# Title Page

**Title:** An observation of attempted infanticide and female-female cooperation in wild plains zebras (*Equus quagga*)

**Short title:** Infanticide and cooperation in wild plains zebra

Severine B.S.W. Hex[1,*,**] Margaret Mwangi[2], Rosemary Warungu[2] & Daniel I. Rubenstein[1, ***]

[1] Department of Ecology and Evolutionary Biology, 106A Guyot Hall, Princeton University, Princeton, NJ 08544-2016, USA

[2] Mpala Research Center, Laikipia, Kenya

* Corresponding author's email address: shex@princeton.edu

** ORCID: https://orcid.org/0000-0002-9142-6917

*** ORCHID: https://orcid.org/0000-0001-9049-5219

# Abstract

Male infanticide has been reported in a wide range of taxa as a strategy for redirecting maternal investment and increasing a male's chance of siring future offspring. Plains zebras (*Equus quagga)* possess many of the social organization and life history traits found to favor infanticide. However, most documented cases are from captive animals, while it has not been detected in studies of free-ranging populations. Here, we report an apparent infanticide attempt in which the historical associations of all participants were known. In addition, we report the first instance of non-kin female-female cooperative defense against male aggression in this species. We discuss why this behavior may not have been observed by other longitudinal studies. We then explore how intraspecific and inter-individual variation may factor into its relative rarity, how the reproductive biology of plains zebras relates to this behavior, and how female-female cooperation between non-kin can operate as an effective counterstrategy.


**Keywords** equids, Equidae, ungulate, third-party intervention, sexual conflict

# 1. Introduction

In social systems where the interests of males and females regularly collide, such as in stable, mixed-sex associations, intersexual conflicts of interest often emerge. One of the most extreme forms of intersexual conflict is male infanticide, whereby an adult male kills the dependent offspring of a female. A widespread phenomenon across diverse taxa (Hrdy, 1979; Hausfater & Hrdy, 2017), infanticide has been proposed to be a major selective force shaping mating systems and social dynamics, such as the evolution of monogamy in primates (Borries et al., 2011; Opie et al., 2013; but see Lukas & Clutton-Brock, 2014), as well as the emergence of female counter-strategies such as sexual promiscuity to obfuscate paternity (Balme, 2013), sexual segregation (Dahle & Swenson, 2003), and female gregariousness (Grinnell & McComb, 1996). However, other studies have argued that infanticide is a consequence rather than a cause of social variation (Lukas & Huchard, 2014).

Though there are a variety of hypotheses for why male infanticide might occur (for excellent discussions of adaptive and maladaptive explanations, see Palombit, 2015; Hausfater & Hrdy, 2017), a common explanation is the *sexual selection hypothesis*, which posits that infanticide is advantageous to males because it removes the vessel of a competitor's genes while shortening the female's latency to estrus and/or improving her condition and future fertility (Palombit, 2015). In a meta-analysis of 260 mammalian taxa, male infanticide was found to be most strongly predicted by the absence of seasonal reproduction, occurring most often in species living in stable, mixed-sex groups with a female-biased sex ratio where reproduction is monopolized by a few males who have relatively short reproductive tenures compared to female inter-birth intervals (Lukas & Huchard, 2014). This study concluded that infanticide acts to increase a male's fitness by directly reducing another male's reproductive success and by redirecting maternal investment to a male's future offspring, and highlighted that social organization was critically important in predicting its emergence.

Plains zebras (*Equus quagga*) meet these predicted requirements, occupying complex social worlds where males and females live in stable, female-biased social groups. The core social unit of plains zebra society is a type of uni-male multi-female unit (UM-MF unit) referred to as a "bonded true harem" (hereafter simply "harem"), defined as "*a stable group consisting of a single breeding male maintaining tenure in a group with two or more unrelated females across more than one reproductive event for at least one of the females"* and in in which the unrelated females form stable bonds with one another (Hex et al., 2021). In plains zebras, the harem consists of a single reproductive stallion, 2-5 typically unrelated adult females, and their dependent offspring who generally disperse when they reach sexual maturity (approx. 2.5 years old), though young females may remain in their natal harem if their father is deposed (Simpson et al. 2012; pers. obs.), and young males may delay dispersal until they are as old as 4 (Klingel 1965, 1974; Simpson et al. 2012; pers. obs.).Young males join bachelor groups, where, in our population, they may remain until they are between 5-12 years old before forming their first bonds with females and beginning their reproductive lives. Harems are relatively stable across time, with composition remaining unchanged for 3.5 years on average (Tong et al., 2015), though some bonds can persist much longer, up to 12 years (pers. obs.). As a result, there is great potential for skew in reproductive success between males, especially between stallions and bachelors, who do not breed (Rubenstein & Nuñez, 2009).

