

Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation danger from lions

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Prey species must adapt their behavior to avoid predation. As a key prey item for lions (*Panthera leo*), plains zebras (*Equus burchelli*) were expected to respond to immediate threats posed by lions in their area. In addition, zebras were predicted to exhibit behavior tuned to reduce the potential for encounters with lions, by modifying their movement patterns in the times of day and habitats of greatest lion danger. We studied a population of approximately 600 plains zebra living in OI Pejeta Conservancy, Kenya. We found that zebra abundance on or near a grassland patch was lower if lions had also been observed on that patch during the same day. Predation danger was highest in grassland habitat during the night, when lions were more active. Zebra sightings and global positioning system radio collar data indicated that zebras also reduced their use of grassland at night, instead using more woodland habitat. Zebras moved faster and took sharper turns in grassland at night. It is hypothesized that these more erratic movements assist zebras in avoiding detection or capture by lions. *Key words*: antipredator behavior, habitat choice, ungulates. [*Behav Ecol*]

A central question in ecology is to what extent prey behavior and populations are determined by pursuit of resources versus avoidance of predation. Animals modify their habitat preferences and movement patterns to reduce their likelihood of being encountered or captured by predators (Bowyer et al. 1999; Fortin et al. 2005) while at the same time meeting their resource needs. As an important prey species for lions (*Panthera leo*) (Hayward and Kerley 2005), plains zebra (*Equus burchelli*) may offer insight into the ways in which predation shapes the behavior of prey. Plains zebras are grazers living in the savannah ecosystems of East and Southern Africa.

In a set of 3 adjacent, unfenced ranches, covering 500 square kilometers, zebra abundance within a ranch over a 1-week period inversely correlates with local predator abundance during that period (Rubenstein and Hack 2004). Such coupling of predator–prey population movements suggests that zebras can respond to specific threats by leaving areas after detecting predators. But zebras cannot always rely on detecting lions and moving away from them because lions are highly mobile and stealthy. Therefore, in addition to responding to immediate lion presence, zebras may also exhibit behavior tuned to reduce the potential for encounters with predators. To lessen the chance of being found by lions, we expect that zebras modify their movement patterns in the times of day and habitats of greatest predation danger.

In this paper, we examine 2 aspects of zebra antipredator behavior. First, we determine how zebras respond to the presence of lions in the immediate vicinity. The savannah landscapes inhabited by zebras are typically a mosaic of grassland and woodland areas. Spatial and temporal variation in danger arises as lions move among patches. If a lion group is on

a grassland patch, zebras can reduce their predation danger in the short term by avoiding this patch. Thus, zebras are predicted to move away from specific locations when lions move into the area.

Second, we hypothesize that zebras exhibit consistent responses to 2 environmental correlates of predation danger: time of day and habitat. In most areas, lions hunt principally at night, resting at other times (Schaller 1972). When lions do hunt during the day, they do so in bushier habitat that offers cover to hide behind (Elliott et al. 1977). The darkness of the night provides adequate concealment for lions, allowing them to hunt in open areas (Elliott et al. 1977; Funston et al. 2001). Darkness is expected to increase the danger of being in open areas for a zebra because lions are more likely to be present in these habitats at night. We expect zebras may therefore increase their use of bushy habitat at night. Zebras can greatly reduce their risk of being killed by avoiding encounters with lions. Over 75% of lion–zebra encounters result in lions hunting the zebra (Mills and Shenk 1992; Funston et al. 2001).

In choosing habitat, zebras must consider other needs besides safety. Zebras must continue finding forage and water while avoiding lions. Due to their digestion system of hindgut fermentation, zebras must graze frequently throughout the day and night (Janis 1976; Illius and Gordon 1992). Zebras spend about 60% of their time grazing (Neuhaus and Ruckstuhl 2002). Thus, they cannot simply move to a safe area and wait out lions. As grazers, zebras generally prefer grassland (McNaughton and Georgiadis 1986). We expect, however, that they modify this preference in response to temporal variation in lion habitat use.

