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ARTICLES

Male infanticide in captive plains zebra, *Equus burchelli*

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On the assumption that infanticide exists in plains zebra, as reported for horses, *Equus caballus*, we tested the following hypothesis. Introducing a new zebra male into a herd of breeding females should increase foal mortality in comparison with herds in which the sire of the foals is still present. The younger the foal, the more likely infanticide should be. We collected data from five herds in two zoological gardens in the Czech Republic. We found nine records of infanticide in plains zebra and three cases of abortions that were probably induced by forced copulation. We analysed additional indirect data to investigate the possibility of introduced males causing other abortions. Abortions were three times more likely in herds with introduced males than with only fathers present. Postnatal mortality of the foals was four times greater with introduced males than with fathers. No indication of a sex preference was observed for infanticide by a new male for either abortions or postpartum deaths. When we combined all records involving introduced males, the probability of foal death was greatest when the new male joined the herd just after conception and decreased with increasing time between conception and date of the new male introduction (the chance of a foal surviving was less than 5% just after conception and more than 50% at the time of delivery). Mortality of foals did not depend on whether the new male was introduced before or after the foal was born. Survival increased to more than 60% after the foal reached 1 month of age. Our results suggest that captive plains zebra show the highest occurrence of infanticide reported among ungulates.

Male infanticide is defined as the killing of newborns or young juveniles by a conspecific adult male. This phenomenon has been reported in various species such as primates (Hrdy 1977; Agoramoorthy & Rudran 1995), carnivores (Packer & Pusey 1984; Breden & Hausfater 1990; Hessing & Aumiller 1994) and rodents (Huck et al. 1982; Elwood & Ostermeyer 1984; Labov et al. 1985; Dobson 1990; Coulon et al. 1995) with a few records for ungulates (Duncan 1982; Kolter & Zimmermann 1988; Ryder & Massena 1988; Boyd 1991; Bartoš & Madlafousek 1994; Monard et al. 1997; Lewison 1998). There are reports of stallions killing foals in zebras (plains zebra: Joubert 1972; mountain zebra, *Equus zebra*: Penzhorn 1984), but the circumstances of these incidents are not known. Horses (*E. caballus*, *E. przewalskii*) and plains and mountain zebras have a similar social organization (Klingel 1978; Rubenstein 1986). Because intentional male infanticide and feticide (killing the fetus) have been reported for horses (Duncan 1982; Berger 1983; Ryder & Massena 1988; Boyd 1991), we presumed that they also occur in plains zebras.

Plains zebras have a gestation period of 361–385 days (Wackernagel 1965; Klingel 1969). The first fertile oestrus occurs within 7–9 days postpartum (Wackernagel 1965; Klingel 1969; Smuts 1976) and conception rates have been reported to be 0.5–0.79 (Klingel 1969; Smuts 1976). Therefore, at least 50% of zebra mares conceive when still lactating. This means they are investing in two offspring at the same time. Presumably a new stallion benefits more from inducing abortions than killing suckling foals. The stallion can reproduce immediately and the mare saves energy for the next foal. Berger (1983) reported a possible case of forced copulation in a plains zebra mare leading to a termination of pregnancy at the National Zoological Park in Minnesota, although Kirkpatrick & Turner (1991)

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doubted that the copulation caused the abortion in this case, as their data differed from those of Berger (1983).

