water are more scarce (Boutton et al. 1988a, Boutton et al. 1988b, Feng et al. 2013) and susceptibility to predation is increased (Valeix et al. 2009). This means that a variable share of the females of a population give birth in less favourable conditions than the others, potentially exposing their offspring and themselves to a higher mortality risk. An interesting and yet unanswered question is therefore: for such species, to what extent does giving birth in

90 the dry unfavourable season reduce the probability of survival of both the newborn and its
91 mother?

92 To date, we lack empirical studies exploring juvenile survival and reproductive costs
93 both in species reproducing year-round and in tropical large herbivores in general (Clutton-
94 Brock and Sheldon 2010, Burthe et al. 2011, Festa-Bianchet et al. 2017, but see Lee et al.
95 2017). In this study, we investigated the effect of the season of birth on the annual survival of
96 young and mares in relation to environmental conditions in wild plains zebras (*Equus*
97 *quagga*). We explored the impact of the duration of the dry season, which varies according to
98 the timing of rainfalls, on the cohort-specific annual survival of foals, yearlings and adult
99 females. We took advantage of a long-term individual-based monitoring program of plains
100 zebras conducted in Hwange National Park (HNP) in Zimbabwe. Even if their environment is
101 seasonal (Chamaille-Jammes et al. 2006), plains zebras breed year round in this ecosystem
102 (Fig. 1), and are exposed to a high inter-annual variability in the duration of the dry season.
103 This constitutes an adequate framework to study the impact of the timing of reproduction on
104 the survival of young and females in seasonal tropical environments.

105 Specifically, we hypothesised that the dry season, and in particular long dry seasons
106 which lead to harsh conditions for herbivores, should decrease plains zebra foal survival until
107 weaning (0 to 6 months old) because this period corresponds to the most vulnerable stage
108 (Caughley 1966, Festa-Bianchet 1988). Similarly, harsh environmental conditions during
109 early life should decrease foal survival between weaning and complete independence from
110 the mother (6 to 12 months old) because they are arguably less vulnerable, are still growing
111 and cannot rely on their mother anymore for food provisioning and protection (Smuts 1976,
112 Côté and Festa-Bianchet 2001). We expected a comparatively smaller effect of exposure to
113 harsh conditions on yearling (1 to 2 years old) survival than on foal, because older individuals
114 should have more resources to survive through periods of low food availability (Gaillard et

al. 2000). Regarding mares, we expected that costs of reproduction would be reflected in a lower survival of reproductive females compared to non-breeding ones. Indeed, a dependent foal imposes additional energy expenditure for reproduction whereas the amount of energy available to the mother is limited (energy allocation hypothesis; Cody 1966, Williams 1966). Alternatively, one could expect the opposite, with reproductive females coping better than breeding females as non-reproductive females could be those of lower phenotypic quality, explaining that they do not even breed (Reznick et al. 2000, Hamel et al. 2009), and overall would be more vulnerable to environmental harshness.

## Materials and methods

### *1. Context of the study*

#### *1.1. Study site*

HNP (19°00' S, 26°30' E), Zimbabwe, covers 14,651 km$^2$ of bushlands, woodlands (mostly *Colophospermum mopane*, *Combretum spp.*, *Acacia spp.*, *Baikiaea plurijuga* and *Terminalia sericea*, Rogers et al. 1993) and scrublands interspersed with grassland (Arraut et al. 2018), and is located between 900 and 1,100m a.s.l.. Average annual rainfall is approximately 600mm, with marked inter-annual variations (Chamaille-Jammes et al. 2006). On average, 98% of the rainfall events occur during the wet season, generally from October to April (Chamaille-Jammes et al. 2006, Chamaille-Jammes et al. 2007). 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 > 8km from a waterhole are rare, even in the dry season (Chamaille-Jammes et al. 2007). The densities of lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*), the two main predators of plains zebra, are relatively high (Loveridge et al. 2007, Drouet-Hoguet 2007). There is no hunting in the park.

### *1.2. Study species*

Plains zebras live in harems composed of a stallion, several mares and their offspring under two years old (Klingel 1969). Females give birth to a singleton year round in most of their geographic range, including Zimbabwe (Dasmann and Mossman 1962, Barnier et al. 2012), even if a birth peak can occur from January to March in this area (Fig. 1). Gestation length ranges between 340 and 390 days and foals are weaned around 11 months of age (Smuts 1976). Plains zebra foals are considered as "followers" on the hider-follower gradient (Lent 1974), as they stand and follow their mother a couple of hours after birth (Sinclair2000). Plains zebras are grazers (*sensu* Hofman 1989), feeding virtually only on grasses, hence the availability of their food resource is directly linked to rainfall amount and distribution within the year, as well as with the general availability of habitats having a grass layer (DuPlessis 2001). As the other large herbivores occupying African savannas, the plains zebra is generally considered to be located more towards the capital end of the capital-income breeder continuum (Jönsson 1997, Stephens et al. 2009), even if there is currently little empirical assessment of this tactic of energy allocation (but see Ogutu et al. 2014). In HNP, the population of plains zebras is mostly resident thanks to the artificial waterholes providing water year round inside the park, but some seasonal shifts in home-ranges have been observed for some harems (unpublished GPS data).

