

Demography of plains zebras (*Equus quagga*) under heavy predation

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Abstract In natural ecosystems, ungulate densities show strong temporal variations. The ecological processes driving these fluctuations are complex: food limitation and predation are both important and can interact. Survival rates are central to this debate, but data are sparse for tropical ecosystems. Here, we estimate age- and sex-specific survival rates for plains zebra in Hwange National Park, a nutrient-poor savanna with a high predator–prey ratio. We estimated survival from a detailed Capture-Mark-Recapture (CMR) monitoring based on 248 individual life histories, for the first time in an African grazer. We controlled for variations in detection probabilities among adult females, which resulted from their social structure. As

expected, annual survival was low during the first year (0.441); increased in yearlings (0.560) and peaked at 0.795 and 0.847 in adult males and females respectively. The survival of adult females was lower during the dry season, which probably resulted from higher predation due to predictable movements of zebras to waterholes. Survival at all ages was low compared to ungulates without predators. The demographic model we constructed showed a declining trend ($\lambda = 0.94$), which was consistent with the data from road counts ($\hat{\lambda} = 0.92$). Life Table Response Experiment (LTRE) analyses using the Serengeti and Kruger populations as references showed that the main cause of this declining trend in the Hwange population was low survival in yearling and adult females; low foal survival also contributed. In this ecosystem, predation is likely to be the main ecological process causing low survival, and therefore a decline in the zebra population.

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Introduction

Ungulates are a central component of natural ecosystems (Danell et al. 2006), so a good knowledge of their ecology is essential to understand the structure and functioning of ecosystems, and also for their conservation and management (Sinclair et al. 2006). Long-term studies on African ungulates show that their populations often experience strong variations in size (Du Toit et al. 2003). Dry season food resources influence juvenile mortality, and consequently population size, in several ungulates (Mduma et al. 1999; Owen-Smith et al. 2005). Likewise, predation plays an important role in the decline of some prey populations

(Harrington et al. 1999; Power 2002; Tambling and Du Toit 2005). The ecological processes driving fluctuations in African ungulate populations are complex and not fully understood, and getting accurate estimates of demographic parameters, especially survival, is of course central to this debate.

Most studies of survival in Northern hemisphere ungulates (Loison et al. 1999; Coulson et al. 2001; Festa-Bianchet et al. 2003; Catchpole et al. 2004; Toïgo et al. 2007) have used Capture-Mark-Recapture (CMR) analyses to account for imperfect detection, which is necessary to obtain unbiased estimates of survival (Lebreton et al. 1992; Nichols 1992; Gimenez et al. 2008). These studies have improved our understanding of population dynamics of several species, and have allowed the ecological and environmental factors that shape variation in survival to be identified. Longitudinal studies based on individuals have also been used to estimate survival patterns in African ungulates, such as the kudu *Tragelaphus strepsiceros* (Owen-Smith 1990) and the elephant *Loxodonta africana* (Moss 2001), but only two studies of African ungulates, one on the impala *Aepyceros melampus* (Gaidet and Gailard 2008) and one on the giraffe *Giraffa camelopardalis* (Suraud et al. 2012), accounted for imperfect detection by using a CMR method.

During the last decades plains zebras (*Equus quagga*) have been extirpated from parts of their range, and many populations have declined (Moehlman 2002). However, our understanding of their population dynamics is still rather limited (Hack et al. 2002). Their populations can be limited by top-down or bottom-up processes, since resources limit plains zebra in Laikipia, where predator densities are low (Georgiadis et al. 2003), but in the Serengeti the zebra population is limited by low foal survival, apparently due to predation (Grange et al. 2004). In general, within African ungulate communities, zebras tend to be more sensitive to top-down processes than grazing bovids (Grange and Duncan 2006). In previous studies, survival patterns of plains zebra populations were assessed using life tables and age ratios (Spinage 1972; Georgiadis et al. 2003; Grange et al. 2004), so they are likely to be biased because of the strong assumptions inherent to these methods (see e.g., Caughley 1977). As carcasses of juveniles disappear faster than adults, the young age classes are under-represented in the dead sample. There is therefore a need for accurate information on age- and sex-specific survival patterns to understand the population dynamics of plains zebra.

Here, we report the results of the first demographic analysis based on a CMR study on an African grazer, using the monitoring of individually known zebras between 2004 and 2011 in Hwange National Park, Zimbabwe. The main objective was to test the hypothesis that zebra survival in

