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Original article

Inter-birth interval in zebras is longer following the birth of male foals than after female foals

 Florian Barnier^{a,*}, Sophie Grange^a, Andre Ganswindt^{b,c}, Hlengisizwe Ncube^d, Patrick Duncan^a
^a CNRS Centre d'Etudes Biologiques de Chizé, 79360 Beauvoir-sur-Niort, France^b Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa^c Department of Production Animal Studies, Faculty of Veterinary Science, University of Pretoria, Private Bag X04, Onderstepoort 0110, South Africa^d Department of Forest Resources and Wildlife Management, National University of Science and Technology, P. O. Box AC 939 Ascot, Bulawayo, Zimbabwe

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ABSTRACT

Mammalian reproductive rates vary among individuals for physiological and environmental reasons. This study aims to determine reproductive rates from an individually monitored population of wild Plains zebras *Equus quagga*, and to assess the sources of variability in inter-birth intervals. The animals were monitored, where possible, every six months from 2004 to 2011. Thirty nine intervals corresponding to 65 births in 26 mares were identified, using direct observations and faecal steroid monitoring. Mean foaling rate of the population is 0.74 foal/year, and comparable with the literature. There was no significant effect of mother's age, nor of the season of previous birth on the length of inter-birth intervals. Inter-birth interval was significantly longer when the first foal was a male. This finding indicates that additional costs of having a son may delay future reproduction and thus reduce the total number of offspring a mare can have during her lifetime. Individually-based data provide critical information on the determinants of reproductive rates, and are therefore a key to understanding the causes of variations in life-history traits.

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1. Introduction

The dynamics of animal populations are affected by variations in rates of survival, reproduction and dispersion (Caughley, 1977). Processes acting on these rates operate at the individual level: understanding how these processes affect the life histories of individuals is therefore essential in order to understand the dynamics at the population level.

Reproduction is a process requiring large amounts of resources: since their availability varies in time and space, animals are generally limited by the amounts they can allocate to any one process. When investing in offspring, females make a trade-off between the growth of the offspring and their own growth and/or body reserves, and thus their chances of survival and of reproducing successfully in the future (Stearns, 1992). For example, in ungulates, the increased foraging demands caused by the high energy costs of lactation can jeopardize the females' own survival (White and Berger, 2001). Spreading reproductive events over longer time intervals can provide a period of recovery after

reproduction during which females can finish their growth and/or accumulate body reserves and thus invest in their survival and prepare future reproductive output (Proaktor et al., 2008). Variations in the length of the interval between consecutive births can therefore provide valuable information about the costs of reproduction, and about the determinants of the levels of reproductive investment made by individual females.

Few studies have looked at the interacting factors influencing the interval between birth and conception of individual animals in the wild, essentially because of the lack of continuous observation of known individuals (but see Bercovitch and Berry, 2010). This study is part of a long-term programme aimed at understanding the dynamics of the savannah ecosystem in the Hwange region of Zimbabwe, and the processes limiting populations of herbivores are central in the programme. We have measured reproduction and survival in Plains zebras (*Equus quagga*) using a long-term, individually-based approach.

Reproductive rates in Plains zebra populations have been determined in only two previous studies, and in both cases by examining shot animals: in the Kruger National Park the pregnancy rate was 79% (Smuts, 1976) and in the Serengeti 88% (Grange et al., 2004). In this paper we describe a non-invasive approach for measuring reproductive rates in a population of wild Plains zebras,

* Corresponding author. Tel.: +33 0 49 09 96 02; fax: +33 0 5 49 09 65 26.
E-mail address: florian.br@gmail.com (F. Barnier).

by calculating the mean foaling rate of the population, and subsequently testing for sources of variation in the inter-birth intervals of individually observed females. Previous studies on free-ranging horses and captive Plains zebras showed that reproduction in mares, including birth sex-ratios, can be affected by factors such as maternal age, which can have a powerful influence on investment in reproduction by mares (Pluhacek et al., 2006).

