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SHORT COMMUNICATION

A rare fight in female plains zebra

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Abstract We describe a fight between two female plains zebra (*Equus burchelli*). Plains zebra are ungulates with stable social groups known as harems. Female aggression rarely escalates to the level we observed. The fight immediately followed the birth of a foal to one of the females. The initiating female repeatedly kicked and bit the mother, who reacted aggressively and by guarding her foal. We present hypotheses on the causes underlying this rare event.

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Introduction

In polygynous species, fights usually occur amongst males, who compete for access to mates. Fights tend to be rare in females, whose fitness is rather limited by energy and time investments in reproduction (Emlen and Oring 1977; Clutton-Brock and Harvey 1978). For grazing ungulates in savannah, forage resources tend to be widely distributed and difficult to monopolize. Therefore, the resource benefits to a female of winning an aggressive encounter are typically low, relative to the costs of fighting (Maynard Smith and Parker 1976; Matsumura and Kobayashi 1998). Certain female groups form relatively stable and persistent social bonds (Wrangham 1980), which permit habitual dominance relations to emerge (Beacham 2003). Moreover, such relationships facilitate individuals detecting the likely outcome of an aggressive interaction. With greater certainty about how a fight will end, individuals have lower motivation to be aggressive.

Certain equid societies contain stable female groups known as harems, each defended by a male. We find harems in plains zebra (*Equus burchelli*), mountain zebra (*E. zebra zebra*), and in both feral horses subspecies (Oakenfull et al. 2004): *E. ferus caballus* (Rubenstein 1986; Rubenstein 1994) and the Przewalski horse (*E. ferus przewalskii*) (King 2002; Feh and Munkhtuya 2008). In addition to the stallion male and one to several females, the harem contains dependent offspring. Both sexes disperse on maturity, at approximately 2 years of age. In plains zebra, multiple harems form unstable herds, which may

also contain bachelor males (Rubenstein 1994). The membership of a harem remains stable for months to years. The females of plains zebra harems form stable dominance hierarchies in captivity (Pluhacek et al. 2006) and consistent leadership roles in the wild (Fischhoff et al. 2007a, b).

In equids, we can classify a continuum of aggression (Ginsberg 1988). Before any high-level aggressive acts, a pair of individuals will usually proceed through a series of escalating interactions (Rubenstein and Hack 1992). At the lowest level, we have supplants, and threats such as when an individual shakes its head at another, or moves towards it with ears back and head lowered. At the next level is kicking with one hind leg in the direction of a target individual, without necessarily making contact. If the contest escalates further, we may observe full-force kicking with both hind legs. Finally, zebras will chase each other, rear up to kick with forelegs, and attempt to bite the neck or hock of the opponent.

Aggression rates among wild female plains zebra have not, to our knowledge, been quantified in the scientific literature. Based on our field experience, aggression appears to be almost uniformly at a low level of intensity, for example, displacement without physical contact. Here, we provide the first description, and accompanying video, of a severe fight between two zebra. We explore possible explanations, both adaptive and pathological, for why this unusual fight may have occurred.

Description of fight

The fight occurred between two females in the same harem. We observed this encounter on 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, gathering data on associations, movement, and demography. We individually identify zebras based on their stripes. In periodic surveys of the population, we drive a set route through the reserve, searching for herds. When we encounter a herd, we record its spatial coordinates, habitat, and the phenotype and identity of each individual (Fischhoff et al. 2007a, b, 2009). We conduct a survey at an interval of typically 1 week, and ranging between 1 day and 1 month.

On July 14, 2005, during the course of a survey, we observed a foal which we believe had been born minutes before our arrival. The foal was lying on the ground, visibly wet. Zebras wet from rain typically appear dry soon after rain and cloud cover dissipate. Thus on a dry day like this one, it is likely that a newborn foal would remain wet with amniotic fluid only briefly.

We stayed to observe the behavior of the group and make a video record. Initially, we focused the video camera on the foal and its mother; as the females began to fight, we attempted to keep all three individuals in the frame. The 3 min, 30 s video is available as a Supplement (S1). As soon as we began recording, at 11:13 a.m. and less than a minute after our arrival at the scene, the foal attempts to stand up (S1, 0 min, 0 s). On standing, the foal is closest to a female, 2001_374, different from its mother, 2001_311 (Fig. 1). (Hereafter, we refer to these individuals as 374 and 311.) The mother is lying on the ground, while 374 is grazing.

This description highlights key events from the video. To further facilitate comparisons with other studies' results, we sample agonistic behaviors visible in the videotape. We record four behaviors: bite threat, bite, kick threat, and kick (Feist and McCullough 1976; Heitor et al. 2006). Bite threats are instances when one individual opens its mouth in the direction of the other, without making contact. Kick threats are defined as occasions when an individual raises one or more back legs and projects them backward, but again without making contact. In a bite or kick, contact is seen with mouth or hoof. In the case of bites, we further record the duration of contact between the aggressor's mouth and its victim. We compute the frequency of occurrence of each behavior, and mean bite duration, during the 3 min of fighting that we recorded.