Postpartum infanticide, however, can also improve the male's chances of reproducing. Keiper (1979) suggested that lactating mares are more likely to abort than mares with no dependent offspring. As argued by Boyd (1991), the nutritional stress imposed by the demands of lactation may impair a mare's body condition and subsequent reproductive performance (Berger 1986). New Forest pony mares nursing foals, for example, had a body condition score twice as poor as that of barren mares (Pollock 1980, cited in Boyd 1991). Removal of the foals brought about an immediate improvement in body condition while mares who nursed their foals for 2 years were in poor condition for that period; although they bred in the second year, they failed to foal. Domestic mares in poor body condition during gestation and lactation have lower conception rates and higher embryonic mortality then mares in good condition (Henneke et al. 1984). Keiper (1985) found that a population of feral mares in which the duration of lactation was shortened by removal of the dependent foals had an average foaling rate of 74%, while for mares in a population where foals were not removed this was only 57%. Thus, killing foals before peak lactation occurs would improve the stallion's chances of the mare conceiving by him and carrying his foal to term (Boyd 1991). Kaseda et al. (1995) showed that mares that disperse more often have lower fecundity. This may be due, at least in part, to infanticide and/or feticide in free-ranging populations.

On the assumption that infanticide exists in zebra, as reported for horses, we tested the following hypothesis. Introducing a new male zebra into a herd of breeding females should increase foal mortality in comparison with herds in which the sire of the foals was still present. The younger the foal, the more likely infanticide should be.

METHODS

The data were collected from zoological gardens at Dvůr Králové nad Labem and Prague, Czech Republic. Five breeding herds of plains zebras of four subspecies were available: Damara's zebra, *E. b. antiquorum*, maneless zebra, *E. b. borensis*, Grant's zebra, *E. b. boehmi*, and Chapmann's zebra, *E. b. chapmanni*. Herd sizes ranged between three and eight breeding mares, which were 2–20 years old. The enclosures varied between 800 and 1400 m^2 in size. There was almost no vegetation in the enclosures but food was available ad libitum and all the mares were in good condition. For each foal we collected data on date of birth, date of death, mother and sire identity, and the date of introduction of an unrelated stallion (new male). Any foals injured by the new male that were in need of veterinary treatment and separated from the herd were regarded as dead in the analysis. The usual weaning time of 9 months of age (Smuts 1976) was taken as the criterion for survival.

Since the observations were proportions of dying foals derived from binary data, their variation was analysed with SAS after categorical data analyses (Stokes et al. 1997).

RESULTS

As expected, we found records of infanticide in captive plains zebra. We documented nine attacks resulting in heavy injuries or death of the foal (Table 1). We also recorded three cases of abortions that were probably induced by forced copulation (Table 2).

First we investigated the possibility of new males causing abortions. To cover all abortions in the evaluation, we considered all cases of foals found dead on the day they emerged (N=35, all being reported as abortions by the keepers) as 'abortions'. These abortions were compared with all other cases of parturition when the foal survived the day of delivery. The analysis was performed in two steps. First, we compared the survival of the progeny of all males involved (N=8), both new males and fathers. In total 161 foals were considered, of which 35 were aborted and 126 survived. The proportion of abortions was almost twice as high for new males (15 abortions, 33.3%, N=45) than for fathers (20 abortions, 17.2%, N=116; χ^2_1=4.94, P<0.05). Then we scored only those males (N=3) that were both new males and fathers. Eighty-three foals were available, 18 of which were aborted and 65 survived. In this case, the proportion of abortions for new males (13 abortions, 35.1%, N=37) was three times that for fathers (five abortions, 11.6%, N=46; χ^2_1=6.57, P<0.01). Since this comparison may be taken as a repeated measures application, we applied Mantel–Haenszel statistics. This showed a strong association between abortions and whether the male was a father or new male, adjusting for the effect of individual males (χ^2_1=6.95, P<0.01).

We also analysed postnatal mortality of the foals. Again, the analysis was performed in two steps. First, we compared foal mortality for all males involved (N=8). In total 173 foals were born and 17 died. The mortality was much higher for new males (eight died, 18.6%, N=43) than for fathers (nine died, 6.9%, N=130; Pearson chi-square test: P=0.037). We compared the foal mortality for males that experienced both situations (N=6). In this case, 99 foals were born in total and 11 died. The proportion of postnatal mortality for new males (eight died, 20.0%, N=40) was significantly higher than with fathers (three died, 5.8%, N=59; Pearson chi-square test: P=0.026). Mantel–Haenszel statistics indicated that a male induced a higher proportion of postnatal mortality when he was a new male than when he was a father (χ^2_1=3.70, P<0.05).