Plains zebras are common herbivores of African savannahs, distributed from East to Southern Africa (Moehlman, 2002). They foal throughout the year and their gestation length is just over a year (with a mean gestation length of 371.2 days, Wackernagel, 1965). The minimum interval between foaling and conception is 8–10 days (King, 1965) and the shortest intervals between consecutive births so far observed were 378 and 385 days (Klingel, 1969); Wackernagel (1965) estimated the mean interval to be 13.9 months (417 days). Variability in the inter-foal interval therefore exists, but there is no information on the determinants of this variability in wild Plains zebras.

Zebra females can foal at three years of age, but they may grow until six years of age (Smuts, 1975), so we hypothesise that the trade-off between growth and reproduction would lead to longer inter-foal intervals in young females. Further, older females can be expected to have different intervals compared to prime-aged animals: the intervals could be lengthened through the process of senescence. This was true in the Serengeti, as senescent females had lower reproductive rates than prime-aged females (Grange et al., 2004).

The environment of Hwange is highly seasonal, with average annual rainfall of 606 mm, of which only 10 mm fall during an average dry season which lasts 6 months (May–October, Valeix et al., 2007). Dry season births are likely to be more costly due to the poor availability of adequate resources, thus females giving birth during this season may need more time before conceiving again. In the Kruger National Park, which has a similar environment to that of Hwange, Plains zebras have a clear birth peak in the wet season (Smuts, 1976): a longer inter-foal interval after a dry season birth could be a mechanism leading to more frequent foaling in the wet season, we therefore expected to find longer intervals after foals born in the dry season in our population. Finally, intervals should be longer after giving birth to a male foal, as males are generally more costly to raise in mammals (Bercovitch et al., 2000; Fernández-Llario et al., 1999; Rutkowska et al., 2011) including horses (Duncan et al., 1984; Cameron and Linklater, 2000).

In this paper, we report the duration of intervals between births in a population of Plains zebra, calculate the foaling rate, and attempt to disentangle the factors determining the length of the inter-foal intervals. We hypothesize that:

- (1) The age of a female should influence the inter-foal interval, with younger and senescent females having longer intervals between successive births
- (2) Females giving birth during the dry season should have a longer interval to the next birth
- (3) The interval to the next birth should be longer after giving birth to a male foal

2. Materials and methods

2.1. Study area

The study was based in Hwange National Park, which covers approximately 15,000 km² of semi-arid savannah in western Zimbabwe (19°00'S, 26°30'E). Long-term (1928–2005) mean annual rainfall is 606 mm (Valeix et al., 2007) with a dry

(May–October) and a wet (November–April) season. The vegetation is dominated by deciduous woodlands and shrublands, with patches of grasslands (Rogers, 1993). The presence of 30 artificial waterholes in the northern part of the Park in most years maintains drinking water, and a relatively high density of large mammals, particularly during the dry season. The study population of Plains zebra moved freely since there are no fences, within the Main Camp area (approximately 1000 km²) in the northern part of the Park.

2.2. Field observations

Observations started in July 2004 and fieldwork sessions were conducted twice a year (around July–August during the dry season and around January–February during the wet season) up to March 2011. Zebras were identified individually from their unique stripe patterns. Re-sightings of animals was opportunistic, with a focus on waterholes and a plain where zebras often concentrate during the wet season. A database was built up which includes individual photos (both sides of each zebra) for recognition and the sightings of every animal.

Ninety females were identified and monitored to determine their pregnancy status using steroid concentrations in the faeces where possible (Ncube et al., 2011) and to have accurate estimates of their foaling dates. As re-sightings of individuals were opportunistic, not all foals were sighted immediately after birth: we estimated the age of the foal when first sighted using the criteria of Smuts (1974) and Penzhorn (1982). The foaling date was taken as the mid-point between the earliest and latest possible dates of birth with regard to these criteria. Neonatal mortality could be determined, but only for females which were followed closely: heavily pregnant females close to foaling have swollen udders, and if a foal is lost the udder involutes within about 5 days (Smuts, 1976). One pregnant female whose abdominal profile was no longer large and whose udders had been swollen and then returned to normal 5 days after, was noted as having foaled and lost her foal, as none was observed with her. Foaling date was taken as the mid-point between last sighting with swollen udders and the next sighting. Suckling and maternal behaviour were used to determine maternity, and the sex of the foal was determined as soon as possible after the first sighting. Mares of known age were classified into three age classes (Young: 3–5, Prime: 6+ years) and a few obviously old females were classified as Senescent: old horses, like other large mammals show a number of features summarised in http://www.vetstream.com/dalehead/html/pdf/Factsheets/Horse/24_269864.pdf. With personal experience of horses, one of us (P. Duncan) classed as Senescent animals which had “Sagging topline resulting in a 'sway' or dipped back with prominent withers”.

