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

Lucie Thel[1], Christophe Bonenfant[1, 4] & Simon Chamaillé-Jammes[2, 3, 4]

Author details[1]

[1] Laboratoire de Biométrie et Biologie Évolutive, Unité Mixte de Recherche 5558, Bâtiment 711, Université Lyon I, 43 Boulevard du 11 novembre 1918, F-69622 Villeurbanne Cedex, France.

[2] CEFE, Université Montpellier, CNRS, EPHE, IRD, Montpellier, France.

[3] Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa.

[4] LTSER France, Zone Atelier "Hwange", Hwange National Park, Bag 62, Dete, Zimbabwe-CNRS HERD (Hwange Environmental Research Development) program.

Corresponding author: Thel Lucie, lucie.mc.thel@gmail.com

[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 survival of juveniles and reproductive females remains mostly unknown. This holds particularly true in tropical ecosystems where the demographic processes underlying population dynamics are often poorly studied. We investigated survival rates in 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 early juvenile survival (< 6 m.o.), whereas late juvenile and yearling survival rates, which were higher on average, decreased with increasing length of the dry season. Female survival was high but decreased with increasing exposure to the dry season in non-reproductive females 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 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 mothers during the last months of gestation and by newborns during their first year of life (Lindström 1999, Beckerman et al. 2003, Kiffner and Lee 2019). For instance, exposure to harsh winters reduce fawn survival in red deer (*Cervus elaphus*, Loison and Langvaten 1998). In reindeer (*Rangifer tarandus*), high rain-on-snow during the gestation period increases the negative effect of a low body mass of the mother on her probability to have a calf at heel during the next summer (Pigeon et al. 2022). For capital breeders, female usually enter a reproductive phase if they reach a threshold body mass (Jönsson 1997). The energy reserves built prior to reproduction critically contribute to the female's ability to feed the fetus during pregnancy and the newborn during lactation. The level of reserves thus affects 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.

In temperate and boreal ecosystems, the timing of birth contributes to generate silver-spoon effects on life history traits (sensu Grafen 1988). Timing of birth is associated with early-life survival in the roe deer (*Capreolus capreolus*, Plard et al. 2015), and individual fitness in the collared flycatcher (*Ficedula albicollis*, Spagopoulou et al. 2020). 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; Grovenburg et

al. 2012) and 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 must cater to 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 timing 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 1993). In red deer, the later in the year a hind gives birth, 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 influences 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 (Owen-Smith and Ogutu 2013). Although some large herbivore species give birth within a relatively short time window in such environments (e.g. 80% of birth occur within 3 weeks in 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 therefore give birth in less favorable conditions than others (Boutton et al. 1988a, Boutton et al. 1988b, Feng et al. 2013), potentially exposing themselves and their offspring to

a higher risk of mortality (Valeix et al. 2009) and creating cohort effects (i.e. individuals presenting similar life histories because they experience the same environmental conditions, Lindström 1999). An interesting and yet unanswered question is therefore: for such species, to what extent does giving birth in the dry unfavourable season reduce the probability of survival of both the newborn and its mother?

In order to grasp a better understanding of the phenology of reproduction and the factors that can influence it, more empirical studies exploring juvenile survival and reproductive costs both in species reproducing year-round and in tropical large herbivores are needed (Clutton-Brock and Sheldon 2010, Burthe et al. 2011, Festa-Bianchet et al. 2017, but see Lee et al. 2017, MacKay et al. 2018). In this study, we investigated the effect of the season of birth on the annual survival of young and mares in wild plains zebras. We explored the impact of the duration of the dry season, which varies according to the timing of rainfall, on the cohort-specific annual survival of foals (i.e. individuals of the same age), yearlings and adult females. We took advantage of a long-term individual-based monitoring program of plains zebras conducted in Hwange National Park (HNP) in Zimbabwe. Although their environment is seasonal (Chamaille-Jammes et al. 2006), plains zebras breed year round in this ecosystem (Fig. 1), and are exposed to a high inter-annual variability in the duration of the dry season. This constitutes an adequate framework to study the impact of the timing of reproduction on the survival of young and females in seasonal tropical environments.

We hypothesised that the dry season, and in particular long dry seasons which lead to harsh conditions for herbivores, should decrease the survival of plains zebra foal until weaning (0 to 6 months old) because this period corresponds to the most vulnerable stage of life (Caughley 1966, Festa-Bianchet 1988). Similarly, harsh environmental conditions could reduce the survival of foals when they become independent from their mother (between 6 and 12 months old). Older foals are arguably less vulnerable, but are still growing and cannot rely

on their mother anymore for food provisioning and protection (Smuts 1976, Côté and Festa-Bianchet 2001). We expected a comparatively smaller effect of exposure to harsh conditions on yearling (1 to 2 years old) survival than on foal survival, because older individuals 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-reproductive females. Indeed, reproductive females spend more energy than non-reproductive females because they have to raise a foal (energy allocation hypothesis; Cody 1966, Williams 1966). Alternatively, one could expect the opposite, with reproductive females coping better than non-reproductive females. The latter could be 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 (Weladji et al. 2008).

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 (*Combretum spp.*, *Terminalia sericea*, *Colophospermum mopane*, *Acacia spp.*), woodlands (mostly *Colophospermum mopane* and *Baikiaea plurijuga*, Rogers et al. 1993) and scrublands interspersed with grasslands (Arraut et al. 2018). Dominant grass species in HNP are *Aristida sp.*, *Bothriochloa radicans*, *Cynodon dactylon*, *Digitaria eriantha*, *Eragrostis sp.*, *Heteropogon contortus*, *Panicum maximum*, *Pogonarthria squarrosa and Schimidtia pappophoroides (unpub. data).* Altitude varies 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 a 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 can give birth to a singleton at any time of the year in most of their geographic range, including Zimbabwe (Dasmann and Mossman 1962, Barnier et al. 2012), even if a birth peak occurs from January to March in this area (Fig. 1). Gestation length ranges between 340 and 390 days and foals are weaned between 6 and 12 months of age (Smuts 1976, Owen-Smith and Mason 2005, Pluháček et al. 2007). 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 (Du Plessis 2001). Similarly to the other large herbivores occupying African savannas, the plains zebra is considered to be a capital breeder (Jönsson 1997, Stephens et al. 2009), although there is currently little empirical assessment of its energy allocation strategy (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 around August, during field sessions (hereafter called "sessions", n = 24 sessions, *mean session duration* ± *SD* = 45 ± 25 days, *range* = 13 - 88 days). Individuals of more than 24 months were identified as adults while the age of the young individuals was determined more accurately based on their relative size compared to adults, using the criteria of Smuts (1975) and Penzhorn (1982), and photographs of individuals of known age from HNP. We also attributed an accuracy to this age estimation, based on our experience from the field. The age of very young foals was considered accurate to a few days, whereas young seen at an older stage for the first time could be attributed an age ± 2 months, for instance.