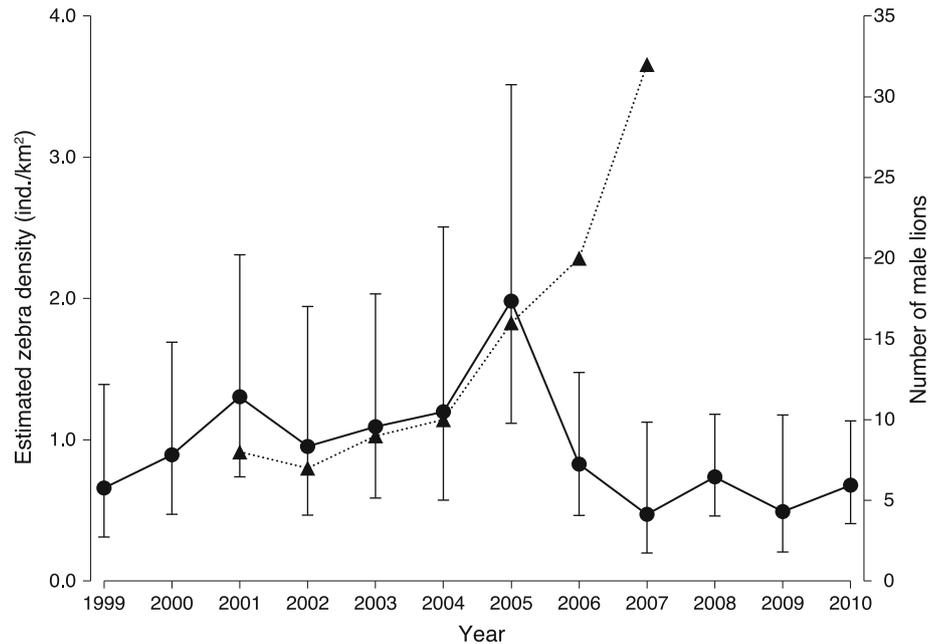
this ecosystem, including a complete guild of large herbivores and their predators, would be lower than in equid populations without predators. The population declined after 2005 (Fig. 1), and we expected that it would be limited by low survival since the predation pressure on zebras is higher in Hwange than in other African systems. The ratio to predator biomass on zebra biomass is 0.10 in Hwange, compared to 0.08 in Kruger, 0.03 in Ngorongoro, and 0.01 in Serengeti (Fritz et al. 2011). Moreover, the study area in the northern part of Hwange shelters the highest densities of lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) in this Park (Drouet-Hoguet 2007; Loveridge et al. 2007). Age- and sex-specific survival was estimated for zebras: we expected low survival during the first year of life (as in the Serengeti, Grange et al. 2004), and lower survival in all age classes than in predator-free populations. Like wild horses, zebra stallions compete for mates and protect their harems from predators (Klingel 1975) and in many equids, secondary sex ratios are biased in favor of adult females (Berger 1983), so we expected lower survival in adult males compared to females. Temporal effects (time, year and season) were tested on survival and detection probabilities: since there is practically no rain in the long dry season (6 months), we expected lower survival in the dry season. Finally, we investigated which demographic parameters were the most influential in driving the observed demographic patterns. We first built a demographic model (matrix model, Caswell 2001) using age-specific survival and information on age-specific reproduction (Barnier et al. 2012). We then compared the population growth rate obtained from this demographic model with observed trends in the population during the study period. Lastly, we performed two Life Table Response Experiment (LTRE) analyses to measure the relative contribution of demographic parameters to the observed variation in the population growth rate (λ) between this zebra population (declining) and two stable populations (Serengeti and Kruger).

Methods

Study area

Hwange National Park covers 14651 km² in western Zimbabwe. This system is near natural as there is very little hunting in the Park by people, and commercial hunting of lions outside the Park was stopped between 2005 and 2010 (Loveridge et al. 2010). This study was conducted in the Northern part of the Park and the adjacent Forestry area, ca. 1500 km² around Main Camp. The vegetation is typical of southern African dystrophic wooded savannas with patches of grasslands (Rogers 1993). The long-term average annual

Fig. 1 Zebra densities during the dry season (black circles; solid line) and the number of adult male lions in the Main Camp area (black triangles; dotted line; data from Loveridge et al. 2010). Error bars represent 95 % confidence intervals



rainfall at Main Camp is 606 mm (Chamaillé-Jammes et al. 2006), and the rainfall pattern divides the year into two distinct periods: a dry season (May–October) and a wet season (November–April). About 30 artificial waterholes have been dug in the northern and eastern parts of the Park, and these allow water-dependent large mammals to use the area year-round. Observations started in July 2004, and fieldwork sessions have been conducted every 6 months since then (in July–August during the dry season and in January–February during the wet season). The data collected between July 2004 and February 2011 are used here.

Identification and monitoring

We identified and monitored zebras in the main camp area, where waterholes and an abandoned airstrip attract many grazers and provide a good visibility for field observations. Zebras were individually identified from variations in their stripe pattern (Klingel 1967), based on photos of both sides. When zebra groups were encountered the observer first determined the group composition (number of individuals, age class, sex), then photographed individuals present in the group. Since zebra groups were generally encountered many times during a 2 month-session, by the end of a field session each individual present in a group was photographed at least once. A folder with individual photos was used to visually identify individuals in the field, and thereafter photos of all individuals seen in the field were compared to the digital photo database. This procedure based on the identification of unique stripe patterns from photos allowed avoiding potential misidentifications.

We determined the sex of zebra individuals by observing the genitals. We estimated the age of the foals and yearlings when first sighted using the criteria of Smuts (1975) and Penzhorn (1984), and photographs of foals of known age in the Hwange population. When a zebra was identified for the first time, it was aged as accurately as possible; for this analysis it was classified into one of these three main age-classes: foal (including “young foal” of 0–6 months-old and “old foal” of 6–12 months-old), yearling (including “young yearling” of 12–18 months-old and “old yearling” of 18–24 months-old), or individuals over 2 years-old (adults). A database was built and included over 11000 sightings, with photos of both sides of each individual, biological characteristics (age, body condition, predation marks, and reproductive status), and group composition. Fifty individuals (in 9 family groups) were first identified in July 2004. This database was updated continuously since then.

CMR modeling

Plains zebra typically lives in harems; i.e., mares and their offspring associate with a specific male for up to several years. Young zebras of both sexes disperse around 2 years of age: young males join a bachelor group and young females integrate a new harem. During fieldwork, all members of a specific harem are therefore seen at the same time, inducing heterogeneity and dependency in individual sightings (i.e., captures in a CMR framework). Ungulates generally show a marked age-dependence in survival, which is low in the first year, higher in yearlings, reaching

a maximum during early prime-age stage, and declining in old age (Gaillard et al. 2000). Since we can recognize 3 main age-classes for individual zebras identified in the field (foal, yearling, and adult) and considering associations between adult females within the same harem and their stallion, for the sake of simplicity, we chose to run a set of CMR models on three distinct datasets: a first one for adult males (harem stallions; $n = 36$) to estimate male adult survival, a second one for adult females ($n = 80$) to estimate female adult survival, and a third one on young zebras, i.e., individuals first identified as foal or yearling ($n = 132$) to estimate foal (0–12 months-old) and yearling (12–24 months-old) survival. The strong social structure generates various patterns of heterogeneity (see “GOF tests” below), which justifies partitioning the analysis of survival into three broad groups in order to avoid obtaining an overly complex model.