### *1.3. Seasonality and plains zebra life histories*

Following the protocol presented in Grange et al. (2015), we recorded the presence of individually identified plains zebras between 2008 and 2019 using visual identification of their unique stripe pattern. Observations 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* ± *SD* = 45 ± 25 days, *range* = 13 - 88 days). When first sighted, individuals were classified according to three age-classes: foal

165 (from birth to 12 months old), yearling (12 to 24 months old) and adults (> 24 months old).
166 The age of the young individuals was then determined more accurately based on their relative
167 size compared to adults, using the criteria of Smuts (1975) and Penzhorn (1984), and
168 photographs of individuals of known age from HNP. We also arbitrarily attributed an
169 accuracy to this age estimation, based on our experience from the field. The age of very
170 young foals was considered accurate to a few days, whereas young seen at an older age for
171 the first time could be attributed an age ± 2 months, for instance.

172 The main goal of this study was to explore the effect of seasonality as a categorical
173 (i.e. wet season versus dry season) or continuous (i.e. duration of the dry season) variable on
174 the survival of young and mares, accounting for the reproductive state of the mare and the
175 age-class of the young. We also assessed the probability of transition between reproductive
176 and non-reproductive states in mares from one session to the next. Explanatory variables are
177 described in the following sections and summarised in Table 1.

178 *2. Explanatory variables*

179 For each year, we identified the transition date between wet and dry season using 500m
180 spatial resolution, bi-monthly Normalised Difference Vegetation Index (NDVI) records from
181 the NASA website (MOD13A1 product, computed from atmospherically corrected bi-
182 directional surface reflectances masked for water, clouds, heavy aerosols, and cloud shadows;
183 temporal resolution: 15 days; https://modis.gsfc.nasa.gov) and daily rainfall records from the
184 Climate Hazards Center website (Rainfall Estimates from Rain Gauge and Satellite
185 Observations, https://www.chc.ucsb.edu). During the study period and according to our
186 estimations, the wet season in HNP started between the 1st of November and the 19th of
187 December, while the dry season started between the 9th of May and the 29th of July (Fig. 1,
188 Online Resource 1). We attributed a season to each session according to the date of the
189 session (variable *season*, Table 1). We also estimated the proportion of days of dry season

between the first day of the session *s* and the first day of the following session *s+1* (variable *pds*, namely "proportion of dry season", Table 1). We defined three age-classes among the young: "younger foals" of less than six months old, "older foals" aged between six and 12 months old, and "yearlings" between one and two years old (Gaillard et al. 2000, Table 1).

## *3. Statistical analysis*

### *3.1. Capture-Mark-Recapture framework*

We used a Capture-Mark-Recapture (CMR, Lebreton et al. 1992) framework to account for the variability of the probability of recapture (i.e. re-observation) of the individuals of this population (Grange et al. 2015). We considered each session as a discrete event, summarised by its starting date. As the time interval between two successive sessions varied, we used the *time.intervals* argument of the *process.data* function to correct survival estimates for the duration of exposure to mortality risk (*RMark* package, Laake 2013). For this, we calculated the proportion of time elapsed between two successive sessions in relation to a year of 365 days: $\Delta t_{session2\text{-}session1} = (Starting\ date_{session2} - Starting\ date_{session1}) / 365$. We performed all CMR analyses using the program MARK (www.phidot.org/software/mark) and the R statistical software (version 4.3.1, www.r-project.org), thanks to the package *RMark* (Laake 2013). The goodness-of-fit tests (GOF tests: see below) were conducted with the R package *R2ucare* (Gimenez et al. 2017).

### *3.2. Survival of the young*

Similarly to previous demographic analyses performed on these data (Grange et al. 2015, Vitet et al. 2020, Vitet et al. 2021), we built capture histories for each individual as follows: 0 corresponded to "no sighting of the individual during the session", and 1 corresponded to "at least one sighting of the individual during the session". We ran the analyses on individuals of known date of birth with an accuracy ranging from 0 to ± 90 days ($n$ = 310). The dataset contained individuals observed at least once in the field ($n$ = 290) and individuals never

observed in the field but whose mother was detected to be pregnant ($n$ = 20). For the latter, the date of parturition was estimated based on opportunistic faecal sampling from the mare and subsequent 20-oxopregnanes and oestrogens enzyme immunoassay (Online Resource 2, Ncube et al. 2011). We recorded these individuals as being identified at birth only and never seen again, assuming no foetal loss or abortion as usually reported in large mammals. All the individuals born in the same cohort (i.e. which had the same session as the one closest to their date of birth) were considered to have experienced the same environmental conditions (i.e. *season* and *proportion of dry season* variables). Because of the imperfect detection, we kept sub-adults and adults (> 2 years old) in the model to get better estimations of yearling survival. In other words, individuals re-observed only at an age of 2 years or more but missed during the previous sessions still contributed to the estimation of survival of the young, even if adult survival *per se* was not presented in this analysis.