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

2. Explanatory variables

For each year, we identified the transition date between wet and dry season using 500m spatial resolution, bi-monthly Normalised Difference Vegetation Index (NDVI) records from the NASA website (MOD13A1 product, computed from atmospherically corrected bi-directional surface reflectances masked for water, clouds, heavy aerosols, and cloud shadows; temporal resolution: 15 days; 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). 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, while the dry season started between the 9th of May and the 29th of July (Fig. 1, Online Resource 1). We attributed a season to each session according to the date of the 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 corresponding to "no sighting of the individual during the session", and 1 corresponding to "at least one sighting of the individual during the session". We ran the analyses on individuals whose date of birth was known with an accuracy ranging from 0 to ± 90 days, based either on direct observation in the field or on hormonal assay of the feces of the female (n = 310). Indeed, 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. We assigned all the individuals born close to the same session to the same cohort and assumed that they experienced the same environmental conditions during the last months of gestation and beginning of lactation (i.e. *season* and *proportion of dry season* variables). Based on the rich literature dealing with northern ungulates which breed synchronously during a restricted period, a cohort is generally defined as the ensemble of individuals born during the same year (Gaillard et al. 1993, Gaillard et al. 2003). However, working on annual cohorts is less meaningful in the case of asynchronous breeders, for which births are more spread out and can happen during different seasons. In our situation, it made more sense to define a cohort at the seasonal scale, such as Lee et al. (2017) did to study juvenile survival of giraffes *Girafa camelopardalis*. We kept sub-adults and adults (> 2 years old) in the model to get better estimations of juvenile and 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 the focus of another analysis. Indeed, because detection of individuals is imperfect, a zebra can be unseen for several years in a raw, even if still alive. If a foal is only seen again at the adult stage but adult stage is not included in the juvenile survival analyses, these individuals would be considered as dead and juvenile survival would be overall biased low.

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 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-state capture-recapture model (Lebreton et al. 2009). We built capture histories for each individual as follows: 0 corresponding to "no sighting of the mare during the session", 1 corresponding to "all sightings of the mare without any dependent juvenile during the session" and 2 corresponding to "at least one sighting of the mare with a dependent juvenile during the session". We considered a dependent juvenile (corresponding to our "younger foal" age-class) as an individual that was still suckling and entirely relying on its mother's milk to feed, so under 6 months of age.

As there were too few observations to conduct the GOF tests of the multi-states model, we conducted the GOF tests on the single-state model instead (i.e. without taking into account reproductive states). The tests revealed overdispersion (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-dependence (χ^2 = 112.13, df = 21, P < 0.01) and transience (χ^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 overdispersion in the analyses. We accounted for trap-dependence by adding a trap-dependence effect (*td* variable, Table 1) in the recapture model. To take into account transience, we added a categorical variable *sight* in the survival model to differentiate between mares captured for the first time during the survey and mares already captured at least once during the survey, following the method described by Pradel et al. (1997; *sight* variable, Table 1). We evaluated the effect of the *reproductive state* (Table 1), and *season* or *proportion of dry season* on recapture, survival and transition probabilities. Age being not known for most adult females, we were unable to include this variable in the model.

3.4. Model selection

For both juveniles and mares, we conducted model selection by comparing models ranging

from the most complex full time-dependent model (*time* variable, i.e. chronological number identifying the session, Table 1) to the reference model (i.e. depending exclusively on the covariables related to GOF corrections, Online Resource 3). Because of the large number of possible combinations between recapture and survival (and transition for the mares dataset) models, we conducted a sequential model selection. We started by modelling recapture, then survival and finally transition probabilities (Lebreton et al. 1992). We conducted a first model selection to identify the best recapture model, while survival model was set to depend exclusively on the covariables related to GOF corrections (i.e. *age-class* for young individuals and *sight* for mares) and transition probability was set constant for mares. We then modeled survival probability using the best recapture model and constant transition probability for mares. We eventually selected the best transition probability model with the best recapture and survival models for mares.

We used the Akaike Information Criterion adjusted for small sample sizes (AICc) and we selected the model with the lowest number of parameters for models having a ΔAICc < 2 (i.e. models receiving substantial empirical support, Burnham and Anderson 2002, Arnold 2010) when compared to the best model (parsimony principle, Burnham and Anderson 2002). In order to estimate the overall explanatory power of the variables *time in dry season* versus *season*, we calculated the cumulated weight of all the models including the effect of the *proportion of dry season* or the *season* on the probability of survival. The weight of the model *i* was calculated as follows:

$$weight_i = e^{-\Delta AICi/2} / \Sigma(e^{-\Delta AICi/2}),$$

where ΔAIC_i is the difference between the AIC of the best model and the model *i*. We also report the number of models within a ΔAIC < 7 (i.e. models receiving substantial or some form of empirical support, Burnham and Anderson 2002, Arnold 2010) from the best model which included the effect of the *proportion of dry season* or the *season* on the probability of

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

Results

1. Survival of the young

Results on recapture probabilities of juveniles are presented in Online Resource 5. In summary, recapture probability was best described by an effect of *trap dependence* and *proportion of dry season*. Recapture probability ranged between 0.293 ± 0.039 SE, 85% CI [0.240; 0.353] and 0.483 ± 0.030 SE, 85% CI [0.440; 0.526] over the study period. According to the most parsimonious model, survival varied between age-classes (see Online Resource 3 for the detailed model selection). The early juvenile survival was lower (φ = 0.458 ± 0.044 SE, 85% CI [0.395; 0.522]) than the late juvenile and yearling survival, which decreased with the *proportion of dry season* (β = -0.026 ± 0.016 SE, 85% CI [-0.049; -0.002]). The predicted probability of survival of older foals and yearlings (pooled together) varied from 0.850 ± 0.095 SE, 85% CI [0.661; 0.943] when the *proportion of dry season* was the shortest (i.e. 9 % of the time) to 0.480 ± 0.120 SE, 85% CI [0.316; 0.648] when the *proportion of dry season* was the longest (i.e. 80 % of the time, Fig. 2). The *season* variable was not retained in the best models of either the CMR or the GLM approaches (Online Resource 4). Even though non-significant, a quick exploration of late juvenile survival and yearling survival according to the season and time showed that it was likely lower and more variable during the dry (0.536 ± 0.221 SD) than during the wet season (0.707 ± 0.172 SD). Overall, the cumulated weight of the models including the effect of the *proportion of dry season* on the probability of survival was 0.738 (n = 15 models in a ΔAIC < 7), whereas the cumulated weight of the

models including the effect of the *season* was only 0.214 (n = 9 models in a ΔAIC < 7).