At approximately 0:17 on the tape, the mother stands up, puts her mouth close to the ground, and appears to lick the soil. Female 374 then approaches and puts her face to the ground in the same place (0:24), interposing herself between the mother and foal. During this period, we observe the partially ejected placenta of 311.

Female 374 puts her head next to that of 311, then moves her head up so as to cause 311 to do the same (0:27–0:28). We frequently observe males engaging in such "nose-to-nose" interactions; this is a form of mutual

Fig. 1 A newly born foal attempts to stand. The individual lying on the *right* (partially visible) is the mother, female 311. Female 374 is standing and grazing on the *left*

Fig. 2 Female 311 (mother, *left*) and female 374 (*right*) both inspect foal

Fig. 3 Female 311 (mother, *right*) stands over her foal as female 374 (*left*) attacks the mother

evaluation in equids (Rubenstein and Hack 1992). The mother backs away, as 374 opens her mouth and attempts to bite her (0:32), the first aggressive act. As 374 bites the mother, the two make a tight circle that brings the mother between the foal and the attacking female (0:32–0:34). The attack further escalates as female 374 kicks at 311 with her hind legs (0:46–0:47). Through these actions, 374 maintains the position closest to the foal, while 311 appears to be attempting to move towards the foal, but fails to respond aggressively to 374. The foal attempts to get up, only to be knocked down by the fight (0:49–0:50).

As 374 briefly runs away, the mother, 311, stays behind and inspects the foal (0:52–0:53). The attacking female returns; for several seconds, both females put their noses next to the foal (0:54–0:56) (Fig. 2). She then recommences attacking the mother, pushing the mother so that she, in turn, knocks down the foal (0:57). The mother turns a circle around the foal and appears to push female 374 away with her body, then remains close to her foal (0:58–1:00).

Table 1 Summary of agonistic events during fight

Measure	Action	Actor	
		311	374
Count	Bite	1	11
	Bite threat	3	1
	Kick	4	6
	Kick threat	8	4
Rate (min^{-1})	Bite	0.3	3.7
	Bite threat	1.0	0.3
	Kick	1.3	2.0
	Kick threat	2.7	1.3
Duration (s)	Bite	1.0	10.4

We record all instances of bites, bite threats, kicks, and kick threats by the two fight participants. The observation period is 3 min of video from the first occasion of aggression to the end of the video. Female 311 is the mother of a newborn foal; female 374 is a harem-mate. Event rates are computed over the 3 min. Bite duration is the average over all bites for each actor

At 1:24, the mother moves away from 374 to stand by her foal and lick it (1:26–1:59), until interrupted by 374 charging in to resume her attack on the mother. The pair repeatedly circles around the foal. In Fig. 3, we see the mother standing directly over her foal, and blocking 374 from reaching the foal. Female 374 is biting the mother, while female 311 is in an aggressive posture, with ears down and with her rear legs situated so as to enable her to kick at 374.

During most of the last 2 min of footage 374 is biting at the mother's neck. As female 374 kicks, charges, and bites, the mother 311 generally responds by moving away from 374 and close to her foal. However, the mother also aggressively fights back on several occasions, attempting to bite (without contact) at 1:13 and 2:18, and kicking with back legs at 1:23 and 2:58.

At 11:18 a.m., 1 min after the end of the video, 374 stopped attacking the mother. We remained with the group for approximately five more minutes. During this time, 374 grazed while 311 grazed or licked her foal. Neither female nor the foal suffered any visible injuries.

No other zebras became involved in the fight. One other harem female and the stallion both briefly came within 10 m of the pair but did not make contact with them.

Summary statistics of agonistic events during fight

We provide summary statistics of agonistic behavior by both females during the fight in Table 1. We also provide the times of each agonistic behavior, as a data file (Supplement 2). The aggregate data are consistent with female 374 being the main aggressor and female 311, the mother,

being the victim. Female 374 bites and kicks more often than does female 311. When female 374 bites, she does so for longer periods; her longest bite lasted 42 s. Female 311 appears to be principally responding to the other's aggression: all aggressive acts by female 311 come either during a bite by female 374, or within 4 s of an agonistic behavior by 374. Female 311 is the more frequent actor of the lower-intensity agonistic behaviors: threatened bites and kicks.

Life history of fight participants

The two females were first seen in 2001, in separate harems. Female 311 was in the 6- to 12-month-old age class in 2001, and therefore approximately 5 years old at the time of the fight. Female 374 was already an adult by 2001, and therefore at least 7 years old in 2005. The pair was in the same harem from July 2003 until October 2005, 3 months after the fight. At this time, female 311 was observed with a serious injury to her left back leg. We believe she is now dead, as she was neither recorded with her harem when it was taken over by a new stallion nor seen with a new harem. Female 374 was last seen in March 2009 and so is plausibly still alive.