In a preliminary step, we performed goodness-of-fit tests to check if the dataset of young individuals did fit the CMR model assumptions (Lebreton et al. 1992). The GOF tests of the fully time-dependent model (Gimenez et al. 2018) highlighted possible overdispersion (Test 2.CL: $\chi^2$ = 40.79, $df$ = 16, $P$ < 0.01; Test 3.Sm: $\chi^2$ = 11.05, $df$ = 19, $P$ = 0.92), owing to trap-dependence ($\chi^2$ = 139.35, $df$ = 17, $P$ < 0.01) and transience issues ($\chi^2$ = 70.47, $df$ = 22, $P$ < 0.01). After examination of Test 2.CL, we noticed that overdispersion was mainly caused by three sessions over the 24 available in the dataset, so we considered this lack of fit as marginal and ignored overdispersion in the analyses.

We accounted for trap-dependence by adding a trap-dependence effect in the recapture model (*td* variable, Table 1). As plains zebras' distribution within the park could depend on the seasonal dynamics, we tested the effect of the *season* or *proportion of dry season* in the recapture model. Transience was likely due to the age structure as young individuals often have lower survival in large herbivores (Gaillard et al. 2000) and are thus

less frequently recaptured than adults, leading to a lower recapture probability. Thus, we fitted the survival model with an *age-class* effect (Table 1). We also explored the effect of several poolings of those age-classes (e.g. older foals and yearlings pooled together as one single age-class versus younger foals). We tested the effect of the *season* or *proportion of dry season* in the young survival models (Online Resource 3). For comparison purposes, we also conducted an analysis of the survival of the juveniles using a Generalised Linear Model (GLM) approach instead of a CMR approach (Online Resource 4).

### *3.3. Mare survival*

To study the probability of survival and transition between reproductive states in adult females ($n$ = 322), we used a multi-states capture-recapture model (Lebreton et al. 2009). We built capture histories for each individual as follows: 0 corresponds to "no sighting of the mare during the session", 1 corresponding to "at least one sighting of the mare without her dependent juvenile during the session" and 2 corresponding to "at least one sighting of the mare with her dependent juvenile during the session". We considered a dependent juvenile as an individual that was still suckling, so under 6 months of age. Even if weaning generally occurs around 11 months of age in zebras, juveniles can survive without their mother from 9 months old onwards (Smuts 1976). We chose 6 months to exclude such possibility and match our sessions frequency.

As there were too few observations to conduct the GOF tests of the multi-states model, we conducted the GOF tests on the one-state model instead (i.e. without taking into account reproductive states). The tests revealed overdispersion (Test 2.CL: $\chi^2$ = 49.02, $df$ = 19, $P$ < 0.01; Test 3.Sm: $\chi^2$ = 72.10, $df$ = 20, $P$ < 0.01), trap-dependence ($\chi^2$ = 112.13, $df$ = 21, $P$ < 0.01) and transience ($\chi^2$ = 62.23, $df$ = 21, $P$ < 0.01). After examination of Test 2.CL and 3.Sm, we noticed that overdispersion was mainly caused by five and three sessions over the 24 available in the dataset, respectively. Again, we considered it as marginal and ignored

265 overdispersion in the analyses. We accounted for trap-dependence by adding a trap-
266 dependence effect (*td* variable, Table 1) in the recapture model. To take into account
267 transience, we added a categorical variable *sight* in the survival model to differentiate
268 between mares captured for the first time during the survey and mares already captured at
269 least once during the survey, following the method described by Pradel et al. (1997; *sight*
270 variable, Table 1). We evaluated the effect of the *reproductive state* (Table 1), and *season* or
271 *proportion of dry season* on recapture, survival and transition probabilities. Age being not
272 known for most adult females, we were unable to include this variable in the model.

273 *3.4. Model selection*

274 For both young and mares, we conducted model selection by comparing models ranging from
275 the most complex full time-dependent model (*time* variable, i.e. chronological number
276 identifying the session, Table 1) to the reference model (i.e. depending exclusively on the
277 covariables related to GOF corrections, Online Resource 3). Because of the huge number of
278 possible combinations between recapture and survival (and transition for the mares dataset)
279 models, we conducted a sequential model selection starting by modelling recapture, survival
280 and then transition probabilities (Lebreton et al. 1992). We conducted a first model selection
281 to identify the best recapture model, while survival model was set to depend exclusively on
282 the covariables related to GOF corrections (i.e. *age-class* for young individuals and *sight* for
283 mares) and transition probability was set constant for mares. We then modelled survival
284 probability using the best recapture model and constant transition probability for mares. We
285 eventually selected the best transition probability model with the best recapture and survival
286 models for mares.

287 We used the Akaike Information Criterion adjusted for small sample sizes (AICc) and
288 we selected the model with the lowest number of parameters for models having a $\Delta$AICc < 2
289 when compared to the best model (parsimony principle, Burnham and Anderson 2002).