There was no significant difference in the incidence of deaths between pre- and postnatal periods (comparison of proportion of deaths with new male present calculated for males who were with the herd in both situations: χ^2_1=2.22, NS).

Where the foal's sex was known, there was no indication of male foals being preferred for infanticide by a new male either in abortions (four out of seven were males; Pearson chi-square test: P=1.000) or in foals that died postpartum (five out of the nine foals that were attacked were males; Table 1).

For the next step, we combined all records of herds with new males. However, we excluded cases if the date of

Table 1. Nine recorded cases of an attack by a new male in the herd on a foal resulting in heavy injuries or the death of the foal

Year and zoo	Subspecies	Sex	Age	Notes
1974 Prague	*E. b. antiquorum*	M	13 days	The foal died from necrosis caused by bites to the limbs
1986 Dvůr Králové	*E. b. boehmi*	M	Newborn	The male introduced into the herd 5 days before the delivery killed the foal shortly after parturition by kicking and biting
1986 Dvůr Králové	*E. b. boehmi*	M	18 days	The foal was consistently attacked by the male during the first 2 weeks of life and was then separated from the herd
1988 Dvůr Králové	*E. b. antiquorum*	M	33 days	The male was introduced into the herd when the foal was 16 days old. He attacked the foal and 14 days later the foal had to be separated (with its mother). Two subsequent attempts to return the foal elicited further attacks by the male. When the male was removed, the foal rejoined the herd without any problems
1990 Dvůr Králové	*E. b. antiquorum*	F	10 days	The new male immediately attacked and bit the 10-day-old foal, which was removed from the herd the next day
1992 Dvůr Králové	*E. b. boehmi*	F	Newborn	Three months after a new male was added to the herd, one mare gave birth. The male attacked the newborn foal by biting it, grabbing it by the neck with its teeth, shaking it and tossing it into the air. The foal died the same day
1992 Dvůr Králové	*E. b. chapmanni*	F	Newborn	The male attacked the newborn foal by throwing it up into the air. The foal was immediately separated from the herd
1993 Dvůr Králové	*E. b. chapmanni*	F	6 months and 25 days	The foal was born on 29 September 1992 and the new male was introduced into the herd on 8 November. On 26 March 1993 the foal's mother died. The next day the male started attacking the orphan. Since this resulted in extended injuries, 2 days later the foal was removed from the herd
1997 Dvůr Králové	*E. b. antiquorum*	M	Newborn	The male attacked the foal immediately after its delivery. He grabbed it by the neck with his teeth and threw it into the ditch separating the enclosure from the public. The foal was immediately removed

M: Male; F: female.

Table 2. Three recorded cases of forced copulations inducing abortions

Zoo	Subspecies	Date of copulation	Date of abortion
Dvůr Králové	*E. b. antiquorum*	25–27 May 1989*	28 May 1989
Dvůr Králové	*E. b. borensis*	16–19 February 1991	22 February 1991
Dvůr Králové	*E. b. boehmi*	10–11 October 1992	12 October 1992

*The male was the sire of the aborted fetus. Nevertheless, since he was frequently separated from the herd for periods of 14 days and more, he could have been uncertain of its parentage.