Neither female has a successful record as a mother. The newborn foal of female 311, described here, was absent when the harem was seen next, on August 2, 2005 (17 days later), and never observed again. Female 311 has had no other recorded foals. Female 374 has had one foal, following this incident. Female 374's foal was last seen at an age of less than 3 months in 2008. Our failure to sight it since suggests it has died.

Frequency of high-level aggression

Female aggression has not been a focus of our work on Ol Pejeta or elsewhere; therefore, we do not have an estimate of typical rates of aggressive acts such as bites or kicks. We have observed these events at other times, but have not recorded their frequency. However, bites, kicks or other aggressive acts are typically isolated events between plains zebra females. Normally, such an interaction would last for no more than several seconds, after which individuals return to other activities. Among females, this is our only observation of a continued series of escalated agonistic interactions.

If we consider the fight as a whole, rather than the constituent sequence of agonistic acts, then we can draw some conclusions about how rare such fights are, based on our long-term monitoring of the population. From July 2003 to March 2009, we have observed 4,470 independent zebra herds, as part of our regular survey protocol. Zebra herds are fluid associations among multiple harems, each harem being a relatively stable set of a stallion, several females, and their dependent offspring. If we tally the number of female observations over the 4,470 herds, then we have 19,457 contacts with females. We have individually identified 1,277 adult females. Most individuals have been observed in multiple herds, on different sampling days. We further assume that we observe each female in a herd for approximately 1 min, the time necessary to take her picture, record her reproductive state, and the identity of her stallion. Thus we have a total of 19,457 min, or approximately 320 h, of observations of females. We have observed one fight in 320 h of observation.

Discussion

Continued, violent fights occur regularly among male equids, but the female–female aggression we describe here is rare. This is the only major fight in our study of this plains zebra population, nor are we aware of other descriptions in the literature. Such extreme female aggression appears to be generally rare in feral or wild horses (Feist and McCullough 1976; Heitor et al. 2006; Rubenstein 1994) and captive plains zebras (Pluhacek et al. 2006).

The presence of a new foal seemed to be the precipitating event of the fight. The incident began following a close encounter between the foal and the aggressing female, as the mother lay a short distance away. Throughout the fight, the mother appeared intent on blocking the aggressor's path to her foal. Her threatened bites and kicks appeared to be defensive acts, attempts to ward off continued aggression by female 374.

The mystery about the fight is why the aggressing harem-mate responded to the foal and mother as she did, with such intense and prolonged aggression. Given what we believe to be the rare nature of this encounter, we do not assume that there exists an adaptive explanation. By exploring alternative explanations, we seek to understand why the fight took place.

One hypothesis is that the female 374 had the intent to harm or kill the foal of female 311. The foal was knocked down several times, and it is possible that it incurred injuries that contributed to its disappearance and presumed death in the weeks following the fight. Infanticide has the potential to increase the fitness of female 374, by reducing resource competition for her and her future offspring (Digby 2000). However, our close observation of the fight suggests that the female 374 was not directly aggressive toward the foal. On several occasions it came close to the foal and inspected it, rather than attacking (Fig. 2).

A second hypothesis is that this fight represents continuation of past conflict, or contest over dominance status. Immediately following birth, the mother may be unable to fight back effectively due to physical exhaustion and the need to attend to and protect her foal. If this hypothesis is correct, then we would expect to see such fights to be

initiated by lower-ranking females against a dominant female who is temporarily vulnerable, due to birth or illness. Repeated measures of aggression and dominance in wild zebras would be useful in testing this hypothesis.

Finally, and we believe most plausibly, we may imagine that female 374 mistakenly responded to the foal as her own offspring. Following this mistake, she was attempting to drive the real mother away from the foal. We had not observed female 374 as a mother prior to this incident. However, it is possible that she had a foal that we failed to observe, as we are aware that foals sometimes die within days of birth. At the time of the fight, survival rates during the first year of life were approximately 10–20% in this population (Fischhoff et al., unpublished data). If female 374 had experienced recent or repeated death of her own foals, she may have been more likely to mistake the new foal as hers. In the initial moment of the video, the foal is closer to the second female than to its mother (Fig. 1). The second female may have taken this as a cue that the foal was hers. The proximity of odors and tastes from the amniotic fluid and other hormones may have also been miscues to female 374 that she was the mother. The occasional display of such nonadaptive adoption may be an evolutionary tradeoff of the ordinarily adaptive urge to protect one's own offspring.

We have posited several alternative hypotheses for an adaptive basis for female 374's aggressive behavior. None is entirely convincing. The attacks may have been misplaced, pathological aggression, with origins in behavioral strategies that would be adaptive under different circumstances, or in the present context at a much lower level of intensity.

Over the course of a long-term study, researchers of animal behavior and ecology have the opportunity to witness rare, even aberrant, behavior. We believe that such rare events, combined with an understanding of typical behavior and sampling effort, can yield a richer picture of individuals' complex and dynamic motivations and relationships.

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