290 Following Arnold (2010), we reported the 85% confidence intervals of estimated parameters,
291 in accordance with our AICc model selection procedure. We used the scaled value of
292 *proportion of dry season* in the models to ease model convergence, but for convenience, we
293 back-transformed the coefficients to their initial scale in the Results section.
294

295 **Results**

296 *1. Survival of the young*

297 Results on recapture probabilities of juveniles are presented in Online Resource 5. In
298 summary, recapture probability was best described by an effect of *trap dependence* and
299 *proportion of dry season*, and overall was within the 0.3 - 0.5 range. According to the most
300 parsimonious model, survival varied between age-classes (see Online Resource 3 for the
301 detailed model selection). The average probability of annual survival was lower for younger
302 foals ($\varphi$ = 0.458 ± 0.044 SE, 85% CI [0.395; 0.522]) than for the two other age-classes, which
303 had a similar survival that decreased with the *proportion of dry season* ($\beta$ = -0.026 ± 0.016
304 SE, 85% CI [-0.049; -0.002]). The predicted probability of survival of older foals and
305 yearlings varied from 0.850 ± 0.095 SE, 85% CI [0.661; 0.943] when the *proportion of dry*
306 *season* was the shortest (i.e. 9 % of the time) to 0.480 ± 0.120 SE, 85% CI [0.316; 0.648]
307 when the *proportion of dry season* was the longest (i.e. 80 % of the time, Fig. 2). The *season*
308 variable was not retained in the best models of both the CMR or the GLM approaches. Even
309 though non-significant, a quick exploration of survival probabilities according to the season
310 and time in older foals and yearling survival showed that it was likely lower and more
311 variable during the dry (0.536 ± 0.221 SD) than during the wet season (0.707 ± 0.172 SD).
312 Note that an alternative, simplest, analysis based on a GLM approach provided similar results
313 (Online Resource 4).

314 *2. Mare survival*

315 Overall, the recapture probability was higher for mares than for young individuals, generally
316 around 0.7 (Online Resource 5). The best model for survival probability included an additive
317 effect of *sight*, *proportion of dry season* and *reproductive state*, and an additive effect of *time*
318 and *reproductive state* for transition probability (see Online Resource 3 for the detailed
319 model selection). As the *sight* variable had a significant effect on the probability of survival,
320 we present results for mares in their second and following observations only, because results
321 relying on the first observation of a mare are less robust and informative. The *proportion of*
322 *dry season* had a negative effect on survival ($\beta$ = -0.035 ± 0.011 SE, 85% CI [-0.050; -0.019],
323 Fig. 3a). The probability of survival of reproductive females varied slightly from 0.995 ±
324 0.006 SE, 85% CI [0.970; 0.999] when the *proportion of dry season* was the shortest to 0.945
325 ± 0.059 SE, 85% CI [0.768; 0.989] when the *proportion of dry season* was the longest.
326 Although the interaction between the *proportion of dry season* and the reproductive state of
327 the females was not retained in the best model, we noted that the probability of survival of
328 non-reproductive females appeared to vary more largely, from 0.966 ± 0.019 SE, 85% CI
329 [0.924; 0.985] to 0.703 ± 0.057 SE, 85% CI [0.615; 0.779] as the *proportion of dry season*
330 increased.
331 The probability of transition between reproductive states was not dependent on either
332 the *season* or the *proportion of dry season* as neither of these variables were selected in the
333 best model, but was highly variable according to *time*. As could be expected from the
334 phenotypic quality hypothesis, the probability for a mare to switch from the reproductive to
335 the non-reproductive state between two consecutive sessions was higher (from 0.582 ± 0.094
336 SE, 85% CI [0.443; 0.709] to 0.961 ± 0.015 SE, 85% CI [0.933; 0.978]) than the probability
337 to transition from the non-reproductive to the reproductive state (from 0.049 ± 0.018 SE, 85%
338 CI [0.028; 0.083] to 0.475 ± 0.093 SE, 85% CI [0.346; 0.608], Fig. 3b). Based on the model
339 including the season and reproductive state as explanatory variables for the probability of

transition, the average probability to be reproductive one year later was not different between reproductive females (0.423) and non-reproductive females (0.420).

## Discussion

Our study shows that even if the general survival pattern of mammalian populations (Caughley 1966, Gaillard et al. 2000) also fits plains zebra in a tropical context, the expected negative effects of the duration of dry season on juvenile survival was not consistently observed across all age classes. We found the year-round breeding strategy of female plains zebras to have little consequences for early survival of foals, and we relate it to the long gestation length and the possible strategy of energy allocation of mares to their offspring. We document, however, a within-year and between years variability of young survival rates with potential consequences for population dynamics.

In contrast with the younger foals, older foals and yearlings had a lower survival when experiencing long dry seasons. To our knowledge, studies so far mostly addressed the difference between juvenile and adult survival, but comparisons of survival between different "young" age classes remains rare. Georgiadis et al. (2003) modelling work suggested a higher sensitivity of the survival of plains zebra foals under one year of age to fluctuations in rainfalls than adults. Sensitivity to environmental conditions of young individuals is a commonly observed pattern, even in tropical herbivores: for instance, juveniles and yearlings' survival is highly correlated with the preceding annual rainfalls in the greater kudu (*Tragelaphus strepsiceros*, Owen-Smith 1990) and calf survival decreases during the dry season in the wildebeest (*Connochaetes taurinus*, Mduma et al. 1999). Young plains zebras are weaned around 11 months (Smuts 1976), but they only reach their adult size around three years of age (Smuts 1975). During this critical period, older foals and yearlings, which are still growing, remain more vulnerable than adults in the face of poor environmental

conditions or predation, explaining their lower survival.