introduction was not known; hence the number of cases differs from previous analyses. We tested whether there was any relationship between the probability of death and the age of the foal, and the time when the new male joined the herd (counted in days to the date of delivery and/or abortion). First, we applied a logistic regression procedure on the age of the foal. The data points separated into two groups (Fig. 1) and there was no maximum likelihood estimate. The majority of the foals that died when a new male joined the herd were very young; those older than 7 months mostly survived. The time when the new male joined the herd appeared highly influential (records for two males were not available and hence these males were excluded; logistic regression, whole-model test: $\chi^2_1=15.57$, $P<0.001$; analysis of maximum likelihood: $\chi^2_1=10.54$, $P<0.001$) and the model fitted well (association of predicted probabilities and observed responses: concordant: 77.6%, discordant: 22.2%). The probability of foal death was greatest when the new male joined the herd just after conception and decreased with increasing time between conception and date of the new male introduction (Fig. 2). To see if there was an interaction between the foal's age and the time of the new male's arrival in the herd, we applied a multiple logistic regression on the data, but the analysis of maximum likelihood revealed no significant interaction ($\chi^2_3=0.03$, NS).

DISCUSSION

As predicted, we found evidence of male infanticide in captive plains zebra. Mortality rates increased when there was a new male in a herd in pre- as well as postnatal

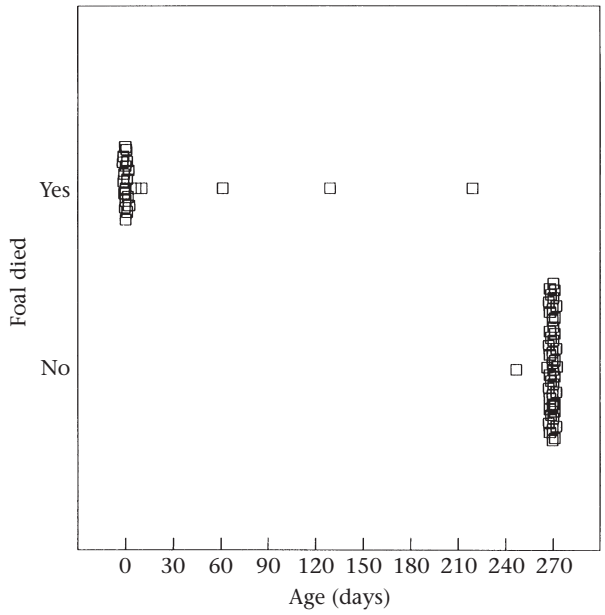

Figure 1. The relationship between age and time of foal death. As there were many overlapping data points for ages 0 and 270, they are placed randomly near their actual location.

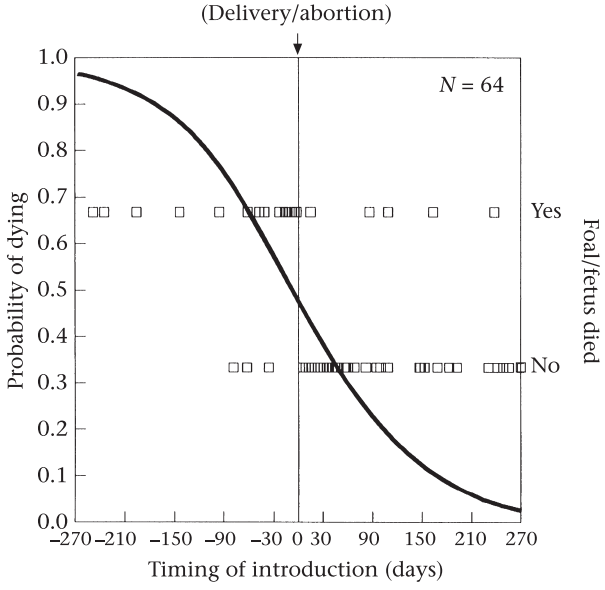

Figure 2. Logistic regression curves superimposed on data showing the relationship between the foal's probability of death and the time the new male was introduced into the herd relative to the day of parturition and/or abortion, shown as zero. Day of conception was between −385 and −361 days.

phases of the foal's ontogeny. We have three records of direct observations of possibly feticidal behaviour of zebra males. The new male forced copulation with the pregnant mare which was followed by abortion as suggested in previous reports (Berger 1983; Penzhorn 1985), although results obtained in horses indicate that forced copulation and induced abortion are not common events among feral herds (Kirkpatrick & Turner 1991). Nevertheless, our indirect data suggest a much higher incidence of possible feticide. The incidence of abortions with a new male present was 33% of all fetuses. This suggests that captive plains zebra might suffer from feticide to a greater extent than wild horses (Berger 1983; Kirkpatrick & Turner 1991). Our study was based on the behaviour of captive animals, however, which may be the product of environmental circumstances and it is difficult to know if the same occurs in the wild. Field studies are required to answer this question.