2. Mare survival

The recapture probability was higher for mares than for young individuals, within the range 0.449 ± 0.033 SE, 85% CI [0.402; 0.496] - 0.849 ± 0.083 SE, 85% CI [0.690; 0.934] (Online Resource 5). The best model for survival probability included an additive effect of *sight*, *proportion of dry season* and *reproductive state*. The best model for transition probability included an additive effect of *time* and *reproductive state* (see Online Resource 3 for the detailed model selection). As the *sight* variable had a significant effect on the probability of survival, we present results for mares in their second and following observations only. Results relying on mares observed multiple times are a better representation of the average behaviour of the population than those from mares observed for the first time or only once because the latter could be transient young adult females. The *proportion of dry season* had a negative effect on survival (β = -0.035 ± 0.011 SE, 85% CI [-0.050; -0.019], Fig. 3a). The probability of survival of reproductive females varied slightly from 0.995 ± 0.006 SE, 85% CI [0.970; 0.999] when the *proportion of dry season* was the shortest to 0.945 ± 0.059 SE, 85% CI [0.768; 0.989] when the *proportion of dry season* was the longest. Although the interaction between the *proportion of dry season* and the reproductive state of the females was not retained in the best model, we noted that the probability of survival of non-reproductive females appeared to vary more largely, from 0.966 ± 0.019 SE, 85% CI [0.924; 0.985] to 0.703 ± 0.057 SE, 85% CI [0.615; 0.779] as the *proportion of dry season* increased. Overall, the cumulated weight of the models including the effect of the *proportion of dry season* on the probability of survival was 0.964 (n = 3 models in a ΔAIC < 7), whereas the cumulated weight of the models including the effect of the *season* was only 0.024 (n = 0 models in a ΔAIC < 7).

The probability of transition between reproductive states was not dependent on either

the *season* or the *proportion of dry season* as none of these variables were selected in the best model, but was highly variable according to *time*. The probability for a mare to switch from the reproductive to the non-reproductive state between two consecutive sessions was higher (from 0.582 ± 0.094 SE, 85% CI [0.443; 0.709] to 0.961 ± 0.015 SE, 85% CI [0.933; 0.978]) than the probability to transition from the non-reproductive to the reproductive state (from 0.049 ± 0.018 SE, 85% CI [0.028; 0.083] to 0.475 ± 0.093 SE, 85% CI [0.346; 0.608], Fig. 3b). Based on the model 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 highlighted an influence of duration of dry season on the survival of some juvenile age-classes. We found the year-round breeding strategy of female plains zebras to have little consequences on early survival of foals, which could be related to the long gestation length and the capital breeding strategy of energy allocation to reproduction. We documented, however, a within-year and between years variability in young survival rates with potential consequences for population dynamics.

Although we did not find major evidence for an effect of the season as a categorical variable, possibly because our field sessions sometimes happened at different stages of a given season due to variability in their timing, we identified a marked effect of the duration of the dry season, a more accurate variable to estimate the possible influence of harsh conditions on survival. In contrast with early juvenile survival, late juvenile survival and yearling survival were lower during long dry seasons. Georgiadis et al. (2003) suggest in their theoretical approach that plains zebra foals under one year of age are more sensitive to fluctuations in rainfall 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 rainfall 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 only reach their adult size around three years of age and adult body mass around five years of age (Smuts 1975). During this critical period, older foals and yearlings showed a decreasing survival with increasing time spent in dry season. This decrease in survival could result from energy allocation to body growth that may induce a higher vulnerability to poor environmental conditions or predation (Grange et al. 2004).

Reproductive 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 (Clutton-Brock et al. 1989), with the period of best food quality or availability (Bronson 1989). In mammals, this matching between food resources and costly reproductive events should minimise subsequent fitness costs such as a lower survival, litter size or probability of reproducing again at the following opportunity. Accordingly, most of the plains zebra mares in HNP gave birth during the wet season (Fig. 1). Our results suggest that when environmental conditions are harsher (longer dry seasons), mothers appear to buffer the costs for the dependent foal (i.e. younger foal). This supports the idea that plains zebras might be capital breeders, with females engaging in reproduction conditional to a sufficient acquisition of energy prior the reproductive period. This would increase their ability to cope with their offspring's requirements in case of an unexpectedly long dry season. However, dry season births do not mean death sentence for either the foal or the mare. Plains zebras are able to survive on rather low quality grasses, even if these may not allow them to not loose condition in the dry season (Duncan et al. 2024). Therefore, reproductive timing leading to dry season births may not have been selected against so strongly. Additionally, the presence of

permanent waterholes in the study area greatly removes the effect that drought usually have on herbivores via reduced water availability.

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 season. Juveniles could thus benefit from their mother's protection during the harsher season and enter the age of independence during the most favourable one. Similarly, Lee et al. (2017) showed that giraffes born during the dry season experienced a higher survival probability in Tanzania. Even though most of the plains zebras' births in our population happened during the wet season, ensuring sufficient food resources for the mother at a critical stage of their reproductive cycle, the birth peak also extended towards the beginning of the dry season (Fig. 1), which might be more favourable to the offspring. Such a phenomenon could illustrate a potential trade-off between minimising mother's reproductive costs and maximising juveniles' survival, as it has been described in primates (Dezeure et al. 2021).

However, the strength of this trade-off might not be so large. The length of the dry season only had a small impact on the survival of reproductive females, whose survival always remained very high (~ 0.95 or above). Our results also suggest that reproductive females are not more sensitive, and possibly are less sensitive, than non-reproductive females to environmental conditions. Females engaging in reproduction thus appear to not only be able to buffer the effect of the environment on their young foal, but also to bear the costs of reproduction, even under harsh conditions, with minimal impact. As shown by the similar probability of transition to the reproductive state both from the non-reproductive and the reproductive state the previous year (0.420 and 0.423 respectively), reproductive females are as able as non-reproductive females to engage in future reproduction. All these results point toward the fact that reproductive females might be those of higher reproductive potential, or experience. If these effects have been well described and studied in temperate or boreal

ungulates (e.g. Hamel et al. 2009), our results generalise these observations to tropical species. As both reproductive and non-reproductive females can be found in the same harems, with thus similar landscape use, we can rule out that differences in habitat availability or habitat selection strategies explain the observed contrasts between females of different reproductive states. Given the importance of age and dominance status (which are often related in equids) on reproduction previously demonstrated in horses and zebra species (Lloyd and Rasa 1989, Pluháček et al. 2007, Rubenstein and Nuñez 2009), we suspect that they are key traits underlying the observed difference. Unfortunately, age, which was sometimes available (dominance status was not) could not be included in our analysis without reducing its power.