2.3. Faecal sample collection, extraction and hormone assays

In order to determine the pregnancy status between two observed births we collected dung samples from individuals (Ncube et al., 2011): 149 samples from 52 mares were collected from mares which were observed defecating, between January 2007 and March 2009 and analysed for 20-oxopregnane and oestrogen concentrations. We collected a sub-sample representative of the dung pile, and dried it within 48 h, either air-drying or in a low heat (40 °C) field oven. The samples were packed in plastic bags and stored dry at room temperature until assayed.

Dried faecal matter was pulverized and sifted using a mesh strainer to remove fibrous material (Fieß et al., 1999). Approximately 0.1 g of each powdered faecal sample was extracted by vortexing for 15 min with 80% ethanol in water (3 ml) according to the procedure described by Ncube et al. (2011). The resulting extracts were measured for unconjugated oestrogens and 20-

oxopregnanones using enzyme immunoassays for oestrogens (E_t ; Palme and Möstl, 1994) and 5β -pregnane- 3α -ol-20-one (5β -20-one; Schwarzenberger et al., 1996), which have been previously used to reliably diagnose pregnancy in Plains zebra (Ncube et al., 2011). Assay procedures followed standard protocols (e.g. described by Ganswindt et al., 2002). Sensitivities (90% binding) of the assays were 1.0 pg/well for E_t and 0.3 pg/well for 5β -20-one, respectively. Intra- and interassay coefficients of variation ranged between 3.1% and 9.3% for E_t , and 6.4% and 16.7% for the 5β -20-one measurements.

2.4. Pregnancy determination

For females of unknown pregnancy status between two consecutive births, faecal steroid hormone concentrations were used to determine the possibility of a pregnancy. The criteria from Ncube et al. (2011) were used to ascertain the pregnancy status of the mare in between the two births: high levels (> 200 ng/g DW) of faecal 20-oxopregnanones associated with high (> 160 ng/g DW) faecal oestrogen levels indicate mid-pregnancy; high faecal 20-oxopregnanones and low (< 160 ng/g DW) faecal oestrogen levels indicate late pregnancy. At least two samples were used to ascertain the pregnancy status. Females which were determined to have had another pregnancy in the interval between the two observed births were removed from the dataset. Intervals between observed births which were longer than two mean gestation periods (740 days), and for which we did not have information on the pregnancy status of the mare were also excluded from the dataset. In total 65 births and 39 foaling intervals in 26 mares could be identified.

2.5. Statistical analyses

The intervals were not normally distributed (Shapiro–Wilk's test, $p < 0.01$), and were close to a Gamma distribution. We used a Generalized Linear Mixed Model (GLMM) using function `glmmPQL` of package MASS in R-software version 2.12.2 (R Development Core Team, 2011) specifying that the response variable follows a Gamma distribution. We treated age of the female (Young, Prime or Senescent), season of initial foaling (Dry or Wet), and sex of the initial foal (Male or Female) as fixed factors. The identity of the female was treated as a random factor. Effects were considered significant when $p < 0.05$. Only 38 intervals were used in the analysis, as the sex of one foal was unknown.

3. Results

Births occurred in both wet and dry seasons. The mean interval between two births was 480 days (SE = ± 116 days, range = 375–821 days). The average foaling rate of the population was therefore 0.74 foal/year (the foaling rate was calculated as 365/mean foaling interval). The sex-ratio at birth (21 males, 35 females) was not significantly biased ($\chi^2 = 3.5$, $df = 1$, $p = 0.06$), but mares tended to produce more females than males during our study period.