Since the same zebra groups were observed almost every day or at least several times a week for 1–2 months in both dry and wet seasons, some foals were monitored from birth ± 2 days (20 %; $n = 93$), but most were first identified when aged 3 days–6 months (64 individuals, i.e., 68.8 %; $n = 93$), and 13 individuals were first identified after 6 months-old (i.e., 14 %; $n = 93$). To estimate foal and yearling survival, we therefore used a CMR model based on staggered entry data for young zebras (i.e., individuals first identified at 0–6, 6–12, or 12–18 months-old; see details below). We also included data derived from a study of reproduction in mares conducted between 2007 and 2009 using hormone assays in 152 fecal samples, which provided reliable criteria to detect pregnancy (Ncube et al. 2011). It allowed us to estimate the number of missed foals in the field when mares were detected pregnant but the foal was not seen alive during the following session. During our study period, 93 foals were identified in the field and 23 were not (i.e., a pregnancy was detected and no foal was seen with the mare afterwards). In this last case, we marked the foal as being identified at birth and then reported as dead (life history: 10000 etc.). Fetal loss in horses is a maximum of 10 % (Chevalier-Clément 1989). If this loss occurred in these zebras it would lead to a negligible change in the population growth rate estimated from the population projection models (-0.8 % decline in the asymptotic λ , see below). Finally, 16 individuals first identified at 12–18 months-old were also included in the dataset on young zebras, reaching a total of 132 individual life histories.

CMR models were based on 248 individual life histories: 116 adults (36 harem stallions and 80 females) and 132 young zebras (see below for details on age-classes; Table 1). Three datasets were built, corresponding to adult males, adult females, and to young zebras (first identifications at foal and yearling stages combined). For

Table 1 Number of individuals included in CMR models with their associated status at first identification

Age class	Sex	Group	<i>N</i>
Adult	Male		36
Total for CMR models on adult males			36
Adult	Female	1 [§]	14
		2 [§]	21
		3 [§]	25
		4 [§]	20
Total for CMR models on adult females			80
Young [#]	NA	1*	103
		2*	13
		3*	16
Total for CMR models on young zebras			132

[§] Adult females classified into distinct spatial groups

[#] Staggered entry data (6-month age-classes starting from birth date) for young zebras (pregnancy data and individuals first identified as foal or yearling)

* The groups of young zebras are based on their age at first identification: group 1 = foals not seen when pregnancy was detected ($n = 23$) and individuals first identified at 0–6 months-old ($n = 80$), group 2 = individuals first identified at 6–12 months-old, and group 3 = individuals first identified at 12–18 months-old

each of the three datasets, a set of CMR models was then run with the E-SURGE program (Choquet et al. 2009a). For models on adult zebras, the study period encompassed 14 occasions of capture (time covariate) over 8 years, corresponding to 7 dry and 8 wet seasons. The location of each observation was recorded in order to classify individual harem mares into distinct spatial groups. We then incorporated both additive and interactive combinations of temporal (time, year and season) and individual (spatial groups for mares) effects on both survival and detection probabilities. For CMR models on young zebras, 16 occasions of capture were defined as follows: the first occasion of capture represented the first age-class (0–6 months-old), and then successive recaptures were compiled every 6 months (i.e., 6–12 months-old, 12–18 months-old, ... 90–96 months-old). This CMR structure allowed considering a staggered entry of young zebras. Three groups were defined: 103 “young foals” first identified at 0–6 months-old (including 23 detected pregnancies with no birth or foal observed thereafter, and 80 foals observed in the field), 13 “old foals” first identified at 6–12 months-old, and 16 “young yearlings” first identified at 12–18 months-old. CMR models were constrained to define five age-classes: 0–6 (“young foal”), 6–12 (“old foal”), 12–18 (“young yearling”), 18–24 (“old yearling”), and >24 months-old (adult). Models with constant parameters and an effect of time on survival and detection

probabilities were tested (notations as in Lebreton et al. 1992; see Table 2).

We could not test the effect of sex for young zebras as 32 individuals (24 %, $n = 132$) were not sexed (including foals which were never seen, but detected during pregnancy stage). We did not use the estimate of adult survival (>24 months-old) derived from the dataset on young zebras (0.768), since it was likely to be underestimated. In this population, young zebras disperse at about 2 years of age (24.6 months \pm 1.2 SE; $n = 32$). Moreover, because of the high mortality of foals and yearlings (see “Results”), few young zebras survived to adulthood during our study period. Finally, we could not look for actuarial senescence (i.e., an increasing mortality rate with age) because the oldest zebras whose age was known accurately were only 5 years of age, well before the onset of actuarial senescence generally reported in ungulates (7–8 years of age, Gaillard et al. 2000).

GOF tests

Program U-CARE was first used to perform the goodness-of-fit (GOF) test of the fully time-dependent model (i.e., the Cormack-Jolly-Seber model, Lebreton et al. 1992) to detect problems in the data structure of our three datasets (Choquet et al. 2009b). The CJS model satisfactorily fitted survival patterns of adult males (global test: $\chi^2 = 13.4269$, $df = 24$, $P = 0.95855$, see Table 3 for further details) and young zebras (global test: $\chi^2 = 20.5072$, $df = 22$, $P = 0.55134$, see Table 3 for further details). However, the CJS model fitted survival patterns of adult females poorly (global test: $\chi^2 = 114.378$, $df = 33$, $P < 0.001$, see Table 3 for further details), apparently due to trap-dependence (signed statistic for trap-dependence = -6.566 , $P < 0.001$).