In addition to spending more time in bushy habitat, zebras may alter their movements at night to reduce the probability of a lion successfully stalking them. At night, lions search for and stalk zebras actively, rather than waiting in one position as they do when hunting during the day (Schaller 1972; Elliott et al. 1977). By changing their location and trajectory frequently, zebras may decrease the likelihood of being caught by lions. Such movements may be more important in open

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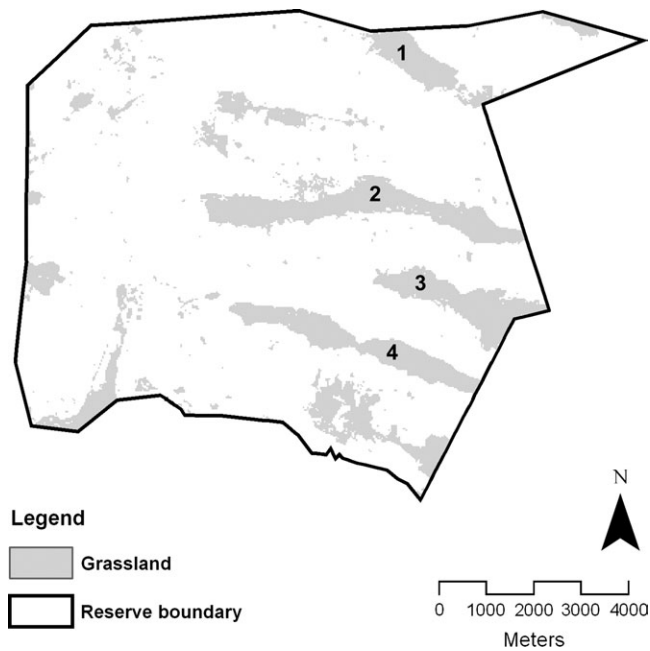


Figure 1
Map of study area showing habitat types. Dark areas are grassland and white is woodland. The surrounding line is the reserve boundary fence. Numbered patches are those used in analysis of zebra response to lion presence on a patch.

habitat where zebras and lions are more likely to encounter each other. We may expect higher potential encounter rate between zebras and lions on grassland due to lions' frequently observed preference for hunting in the open at night (Elliott et al. 1977; Funston et al. 2001). Zebras are expected to primarily use grassland during both day and night because they are grazers.

MATERIALS AND METHODS

Study site and species

We studied a population of approximately 600 plains zebras in the 90 km² Sweetwaters Reserve of Ol Pejeta Conservancy (0°00'N, 36°56'E). Sweetwaters is a semiarid bushed grassland in the Laikipia ecosystem of central Kenya. At the time of the study, an elephant-proof fence prevented zebras from leaving or entering the reserve. Average annual rainfall for the period 1996–2004 was 726 mm (standard deviation = 229 mm) (Ol Pejeta Conservancy records). Most rainfall occurs in April or November.

For our habitat map, we used a ground-truthed 2002 Landsat image that was classified into 5 vegetation types (Ol Pejeta Conservancy GIS database, 2004). For the present paper, we defined 2 habitat types: woodland and grassland. Woodland included 3 vegetation types (thick bush/riverine forest, medium bush, and light bush), whereas grassland included 2 types (open grassland and short grass) (Figure 1). Based on this classification, 18.6% of the total area was grassland and the rest was woodland. The grassland areas ranged in size from less than a hectare to 600 hectares. Dominant grass genera were *Cynodon*, *Themeda*, and *Pennisetum*. Between the grassland patches were *Acacia* and *Euclea* woodlands.

Plains zebras are large-bodied (~200 kg) grazing ungulates inhabiting grasslands of East and Southern Africa. They drink approximately once every day. The core social group is the harem composed of 1 stallion male and 1–8 females, as well as

their dependent offspring. Males and females disperse at sexual maturity. Males join bachelor groups until they acquire a harem of their own. Multiple harems form unstable herds, which may also contain groups of bachelor males (Rubenstein 1994).

Sampling methods

We gathered zebra data using both global positioning system (GPS) radio collars and direct observations. We used radio collar data to analyze habitat preferences and movement properties. In July 2005, we radio collared 4 adult zebras, including females in 3 harems and 1 bachelor male. July was a month in the middle of the dry season. The collars were prototypes of a novel design (Zhang et al. 2005). We programmed the collars to record displacements of less than 10 m as a displacement of zero to account for GPS error. The units provided GPS fixes every 8 min. Due to technical failures, the radio collars stopped collecting data after 4–15 days (Bachelor: 9 days, 1064 locations; Female 1: 15 days, 655 locations; Female 2: 11 days, 1899 locations; Female 3: 4 days, 481 locations).