Plains zebras do not have seasonal reproduction and females cycle year round, with an estrus of 2-9 days followed by a diestrus of 17-24 days (King, 1965). This aseasonal reproduction meets another of the predictions derived from Lukas and Huchard's (2014) meta-analysis. Though mares exhibit a post-partum estrus 8-10 days after foaling (King, 1965), infanticide has been reported to occur in this species. Both infanticide and feticide, when a male persistently attacks and/or forces copulations on pregnant females to induce abortions, have been observed at relatively high rates in captive plains zebras (Pluháček & Bartoš, 2000; Pluháček & Bartoš, 2005). However, the extent to which infanticide occurs in *wild* plains zebras is contentious. There have been a few reports of infanticide in other feral (Berger, 1986; Gray, 2009) and semi-feral equids (Duncan, 1982; Feh & Munkhtuya, 2008; Dorj & Namkhai, 2013). Recently, Britnell and colleagues (2021) reported perhaps the most comprehensive evidence to date of infanticide in wild Cape Mountain zebras (*Equus zebra zebra),* which share many aspects of their ecology with plains zebras. This report included an observation of attempted infanticide by bachelor males, along with descriptions of three necropsied foals with injuries the authors considered consistent with infanticide, including kick marks, bitten ears, massive internal injuries, broken ribs, and broken necks.

In contrast, while there are many videos and documentaries on the internet documenting anecdotes of infanticide in wild plains zebras, there has only been a single published report to date (Ransom & Kaczensky, 2016). Other studies have reported no occurrence of infanticide in their populations, including a longitudinal survey which found no significant effect of stallion turnover on infant mortality in a population that had been monitored for 16 years (Vitet et al., 2021). This inability to detect a population-level signature of infanticide led the investigators to conclude that infanticide, if it occurs at all, is likely a rare occurrence with no significant demographic impact on plains zebra populations. There is also disagreement as to whether infanticide in equids represents an adaptive reproductive strategy under sexual selection (e.g. Britnell et al., 2021), or is a maladaptive, social pathology induced by unnatural or stressful social conditions (e.g. Feh & Munkhtuya, 2008), as there appears to be intraspecific variation in its incidence.

Vitet and colleagues (2021) proposed the presence of sufficiently effective female counterstrategies, namely female-female cooperation, as one potential reason for why infanticide does not appear to be a strong demographic driver in plains zebras. Coalitionary support as a strategy to defend against infanticide has been observed in other taxa (African lions *Panthera leo,* Packer et al.,1990; Temminck's red colobus *Procolobus* *badius temminckii*, Starin, 1994), almost always occurring between close kin. Among equids, the degree of social integration between unrelated feral horse females was significantly negatively correlated with degree of male harassment, suggesting female social bonds play a role in reducing male harassment (Cameron et al., 2009), and there has been at least one report of a female intervening on behalf of a half-sister against an infanticidal male (Feh & Munkhtuya, 2008). However, to our best knowledge, such cooperative behavior towards male aggression has not yet been reported in the literature for female plains zebras.

Here, we describe, with accompanying video examples, an instance of apparent attempted infanticide in a monitored population of wild plains zebras in which the relationships and history of associations between all participants are known. In addition, we report the first description of female-female cooperation, likely between non-kin, in a high-risk situation involving extended male aggression in wild plains zebras. We then explore the possibilities for why infanticide appears to be rare in wild populations, how the reproductive biology and socioecology of plains zebras might explain its presence, and how female-female cooperation could operate as a highly effective counterstrategy.

# 2. Study area and observational methods

The event occurred on the Eastern Sector of Ol Pejeta Conservancy (0°00 N, 36°56 E), a semi-arid, bushed grassland in the Laikipia ecosystem of central Kenya. We have been monitoring this population since 2001, collecting data on associations, movement, and demography.

During census loops, we drive a set route through the reserve in search of harems/herds. Upon locating a harem, we record the spatial coordinates and habitat, as well as the identity, phenotype, reproductive state, and group membership of each individual (Fischhoff et al., 2007, 2010). We conduct a survey of the population at a typical interval of 1 week (range: 1 day -1 month). Harem size in our population (5 ± 1.3 members, range 2-13) is comparable to those reported in other populations (Klingel 1965; Vitet et al., 2021). We are able to individually identify zebras based on their unique stripes (Figure 1 for example ID cards).