Social bonds between zebra mares are likely to have caused this heterogeneity in detection. To correct this bias, we performed a hierarchical cluster analysis with R software version 2.12.0 (function “hclust”, R Development

Core Team 2011) to classify the adult females into different spatial groups according to their geographical locations. The GPS coordinates of zebra sightings were used to estimate the home range of each adult female (function “mcp”). This cluster analysis allowed 4 groups to be defined whose members used closely similar home ranges. After including spatial groups in the analysis, we still detected heterogeneity in the data using the GOF tests (global test: $\chi^2 = 51.314$, $df = 32$, $P = 0.017$, see Table 3 for further details), including some trap-dependence (signed statistic for trap-dependence = -2.188 , $P = 0.029$). We then analyzed the results of tests 3.SR and 2.CT (Table 3) to identify the cause of heterogeneity detected in adult females (Fletcher et al. 2012). Tests 3.SR and 2.CT did not reveal any heterogeneity within the 4 groups (see Table 3 for further details). To account for any other potential heterogeneity in the detection of adult females, we finally used multi-event models including hidden detectability levels. Such models include a detection probability that varies randomly across time. In these mixture models individuals are distributed between a state of high detection probability H and a state of low detection probability L (see Choquet et al. 2009a for further details). The implementation of these models in E-SURGE involves building three matrices corresponding to the initial states, the transition probabilities and the encounter rates, respectively. These matrices stand as follows:

- initial state: $P\Pi = [\pi \ *];$
- transition probabilities: $P\Phi = \begin{bmatrix} \phi & - & * \\ - & \phi & * \\ - & - & * \end{bmatrix};$
- encounter rates: $PB = \begin{bmatrix} * & p \\ * & p \\ * & - \end{bmatrix};$

where “*” indicates the complementary parameter, π is an initial state parameter to be fixed, ϕ is a transition parameter to be estimated, p is an encounter rate to be estimated, and “-” indicates parameters constrained to zero.

Table 2 Effects tested on survival and detection probabilities in CMR models

Formula in E-SURGE	Description	Dataset used
i	Constant: probabilities are constant	Adult male, adult female
t	Time: probabilities vary with time (i.e., at each capture session)	Adult male, adult female, young
$t(1\ 3\ 5\ 7\ 9\ 11\ 13, 2\ 4\ 6\ 8\ 10\ 12\ 14)$	Season: probabilities vary between the wet and dry seasons	Adult male, adult female
$t(1\ 2, 3\ 4, 5\ 6, 7\ 8, 9\ 10, 11\ 12, 13\ 14)$	Year: probabilities vary across years (2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011)	Adult male, adult female
g	Spatial group (4 distinct groups; see Table 1)	Adult female
g	Groups based on age at first sighting	Young
$a(1\ 2, 3\ 4, 5)$	Age (models structured in 5 age-classes: see text)	Young

Table 3 Results of the GOF tests

Dataset	GOF tests	Group	Statistic	p two-sided
Adult male	Global test: χ^2	NA	13.4269	0.95855
Young [#]	Global test: χ^2	All	20.5072	0.55134
Adult female	Global test: χ^2	NA	114.378	<0.001
Adult female	Global test: N(0,1) signed statistic for trap-dependence	NA	-6.566	<0.001
Adult female ^S	Global test: χ^2	All	51.314	0.01659
Adult female ^S	Global test: N(0,1) signed statistic for trap-dependence	All	-2.188	0.02867
Adult female ^S	Test 3.SR: N(0,1) signed statistic	1	0	0.5
Adult female ^S	Test 3.SR: N(0,1) signed statistic	2	0	0.5
Adult female ^S	Test 3.SR: N(0,1) signed statistic	3	0	0.5
Adult female ^S	Test 3.SR: N(0,1) signed statistic	4	0	0.5
Adult female ^S	Test 2.CT: N(0,1) signed statistic	1	-1.9038	0.05693
Adult female ^S	Test 2.CT: N(0,1) signed statistic	2	NA	NA
Adult female ^S	Test 2.CT: N(0,1) signed statistic	3	-0.90619	0.36483
Adult female ^S	Test 2.CT: N(0,1) signed statistic	4	-1.0009	0.31687

[#] Staggered entry data (6-month age-classes starting from birth date) for young zebras (pregnancy data and individuals first identified as foal or yearling)

^S Dataset with adult females classified in 4 spatial groups

Model selection was based on the lowest Akaike information criterion (AIC), as well as the lowest number of parameters (parsimony). For adult females, the coefficient of dispersion using four spatial groups was $\hat{c} = 1.60$, indicating a slight over-dispersion in the data. In this case, multi-event models were therefore classified according to QAIC_c (QAIC is the criterion modified for over-dispersed data; and “c” indicates a weighted QAIC for small sample size, Burnham and Anderson 2002).

Since the time step for CMR modeling was 6 months, annual survival and detection probabilities were derived from the products: $\Phi_{annual} = (\Phi_{model})^2$ and $p_{annual} = (p_{model})^2$. The standard error and the confidence interval were obtained based on the classical formulas for the variance of a product of random variables (Goodman 1962).

Population modeling

We modeled the dynamics of this zebra population with a pre-breeding census matrix model (Caswell 2001). Using a birth-pulse model is appropriate considering that in Southern Africa zebra births occur mainly during the wet season (Smuts 1976). In this population, the exact first age at reproduction was determined for two zebra females (2.83 and 3.58 years respectively; i.e., 3.21 years in average). Following our observations and data in the literature we thus considered that first reproduction of zebra females occurred at 3 years of age (Smuts 1976; Rubenstein 2010) and that they reproduced fully from this age onwards. We therefore defined an age-structured model with 3 classes ($1 \leq \text{age} < 2$ years-old; $2 \leq \text{age} < 3$ years-old; and $\text{age} \geq 3$ years-old):

$$\begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & F_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & S_3 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix}_t$$

Where N_x is the number of individuals of age x , S_x is the survival probability of individuals of age x and F_x is the net fecundity of individuals of age x .

The model was based on females, assuming that male numbers were not limiting female reproduction. The sex ratio at birth was taken as balanced. Age-specific survival was derived from the CMR modeling (this paper) and fecundity was estimated at 0.74 (females ≥ 3 years-old, Barnier et al. 2012) from long-term monitoring of reproduction in this population. Since the age of reproductive females was generally not known, fecundity was considered to be independent of age. The net fecundity was defined as follows:

$$F_x = S_0 \times \sigma \times f_x$$

where S_0 is the foal survival rate, σ is the sex-ratio at birth (0.5 in these analyses) and f_x is the number of foals alive at birth produced by females of age x . The demographic model was studied with program ULM (Legendre and Clobert 1995).