When a new male was absent, the proportion of abortions in our study was less than one-third of that when he was present. The proportion of abortions was high even though forced copulation, a conspicuous behaviour, was rare. Some abortions, however, could also be attributed to stallions harassing mares without forced copulation (see also Réale et al. 1996).

We documented nine records of fatal attacks to foals of various ages exclusively by new males. Nevertheless, the chance of a foal dying was four times higher with a new male present. This agrees with previous reports on horses (Duncan 1982; Ryder & Massena 1988; Monard et al. 1997). Thus, the plains zebra is the third equid species (after *E. caballus* and *E. przewalskii*) in which male infanticide has been documented. The possibility of infanticide has also been discussed for mountain zebra, *E. zebra*. While Penzhorn (1984) did not record any aggression by stallions towards foals, he admitted later the possibility of induced abortions by repeated forced copulations after take-over by a harem stallion (Penzhorn 1985). In our survey, we recorded one attack by a new male mountain zebra on a 7-day-old foal in the zoo at Dvůr Králové. The foal was rescued and removed. Owing to inaccuracy in other data on the mountain zebra, we could not incorporate data on that species into our study. Nevertheless, it also seems likely that infanticide occurs in captive mountain zebra.

The attacked zebra foals were injured mainly on the neck, head and limbs (Table 1) as was the case for horse foals (Duncan 1982; Ryder & Massena 1988). In the recorded cases, the zebra males hurt the foals more by biting than kicking with their hindlegs. This was also similar in horses. Biting shows intentional attacks, because teeth are offensive weapons among equids (Carson & Wood-Gush 1983).

In horses, Duncan (1982) and Ryder & Massena (1988) recorded attacks only on male foals. In contrast, four (44.4%) of the infanticidal attacks in our study were directed to female foals. This difference may be because a horse stallion can take a female foal as a potential mate for the future (Duncan 1982) whereas in plains zebra, the young mares are excluded from their natal herd when they reach their first oestrus (Klingel 1969; Smuts 1976). Thus, they are unlikely to be a future mate for the new male.

Because of the zebra's reproductive biology (Wackernagel 1965; Klingel 1969; Smuts 1976), to increase his chances of breeding, the new male should kill another male's offspring in the earliest possible stages. Our results strongly suggest this is the case. When a new male was present, the majority of the foals died either prenatally or shortly after delivery. Few older foals died.

The time of the new male's introduction into the herd appeared to be critical. The sooner the new male arrived after conception of the female with another male, the less likely her offspring was to survive. Mortality of foals was higher whether the new male was introduced before or after the foal's birth. With a few exceptions (e.g. as in Table 1), the foal's chances of survival increased after 1 month of age.

Our results were obtained from captive herds. Hence, a question arises if they are simply an artefact of captive breeding or if they apply to wild zebra populations. As discussed above, by killing young unrelated foals, a stallion may benefit by freeing the mares from the physiological stress of lactation, which improves their chances of producing a foal by him the following season (Boyd 1991). This is a factor thought to be sufficient to induce male infanticide even in a strictly seasonal breeder such as red deer, *Cervus elaphus* (Bartoš & Madlafousek 1994). Therefore, we expect male infanticide will occur in plains zebra living in the wild.

As a result of our study, we recommend that in zoos zebra males are introduced only to herds containing nonpregnant mares and foals at least 1 month old, which are less likely to be attacked.

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