While functioning, the collars occasionally missed fixes when their solar-charged batteries were in a depleted state. We excluded all observations more than 8 min from the previous location. We computed step length and turning angle between successive locations. Step length is the straight line distance between successive locations. Turning angle is the angle subtended by 2 successive steps. A turning angle of zero indicates no change in direction, whereas a complete reversal in direction results in turning angle of 180°. We assigned positive values to right turns and negative values to left turns. We computed turning angle only for successive steps that both had nonzero displacement.

Before using the radio collar data to analyze habitat use and movement patterns, we subsampled the data by time to remove autocorrelation in step length or turning angle. We first parsed the data for each individual into paths defined as a sequence of steps uninterrupted by any intervals greater than 8 min. For each path, we determined whether there was significant autocorrelation in step length or turning angle (Turchin 1998). We examined autocorrelation in turning angles using a runs test on successive turns. We classified turns as either left or right (Turchin 1998). We computed the step length autocorrelation function (ACF) for lags of up to 6 time steps. We calculated the Ljung-Box Q statistic to determine if there was significant autocorrelation. When we found significant autocorrelation in a path, then we systematically subsampled the data at increasing time intervals of 16, 24, 32 min, and so on until 80 min. We then calculated the ACF and Q statistic for each subsampled path to determine whether there existed a minimum subsampling interval that yielded a path without autocorrelation. This analysis indicated that no path contains autocorrelation beyond 32 min. Therefore, we subsampled data for each individual so that points were no less than 40 min apart. We assumed the resulting data points were independent with respect to habitat choice as well as movement properties.

To test how zebras respond to lion arrival on a plain, we used only direct lion and zebra sightings. Every 3 days, we drove sampling loops for zebras throughout the field site. For each herd of zebras, we recorded group size and identified all individuals. We were able to distinguish individuals based on their unique stripe patterns. Lion data included our own chance encounters while driving zebra loops. To these data, we added lion observations by both Ol Pejeta rangers and Ol Pejeta tour guides. The rangers walked all areas of the reserve daily. Ol Pejeta operated night game drives for tourists on most nights. Ol Pejeta staff also recorded location, date, and time of all lion sightings. All lion sightings

were assigned northing and easting in the field or subsequently, based on local names that were accurate to within 100 m. The lion population on Sweetwaters during the study period ranged from 20 to 30 (Ol Pejeta Conservancy, unpublished data). For both species, the data presented here were from July 2003 to August 2005.

Analysis

Zebra response to lion presence

To test if zebra tended to abandon an area when lions arrive, we compared the numbers of zebras using a patch on a day when we observe lions in that patch to zebra abundance on days when we did not find lions in that patch. We defined a grassland patch as an area of the reserve containing a large ($>1 \text{ km}^2$) polygon of contiguous grassland pixels in the habitat map (Figure 1). We considered small polygons near a large patch to be part of that large patch. We used zebra sightings from 4 patches, numbered in Figure 1.

We assigned lion and zebra sightings to a patch if they were on or within 100 m of the patch. Because all the individuals in a zebra harem move together, we used stallions as representatives of their harem. We assumed that each bachelor male sighting was independent. To test for the effects of lion presence on zebra numbers, we used a 2-way mixed model analysis of variance (ANOVA), with lion presence as fixed effect and patch as random effect. We included 324 counts of zebra on a patch. For 90 of these, we observed at least one lion on that patch on the same day.

Lion activity by time of day

To evaluate whether Sweetwaters lions were more active at night than during the day, we computed a frequency distribution of lion observations by hour. We assumed that the number of sightings in an hour provided a reliable index of lion activity in that period. We limited this analysis to the hours between 0600 and 2300, when people were awake in the reserve. Over this period, sampling effort may not have been equal between daylight and nighttime hours. Effort was likely to be greater during the day than at night, when only several tourist vehicles operated. Thus, there may have been a bias against lion sightings at night.