Breeding females usually time their reproduction to match the most costly part of the reproductive cycle, corresponding to the late gestation and early lactation in large herbivores (Sadleir 1982, Clutton-Brock et al. 1989), with the period of best food quality or availability (Bronson 1989). This matching between food resources and costly reproductive events should minimise subsequent fitness costs like a lower survival, litter size or probability to reproduce after a successful reproduction. Accordingly, most of the plains zebra mares in HNP gave birth during the wet season (Fig. 1). The clear and striking result of our study is that, when environmental conditions are harsher (longer dry seasons), mothers appear to buffer the costs for the dependent young (i.e. younger foal). This suggests that plains zebras might be capital breeders, with females engaging in reproduction conditional to a sufficient acquisition of energy during the prior non-reproductive period. This would guarantee their ability to cope with their offspring requirements in case of an unexpectedly long dry season. Only in the case of extreme drought reproductive mares and their dependent foals have been found to experience higher mortality than usual (Joubert 1974). In our system, the impact of droughts on plains zebras, which are able to feed on rather low quality grasses, is likely buffered by the presence of permanent waterholes. Combining these demographic data with explorations of the existence of accumulation and storage of energy by the females during favourable periods would help in clarifying the plains zebra's reproductive strategy. Also, it would shed light on the validity of the capital-income breeder concept in tropical herbivores. Indeed, such a classification has so far rarely been used in these systems because of the lack of adequate demographic data, contrary to temperate ecosystems where it is a common conceptual framework (e.g. Kerby and Post 2013, Apollonio et al. 2020).

Given our results and somewhat counterintuitively, the optimal timing of birth in order to minimise mortality risks of young plains zebras should be the beginning of the dry

390 season. Juveniles could thus benefit from their mother's protection during the harsher season
391 and enter the age of independence during the most favourable one. Similarly, Lee et al.
392 (2017) showed that giraffes (*Giraffa camelopardalis*) born during the dry season experienced
393 a higher survival probability in Tanzania. Even though most of the plains zebras' births in our
394 population happened during the wet season, ensuring sufficient food resources for the mother
395 at a critical stage of their reproductive cycle, we note that the birth peak also extended
396 towards the beginning of the dry season (Fig. 1), which is more favourable to the offspring.
397 Such a phenomenon could illustrate a potential trade-off between minimising mother's
398 reproductive costs and maximising juveniles' survival, as it has been described in primates
399 (Dezeure et al. 2021).
400 The strength of this trade-off might not however be so large. Indeed, the length of the
401 dry season had only a small impact on the survival of reproductive females, whose survival
402 always remained very high (~ 0.95 or above). Data also suggested that reproductive females
403 are not more sensitive, and possibly are less sensitive, than non-reproductive females to
404 environmental conditions. Females engaging in reproduction thus appear to not only be able
405 to buffer the effect of the environment on their young foal, but also to bear the costs of
406 reproduction, even under harsh conditions, with minimal impact. They are also able to engage
407 in future reproduction as quickly as non-reproductive females. All these results point toward
408 the fact that females that reproduce might be those of high intrinsic phenotypic quality, or
409 experience. Again, if these effects have been well described and studied in temperate or
410 boreal ungulates (e.g. Hamel et al. 2009), our results generalise these observations to tropical
411 species. Although this was not the goal of this research, getting a more mechanistic
412 understanding of what makes some females more prone to reproduce would be interesting. As
413 both reproductive and non-reproductive females can be found in the same harems, with thus
414 similar landscape use, we can rule out that differences in habitat availability or habitat

415 selection strategies explain the observed contrasts between females of different reproductive
416 states. Given the importance of age and dominance status (which are often related in equids)
417 on reproduction previously demonstrated in horses and zebra species (Lloyd and Rasa 1989,
418 Pluháček et al. 2007, Rubenstein and Nuñez 2009), we suspect that they are key traits
419 underlying the observed difference. Unfortunately, age, which was sometimes available
420 (dominance status was not) could however not be included in our analysis without reducing
421 its power.

422 Overall, we document marked variations in demographic rates (juvenile survival and
423 females' reproductive rates) of plains zebras in HNP, both between seasons and across the
424 years, partly accounted for by the duration of the dry season. This creates cohort effects,
425 which have been documented in many long-lived species in temperate areas (see Sæther
426 1997, Gaillard et al. 2003 for reviews in large herbivores, Kiffner and Lee 2019) but so far
427 haven't been much studied in tropical ecosystems (e.g. in the greater kudu, Owen-Smith
428 1990). Here, our results indicate that juvenile survival of plains zebras is structured according
429 to two levels of temporal variation, the seasonal and yearly levels. These two sources of
430 juvenile survival variation have the potential to generate more cohorts of individuals with
431 contrasting life histories in the population than for seasonal breeding species. This particular
432 pattern of juvenile survival variability might destabilise plains zebra population dynamics
433 because of cohort effects (Lindström and Kokko 2002) and reduce the long-term stochastic
434 population growth rate because of its sensitivity to the temporal variance of demographic
435 rates (Tuljapurkar 1989).