In addition, between July and October 2021, a subset of 22 harems (115 individuals), including the harem involved in the reported event, were part of a more intensive ongoing study involving routine focal follows of harems which last on average 3 consecutive hours. Harems from this subset are systematically prioritized so they can be re-sighted and followed at relatively regular intervals (median inter-follow interval 14 ± 6 days, range 2-29), though a degree of opportunism is included in the search protocol to maximize contact time with a given harem. When a harem is found, continuous video and audio recordings are collected of focal individuals (1 hour per focal) and scan samples are collected every 30 minutes recording spatial coordinates, habitat, nearest neighbor, and the behavior of all members. With these data, we are able to construct proximity networks using the R packages igraph (Csardi & Nepusz, 2006) and ggnetwork (François, 2021) to inspect the associations of harem members over time. Finally, all instances of other behaviors of interest are recorded, including travel initiations and follows, queue order, affiliation, and aggression. We amassed a total of 290.5 contact hours, amounting to an average of 13 hours (range: 6-23 hours) spent with each harem.

Table 1: Aristocrats harem membership prior to the observed infanticide attempt. *Edmund was last seen with the harem on the 22nd of May.

| Individual name | Sex | Reproductive State | Year First sighted | Member since |
|---|---|---|---|---|
| *Edmund | Male | Stallion | 2008 as bachelor | 2009 (until May 2021) |
| Aethelwulf | Male | Stallion | 2009 as infant | May 2021 |
| Matilda | Female | Pregnant | 2008 as adult | 2012 |
| Elanor | Female | Nonlactating | 2017 as adult | 2018 |
| Antoinette | Female | Nonlactating | 2012 as infant | 2010 |
| Isabella | Female | Pregnant | 2008 as adult | 2013 |
| Victoria | Female | Pregnant | 2020 as adult | 2020 |

# 3. Results

## *3.1. Description of the event*

(Fig. 1 here)

On August 3rd, 2021, at approximately 09:00, we encountered the 6-member Aristocrats harem (Table 1). Upon arrival, we observed a new foal who appeared to have been born that morning to Matilda (Figure 1, Supplementary material 1). The foal was unsteady on its legs, and its curly baby-pelt was still wet with amniotic fluid about the underbelly, where the vestiges of the umbilical cord remained. Both the foal and mother's hind legs were still stained with blood from the birth, and the placenta lay less than 100 meters away, visibly fresh, and only just beginning to draw in white-headed vultures (*Triconoceps occipitalis*) and a raptor to feed (Supplementary material 2). All of these observations suggested to us that the foal had not been born more than a few hours prior to our arrival that morning.

Beside Matilda stood another female member of the harem, Elanor (Figure 1), while the other three mares of the harem grazed several hundred meters away. Nearby grazed the new stallion, Aethelwulf, who had been the resident male for just over two months (Figure 1). At 09:09 we commenced our routine focal follow of the Aristocrats, during which we witnessed the following events.

Matilda expressed elevated levels of aggression towards Aethelwulf, kicking at him whenever he approached within a body length and keeping herself interposed between him and her foal (Figure 2, Supplementary material 3). In contrast, Elanor was frequently permitted to graze within a single body length, often standing beside the newborn foal without receiving aggression. Aethelwulf would not retreat after Matilda's threats, as we generally see from stallions or other harem members who accidentally approach too near (pers. obs.), instead returning her kicks in kind (Figure 3).

(Fig. 2 and 3 here)

At approximately 09:12 we witnessed Aethelwulf's first attack, where he appeared to lunge for the foal after Matilda's threats towards him left her further from her foal. (Supplementary material 4). Matilda interposed, kicking Aethelwulf, who bit her in retaliation, before moving the foal away by pushing its body with her head. Elanor approached at a trot and interposed between the parties while Matilda retreated, and then stopped to graze between Matilda and Aethelwulf. Elanor remained beside Matilda for 4 minutes, during which time the foal was positioned between the two mares as it attempted to nurse, before she moved a few body lengths away to graze. At 09:20 Matilda approached Elanor, where the two grazed within a body length of one another for 4 minutes, until Aethelwulf approached within two body lengths. At 09:34 Aethelwulf attacked again, and he and Matilda exchanged kicks before Elanor trotted between the parties, and remained near Aethelwulf until he retreated before returning to graze near Matilda.

At 10:00 another attack was witnessed. Aethelwulf first kicked at Elanor before charging after Matilda, appearing as though attempting to get around her to the foal  while she continually turned her haunches into him to keep herself positioned between them (Supplementary material 5). Aethelwulf pursued Matilda as she walked away, repeating his bites and apparent attempts to maneuver around Matilda and get to where the foal was (Supplemental material 6). Elanor intervened in both instances, interposing between the parties, where she directed her attention toward Aethelwulf and stayed near him while Matilda retreated with her foal. During this time, one of the distant harem members, a female named

Antoinette, approached within 50 meters and watched the fighting, though at no time did she become involved in the event.

