

Further evidence for male infanticide and feticide in captive plains zebra, *Equus burchelli*

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A b s t r a c t. The captive plains zebra are characterised by a high incidence of male infanticide and feticide. One of the most common reasons why infanticide and feticide occur is the introduction of a new male into a herd. In the present study, we used twice as much data, including nine plains zebra herds from four Czech zoos, compared to our previous study on this topic. As a result, both of the statistical models that we tested were significant. The probability of the death of a foal was greatest when a new male was introduced into the herd just after conception. The probability of a foal to die in the presence of the new male was nearly 100% during the first two months of age and decreased as the foal aged. The foal's probability to die, depending on the timing of the introduction of a new male or the foal's age, was neither affected by the zoo nor the subspecies. In this paper, we also describe a fourth case of male feticide in plains zebra. Our results demonstrate the highest occurrence of infanticide and feticide among ungulates caused by males.

Key words: equid, infant mortality, zoo

Introduction

Male infanticide is the killing of dependent young by an adult male of the same species. Male feticide is defined as the abortion of a foetus due to harassment or forced copulation by an adult male of the same species. These phenomena have been described in relation to social organisation in a few species: the red deer *Cervus elaphus* (Bartoš & Madlafousek 1994), the common hippopotamus *Hippopotamus amphibius* (Lewison 1994), the Indian rhinoceros *Rhinoceros unicornis* (Dinerstein & Price 1991, Dinerstein et al. 1988), the Przewalskii horse *Equus przewalskii* (Boyd 1991, Kolter & Zimmermann 1988, Ryder & Massena 1988, Zharkikh 1999) and the feral horse *E. caballus* (Berger 1983, 1986, Duncan 1982, Monard et al. 1997).

Plains zebra *Equus burchelli* form harems that contain between one to six adult females and one adult male (Klingel 1969, Monfort & Monfort 1978, Smuts 1976a). The mares are exclusively mated by the harem male (Rubenstein 1986). Therefore, the paternity of the young within the harem is apparent. The male in each harem acts to defend all members of the harem, which includes the protection of the foals from predators (Klingel 1967, Smuts 1976a). Therefore, the male of a harem makes invests greatly in the foals. After taking over a harem, a new male can gain reproductive advantage by killing the dependent foals or by forcing the females to abort. This enables him to invest only into his own offspring within a relatively short period of his presence in a harem.

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We have previously published the first evidence of male infanticide in captive plains zebra (Pluháček & Bartoš 2000). The results dealing with the relationship between the death of a foal and its age did not reach level of significance due to the use of a small sample size. Therefore, in the present study we used a sample size that was twice as large to provide further evidence to support and extend our previously published results. In this study we tested the prediction that the younger the foal is, the more likely infanticide will occur. We also tested the prediction that the sooner a new male is introduced into the herd after conception, the higher the probability is for a foal to die.

Material and Methods

We collected data from zebras located in four zoological gardens in the Czech Republic: Dvůr Králové nad Labem, Liberec, Lešná – Zlín and Praha. Nine different herds of four different subspecies of plains zebra were used in the study: Grant's zebra – *E. b. boehmi*, Chapman's zebra – *E. b. chapmani*, Damara zebra – *E. b. antiquorum* and maneless zebra – *E. b. borenensis*. The herd sizes ranged between having two to eight mares, which ranged in age from 2–24 years old. The enclosures for the eight herds varied between 400 to 2200 m² in size. There was almost no vegetation present in any of the enclosures. However, food was available ad libitum and all of the mares were in good condition. It must be noted that the herd of Damara zebra in the Dvůr Králové zoo was kept from May until September in a 16 600 m² grass enclosure. The winter enclosure for this herd was only 350 m² in size, with no vegetation; however, food was available ad libitum for this herd. For each foal that was born, we collected the date of birth, the date of death (if it occurred), the identity of the dam and sire, the subspecies, the zoo and the date of introduction of an unrelated stallion (a new male) into its herd. Incomplete records were omitted from the analysis. Any foals that were injured by a new male and were in need of veterinary assistance and, consequently, separated from the herd, were regarded as dead in the analysis. The typical weaning age of 9 months was considered as the criterion for survival (Smith 1976b).

All analyses were based on binary data. The variation of this data was analysed with SAS (v. 9.1) using categorical data analyses (Stokes et al. 2000).

Results

In the present study, we collected data on 394 foals that were born in the investigated zoos from 1973 to 2000. The relationship between the age of a foal and its probability of dying is shown in Fig. 1 (logistic regression, whole model test: $\chi^2 = 11.15$; $P < 0.001$; $N = 108$; analyses of maximum likelihood: $\chi^2 = 9.67$; $P < 0.01$ and the model fitted well association of predicted probabilities and observed responses: concordant: 74.3%, discordant: 25.4%). The probability of foal to die was almost 100 % during the first two months of life, and then the probability declined sharply. We found that the sooner a new male arrived after the conception of the female with another male, the less likely that her offspring would survive (Fig. 2; logistic regression, whole model test: $\chi^2 = 101.74$; $P < 0.001$; $N = 105$; analyses of maximum likelihood: $\chi^2 = 10.73$; $P < 0.01$; association of predicted probabilities and observed responses: concordant: 99.7%, discordant: 0.3%). The foal's probability to die depending on the timing of the introduction of a new male or the foal's age was neither affected by zoo nor subspecies (multiple logistic regression; zoo: $\chi^2 = 2.62$; $df = 3$; NS and subspecies: $\chi^2 = 6.27$; $df = 3$; NS).