## Acknowledgments

This long-term demographic survey was initiated by Patrick Duncan, who also took part in many of the field sessions. The authors are therefore indebted to him, and also acknowledge all the other people involved in data collection over the years, in particular S. Grange, F. Barnier, H. Ncube, C. Vitet and A. Duncan. J. Dezeure assisted with NDVI and rainfall data retrieval.

## Declarations

**Funding**: This work was supported by a PhD grant from the "Ministère Français de l'Enseignement Supérieur, de la Recherche et de l'Innovation" through the "Ecole Doctorale E2M2" of the "Université Claude Bernard Lyon 1" attributed to LT.

**Conflict of Interest**: The authors declare that they have no conflict of interest.

**Ethical approval**: Ethics approval was not required for this study according to local legislation [Parks and Wildlife Act].

**Consent to participate**: Not applicable.

**Consent for publication**: Not applicable.

**Availability of data and material**: Data available from the corresponding author on reasonable request.

**Code availability**: Not applicable.

**Authors' contributions**: LT, CB and SCJ were involved in the Conceptualization, Investigation, Methodology, Writing, Funding acquisition. CB and SCJ were involved in the Supervision and Validation. LT and CB were involved in the Formal analysis. LT and SCJ were involved in the Data curation. LT was involved in the Visualization. SCJ was involved in the Data collection, Project administration.

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## Tables

Table 1: Set of explanatory variables used in the models investigating survival in young individuals and mares plains zebra (*Equus quagga*), and transition probability between reproductive and non-reproductive states in mares plains zebra (Hwange National Park, Zimbabwe, 2008-2019).

| **Variable** | **Type** | **Description** | **Used in the model(s)** |
|---|---|---|---|
| *Season* | Categorical | "Wet" or "Dry" season | Young & Mares |
| *Time in dry season* | Continuous | Proportion of dry season between two consecutive sessions [range: 9-80 %] | Young & Mares |
| *Time* | Categorical | ID number of the field session [range: 1-24] | Young & Mares |
| *Trap-dependence* | Categorical | The individual has been seen during the previous field session (1) or not (0) | Young & Mares |
| *Age-class* | Categorical | "Younger foal" (less than six months old), "Older foal" (between six and 12 months old) or "Yearling" (between one and two years old) | Young |
| *Reproductive state* | Categorical | The mare is seen with a dependent juvenile (1) or not (0) | Mares |
| *Sight* | Categorical | The individual is seen for the first time (1) or not (0) | Mares |

## Figure legends

Figure 1: Distribution of plains zebra (*Equus quagga*) births per month, estimated from the individual-based monitoring conducted in Hwange National Park, Zimbabwe, between 2008 and 2019 ($n$ = 310 foals). The black line represents the total number of births per month over the complete study period (i.e. all years summed). The coloured areas indicate the seasons: blue = main wet season (approx. mid-December to mid-May), orange = main dry season (approx. August to October), mixed colour = inter-annual variability in the start of the seasons (start of the wet season: November to mid-December; start of the dry season: mid-May to July).

Figure 2: Probability of annual survival of plains zebra (*Equus quagga*) young individuals in Hwange National Park, Zimbabwe (2008-2019), according to the proportion of dry season between two consecutive sessions. Black: younger foals (between birth and six months old), blue: older foals (between six and 12 months old) combined with 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. Dark coloured dots represent the survival predicted by the time model, shaded areas around the dot are proportional to 1/standard error of these predicted values.

Figure 3: a) Probability of annual survival of plains zebra (*Equus quagga*) mares in Hwange National Park, Zimbabwe (2008-2019), according to the proportion of dry season between two consecutive sessions and the reproductive state (for mares in their second and subsequent observations only, see text for details). Red: non-reproductive females, green: reproductive females. Solid lines represent predicted values from the best model. Shaded areas represent 85% confidence intervals of these predicted values. Dots represent females survival predicted

by the time model, vertical bars represent 85% confidence intervals of these predicted values. b) Probability of transition between reproductive and non-reproductive states for plains zebra mares according to the session. Red: from reproductive to non-reproductive state, green: from non-reproductive to reproductive state. Dark coloured dots represent the survival predicted by the time model, shaded areas around the dot are proportional to 1/standard error of these predicted values.

## Figures

Figure 1:

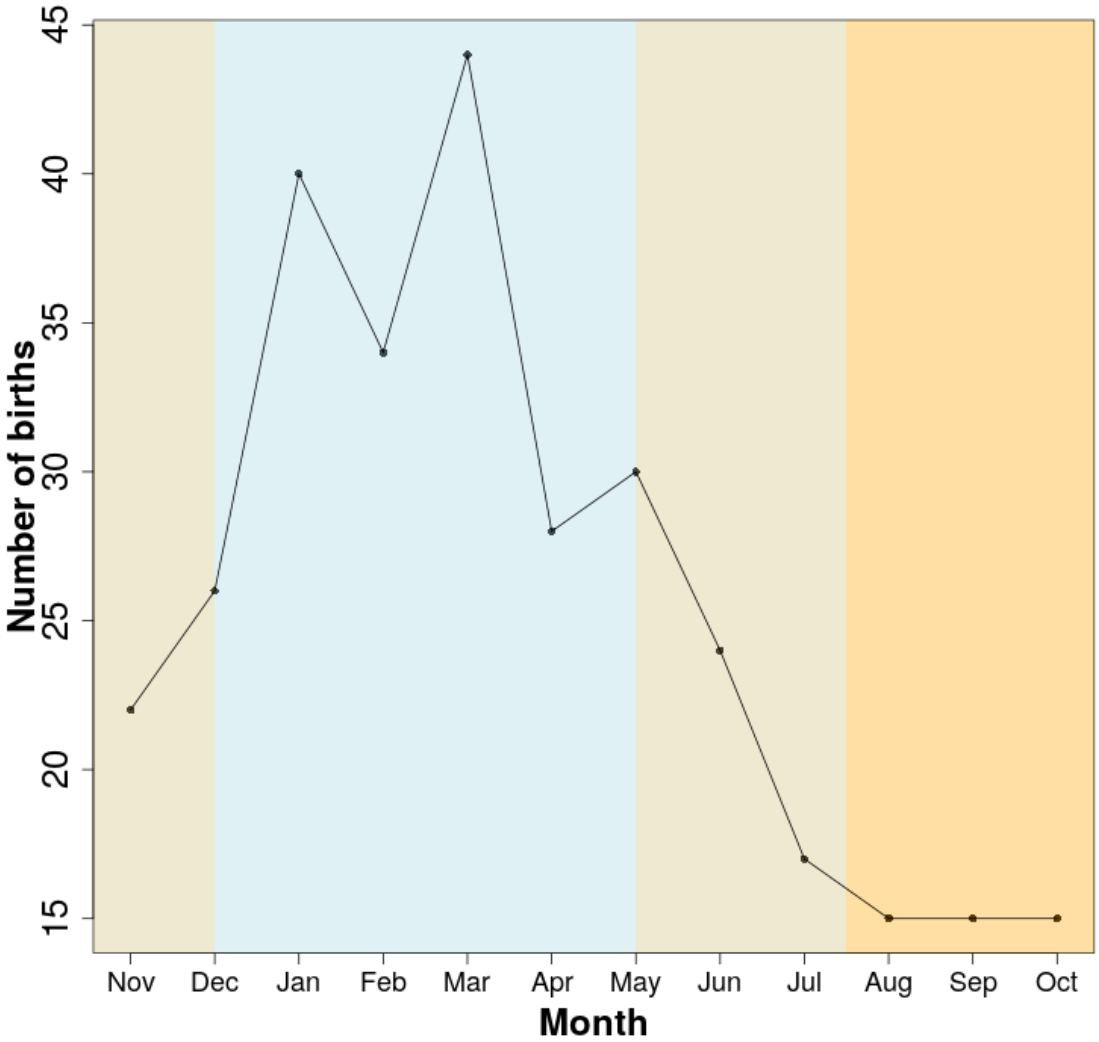
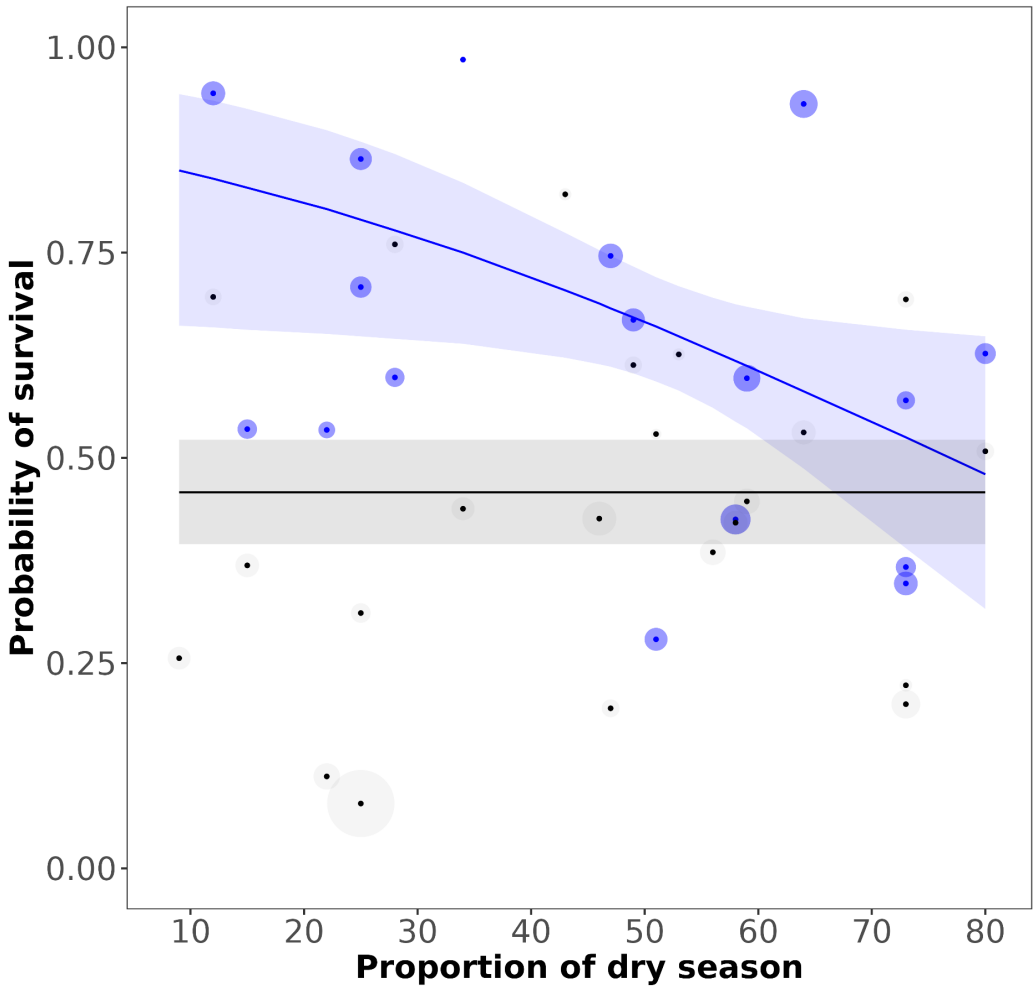