Overall, we documented marked variations in demographic rates (juvenile survival and females' reproductive rates) of plains zebras in HNP, both between seasons and across the years, partly accounted for by the duration of the dry season. Such variations can create cohort effects, which have been documented in many long-lived species in temperate areas (see Sæther 1997, Gaillard et al. 2003 for reviews in large herbivores, Kiffner and Lee 2019) but so far have not been extensively studied in tropical ecosystems (e.g. in the greater kudu, Owen-Smith 1990). The seasonal variation of juvenile survival has the potential to generate short-term and long-term cohort effects on demographic rates (Gaillard et al. 2003). Compared to strictly seasonal breeders, plains zebras have more variable cohort-specific recruitment rates. A potential large juvenile survival variability might limit the long-term stochastic population growth rate because of its sensitivity to the temporal variance of demographic 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. This long-term study benefited from some financial support from the OSU-OREME (CNRS UAR 3282).

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.

References

Apollonio M, Merli E, Chirichella R, Pokorny B, Alagić A, Flajšman K, Stephens PA (2020) Capital-income breeding in male ungulates: Causes and consequences of strategy differences among species. Front ecol evol 8:521767. https://doi.org/10.3389/fevo.2020.521767

Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information Criterion. J Wildl Manage 74:1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Arraut EM, Loveridge AJ, Valls-Fox H, Macdonald DW, Chamaillé-Jammes S (2018) The 2013-2014 vegetation structure map of Hwange National Park, Zimbabwe, produced using free satellite images and software. Koedoe African Prot Area Conserv Sci 60:1–10. https://doi.org/10.4102/koedoe.v60i1.1497

Barnier F, Grange S, Ganswindt A, Ncube H, Duncan P (2012) Inter-birth interval in zebras is longer following the birth of male foals than after female foals. Acta Oecologica 42, 11–1. https://doi.org/10.1016/j.actao.2011.11.007

Beckerman AP, Benton TG, Lapsley CT, Koesters N (2003) Talkin' 'bout my generation: environmental variability and cohort effects. Am Nat 162, 754–767. https://doi.org/10.1086/381056

Boutton TW, Tieszen LL, Imbamba SK (1988a) Biomass dynamics of grassland vegetation in Kenya. Afr J Ecol 26, 89–101. https://doi.org/10.1111/j.1365-2028.1988.tb00960.x

Boutton TW, Tieszen LL, Imbamba SK (1988b) Seasonal changes in the nutrient content of East African grassland vegetation. Afr J Ecol 26, 103–115. https://doi.org/10.1111/j.1365-2028.1988.tb00961.x

Bronson FH (1989) Mammalian reproductive biology. University of Chicago Press, Chicago, USA

Burnham K, Anderson D (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York, USA

Burthe S, Butler A, Searle KR, Hall SJ, Thackeray SJ, Wanless S (2011) Demographic consequences of increased winter births in a large aseasonally breeding mammal (*Bos taurus*) in response to climate change. J Anim Ecol 80, 1134–1144. https://doi.org/10.1111/j.1365-2656.2011.01865.x

Cameron RD, Smith WT, Fancy SG, Gerhart KL, White RG (1993) Calving success of female caribou in relation to body weight. Can J Zool 71, 480–486. https://doi.org/10.1139/z93-069

Caughley G (1966) Mortality patterns in mammals. Ecol 47, 906–918. https://doi.org/10.2307/1935638

Chamaillé-Jammes S, Fritz H, Murindagomo F (2007) Detecting climate changes of concern in highly variable environments: Quantile regressions reveal that droughts worsen in Hwange National Park, Zimbabwe. J Arid Environ 71, 321–326. https://doi.org/10.1016/j.jaridenv.2007.05.005

Chamaillé-Jammes S, Fritz H, Murindagomo F (2006) Spatial patterns of the NDVI-rainfall relationship at the seasonal and interannual time scales in an African savanna. Int J Remote Sens 27, 5185–5200. https://doi.org/10.1080/01431160600702392

Clutton-Brock T, Sheldon BC (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends Ecol & Evol 25, 562–573. https://doi.org/10.1016/j.tree.2010.08.002

Clutton-Brock TH, Albon SD, Guinness FE (1989) Fitness costs of gestation and lactation in wild mammals. Nature 337, 260–262. https://doi.org/10.1038/337260a0

Clutton-Brock TH, Guinness FE, Albon SD (1983) The costs of reproduction to red deer hinds. J Anim Ecol 52, 367–383. https://doi.org/10.2307/4560

Cody ML (1966) A general theory of clutch size. Evolution 20, 174–184. https://doi.org/10.2307/2406571

Côté SD, Festa-Bianchet M (2001) Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127, 230–238. https://doi.org/10.1007/s004420000584

Dasmann RF, Mossman AS (1962) Reproduction in some ungulates in Southern Rhodesia. J Mammal 43, 533–537. https://doi.org/10.2307/1376916

Dezeure J, Baniel A, Carter A, Cowlishaw G, Godelle B, Huchard E (2021) Birth timing generates reproductive trade-offs in a non-seasonal breeding primate. Proc R Soc B 288, 20210286. https://doi.org/10.1098/rspb.2021.0286

Drouet-Hoguet N (2007) Influence des activités anthropogéniques sur la régime alimentaire et la réponse numérique de la hyène tachetée en savane arborée dystrophique dominée par l'éléphant. PhD Thesis Lyon 1 University, France.

Duncan P, Valeix M, Loveridge AJ, Grange S, Barnier F, Ncube H, Périquet S, Vitet C, Davidson Z, Mbizah M, Madhlamoto D, Fritz H, Chamaillé-Jammes S (2024) Population limitation of a non-ruminant in a nutrient-poor ecosystem—predation rather than food. African Journal of Ecology, 62(3), e13294. https://doi.org/10.1111/aje.13294

Du Plessis WP (2001) Effective rainfall defined using measurements of grass growth in the

Etosha National Park, Namibia. J Arid Environ 48, 397–417. https://doi.org/10.1006/jare.2000.0752

Feder C, Martin JGA, Festa-Bianchet M, Bérubé C, Jorgenson J (2008) Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. Oecologia 156, 773–781. https://doi.org/10.1007/s00442-008-1035-9

Feng X, Porporato A, Rodriguez-Iturbe I (2013) Changes in rainfall seasonality in the tropics. Nat Clim Chang 3, 811–815. https://doi.org/10.1038/nclimate1907

Festa-Bianchet M (1988) Birthdate and survival in bighorn lambs (*Ovis canadensis*). J Zool 214, 653–661. https://doi.org/10.1111/j.1469-7998.1988.tb03764.x

Festa-Bianchet M, Douhard M, Gaillard J-M, Pelletier F (2017) Successes and challenges of long-term field studies of marked ungulates. J Mammal 98, 612–620. https://doi.org/10.1093/jmammal/gyw227

Gaillard J-M, Delorme D, Jullien J (1993) Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. Oecologia 94, 57–61. https://doi.org/10.1007/bf00317301

Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A Toigo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. Annu Rev Ecol Syst 31, 367–393. https://doi.org/10.1146/annurev.ecolsys.31.1.367

Gaillard J-M, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends Ecol & Evol 13, 58–63. https://doi.org/10.1016/s0169-5347(97)01237-8

Gaillard J-M, Loison A, ToÏgo C, et al (2003) Cohort effects and deer population dynamics. Ecoscience 10, 412–420. https://doi.org/10.1080/11956860.2003.11682789

Georgiadis N, Hack M, Turpin K (2003) The influence of rainfall on zebra population dynamics: implications for management. J Appl Ecol 40, 125–136. https://doi.org/10.1046/j.1365-2664.2003.00796.x

Gimenez O, Lebreton JD, Choquet R, Pradel R (2017) R2ucare: Goodness-of-Fit Tests for Capture-Recapture Models

Gimenez O, Lebreton JD, Choquet R, Pradel R (2018) R2ucare: An R package to perform goodness-of-fit tests for capture-recapture models. bioRxiv 192468. https://doi.org/10.1101/192468

Grafen A (1988) On the uses of data on lifetime reproductive success. Pages 454–471 in T H Clutton-Brock, editor. Reproductive success. University of Chicago Press, Chicago, Illinois, USA.

Grange S, Barnier F, Duncan P, Gaillard J-M, Valeix M, Ncube H, Périquet S, Fritz H (2015) Demography of plains zebras (*Equus quagga*) under heavy predation. Popul Ecol 57, 201–214. https://doi.org/10.1007/s10144-014-0469-7

Grange S, Duncan P, Gaillard J-M, Sinclair AR, Gogan PJ, Packer C, Hofer H, East M (2004). What limits the Serengeti zebra population? Oecologia 140, 523–532. https://doi.org/10.1007/s00442-004-1567-6

Green WCH, Rothstein A (1993) Persistent influences of birth date on dominance, growth and reproductive success in bison. J Zool 230, 177–186. https://doi.org/10.1111/j.1469-7998.1993.tb02680.x

Grovenburg TW, Klaver RW, Jenks JA (2012) Survival of white-tailed deer fawns in the grasslands of the northern Great Plains. J Wildl Manage 76, 944–956. https://doi.org/10.1002/jwmg.339

Hamel S, Côté SD, Gaillard J-M, Festa-Bianchet M (2009) Individual variation in reproductive costs of reproduction: High-quality females always do better. J Anim Ecol 78, 143–151. https://doi.org/10.1111/j.1365-2656.2008.01459.x

Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78, 443–457. https://doi.org/10.1007/bf00378733

Jackson NJ, Stewart KM, Wisdom MJ, Clark DA, Rowland MM (2021) Demographic performance of a large herbivore: effects of winter nutrition and weather. Ecosphere 12, e03328. https://doi.org/10.1002/ecs2.3328

Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78, 57–66. https://doi.org/10.2307/3545800

Joubert E (1974) Composition and limiting factors of a Khomas Hochland population of Hartmann zebra *equus zebra hartmannae*. Madoqua 49–53.

Kerby J, Post E (2013) Capital and income breeding traits differentiate trophic match-mismatch dynamics in large herbivores. Philos Trans R Soc Lond B Biol Sci 368, 20120484. https://doi.org/10.1098/rstb.2012.0484

Kiffner C, Lee DE (2019) The ecology of browsing and grazing II. In: Population dynamics of browsing and grazing ungulates in the Anthropocene, Springer Nature, Switzerland, pp 155–179. https://doi.org/10.1007/978-3-030-25865-8_6

Klingel H (1969) The social organisation and population ecology of the plains zebra (*Equus quagga*). African Zool 4, 249–263. https://doi.org/10.1080/00445096.1969.11447374

Laake JL (2013) RMark: An R Interface for Analysis of Capture-Recapture Data with MARK

Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62, 67–118. https://doi.org/10.2307/2937171

Lebreton JD, Nichols JD, Barker RJ, Pradel R, Spendelow JA (2009) Modeling individual animal histories with multistate capture-recapture models. Adv Ecol Res 41, 87–173.

Lee DE, Bond ML, Bolger DT (2017) Season of birth affects juvenile survival of giraffe. Popul Ecol 59, 45-54. https://doi.org/10.1007/s10144-017-0571-8

Lent PC (1974) Mother-Infant relationships in ungulates. In: The Behaviour of Ungulates and its relation to management. International Union for Conservation of Nature and Natural Resources, Switzerland, pp 14–55.

Lindström J (1999) Early development and fitness in birds and mammals. TREE 14, 343–348. https://doi.org/10.1016/s0169-5347(99)01639-0

Lindström J, Kokko H (2002) Cohort effects and population dynamics. Ecol Lett 5, 338–344. https://doi.org/10.1046/j.1461-0248.2002.00317.x

Lloyd P, Rasa O (1989) Status, reproductive success and fitness in Cape mountain zebra (*Equus zebra zebra*). Behav Ecol Sociobiol 25, 411–420. https://doi.org/10.1007/bf00300187

Loison A, Langvatn R (1998) Short-and long-term effects of winter and spring weather on growth and survival of red deer in Norway. Oecologia 116, 489–500. https://doi.org/10.1007/s004420050614

Loveridge AJ, Searle AW, Murindagomo F, Macdonald DW (2007) The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biol Conserv 134, 548–558. https://doi.org/10.1016/j.biocon.2006.09.010

MacKay AE, Forsyth DM, Coulson G, Festa-Bianchet M (2018) Maternal resource allocation adjusts to timing of parturition in an asynchronous breeder. Behav Ecol Sociobiol 72, 1-10. https://doi.org/10.1007/s00265-017-2419-9

Mduma SAR, Sinclair ARE, Hilborn R (1999) Food regulates the Serengeti wildebeest: a 40-year record. J Anim Ecol 68, 1101–1122. https://doi.org/10.1046/j.1365-2656.1999.00352.x

Ncube H, Duncan P, Grange S, et al (2011) Pattern of faecal 20-oxopregnane and oestrogen concentrations during pregnancy in wild plains zebra mares. Gen Comp Endocrinol 172, 358–362. https://doi.org/10.1016/j.ygcen.2011.03.027

Ogutu JO, Piepho HP, Dublin HT (2014) Responses of phenology, synchrony and fecundity of breeding by African ungulates to interannual variation in rainfall. Wildl Res 40, 698–717. https://doi.org/10.1071/wr13117

Owen-Smith N (1990) Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. J Anim Ecol 59, 893–913. https://doi.org/10.2307/5021

Owen-Smith and Mason (2005) Comparative changes in adult vs. juvenile survival affecting population trends of African ungulates. J Anim Ecol 74, 762-773. https://doi.org/10.1111/j.1365-2656.2005.00973.x

Owen-Smith N, Ogutu JO (2013) Controls over reproductive phenology among ungulates: allometry and tropical-temperate contrasts. Ecography 36, 256–263. https://doi.org/10.1111/j.1600-0587.2012.00156.x

Penzhorn BL (1984) Age determination in cape mountain zebras *Equus zebra zebra* in the Mountain Zebra National Park. Koedoe 25, 89-102.