Interval lengths from young mares were not longer than intervals from prime age mares (Table 1, $p = 0.77$). There was no significant difference in the length of the intervals between senescent and prime mares (Table 1, $p = 0.11$).

The effect of season on interval length ($p = 0.47$) was not statistically significant, but intervals tended to be longer when the initial birth occurred during the dry season (Table 1). There was an effect of the sex of the foal ($p = 0.04$) on the length of the interval: intervals were longer when the initial foal was a male (Table 1, Fig. 1).

Table 1

Factors influencing the length of the interval between two consecutive births in female Plains zebras. Individual identity was included as a random factor. Age (Young, Prime, Senescent), Season of birth (Dry, Wet) and Foal sex (Male, Female) were considered as categorical (classes used as references are italicised).

Model	N	Factors	P-value	Coefficient \pm SE
Effect of age, season and foal sex	38	Age		
		Young	0.770	-15.19 ± 51.36
		Senescent	0.111	-69.33 ± 41.78
		Season		
		Wet	0.470	-31.19 ± 41.51
		Foal sex		
		Male	0.040	88.10 ± 37.49

4. Discussion

The mean foaling rate of the Hwange zebras was 0.74 foals/year (95% c.i. calculated by bootstrap, $n = 1000$ repetitions, are 0.68–0.79). This reproductive rate is close to the best data in the literature, on the Kruger population (0.79, Smuts, 1976). The Serengeti population may have a higher foaling rate (0.88, Grange et al., 2004), but this may be due to a biased sample, since unlike in the Kruger study there was no specific procedure to ensure that animals were chosen at random (see Grange et al., 2004). The use of individually-based data therefore produces results which are consistent with previous studies; it can however be noted that due to the method used, some very long inter-birth intervals can be missed and lead to an over-estimation of the foaling rate.

We present here for the first time data on the patterns of variability in the interval between consecutive births in a wild population of Plains zebra, and one of the first in a wild ungulate (see Bercovitch and Berry, 2010). Inter-birth intervals depend mainly on the delay between foaling and subsequent conception, since gestation length varies only within narrow limits (Clements et al., 2011). Variation in the length of the inter-birth intervals was high (CV = 23%), and few females had the capacity to sustain successive pregnancies without a break (median interval length = 462 days). This is surprising as female horses in good condition commonly become pregnant in the post-partum oestrus, and so have an inter-foal interval of about 340 days (see Duncan, 1992), and the studied

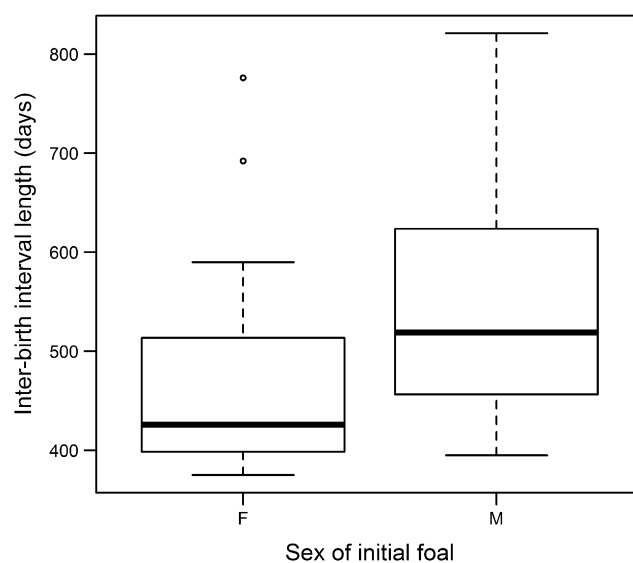


Fig. 1. Length (in days) of the inter-birth interval as a function of the sex of the initial foal in the monitored Plains zebra population of Hwange National Park, Zimbabwe, between 2004 and 2011. F: Female, M: Male.

zebra mares were almost all in good or very good condition (scores 7–8 out of 9 on the scale of Henneke et al., 1983).