Habitat use in day and night

We tested for variation in habitat use between day and night for zebras and lions. The 24-h day was divided into daytime (0600–1800) and nighttime (1800–0600). For lions, we assigned observations to a habitat by matching GPS coordinates to pixels in the habitat map. We assumed the proportion of observations in a habitat was a suitable index of habitat use. For zebras, we similarly assigned radio collar locations to habitats. We used an equal number of observations for each individual. We found the individual with the fewest observations and then randomly selected an equal number of observations from the 3 other individuals. For each species, we counted the number of observations in day and night for each habitat. We used chi-squared tests to evaluate whether habitat use was independent of time period.

We characterized fine-grained temporal variation in zebra habitat use. We plotted the fraction of radio collared zebra sightings in grassland by time of day. For each hour and each individual, we found the fraction of locations that are in grassland. We then computed and plotted the mean fraction across the 4 individuals.

Zebra movement patterns in day and night

Within each habitat type, we compared speed and turning angle of radio collared zebras between day and night. The

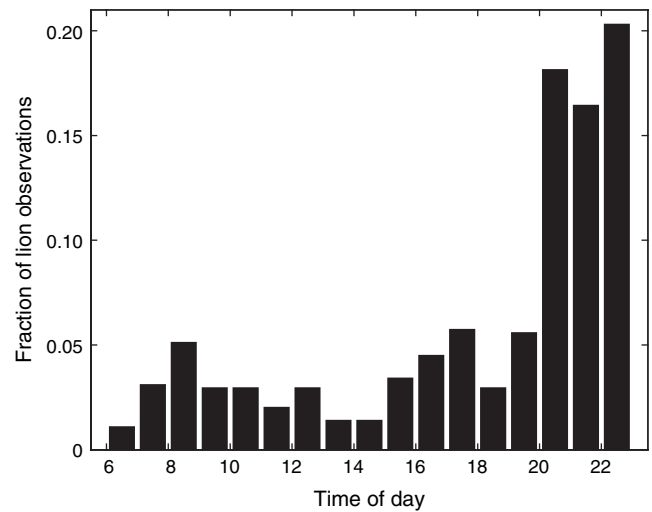


Figure 2

Lion activity by time of day. The plot shows the proportion of lion observations within each of the hours from 0600 until 2300. Lions are observed more frequently after 1800, which suggests that lion activity increases after sunset.

displacement and turning angle values we used were those over the preceding 8-min period of each location that remained after subsampling. For each habitat, we tested how time of day correlated with movement by comparing speed and turning angle distributions between day and night. We used absolute turning angle values, having first determined that turning angles were symmetric around zero using a modified Wilcoxon signed rank test (Fisher 1993). We used permutation *t*-tests because the data did not fit a normal distribution (Good 2000). This test provided an estimate of the difference in the means as well as the 95% confidence interval around this mean.

RESULTS

Response to lion presence

Zebra abundance on a patch was significantly lower on days when lions were also observed on that patch than on days when no lions were observed (mixed model ANOVA, fixed effect, $F_{1,7.05} = 9.44$, $P = 0.02$). We found no evidence for an effect of patch on zebra abundance (mixed model ANOVA, random effect, $F_{3,3} = 0.73$, $P = 0.60$).

Lion activity by time of day

The data showed that lions were most often recorded after 1900 (Figure 2). Over 60% of all lion sightings ($N = 670$) were at night between the hours of 1800 and 2300. Any bias due to sampling effort would tend to reduce the number of our lion sightings at night, when observers were less active. We confirmed that lions were more active at night, as found in other studies (Schaller 1972; Elliott et al. 1977; Funston et al. 2001).

Habitat use by time of day

Comparing night with day, lions shifted toward greater use of grassland at night, whereas zebras increased their use of woodland (Figure 3). Lion habitat use significantly differed between day and night ($\chi^2 = 45.3$, $P < 0.001$, $N_{\text{day}} = 234$; $N_{\text{night}} = 419$). During daylight hours, 43.6% of lion observations were in grassland, whereas at night, 70.4% were in grassland.