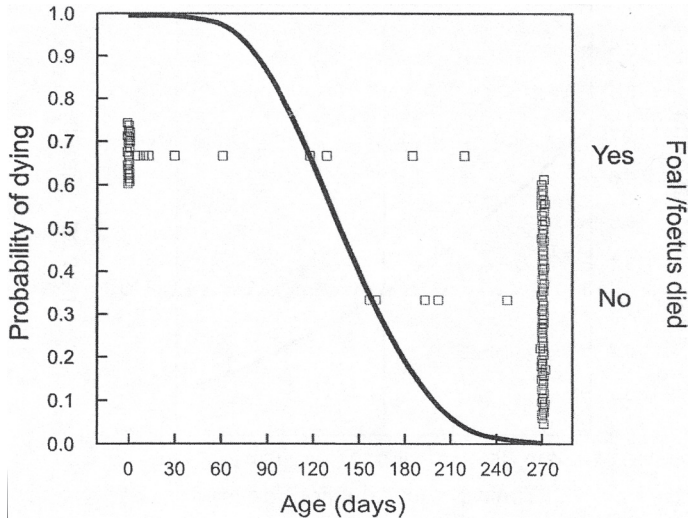


Fig. 1. The relationship between the age of the foal and the probability of dying.

In addition to our previous records (Pluháček & Bartoš 2000), we have recorded the fourth case of male feticide in the Chapman's zebra herd at the Liberec zoo. A pregnant mare was joined with a new male on March 23, 1988. She was seriously injured by the male, who was separated from the herd two days later. The mare aborted two months later. Further, in that same herd, we also recorded five cases of forced mating of two other pregnant females by a new male, though they did not abort. One of these females gave birth to a male foal. He was weak and died at the age of 30 days bearing signs of previous attacks (haematomas and an abscess).

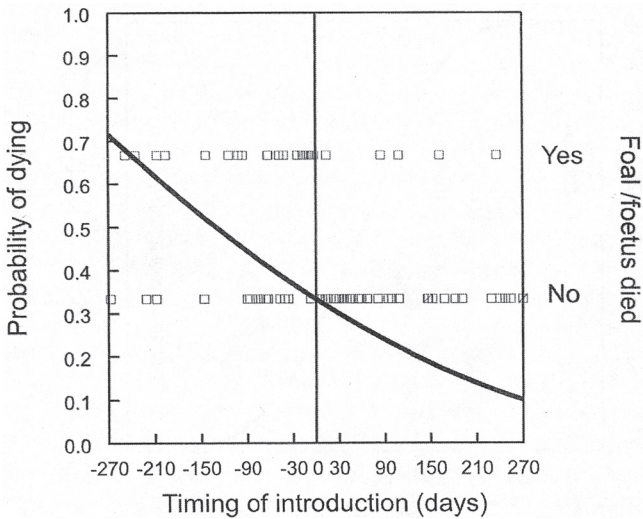


Fig. 2. Logistic regression curve superimposed on the data showing the relationship between the foal's probability of dying and the time of introduction of a new male into the herd (where the day of parturition and/or abortion is equal to 0).

Discussion

Using twice as much data in the present study compared to our previous study (Pluháček & Bartoš 2000), we have supported our previous results and achieved high levels of significance in all the analyses. With the completed data set on the relationship between age and the time of foal death, we could superimpose a logistic regression curve on the data. The curve revealed an extremely high probability of a foal to die during first two months of its life. In terms of the relationship between the foal's probability of death and the time the new male was introduced into the herd relative to the day of parturition and/or abortion, the completed data demonstrated a slightly lower probability to die in the early stages of gestation than in the previous study (Pluháček & Bartoš 2000). Despite this, the general trend remained similar.

With another observed case of male feticide, we have evidence of male feticide occurrence in all four of the studied zebra subspecies. According to the pattern of the logistic regression, which reflected the probability of the foetus to die, it seems likely that the proportion of feticide compared to infanticide may be in fact much higher than that which was recorded. Besides plains zebra (Pluháček & Bartoš 2000 and this study), male feticide has only previously been recorded for the feral horse (Berger 1983, 1986).

Male infanticide has been reported to occur in both captive and feral equid populations (Boyd 1991, Duncan 1982, Monard et al. 1997, Pluháček & Bartoš 2000, Ryder & Massena 1988, Zharikh 1999). To date, there has not been any record of infanticide in the wild plains zebra. Nevertheless, the mortality rate of wild plains zebra foals is twice as high compared to similar ruminants (wildebeest *Connochaetes taurinus* and buffalo *Syncerus caffer*). This led Grange et al. (2004) to conclude that male infanticide could be a major contributor to zebra foal mortality.

Records of male infanticide among ungulates are rare compared to rodents, primates, and carnivores (Agrell et al. 1998, Ebensperger 1998, van Schaik & Janson 2000). Nevertheless, these records are more common among odd-toed ungulates than among even-toed ungulates. Among the odd-toed ungulates, all but one infanticidal attack have occurred within the equid family (Dinerstein & Price 1991, Dinerstein et al. 1988, Duncan 1982, Kolter & Zimmermann 1988, Pluháček & Bartoš 2000, Ryder & Massena 1988). Therefore, equids seem to be the group of ungulates with the largest incidence of male infanticide.

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