Aethelwulf, Matilda, and Elanor grazed from 10:14 until 10:32, with Elanor actively adjusting her positioning as Matilda and Aethelwulf shifted, closely following Matilda's movements to remain interposed, and walking parallel alongside Aethelwulf to herd him away whenever he tried to approach (Supplemental material 7-10). At 10:36 we witnessed the most escalated series of attacks (Supplemental material 11) during which Aethewulf directed repeated aggression towards both Matilda and Elanor. Elanor's involvement became more aggressive, and she performed rump swings, kick threats, and full kicks at Aethelwulf in her attempts to interpose between him and Matilda (Figure 4). During this period, the foal remained by Matilda's side, and Aethelwulf did not succeed in making contact with the foal.

(Fig. 4 here)

Following this period of conflict, the mares began travelling at a trot, followed by Aethelwulf. From 10:38 until 11:20 the mares alternated between travelling and short bouts of grazing, during which time they continued the same behaviors described above. Matilda initiated much of the aggression during this period by threatening or kicking at Aethelwulf whenever he approached her and the foal within a body length, and Elanor continued interposing after every approach by Aethelwulf. From 11:20 until the end of our observation period the mares rested and grazed, often with the foal resting between them, remaining in close proximity with one another while maintaining a distance from Aethelwulf. We did not observe any more attacks from Aethelwulf, though he continued to kick at Matilda in response to her aggression. He spent the remainder of the session watching and following the two mares and foal from a distance, with only intermittent grazing and brief, occasional chases without contact. At the end of our observation period, the other three members of the harem were still at a distance of nearly 200 meters from the four focal animals.

We resighted the Aristocrats two days later on August 5$^{th}$, with all six adult members of the harem travelling in queue from water. Matilda's foal was no longer among them.

## *3.2. Life history and relationships of the participants*

### 3.2.1. The mother: Matilda

Matilda was first seen in 2008 as an adult, making her at least 15 years old. She has been in association with 7 stallions between 2008 until present, the longest bond having been with the most-recent former stallion of the Aristocrats harem, Edmund, whom she was with from 2012 until May 2021. She has had two previous foals, one born in 2011 which did not survive, and a female born the following year (2012) who survived and dispersed to another harem. Incidentally, both foals were born after their probable biological father had been deposed. The 2011 foal had been born during a period of time when Matilda was in a series of brief associations, sighted with 5 different males over the period of seven months, and had only been with the contemporary stallion for between 1-3 months when she gave birth. The 2012 foal, which survived into adulthood, had been born at the beginning of her association with Edmund, whom she had been with for a little over 4 months prior to parturition.

### 3.2.2. The ally: Elanor

Elanor was first seen as an adult on the Western Sector of Ol Pejeta Nature Conservancy in 2017, making her at least 6 years old. The Western Sector has several corridors through which wildlife can travel in and out, meaning that new individuals will occasionally be sighted on the Western Sector that may have originated from beyond the Conservancy. She was first seen with the Aristocrats harem in January of 2018, during Edmund's tenure, after having been separated from her previous harem, which we never sighted again. She has had two foals since her first sighting, one born in 2018 shortly after she joined the harem, which did not survive, and a male born the following year (2019) who is alive today and only dispersed in late May of 2021. Elanor has not had a foal since 2019, meaning there was no possibility that she might have been acting to protect Matilda's foal due to mistaking it as her own or due to postpartum physiological state making her more willing to show maternal care to another foal, which has been suggested to facilitate adoption of non-kin in feral horses (Nuñez et al., 2013) and potentially precipitate conflicts over maternity in plains zebras (Fischhoff et al., 2010).

Elanor and Matilda have been in the same harem since at least the beginning of 2017, and possibly since as early as mid-November of 2016. Despite zebra herds being structured by female relatedness, making it possible that a young female could disperse into a harem containing close kin, relatedness within harems is generally low (Tong et al., 2015). While we cannot completely rule out the possibility that the two are kin without genetic analysis, the evidence suggests Elanor and Matilda are highly unlikely to be kin. There is no overlap in their social histories, which extends as far back as 2008 for Matilda, and it is likely that Elanor originated from beyond the Conservancy, as we first sighted her in an unknown harem on the Western Sector. Given the low average relatedness between harem-mates, the probable age difference between Elanor and Matilda, and the complete lack of overlap in historical associations prior to joining the Aristocrats, we consider it unlikely that Elanor and Matilda's cooperation was the result of kinship.