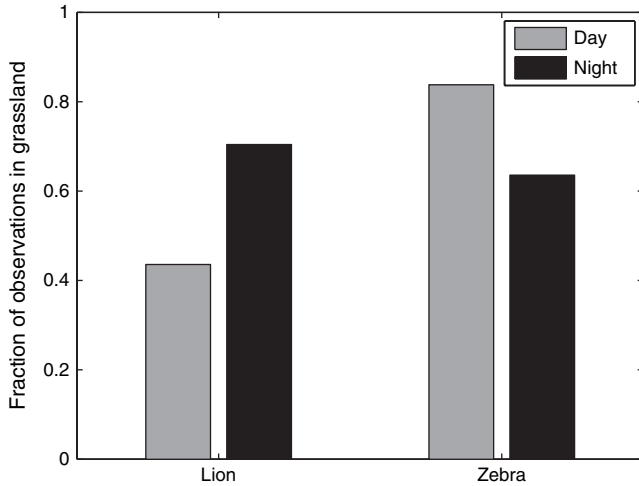


Figure 3 Lion and zebra habitat use by time of day. The plot shows the proportion of observations in grassland during daylight hours (0600–1800) and at night (1800–0600) for both species. Lion data are direct observations from chance encounters, whereas zebra data come from GPS radio collars worn by 4 individuals. Lions increase their use of grassland habitat at night, whereas zebras do the opposite.

Zebra habitat use also varied significantly by time of day ($\chi^2 = 17.0$, $P < 0.001$, $N_{\text{day}} = 183$; $N_{\text{night}} = 153$). In both day and night, zebras used grassland more than they used woodland. However, the percentage of grassland locations decreased from 83.8% in the daytime to 63.6% at night.

In Figure 4, we plotted the fraction of grassland use for each hour of the day, averaged over the 4 radio collared individuals. We noted a precipitous drop in grassland use in the hours between 1600 and 2000. This corresponds to the hours just before and after dusk. Later in the night, grassland use increased, although it remained lower and more variable than during other parts of the day.

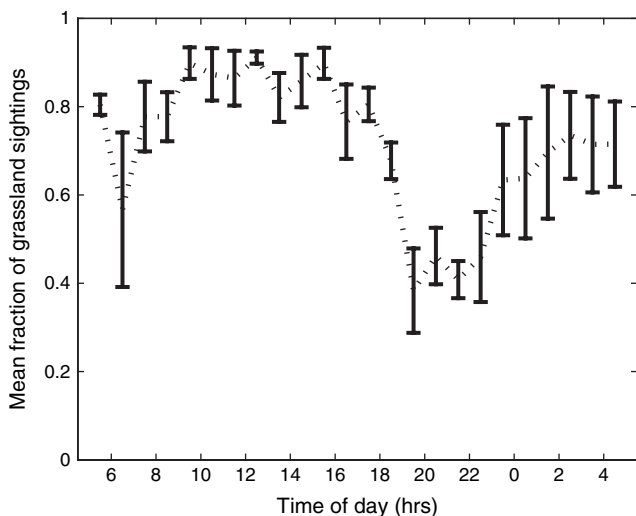


Figure 4 Mean proportion of zebra grassland locations by time of day. For each of 4 radio collared individuals, we compute its average fraction of grassland sightings in each hour of the day. We then compute the average proportion for each hour, across the 4 individuals. Error bars are standard errors around the mean for the 4 zebras.

Movement patterns by time of day in grassland and woodland

Zebras moved differently depending on time of day in grassland, but not in woodland. In grassland, zebras moved faster and took sharper turns during the night than they did in the day. Speed in grassland was significantly higher at night (mean = 0.77 km/h, $N = 100$) than in the day (mean = 0.45 km/h, $N = 155$) ($P = 0.004$, difference in means = 0.32 km/h, 95% confidence interval [CI] 0.12 to 0.51). Turning angle was significantly higher at night (mean = 71.2°, $N = 58$) than during the day (mean = 48.3°, $N = 81$) ($P = 0.016$, difference in means = 22.9°, 95% CI 4.5 to 39.1). Within woodland, we found no evidence for differences between day and night in speed ($P = 0.80$, difference in means = 0.06 km/h, 95% CI -0.48 to 0.56) or turning angle ($P = 0.42$, difference in means = 15.0°, 95% CI -50.9 to 22.3). Mean speed for woodland during the day was 0.59 km/h ($N = 28$) and at night 0.54 km/h ($N = 53$). Turning angle during the day averaged 45.4° ($N = 14$), whereas the mean at night was 60.5° ($N = 21$).