We then compared the population growth rate obtained from the demographic model with the estimate from observed trends of population size derived from road transect counts conducted in the Park between 2005 and 2010. Zebra densities were estimated during the dry season using Distance Sampling software (version 4.1; Thomas et al. 2003) through censuses based on the line-transect method (Chamaillé-Jammes et al. 2009). The annual population growth rate in year t was estimated as $\hat{\lambda} = \frac{N_{t+1}}{N_t}$; where N_t is the population size in year t and N_{t+1} the population size in year $t + 1$. The population growth rate

over a given study period was calculated as $\hat{\lambda} = \left(\frac{N_t}{N_0}\right)^{\frac{1}{t}}$; where N_0 represents the initial population size, N_t the population size in year t , and t is the number of years (Caughley 1977).

Since the Main Camp zebra population was declining (Fig. 1), we compared it with two stable zebra populations to identify the key parameters causing the observed population decline, using LTRE analyses. We used the Serengeti and Kruger populations ($\lambda = 1.01$ and 1 respectively; Grange et al. 2004; Owen-Smith and Mason 2005), as references. LTRE analysis is a retrospective analysis (Caswell 2001) that allows partitioning of the difference in growth rates between a treatment (here zebra in Hwange) and a control (here zebra in Serengeti and in Kruger). This analysis was performed using pre-breeding matrix models for these populations and the “LTRE” function of the R-software (version 2.12.0, R Development Core Team 2011). We used matrix models based on 13 age classes (following the same notations as previously); the last age class represented senescent individuals (≥ 13 years-old):

$$\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_{13} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & F_3 & \cdots & F_{12} & F_{13} \\ S_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & S_2 & 0 & \cdots & 0 & 0 \\ 0 & 0 & S_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & 0 & 0 \\ 0 & 0 & 0 & \cdots & S_{12} & S_{13} \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_{13} \end{bmatrix}_t$$

The demographic parameters for the 3 populations are presented in Table 4. Their contributions to the population growth rate were then compared across different age-classes.

Results

Adult males

The best model for adult male survival included a seasonal effect on the probability of detection (Table 5), with detection probabilities varying from 0.746 [± 0.049 SE; 95 % CI (0.640, 0.830)] in the dry season to 0.923 [± 0.030 SE; 95 % CI (0.840, 0.965)] in the wet season. Survival in the wet season [0.911 ± 0.034 SE; 95 % CI (0.817, 0.959)] tended to be higher than in the dry [0.871 ± 0.040 SE; 95 % CI (0.772, 0.931)], but the difference was not statistically significant, nor was among-year variation with survival estimates varying from 0.701 [± 0.069 SE; 95 % CI (0.561, 0.841)] in 2009 to 0.816 [± 0.066 SE; 95 % CI (0.682, 0.950)] in 2007. The annual survival of adult males therefore appears constant at 0.795 [± 0.052 SE; 95 % CI (0.689, 0.901)].

Table 4 Demographic parameters used in LTRE analyses for the Hwange, Serengeti and Kruger populations (notations explained in the text)

Parameter	Hwange	Serengeti	Kruger
S_0	0.441	0.389	0.454
S_1	0.560	0.847	0.476
S_2	0.847	0.979	0.909
S_3	0.847	0.954	0.909
S_4	0.847	0.954	0.909
S_5	0.847	0.875	0.909
S_6	0.847	0.875	0.909
S_7	0.847	0.875	0.909
S_8	0.847	0.875	0.909
S_9	0.847	0.875	0.909
S_{10}	0.847	0.875	0.909
S_{11}	0.847	0.875	0.909
S_{12}	0.847	0.875	0.909
S_{13}	0.847	0.768	0.909
F_1	0.00000	0.00000	0.00000
F_2	0.00000	0.00000	0.00000
F_3	0.16317	0.13343	0.17933
F_4	0.16317	0.13343	0.17933
F_5	0.16317	0.17174	0.17933
F_6	0.16317	0.17174	0.17933
F_7	0.16317	0.17174	0.17933
F_8	0.16317	0.17174	0.17933
F_9	0.16317	0.17174	0.17933
F_{10}	0.16317	0.17174	0.17933
F_{11}	0.16317	0.17174	0.17933
F_{12}	0.16317	0.17174	0.17933
F_{13}	0.16317	0.17174	0.17933

Adult females

The best model for adult female survival included interactive effects of season and group on the probability of detection (Table 5). The lowest detection probability of 0.392 [± 0.058 SE; 95 % CI (0.286, 0.509)] was observed for the group 4 (20 mares) in the dry season while the highest detection of 0.985 [± 0.015 SE; 95 % CI (0.902, 0.998)] occurred for the group 2 (21 mares) in the wet season. From the selected model, the seasonal survival of adult females varied between 0.864 [± 0.024 SE; 95 % CI (0.809, 0.905)] in the dry season and 0.981 [± 0.018 SE; 95 % CI (0.885, 0.997)] in the wet season. There was no evidence for among-year variation in survival, with estimates varying from 0.749 in 2007 [± 0.064 SE; 95 % CI (0.621, 0.876)] to 0.957 [± 0.065 SE; 95 % CI (0.828, 1.086)] in 2010. The annual survival of adult females was therefore 0.847 [± 0.027 SE; 95 % CI (0.794, 0.900)].

Table 5 Number of parameters (n), deviance and Akaike Information Criterion (AIC) of the 10 best models fitted for adult males and adult females. Bold lettering indicates the selected models