Construction of a proximity network of the Aristocrats harem for July-October 2021 reveals that Matilda and Elanor remained consistently one another's closest associates throughout this period, frequently seen within one body length of the other (Figure 5). The behaviors most frequently observed between these individuals were "social grazing" (grazing in parallel within one body length of one another, often with noses nearly touching), resting in antiparallel (standing side by side with nose to tail, such that tails can switch flies from the partner's face), or resting in perpendicular position (one partner standing perpendicularly behind the other). This consistently close association may explain why

Elanor was the individual to intervene on Matilda’s behalf during this event.

Elanor may also possess an increased tolerance of non-kin juveniles which may predispose her towards assisting in defense/parental duties with other harem members. Elanor has frequently been observed affiliating, playing with, and grooming the offspring of other harem members without aggression (Supplemental material 12).

(Fig. 5a and 5b here)

### 3.2.3. The new stallion: Aethelwulf

Aethelwulf was born in 2009, and has never been the stallion of a harem. In early 2021 he was still a bachelor, and was first seen with the Aristocrats on the 28th of May at the age of 12 years. Aethelwulf is average in age for a stallion in our population (mean 12 ± 3.23 years old, range 5-18 years old). However, he was older than average for a male transitioning from being a bachelor to a stallion, as the average male in our population becomes a stallion for the first time at 7 ± 2.1 years old (range 5-12 years old).

The former stallion of the Aristocrats, Edmund, who was 14 at the time of his disappearance, had last been seen on May 22nd. He has not been sighted since, leading us to suspect he died either shortly before or after Aethelwulf began his tenure as the stallion of the Aristocrats. This means Aethelwulf had been the stallion for just over 2 months (at least 67-73 days) when Matilda’s foal was born. As mares have a mean gestation length of 371.2 days (King, 1965), it is extremely unlikely that Aethelwulf was the father of the foal.

# 4. Discussion

This is one of only a few descriptions of an instance of extended and escalated male aggression directed towards a postpartum female and her newly born foal in wild plains zebras. In addition, this is, to our knowledge, the first report of non-kin female-female cooperation against sustained and persistent male aggression in this species. While we did not observe direct contact between the stallion and foal during our observation period, likely due to the behaviors of the two mares preventing such contact, based upon the stallion's repeated attacks with the apparent intent of accessing the foal, along with his unlikely paternity, we consider this behavior to most likely represent an infanticide attempt.

As we were unable to recover the foal's body, we cannot definitively rule whether the ultimate cause of death was due to infanticide or other causes. Infant mortality is high in plains zebras, ranging from 0.19-0.389 (Geogiadis et al., 2003; Grange et al., 2004). The primary cause of this high mortality rate is thought to be predation, which was estimated to account for 30% of the annual mortality in the Serengeti zebra population (Grange et al., 2004). Lions (*Panthera leo*), spotted hyenas (*Crocutta crocutta*), and cheetahs (*Acinonyx jubatus*) are found on Ol Pejeta, making predation a possible cause of this foal's death. Another possibility is that the foal starved to death in those first two days. Zebra populations in Laikipia, Kenya, are negatively impacted by annual variation in rainfall (Geogiadis et al., 2003). Laikipia county had been experiencing a drought between 2020-2021, which may have influenced some females' abilities to sustain lactation. However, at the time of the event, Matilda's body condition was scored as a "4" out of 5 using the plains zebra body condition scale (Ginsberg, 1988), leading us to suspect it unlikely that Matilda was unable to produce enough milk. Finally, it is possible that Aethelwulf was ultimately successful in his apparent aims to reach the foal and was able to physically harm it, or that he had contacted the foal prior to our arrival and inflicted internal injuries which resulted in its death.

Alternatively, his persistent harassment of mother and foal may have precluded sufficient rest and nutrition for the pair and/or diverted attention from typical vigilance activities, thereby facilitating the direct cause of death. If this was the case, we would argue that the cause of death could still be considered infanticide, as his actions indirectly resulted in the removal of another male's reproductive success. This would be similar to observations of feticide, where persistent, aggressive harassment of pregnant females results in abortion of the fetus, and implies that harassment of new mothers could be another effective infanticidal tactic worthy of closer investigation in this species.

### *4.1. Potential explanations of why infanticide has not been reported in wild plains zebras*

Our observation, though corroborating both dramatic anecdotes from wild plains zebras and numerous reports from captive animals, is at odds with other studies which claim to have never observed infanticide (Vitet et al., 2021). Why might other long-term monitoring projects have failed to observe this phenomenon? We suggest this to be the result of 1) inappropriate sampling to capture its relatively low occurrence, and 2) intraspecific variation in its prevalence.