DISCUSSION

Prey species' responses to predation threat shape many ecological processes: population distribution (Lima and Dill 1990; Heithaus and Dill 2006), resource exploitation by prey (Fortin et al. 2005), and vital rates (Bleich 1999). We may expect that zebras, as a species that experience high predation (Grange et al. 2004), modify their behavior in ways that reduce their exposure to predators. In this paper, we have examined variation in zebra movements and habitat use in relation to danger from lions. First, we investigate zebra response to the specific threat of lion presence in an area used by zebras. Second, we ask whether zebras behave differently at night, when lions are more active.

Our data show that zebras avoid grassland patches where and when lions are present. By avoiding areas in current use by lions, zebras can reduce their chances of encountering their chief predator. In avoiding lions, zebras may be directly perceiving them or responding to cues of other animals. Abandonment of patches used by lions may be an important cause of zebra movement among grass patches. We may expect that lions, in turn, move to patches where zebras are abundant, resulting in cyclical redistribution patterns in both species. Such coupled movements of predator and prey may shape the temporal pattern of zebras' herbivory on a forage patch.

As found for other populations, Sweetwaters lion activity peaks at night (Figure 2). Lions also shift their habitat use from woodland to grassland at night. We find that zebras make an opposite, but incomplete, change in habitat use at night, increasing their use of woodland. Although zebras generally prefer grassland areas, their change in behavior at night may result in reduced lion encounters. Zebras' shift away from grassland begins soon before dusk. This is consistent with the hypothesis that zebras are moving away from the preferred nighttime habitat of lions as a precautionary measure rather than in direct response to pursuit by lions. Over the entire night, the radio collared zebras continued to spend a majority of their time in grassland. This reflects their need to feed continuously, although this may increase their risk of predation.

Zebras' movements at night involve greater speed and sharper turns, in grassland but not in woodland. We suggest that zebras' more rapid and erratic nighttime movements on grassland are a response to heightened danger from lions. Lions hunt at night by active searching rather than lying in

concealment as they do during the day (Elliott et al. 1977). By moving as they do in grassland, zebras may reduce the probability that lions will be able to successfully stalk or capture them, once found. Lions are generally not able to catch a zebra if it has more than a 5-s head start in running away from the lion (Elliott et al. 1977).

We find no evidence for change in zebra movements in woodland between day and night, in contrast to their grassland movements. We hypothesize that this habitat difference is a result of zebras' greater conspicuousness to lions in grassland than in woodland, at night. Under low light conditions, the vision of nocturnal hunters such as lions may be superior to that of zebras. This visual advantage for lions may have greater effect on their ability to find zebras, before zebras detect them, in grassland than in woodland. In woodland, vegetation offers both zebra and lion concealment. At night, darkness is all the concealment that a lion needs, so it hunts in open areas where it can steal up on prey without being seen (Elliott et al. 1977). For zebras, woodland habitat may become more attractive at night because lions tend to hunt in the open. Within woodland, we detect no change in movement style between day and night. If zebras were to move more quickly or erratically in woodland at night, we hypothesize this would make them more conspicuous to lions, without aiding zebras' ability to detect lions through the thick bush.

It is likely that by moving faster, and turning more sharply, zebras are reducing their efficiency in grazing on the grasslands. We would expect grazing zebras to move less. Thus, it appears unlikely that zebras that modify their movements in this way do so to gain resources. Zebras' need to continually graze, even at night, may be expected to impose constraints on the extent to which they can modify their behavior in reaction to lions. We note that our radio collar data come solely from July, when forage is widely available throughout the reserve. July is typically about 2 months following the April rainy season and 3 months before the November rains. It is possible that seasonal variation in grass quality and quantity may change the trade-offs that zebras make between finding food and staying safe.

Behaviors that may be adapted to evade predators, such as those patterns described here, are an important component of predator-prey population dynamics and have implications for conservation. Variation in how individuals respond to predation danger may shape variation in survival. Thus, antipredator movement strategies may mediate effects of predation on population trajectories. In communities with diverse prey assemblages, such as African savannahs, interspecific variation in prey behavioral responses to predation may contribute to prey choice. It is possible that human activities, such as tourism or use of waterholes, may increase ungulates' predation risk by preventing them from using effective antipredator movements. For example, in the congeneric Grevy's zebra (*Equus grevyi*), temporarily fencing off waterholes for livestock during daytime has been suggested as a cause of increased foal mortality because Grevy's zebra must then drink at night when lions are more active (Williams 2002).

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