Class	Survival (Φ)	Detection probability (p)	n	Deviance	AIC [#]	Δ AIC [#]
Adult male	<i>i</i>	<i>ss</i>	3	264.606	270.606	0.000
	<i>ss</i>	<i>ss</i>	4	264.169	272.169	1.563
	<i>ss</i>	<i>yr</i>	9	260.083	278.083	7.477
	<i>i</i>	<i>i</i>	2	274.481	278.481	7.875
	<i>i</i>	<i>yr</i>	8	262.527	278.527	7.921
	<i>ss</i>	<i>i</i>	3	272.576	278.576	7.970
	<i>i</i>	<i>t</i>	14	250.681	278.681	8.075
	<i>yr</i>	<i>ss</i>	9	261.260	279.260	8.654
	<i>ss</i>	<i>t</i>	15	249.884	279.884	9.278
	<i>t</i>	<i>ss</i>	15	253.282	283.282	12.676
Adult female	<i>ss</i>	<i>g</i> * <i>ss</i>	11	648.367	673.548	0.000
	<i>g</i> + <i>ss</i>	<i>g</i> * <i>ss</i>	14	642.693	675.943	2.395
	<i>ss</i>	<i>g</i> + <i>ss</i>	8	660.097	677.771	4.223
	<i>ss</i>	<i>t</i> + <i>g</i>	19	633.038	681.171	7.623
	<i>g</i> * <i>ss</i>	<i>g</i> * <i>ss</i>	17	640.431	682.379	8.831
	<i>g</i> + <i>ss</i>	<i>g</i> + <i>ss</i>	12	654.755	682.560	9.012
	<i>g</i>	<i>g</i> * <i>ss</i>	13	652.606	683.100	9.552
	<i>yr</i>	<i>g</i> * <i>ss</i>	16	644.315	683.290	9.742
	<i>g</i> * <i>ss</i>	<i>g</i> + <i>ss</i>	14	650.068	683.318	9.770
	<i>i</i>	<i>t</i> + <i>g</i>	18	638.379	683.379	9.831

Model notations: survival (Φ), detection probability (p), constant (i), group (g), time (t), season (ss), and year (yr)

[#] Models for adult females classified by the Akaike Information Criterion corrected for over-dispersion and small sample size (QAIC_c)

Foals and yearlings

Foal survival was estimated at 0.510 [\pm 0.052 SE; 95 % CI (0.407, 0.613)] during the first 6 months, and at 0.864 [\pm 0.061 SE; 95 % CI (0.743, 0.985)] between 6 and 12 months-old. First year survival was therefore 0.441 [\pm 0.021 SE; 95 % CI (0.400, 0.481)]. For yearlings, survival was estimated at 0.684 [\pm 0.064 SE; 95 % CI (0.557, 0.811)] between 12 and 18 months-old, and at 0.818 [\pm 0.072 SE; 95 % CI (0.676, 0.960)] between 18 and 24 months-old. Yearling survival was therefore 0.560 [\pm 0.025 SE; 95 % CI (0.510, 0.609)]. We did not find any evidence for time variation in either foal or yearling survival (results not shown).

Demographic analysis and population trends

The data from road counts showed a declining population trend during the study (Fig. 1, $\hat{\lambda} = 0.92$ between 2005 and 2010), although the decline was not significant [\pm 0.23 SE; 95 % CI (0.825, 1.014)]. The population growth rate obtained from the demographic model was similar ($\lambda = 0.94$). The mean generation time (\bar{T}) was estimated at 12.58 years.

The LTRE analysis between the Serengeti and Hwange zebra populations showed that yearling survival contributed the most to the decline of the population in Hwange (Fig. 2). The results indicate that survival contributed more

than net fecundity, and survival of yearlings (51 %) and subadults (2–3 years of age: 32 %) contributed much more than adult survival (12 %). Removing the confounding effect of senescence (because senescence occurred in Serengeti but could not be estimated in Hwange), did not change the pattern markedly, with the highest contribution for yearlings (45 %), followed by subadults (28 %) and adults (23 %). The generation time of zebras was much longer in the Hwange population (13 years) than in the Serengeti population (8 and 9 years, with and without including senescence in survival, respectively) because survival in the non-reproductive young age classes was so

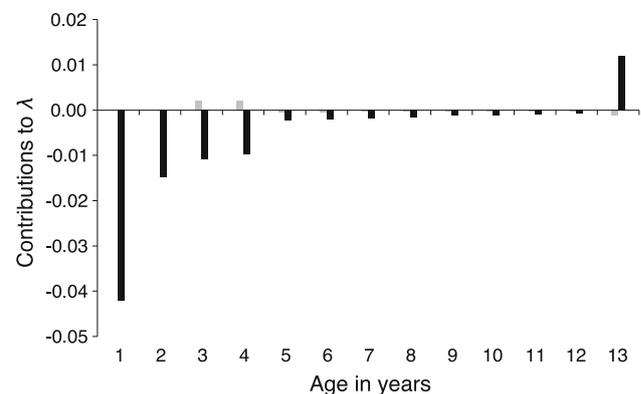


Fig. 2 Contributions of age-specific net fecundity (grey bars) and survival (black bars) rates to changes in λ between Hwange and Serengeti zebra populations

low in Hwange. The LTRE analysis between Hwange and Kruger also showed that survival contributed more than net fecundity, but adult survival (63 %) contributed more than yearling (15 %) and subadult (2–3 years of age: 13 %) survival (Fig. 3).

Discussion

CMR models and survival estimates

Imperfect detection is inherent in studies of individuals in wild populations, so CMR models were used to estimate survival and detection probabilities in this zebra population. With 8 years of monitoring (7 dry and 8 wet seasons), individual life-histories were collected on a relatively long-term basis with high probabilities of recapture. Detection probabilities were generally high (average around 0.80), so individual re-sightings were quite successful, though variable, since the zebras had a higher detection probability during the wet season. This analysis also provides the first empirical demonstration of the necessity of accounting for the effects of social groups on detection probabilities to obtain unbiased survival rates in African ungulates. When these effects were not included in CMR models, adult female survival did not appear to be affected by season or any other factor and was under-estimated (0.825 instead of 0.847). Though detection was imperfect, these conditions should allow reasonably accurate survival estimates to be obtained for this wild population. Few studies have estimated demographic parameters through CMR methods in African ungulates so far. Here we showed that these methods can be efficiently applied on plains zebras and could be developed for other African species.

The estimates of survival confirmed most of the predictions made in the Introduction. Firstly, as in other equid

populations (Berger 1983), the annual survival of adult males appeared slightly lower than in females (0.795 vs. 0.847). Male competition was strong, as in many equid populations: at least two of the known males were injured severely when losing their harems (P. Duncan, personal observation).