Plains zebra populations are often monitored using methods well suited to assessing shifts in demography and social association over time, while behavioral observations are typically ad hoc and of short duration. Rarely do such studies involve long-duration (>1 hour), systematic focal follows of known individuals over the course of several months to years (but see Simpson et al., 2012), a method that increases the likelihood of observing rare social events. This may be especially important in a species in which active socializing necessarily occupies a relatively small portion of their daily time budget due to the demands of being hind gut fermenters that must devote on average 65% of every hour and 50-80% of their total time to grazing (Rubenstein, 1993; Clauss, 2013).

The circumstances that might lead to an infanticide attempt are likely to be uncommon in this species, making it challenging to witness using typical, survey-based monitoring methods. Though the likelihood of male turnover has been found to increase with harem size (Vitet et al., 2021), the average bond length between a stallion and any given mare in our population is 1114 ± 578 days (range 0-2802 days). This stability would reduce the chance of observing a recent turnover event in any given survey. Amongst the captured turnover events, it is likely that only a small proportion of them would possess the suite of circumstances that might favor an infanticide attempt, namely the presence of deeply pregnant females and/or extremely young foals. Furthermore, the long duration of gestation may impose cognitive challenges for a male attempting to assess paternity, and there may be a threshold of time after joining a harem beyond which the paternity of subsequently born foals becomes too uncertain to act upon. Alternatively, the growing bond between stallions and mares over time may shift the dynamics existing between them and make males less likely to attempt infanticide, which has been found to harm stallion-mare affiliative interactions in Przewalski's horses (Feh & Munkhtuya, 2008). Finally, in horses, 5-10% of mares exhibit estrous behavior during pregnancy (Crowell-Davis, 2007), which, if also true in zebras, may further serve to confuse paternity in the event of stallion turn-over while also strengthening social bonds. As infanticide is unlikely to occur if males are uncertain about paternity, turnover events where a male's paternity uncertainty is low are likely relatively uncommon occurrences that even long-running monitoring projects could easily miss. This is especially true if not all infanticide attempts are successful, making it difficult to detect their presence or effect against the background of high infant mortality.

Using our intensive focal sampling regime, however, we have been able to witness various heretofore undocumented behaviors in wild plains zebras. Indeed, the above case study was not the only instance of apparent stallion-mare reproductive conflict and female-female cooperation that we observed in this time period. In a different harem that experienced a brief (~24 hour) stallion turnover, the newcomer male was seen persistently and aggressively separating and driving the only heavily pregnant mare away from this newly acquired harem. The rest of the harem mares were observed apparently trying to reunite with the isolated female. Her closest associate eventually succeeded in joining her, where they remained separated from the harem until their former stallion regained his position the next day. The only explanation we could make for why this particular female was singled out and driven from the harem by the interloper stallion was her reproductive state as a heavily pregnant female due to give birth within a few days to weeks. This behavior was consistent with observations of attempted feticide in captive zebras (Pluhácek & Bartoš, 2005). We should note that this new stallion did not demonstrate such aggressive harassment to any of the other 10 females of the harem, despite aggression being directed towards him by the mares, making it unlikely that he was an abnormally aggressive male, nor have we observed this form of harassment of females by new stallions in other harems. When harassment of mares by new stallions occurs, it generally takes the form of unsolicited attempted mountings or excessive herding. Therefore, aggressive harassment of females involving repeated attacks or isolation from the rest of the harem is not a typical feature of stallion turnover, and the situations in which it would occur are likely infrequent, requiring further investigatory focus using intensive focal follows to characterize.

Another non-mutually exclusive possibility for the apparent rarity of infanticide and its difficulty to observe is that there may be intraspecific and inter-individual variation in the presence or prevalence of this behavior as a reproductive strategy. Studies in captive plains zebras suggest there may be variation in its incidence across subspecies (Pluháček et al., 2006), and there is evidence of within-population individual variation in wild Przewalski's horses (Feh & Munkhtuya, 2008). Even in species in which infanticide is thought of as a common and adaptive reproductive strategy, there can be significant variation in its incidence both across and within populations (Hrdy, 1979; Sommer, 1994; Cords & Fuller, 2010). Infanticide may not always be a fixed, invariable trait, but rather a conditional strategy influenced by sociodemographic factors (Bellemain et al., 2006); characteristics of the male such as his dominance (Palombit, 2003); his age, experience, and/or body size (Cords & Fuller, 2010); and how a male weighs potential benefits (i.e. increased likelihood of fathering future offspring) and opportunity (e.g. age of offspring, experience of mother) against the costs (e.g. coming into physical conflict with the mother and/or other group members, damaging the social bond with that female etc.) (Palombit et al., 2000). There may even be intraindividual variation in whether a male attempts infanticide across time, and how persistent or aggressive his attempts are in the face of female counterstrategies (Cords & Fuller, 2010).