Figure 2:


1.00
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0.00
Probability of survival
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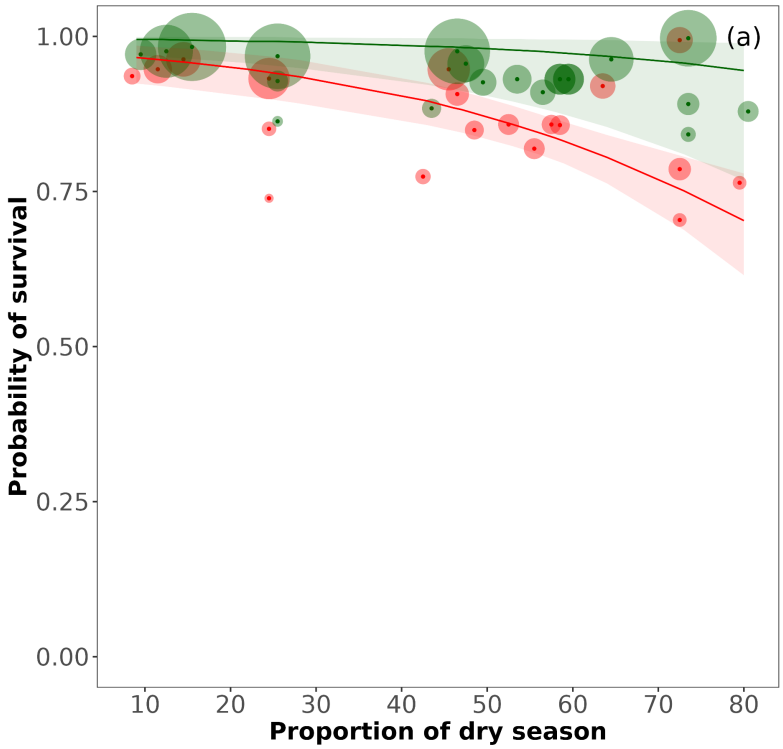
20
30
40
50
60
70
80
Proportion of dry season

Figure 3:


(a)
1.00
0.75
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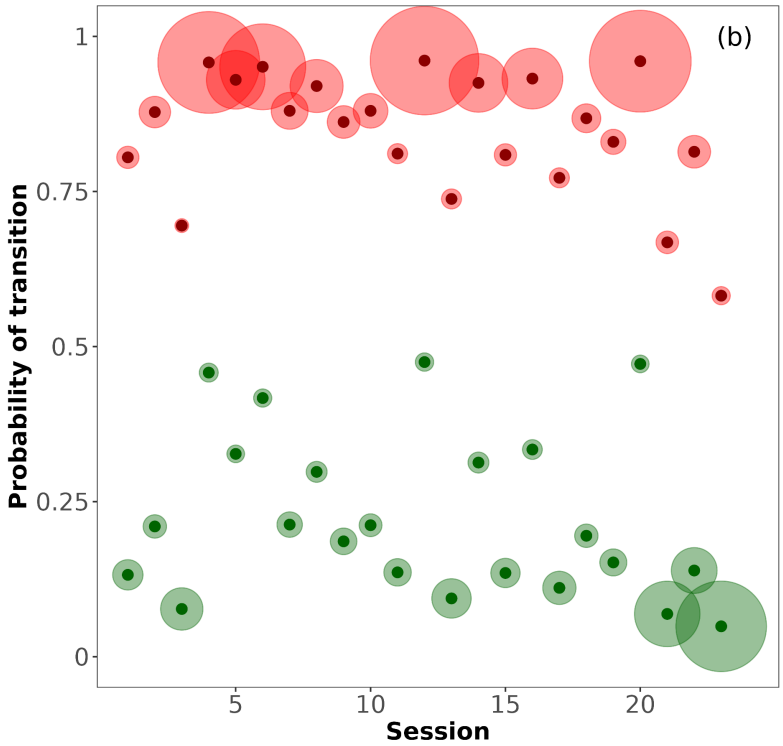
Probability of survival
10
20
30
40
50
60
70
80
Proportion of dry season


(b)
1
0.75
0.5
0.25
0
Probability of transition
5
10
15
20
Session