Secondly, we investigated the impact of predation risk on the survival rates of zebra by comparing them with the survival rates of large herbivores that were not limited by predation. Hwange zebras had lower survival rates compared to the other large herbivore populations (see Table 6). The foals of these zebras had a much lower survival (0.441) than in wild and feral horse populations [0.83 in Kamainawa horses (Cameron et al. 2001), 0.81 in Przewalski horses (Tatin et al. 2009), and 0.62–0.95 in Camargue horses (Grange et al. 2009); Table 6]. Most of these estimates are biased as detection was imperfect and CMR models were not used, but this difference in methodology cannot explain such great disparities. In the case of the Camargue horses, individuals were monitored daily in the breeding season, so detection was perfect.

CMR models for the Hwange population provided a yearling survival of 0.560, whereas other CMR studies on large herbivores indicated a minimum of 80 % for annual survival in yearlings (Festa-Bianchet et al. 2003; Toïgo et al. 2007; Table 6). The annual survival of 80 and 85 % found in adult male and female zebra in Hwange was also low for an adult survival of an ungulate of this size. Many studies on temperate ungulates have reported prime-age survival over 90 % (Gaillard et al. 1993; Loison et al. 1999; Coulson et al. 2001; Festa-Bianchet et al. 2003; Toïgo et al. 2007; Table 6). Since only two individuals can be classified as ‘old adults’ during this study (see Barnier et al. 2012 for the identification of senescent individuals), senescence is unlikely to be the cause of the low adult survival observed in this zebra population.

None of these other populations were affected by sustained predation by large carnivores. In a CMR study on bighorn sheep populations experiencing declines due to predation, Festa-Bianchet et al. (2006) showed that prime-age survival varied from 0.720 to 0.914 in males and 0.792 to 0.899 in females. Consequently, the survival rates of adult zebras in Hwange are in the range expected for ungulate populations under predation.

Thirdly, in African ecosystems the dry season is a critical period for ungulates, especially in Hwange where it spans more than 6 months. The survival of adult males tended to be lower in the dry season. However, the survival of adult females was markedly lower during the dry season (0.864 vs. 0.981 in wet season). In this population, many females were lactating in the dry season, inducing high costs for reproductive mares during the late dry season, a period when food and water are rare. Moreover,

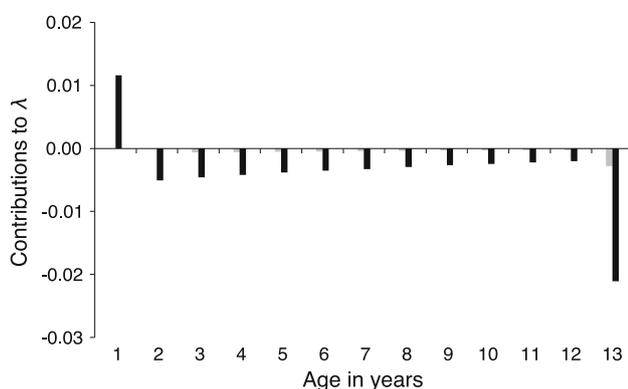


Fig. 3 Contributions of age-specific net fecundity (grey bars) and survival (black bars) rates to changes in λ between Hwange and Kruger zebra populations

Table 6 Survival and fecundity rates of plains zebra and other ungulate populations

Population	Predation	1st year survival	Yearling survival	Adult survival	Fecundity	References
Plains zebra (Hwange)	Yes	0.441	0.624	♂: 0.795 ♀: 0.847	0.74	Barnier et al. (2012); this study
Plains zebra (Serengeti)	Yes	0.389	0.847	0.954 ^a 0.875 ^b 0.768 ^c	0.686 ^a 0.883 ^d	Grange et al. (2004)
Plains zebra (Kruger)	Yes	0.454	0.476	0.909	0.79	Smuts (1976); Owen-Smith and Mason (2005)
Plains zebra (OlPejeta)	Yes	0.13				Rubenstein (2010)
Bighorn sheep	Yes			♂: 0.720–0.914 ^d ♀: 0.792–0.899 ^d		Festa-Bianchet et al. (2006)
Kamainawa horse	No	0.83				Cameron et al. (2001)
Przewalski horse	No	0.81				Tatin et al. (2009)
Camargue horse	No	0.62–0.95				Grange et al. (2009)
Other ungulates	No		≥0.8	≥0.9 ^b		Gaillard et al. (1993); Loison et al. (1999); Coulson et al. (2001); Festa-Bianchet et al. (2003); Toïgo et al. (2007)

^a Sub-adults (3–5 years-old)

^b Prime-age adults (5–12 years-old)

^c Senescent adults (≥13 years-old)

^d Adults (≥5 years-old)

reproductive mares need to drink more often than other animals, spending more time at the waterholes where the risk of predation is high, especially in the late dry season (Valeix et al. 2009a). It remains difficult to identify the causes of reduced survival in ungulate populations coexisting with predators. It can either result from direct predation or an increase in vulnerability to mortality caused for instance by an increased predation risk, disease, or a reduced access to resources.

Demographic consequences of the patterns of survival

The demographic model predicted a decline in the study population ($\lambda = 0.94$), which matched the decline observed in zebra densities in the Main Camp area between 2005 and 2010 ($\hat{\lambda} = 0.92$). We used two stable zebra populations with similar demographic parameters (Serengeti and Kruger populations) to identify those which caused a decline in the Hwange population. LTRE analyses showed that survival made the largest contribution to the decline and was therefore the limiting factor. Yearling survival accounted for the largest decrease of growth rate compared to the stationary zebra population in Serengeti. The comparison with Kruger indicated that adult survival was the main source of the decline in population growth in

the Hwange population, followed by yearling survival. The average reproductive rate (0.74 foals/year) was similar to other zebra populations (Smuts 1976; Grange et al. 2004) and foal survival (0.441) was close to that reported in Serengeti and Kruger [0.39 (Grange et al. 2004) and 0.454 (Owen-Smith and Mason 2005) respectively].