In this case study, we, too, observed intraindividual variation in infanticide attempts by the same male. On August 20th, 2021, a foal was born to another mare of the Aristocrats harem, Victoria. However, in contrast to the above events, we did not witness any aggression directed towards the foal by Aethelwulf, and the harem travelled and stood together for the entire focal follow. It is important to note that our focal follow on that day occurred in the afternoon, meaning we did not have the opportunity to witness his behavior in the hours following parturition. This is an important caveat, as we notice more activity in our zebras in the morning between 8:00-12:00 than in the afternoon between 12:00-16:00. Nonetheless, that infant survived until the end of our study period, and we never witnessed any aggression directed towards either infant or mother by Aethelwulf. Therefore, whether a given male decides to attempt infanticide is likely influenced by a complex suite of social, demographic, and contextual variables, potentially leading to great intraspecific variation in its incidence between and within populations, as well as within a given individual.

### *4.2. Why might plains zebras attempt infanticide?*

The next question is why might infanticide occur in plains zebras? Though plains zebras possess many of the social organization characteristics found to predict its presence, females also possess a post-partum estrus, which theoretically eliminates the benefit of killing a foal. Indeed, Feh & Munkhtuya (2008) reported that infanticide did not reduce interbirth intervals in Przewalski's horses. However, we suggest that, in spite of having a post-partum estrus, nursing a dependent foal imposes costs upon female plains zebras that reduce her chances of conceiving again after parturition. While mares can, in theory, sustain two offspring at once, and in captivity, pregnant mares wean their foals earlier than do nonpregnant females (Pluháček et al., 2007), the actual incidence of females having successful consecutive pregnancies appears to be low in the wild. It has been found that few females actually conceive during their post-partum estrus. Females appear to fall into two distinct reproductive patterns following parturition and during lactation, in which some resume normal estrus cycling after their post-partum estrus and generally conceive around four weeks later, while other females do not resume normal cycling until 10-16 weeks post-partum (King, 1965), effectively experiencing a post-partum anestrus. Nonetheless, it is the case that female plains zebras are theoretically capable of normally ovulating and conceiving while lactating a dependent foal.

However, few mares in the wild appear able to sustain successive pregnancies. The average inter-birth interval in one population was found to be 462 days (Barnier et al., 2012), increasing by an average of 88 days when the offspring was a male. These findings are comparable to those of Klingel (1969), who observed 120 mares across three years and found that only 15% had three foals, while 33% had two, 42% had just one, and 10% had no offspring. Our population follows a similar pattern to those observed by Klingel (1969). When we look at a subsample of 619 mares across a five-year period, 41.6% had only one foal, 15.1% had two, 5.8%

had three, and 1.9% had four, while just two mares managed to have a foal in each of five consecutive years.

This potentially long inter-birth interval is notable when taken relative to the average male-female bond in our population, which is just over 3.5 years. As just over 40% of mares will only have one foal within this period, a given stallion is likely to have only one to two chances to successfully reproduce with each female in the harem before his odds of being deposed begin to increase, especially in larger harems (Vitet et al., 2021). As a result, any foal born in the harem that is not his may be a significant risk to a stallion's reproductive potential by reducing a mare's likelihood of bearing another foal, possibly for many years. Attempting infanticide may act to reduce the latency of a mare giving birth to a surviving foal by redirecting maternal energy to future offspring. In the feral horses of Shackleford island, mares that lose their foals were found to be more likely to conceive, either in the same season or the next, depending on timing of foal death (Rubenstein & Nuñez, 2009). A comparison of interbirth interval between wild plains zebras whose foals did or did not survive would be critical to assessing the extent to which foals impose reproductive costs on mares.