Pigeon G, Albon S, Loe LE, Bischof R, Bonenfant C, Forchhammer M, Irvine RJ, Ropstad E, Veiberg V, Stien A (2022) Context-dependent fitness costs of reproduction despite stable body mass costs in an Arctic herbivore. J Anim Ecol 91, 61–73. https://doi.org/10.1111/1365-2656.13593

Plard F, Gaillard J-M, Coulson T, Hewison AM, Douhard M, Klein F, Delorme D, Warnant C, Bonenfant C (2015) The influence of birth date via body mass on individual fitness in a long-lived mammal. Ecology 96, 1516–1528. https://doi.org/10.1890/14-0106.1

Pluháček J, Bartoš L, Doležalová M, Bartošová-Víchová J (2007) Sex of the foetus determines the time of weaning of the previous offspring of captive plains zebra (*Equus burchelli*). Appl Anim Behav Sci 105, 192–204. https://doi.org/10.1016/j.applanim.2006.05.019

Post E (2003) Timing of reproduction in large mammals. In: Phenology: an integrative environmental science. Springer, Dordrecht, pp 437–449

Pradel R, Hines JE, Lebreton JD, Nichols JD (1997) Capture-recapture survival models taking account of transients. Biometrics 60–72. https://doi.org/10.2307/2533097

Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the costs of reproduction. TREE 15, 421–425. https://doi.org/10.1016/s0169-5347(00)01941-8

Rogers CM and others (1993) A woody vegetation survey of Hwange National Park. A woody vegetation survey of Hwange National Park.. Department of National Parks and Wildlife Management

Rubenstein DI, Nuñez CM (2009) Sociality and reproductive skew in horses and zebras. In: Reproductive skew in vertebrates: proximate and ultimate causes. Cambridge University Press Cambridge, pp 196–226

Sadleir R (1982) Energy consumption and subsequent partitioning in lactating black-tailed deer. Can J Zool 60, 382–386. https://doi.org/10.1139/z82-051

Sæther BE (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. TREE 12, 143–149. https://doi.org/10.1016/s0169-5347(96)10068-9

Sinclair ARE, Mduma SAR, Arcese P (2000) What determines phenology and synchrony of ungulate breeding in Serengeti? Ecology 81, 2100–2111. https://doi.org/10.1890/0012-9658(2000)081[2100:wdpaso]2.0.co;2

Smuts GL (1975) Pre- and postnatal growth phenomena of Burchell's zebra *Equus burchelli antiquorum*. Koedoe 18, 69–102.

Smuts GL (1976) Reproduction in the zebra mare *Equus burchelli antiquorum* from the Kruger National Park. Koedoe 19, 89–132. https://doi.org/10.4102/koedoe.v19i1.1186

Spagopoulou F, Teplitsky C, Chantepie S, Lind MI, Gustafsson L, Maklakov AA (2020) Silver-spoon upbringing improves early-life fitness but promotes reproductive ageing in a wild bird. Ecol Lett 23, 994–1002. https://doi.org/10.1111/ele.13501

Stephens PA, Boyd IL, McNamara JM, Houston AI (2009) Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90, 2057–2067. https://doi.org/10.1890/08-1369.1

Tuljapurkar S (1989) An uncertain life: demography in random environments. Theor Popul Biol 35, 227–294. https://doi.org/10.1016/0040-5809(89)90001-4

Valeix M, Loveridge AJ, Chamaillé-Jammes S, et al (2009) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat

use. Ecology 90, 23–30. https://doi.org/10.1890/08-0606.1

Vitet C, Duncan P, Ganswindt A, Mabika C, Chamaillé-Jammes S (2021) Do infanticides occur in harem-forming equids? A test with long-term sociodemographic data in wild plains zebras. Anim Behav 177, 9–18. https://doi.org/10.1016/j.anbehav.2021.04.012

Vitet C, Duncan P, Gimenez O, Mabika C, Chamaillé-Jammes S (2020) Plains zebras bring evidence that dilution and detection effects may not always matter behaviorally and demographically. Ecosphere 11, e03288. https://doi.org/10.1002/ecs2.3288

Weladji RB, Loison A, Gaillard J-M, Holand Ø, Mysterud A, Yoccoz NG, Nieminen M, Stenseth NC (2008) Heterogeneity in individual quality overrides costs of reproduction in female reindeer. Oecologia 156, 237-247. https://doi.org/10.1007/s00442-008-0961-x

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton, USA.

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. Purple: younger foals (between birth and six months old), brown: 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, blue: 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, blue: 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:

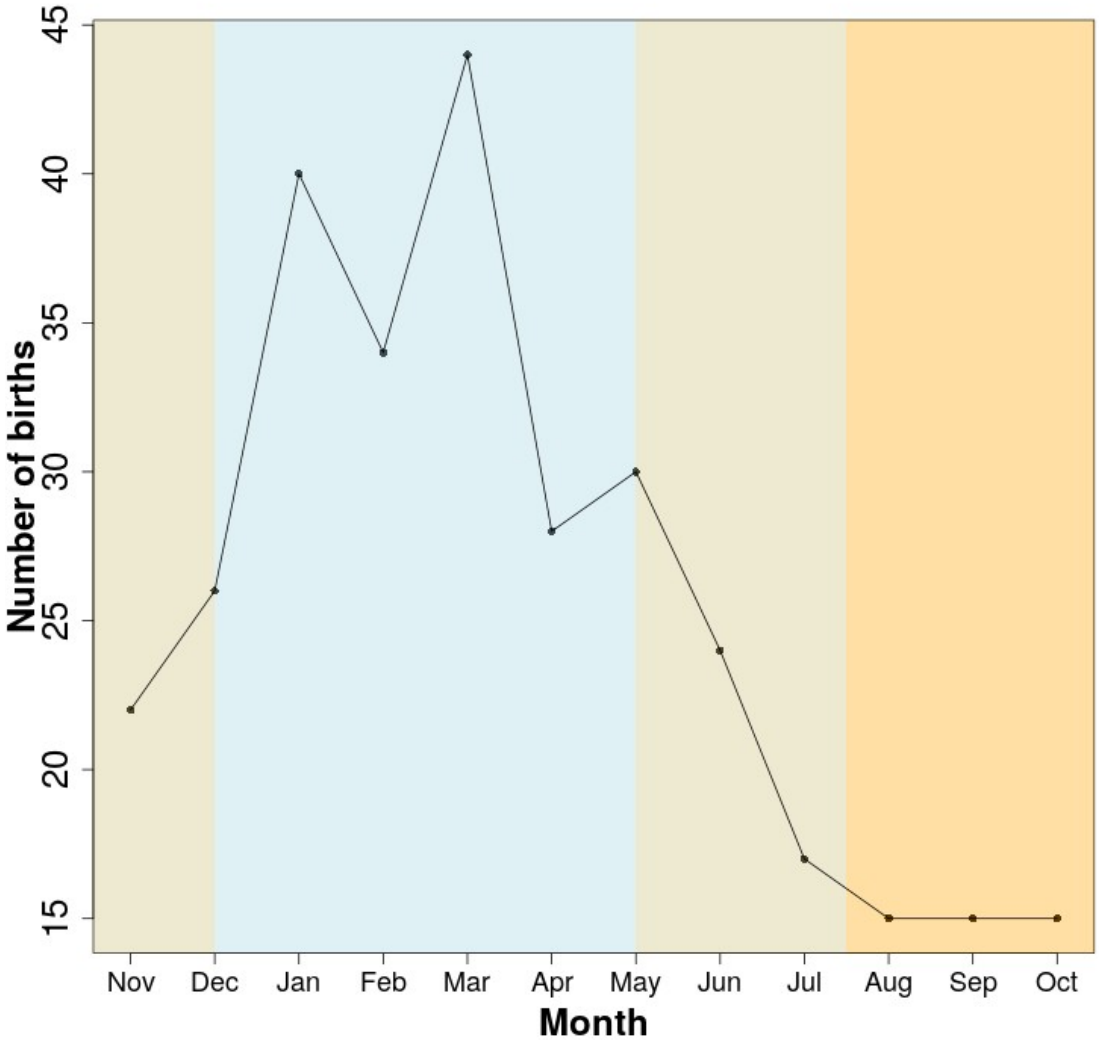


Figure 2:

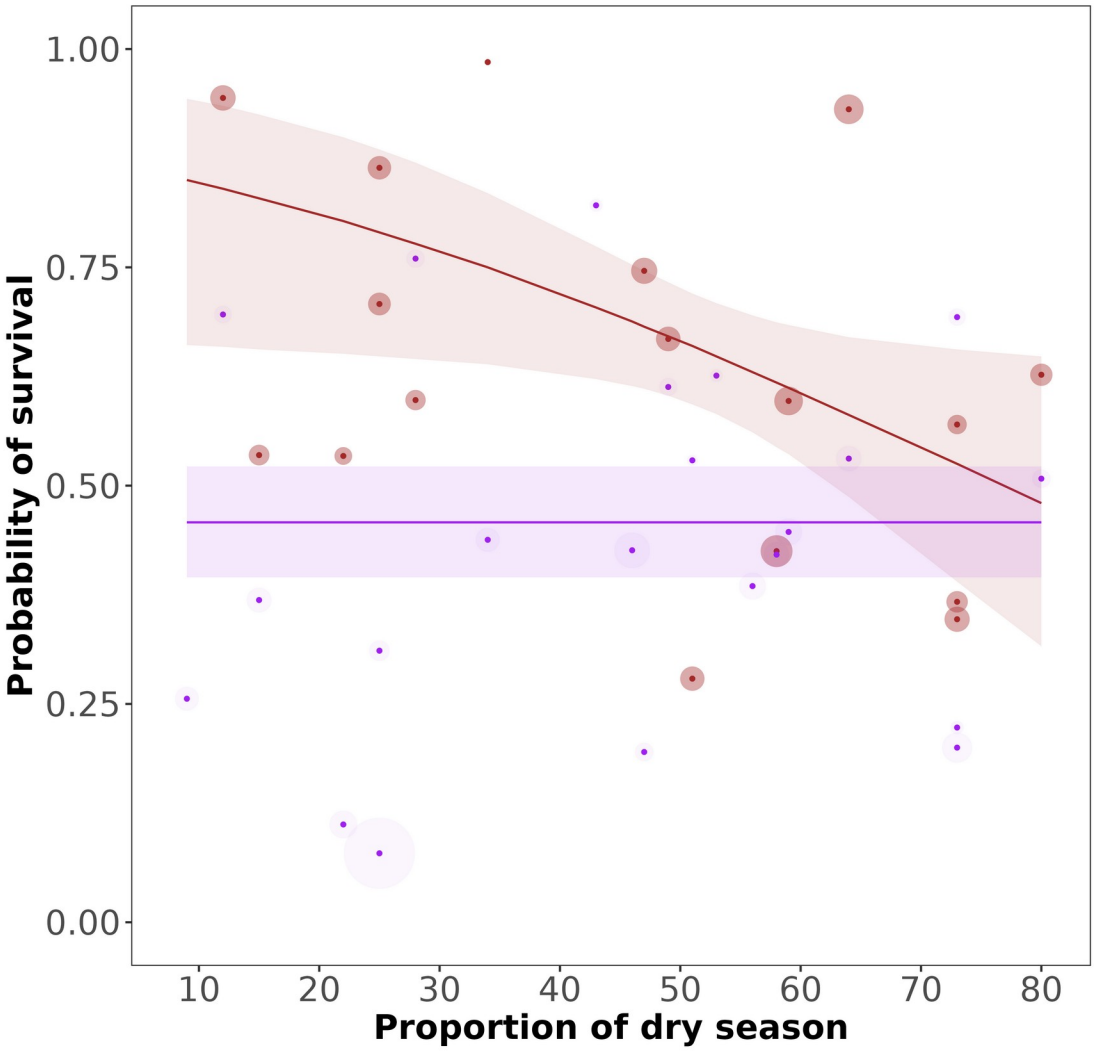
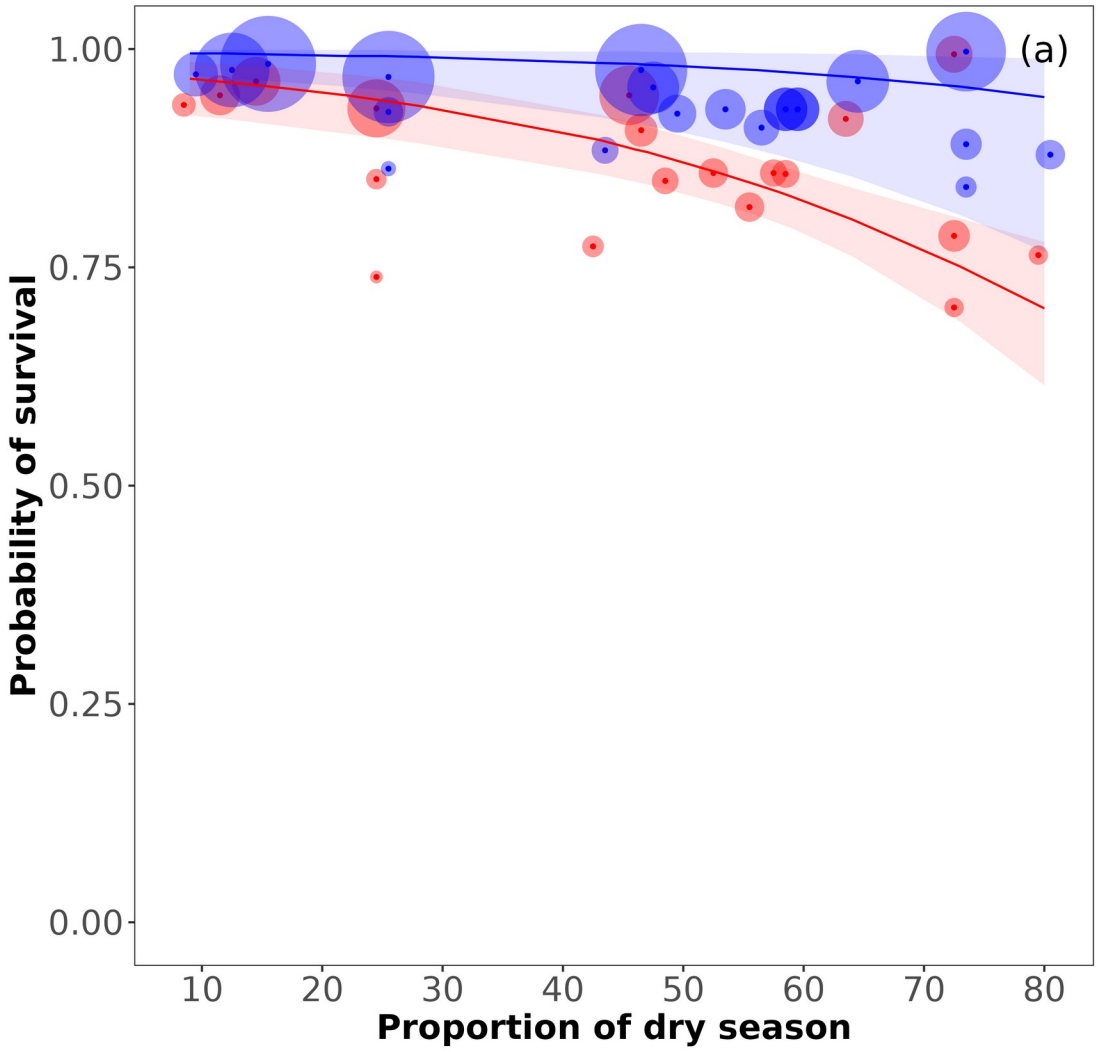
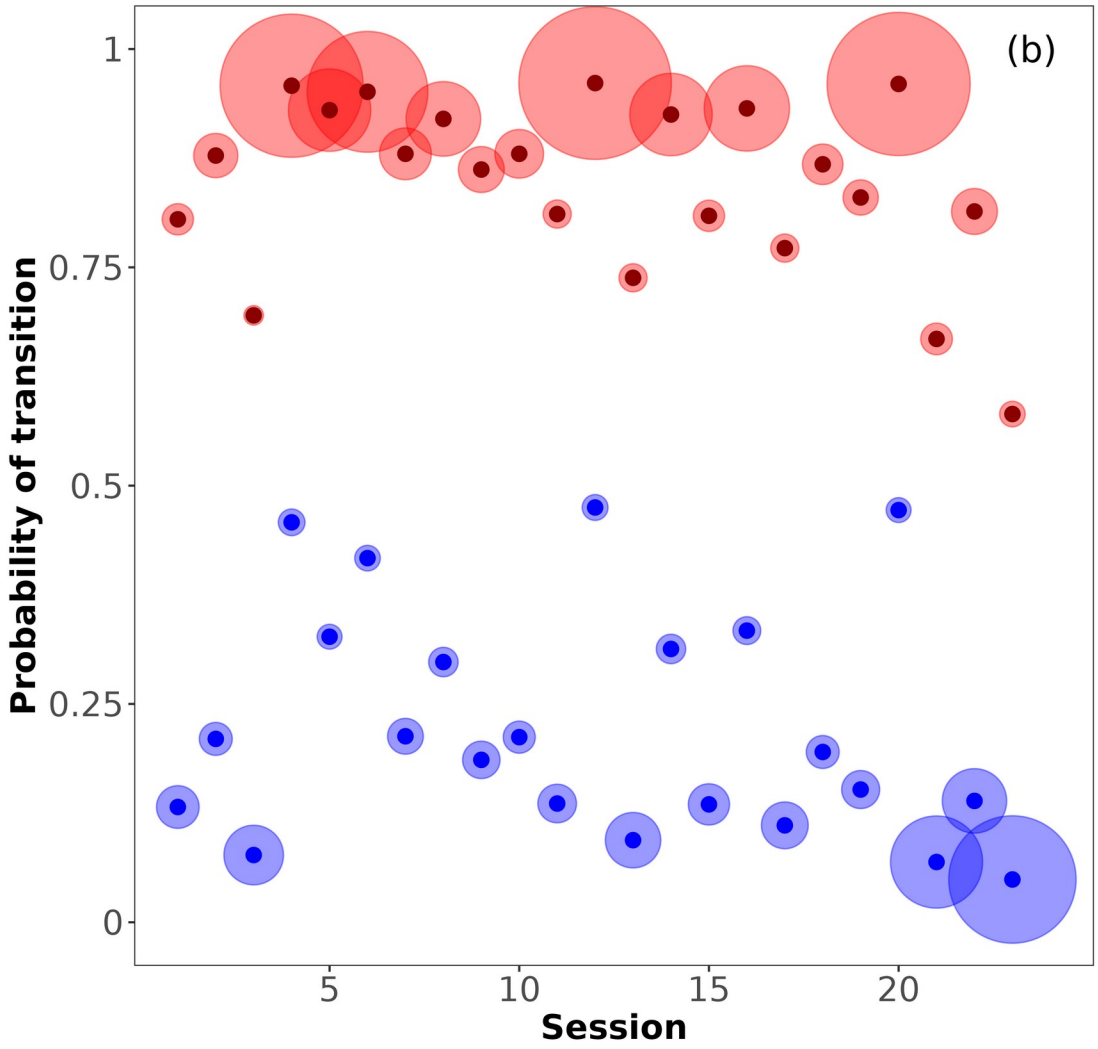

1.00
0.75
0.50
0.25
0.00
Probability of survival
10
20
30
40
50
60
70
80
Proportion of dry season

Figure 3:


(a)
1.00
0.75
0.50
0.25
0.00
Probability of survival
10
20
30
40
50
60
70
80
Proportion of dry season


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