Our findings allowed identifying the relative importance of various demographic parameters in the population dynamics of zebras at Hwange. Firstly, although we could not analyze variations in fecundity among age-classes, and especially the effect of senescence on reproduction, the LTRE analyses showed that the reproductive rate was unlikely to be a limiting factor in this population. Secondly, adult female survival (0.847) in Hwange was quite similar to prime-age survival in Serengeti mares (0.875 Grange et al. 2004). Thirdly, the low survival of the (non-reproductive) yearling age class was a major cause of the low population growth rate compared to the stationary population in Serengeti, and led to a long mean generation time of the Hwange population, which indicates a much lower renewal rate of individuals over years.

In this declining zebra population, the low survival rates of young age classes were not compensated by high reproductive rates, which led the life cycle to slow down, and consequently, the population to decline. Such a

demographic pattern, involving low survival (especially in pre-reproductive age-classes) not compensated by an increase in reproductive output, induces a negative population growth rate associated with a slower life cycle, and seems to be a characteristic feature of populations of large herbivores facing high predation. Generation time is longer in declining roe deer populations (Nilsen et al. 2009); low survival rates in females have also been reported in woodland caribou *Rangifer tarandus* (Wittmer et al. 2005) and bighorn sheep *Ovis canadensis* (Festa-Bianchet et al. 2006) facing cougar *Puma concolor* predation, leading to longer generation times in these declining populations. However, this demographic pattern did not occur in a heavily hunted population of wild boar *Sus scrofa* for which the life cycle was accelerated thanks to earlier reproduction (Servanty et al. 2011). With first reproduction around 3 years of age, a gestation length of one year (Smuts 1976) and only one foal per reproductive event, plains zebras cannot compensate for such low survival in young females, and their populations will decline. In terms of wildlife management, the abundance and diversity of ungulate species contribute to sustaining predator populations, but larger species with lower population growth potentials, like zebras, are more vulnerable to low survival rates (Ogutu and Owen-Smith 2003).

Ecological processes involved

The density of zebras in the study area tended to increase before 2005, and then decreased sharply (Fig. 1). The main ecological processes that have been shown to limit African ungulate populations are bottom-up, i.e., resource limitation, and top-down, e.g., limitation by predation (Grange and Duncan 2006; Hopcraft et al. 2012). We consider that a limitation by food resources after the population peak in 2005 is most unlikely since body condition of adult zebras was good to excellent at all times, in spite of the long dry season: we used a scale based on 5 easily identifiable visual condition classes (Wright et al. 1998), and during the study, stallions scored on average 4.55 (± 0.07 SE, $n = 446$; maximum score = 5) and mares 4.45 (± 0.07 SE, $n = 879$). During the dry season, condition scores remained at high levels (4.53 ± 0.08 SE and 4.39 ± 0.11 SE, for adult males and females respectively). Consequently, any reduction of resources in the dry season had no visible effect on body condition. Further, the long-term population trends of zebra in Hwange were not affected by dry season rainfall (Valeix et al. 2008). We therefore consider that bottom-up processes are weak or absent here.

The predation pressure on plains zebra is higher in Hwange than in other African savanna systems (as measured by the ratio of predator biomass to zebra biomass, see “Introduction”), and a recent study on lions in Hwange

shows that the risk of predation is particularly high in our study area, as the density of lions is high compared to the rest of the Park (Valeix et al. 2009b). A long-term study on spotted hyenas also showed that the Main Camp area has one of the highest densities of this large predator in Hwange (Drouet-Hoguet 2007). The zebra is an important prey of lions in Hwange: it is one of the top five species eaten (Davidson et al. 2013). Consequently, predation on these zebras is potentially high.

There are two lines of evidence that predation is a key process driving the population: first, the mortality rate of adult female zebras in the wet season is 2 % per 6 months, and then it increases to 14 % per 6 months in the dry season; which is much higher than in predator-free populations of large ungulates. Mortality rates also tended to be higher in the dry season in males (see “Results” and models in Table 5). The risk of predation is much higher in the dry season because the zebras, which are water-dependent, can find water only in some 20 waterholes in the Park, so the distribution of the zebras is spatially predictable for the predators. Most lion kills are located within 2 km of a waterhole (Valeix et al. 2009a, 2012), which is coherent with the >5 fold increase in mortality in the dry season.

Secondly, the abundance of the main predator, the lion, was manipulated by management during the study, allowing the hypothesis that the zebra population is limited by predation to be tested. Trophy hunting of lions was suspended in the hunting areas surrounding Hwange National Park in 2005–2010, and the numbers of lions in the study area increased sharply after 2005 (as indicated by the number of male lions, Fig. 1; Loveridge et al. 2010). Before 2005 zebra numbers tended to increase; as expected they decreased after 2005. The hypothesis that predation is a key process in the population dynamics of plains zebra at Hwange is therefore supported by the response of the zebra population to temporal changes in the abundance of lions. A similar phenomenon was observed in the Central District of Kruger National Park where lions and hyenas were culled: after the culling operation, there was a strong increase in zebra foal survival (Reardon 2012). Further, in Ol Pejeta Conservancy, the plains zebra population strongly declined due to the impact of lion predation (0.31 lions/km²), and foal survival was particularly low (0.13; Rubenstein 2010). In Hwange, first year survival (0.441) was quite similar to estimates in two stationary populations [0.389 in the Serengeti (Grange et al. 2004) and 0.454 in Kruger (Owen-Smith and Mason 2005)]. These results indicate that predation pressure on foals is likely to be important, but not sufficient to explain the observed decline of the Hwange population. Despite there being no CMR estimates for yearling survival in other zebra populations,

predation may play a particularly important role in yearling mortality there, too. During dispersal young zebras are likely to be more exposed to predation since they are not well integrated in a particular social group. An interaction between predation and dispersal could therefore explain the low survival of yearlings, especially around Main Camp in Hwange where the predation pressure is high.

This study provides detailed information that reinforces the hypothesis that zebra populations are generally limited by predation in near-natural savanna systems. In Hwange, the concentration of animals around permanent water during the dry season resulted in an increased predation pressure that can negatively impact the population dynamics of prey species, especially lions' preferred ones. Management of artificial water holes can therefore considerably influence the dynamics of wildlife populations, with potentially important effects on the functioning of mammalian communities.

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