There may also be social costs to possessing and raising a foal that have consequences for the entire harem, and especially the stallion. Lactating females need to drink more than non-lactating females, and therefore can sway group movements by leading the harem to water more often (Fischhoff et al., 2007). Water is a risky social environment for harems, as bachelors preferentially select habitat around waterholes to congregate and graze, where they have a greater chance of encountering separated females (Supplemental material 13). This habitat selectivity by bachelors makes each journey to water a potentially costly activity for stallions, increasing their risk of expensive fights or losing females. Stallions also invest in direct protection of the foal, including defending them from extra-harem harassment, such as the approach of interested juvenile females (pers. obs.), a diversion from the already multiplex suite of responsibilities stallions must balance, including deflecting bachelor harassment, socializing with other stallions to reenforce social relationships, and vigilance against predators (Rubenstein, 1994). Stallions may even be important investors in the socialization of foals, as has been suggested in horses (Šandlová et al., 2020). Therefore, the presence of dependent offspring may impose physical costs not only on females, which affects a stallion's likelihood of reproduction, but also on the male himself in the form of increased social and energetic expenditure. A stallion would benefit from ensuring any foals he invests in are his own, potentially incentivizing behaviors to ensure his paternity certainty, including infanticide.

### *4.3. Female-female cooperation as a counterstrategy*

Finally, female counterstrategies may contribute to the apparent rarity of this event in relation to its theoretical benefits for males. This observation of female-female cooperation as a behavioral counterstrategy presents an intriguing piece of evidence for infanticide's existence as a threat in the evolutionary history of plains zebras, suggesting there may have been a selection pressure for cooperation between unrelated females. Partial third-party interventions, where an individual intervenes in a conflict to actively support one of the participants, are both socially and energetically costly by exposing the interferer to potential harm, and are most often explained in terms of kin-selection (white-faced capuchins *Cebus capucinu* Perry et al., 2009; hyenas, Smith et al., 2010; captive white lipped peccaries *Tayassu pecari*, Leonardo et al., 2021), though reciprocity, dominance assurance, and direct benefits can also lead to the emergence of coalitionary support, especially between non-kin (Smith et al., 2010; Leonardo et al., 2021). While this is the first published report of coalitionary support in plains zebras, this sort of cooperative intervention has been observed in other equids (Feh & Munkhtuya, 2008; Cameron et al., 2009), as well as in our population as cooperative defense against unwanted harassment and/or sexual attention from males (pers. obs.).

Elevated aggression towards other group members immediately following parturition has been reported in female plains zebras (Klingel, 1974), who are described as indiscriminately warding off any member of the harem in the first few days. In contrast with these reports, Matilda's aggression during this event appeared to be singularly directed at Aethelwulf, while Elanor was permitted to remain near her and the foal. There were even instances when Matilda initiated proximity between herself and Elanor. This behavior further supports our observation that Elanor was acting in support of Matilda and raises the possibility that such cooperation against male harassment is more prevalent than previously appreciated. The possibility of coalitionary support could significantly affect a stallion's perceived costs of attempting infanticide, especially in a relatively sexually monomorphic species (females 220 kg, males 250 kg; Kingdon, 1979). It could be that, compared to other systems wherein infanticide is more prevalent, females and infanticidal males are relatively evenly matched at this stage in the evolutionary arms race.

## Closing Remarks

The presence of infanticide in the plains zebra remains a controversial phenomenon with limited data in wild populations. This is one of the first reports of an apparent infanticide attempt in wild plains zebras, as well as, to our knowledge, the first report of female-female cooperation in this species. While we agree with previous findings that the demographic signal of this phenomenon is likely low compared to other causes of infant mortality, especially predation, we suggest that infanticide may still represent a real social strategy with potential fitness consequences. We further suggest that infanticide may be direct or indirect, with the harassment and distraction caused by male aggression increasing a young foal's chances of dying by other causes, such as predation or starvation. We urge for further investigation deploying methods amenable to documenting rare social events, namely intensive focal follows of known harems, to fully quantify the incidence of this behavior at the species level, as well as to characterize potential variation in its occurrence at the population and individual scales.

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# Figures

Figure 1: Photographs (from left to right) of Matilda, Elanor, and Aethelwulf. Field notes for identification: Matilda left side—short notch black stripe on middle of back. Elanor left side—large, black “W” shape

on side. Aethelwulf left side—black, right branching phylogeny on side. Photos by S. Hex.

Figure 2: Matilda kicking Aethelwulf while interposing between him and her foal. Still from video by M. Ng'aske.

Figure 3: Aethelwulf kicking Matilda as she pushes her foal away. Still from video by M. Ng'aske.

Fig 4: Elanor kicking at Aethelwulf as she interposes, allowing Matilda and her foal to pass. Still from video by M. Ng'aske.

Fig 5: Social network of Aristocrats harem, showing proximity within (a) one body length and (b) five body lengths. Line width indicates strength of association, with thicker lines denoting more frequent associations. Lines coloured purple are those where the association frequency is greater than the mean association frequency seen within the harem.