There was no significant difference between intervals beginning in the dry season with those beginning in the wet season. This may be due to the small number of births during the dry season (only 17 out of 65). However, only few females supported the cost of foaling during the dry season twice in a row (four females showed dry–dry series, out of twelve dry season births, i.e. 33%), so females may postpone reproduction to give birth to their next foal during the wet season. Some studies on horses have shown that resource limitation reduced the foaling rate in horses, though only in young ones (Duncan, 1992), however more data are needed to demonstrate a seasonal effect in zebras.

Contrary to our predictions, there was no difference in the average intervals of younger and senescent females compared to prime mares. This may be due to the small numbers of young (5) and senescent (5) individuals. In captive Plains zebras, age (and/or dominance) leads to shorter intervals (Pluhacek et al., 2006). If this result is general, then there was no trade-off between growth or body condition and reproduction, so even young and senescent females had abundant resources in these zebras in Hwange and in the captive population.

When females had male foals, the time between foaling and conception was lengthened on average by 88 days (Table 1, Fig. 1). The mares took time to recover after having a male foal, implying that males are more costly to produce. There were no differences in survival of male and female foals (Sophie Grange, unpublished results), so this cannot explain the longer time needed by mares to conceive after giving birth to a male. It has been shown in another monomorphic Perissodactyl, the Black Rhino (*Diceros bicornis*), that the proportion of male calves surviving to their first sighting was positively associated with rainfall prior to and during the time of conception, so to food abundance and, presumably, the body condition of the mothers (Hrabar and du Toit, 2005). Male Black rhinos may therefore be more costly to produce than female, though this result could also be explained by lower intra-uterine and neonatal survival in male calves (see also Monard et al., 1997). As there is no sexual size dimorphism in Plains zebras at birth (Smuts, 1975), this greater energy demand by males cannot be explained by higher requirements of male foetuses during the gestation period, and the extra cost of male foals in zebras can come only after birth.

It has been shown in horses (Duncan et al., 1984), that male foals spend 40% more time suckling than females during the first eight weeks of their lives and, if males do obtain more milk, then they are more costly to produce; it has also been demonstrated that mares in good condition in two horse populations, raised more males (Cameron et al., 1999; Cameron and Linklater, 2000, 2007; Monard et al., 1997). Zebras live in harems, and adult males are subjected to intense competition for females, probably leading to a greater variance in reproductive success for males than for females. Investing more in males in early stages of development, at a cost, could result in better quality of the offspring which could persist into adulthood. Those males could thus be advantaged and have greater reproductive success than their competitors. This would corroborate the hypothesis of Trivers and Willard (1973), that females should bias investment towards the sex that can return greater fitness from additional investment.

There was no significant bias in the sex-ratio of the foals in this study, but a tendency for mares to produce more females. The same tendency was found in the whole monitored population, but still non-significant (58 females, 44 males in identified foals during 7 years of monitoring, $\chi^2 = 1.9$, $df = 1$, $p = 0.17$). The cost of having a male may therefore bias the sex-ratio at birth, and if females can

control the sex of their offspring (see Clutton-Brock and Iason, 1986), mares would be producing more of the less costly females.

In conclusion, large differences exist in inter-birth intervals of zebra mares in the Hwange system, with some females conceiving immediately after giving birth and others waiting over a year before conceiving. This is comparable to findings of Klingel (1969), who observed 120 mares during three years and found that 15% of the females had three foals, 33% had two, and 42% had just one offspring. The cost of producing a son delayed future reproduction, which would reduce the total number of offspring a mare can have during its lifetime. This result supports the conclusion of Cameron and Linklater (2000) that male foals are more costly than females to equid mothers. However, the mechanism is not yet known, and may involve the provision of more milk, or behavioural costs (e.g. more vigilance after producing a male foal). More work is needed to disentangle the other factors determining inter-individual differences in zebra reproductive rates. In this regard, long-term individually-based data can provide the fine-grained data needed to deepen our understanding of how these factors interact to determine foaling rates.

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