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Stable isotope ecology of the endangered Grevy's zebra (*Equus grevyi*) in Laikipia, Kenya

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12/24/10

Abstract

Once common in East Africa, Grevy's zebras (*Equus grevyi*) are now highly endangered for unknown reasons. They share habitat with Plains zebras (*Equus quagga*), which are ecologically similar but not endangered. We suspect that previously unobserved diet differences may be involved in the two species' differential conservation status. This study used $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ stable isotope ratios in tail hair samples of Grevy's and Plains zebras from Laikipia, Kenya to examine these differences. Additionally, three locations with different levels of livestock were compared to see whether livestock presence significantly alters Grevy's diet. I found the first recorded evidence for resource partitioning between Grevy's and Plains zebras. I also found that Grevy's graze significantly less and browse more when livestock are present. Continued overgrazing by livestock could expedite decline of Grevy's zebra populations. I recommend analysis of current management policy and revision to instigate more sustainable livestock farming practices.

Introduction

Analysis of stable isotope ratios in animal tissues is a useful method of obtaining information about the diet of both extinct and extant wildlife (Koch 2007). Although the dietary preferences of extant species can be observed directly in the wild, limitations often render the results of such studies incomplete (Cerling *et al.* 2009). Stable isotope analysis not only provides an alternative to observation in these difficult cases, but can also provide dietary information with a greater level of detail than even the best observational studies. Stable isotope analysis of animal hair can be especially constructive, as it provides a geochemical chronology of diet (Cerling *et al.* 2009). These methods can be used to increase understanding of ecology and physiology of wildlife species or for pinpointing otherwise hidden factors involved in conservation of threatened or endangered species.

Grevy's zebras (*Equus grevyi*), the largest extant zebra species, were once populous and widely distributed throughout much of East Africa. However, this species has declined by over 75% since the 1970s and is now listed as endangered by the International Union for Conservation of Nature (IUCN) and Appendix 1 of the Convention on International Trade in Endangered Species (CITES) (Sundaresan *et al.* 2007; Moehlman *et al.* 2009). Geographically, Grevy's zebras are now present only in isolated locations in Ethiopia and Kenya (Moehlman *et al.* 2009). The cause of this decline is largely unknown; plausible contributing factors may include hunting and diseases such as Anthrax as well as overgrazing and degradation of habitat and resources by farmed livestock (Muoria *et al.* 2007; Sundaresan *et al.* 2007). Because zebras have diets more similar to cattle than any other wildlife species in the East African savannah, zebras are potentially very vulnerable to such overgrazing pressure (Casebeer & Koss 1970). Young *et al.* (2005) showed that zebras in Laikipia, Kenya, use habitat shared with livestock nearly 50% less than livestock-free land. This suggests that zebra dietary needs are not met in overgrazed areas, and that livestock grazing pressure could be related to the decline of Grevy's zebras in East Africa.

Although Grevy's zebras have declined over 90% in Ethiopia (Williams *et al.* 2003), one area where they have managed to retain concentrated populations is the Laikipia-Samburu region of central Kenya (Sundaresan *et al.* 2007). In this area, Grevy's zebras co-habit much of their range with a smaller equid relative, the Plains zebra (*Equus quagga*, formerly *Equus burchelli*). To our present knowledge, Plains zebras have similar social and feeding habits to Grevy's zebras, but are not endangered. Both Plains and Grevy's zebras live in semi-arid savannah regions and have long been assumed to be hyper-grazers, meaning that they eat only grass and no browse (herbaceous or woody plants) at all (Fischhoff *et al.* 2007; Sundaresan *et al.* 2007).

However, apart from casual observation, this assumption has remained unconfirmed. Because both of these species appear to occupy similar habitats, but one has maintained a healthy and stable population whereas the other is highly endangered, we must consider the possibility that present assumptions regarding ecological factors such as diet might be incomplete. I suggest that some difference in diet between Plains and Grevy's zebras may be responsible for or be involved in their differential conservation status.

Several different plant types grow in the semi-arid savannah habitat where Grevy's and Plains zebras live, each of which contain different amounts of the stable isotopes ^{13}C and ^{15}N . Depending on how the proportion of each plant type an animal eats, different proportions of these isotopes relative to ^{12}C and ^{14}N are stored in the animal's hair. Therefore, the ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ can provide information about the diet composition of herbivores (Cerling *et al.* 2009).

Plants in the East African savannah consist of two isotopically distinct photosynthetic classes, called the C_3 and C_4 pathways. These pathways result in fixation of different ratios of $^{13}\text{C}/^{12}\text{C}$ in tissues of animals that eat them. C_3 plants such as trees, herbs and shrubs fix a lower ratio of $^{13}\text{C}/^{12}\text{C}$, are also distinguished by their tendency to leave their stomata open at all times, and thrive in shady, low light woodland areas. C_4 plants such as savannah grasses fix a higher ratio of $^{13}\text{C}/^{12}\text{C}$, can open or close their stomata, and are more tolerant to heat and desiccation than C_3 plants. Depending on the $^{13}\text{C}/^{12}\text{C}$ ratio, zebra hair can show the distinct geochemical signature of a browser (C_3 -eater), a grazer (C_4 -eater), or a mixed feeder (Cerling *et al.* 2009; Koch 2007; Koch *et al.* 1991). Additionally, nitrogen isotope values in tail hair reflect whether any C_3 material eaten consists of plants that do or do not fix nitrogen from the atmosphere.

This study uses stable carbon and nitrogen isotope analysis to determine how much of Grevy's zebra diet in the Laikipia region of Central Kenya is composed of graze (grass) and browse (tree, shrub, and herb) material. The diet composition of Grevy's zebras are compared across three locations in Laikipia with differential, increasing livestock presence (Lewa Wildlife Conservancy, Mpala Research Centre and Wildlife Foundation, and Westgate unmanaged community lands) in order to investigate the impact of livestock grazing pressure on Grevy's diet. Additionally, the diet compositions of Grevy's and Plains zebras are compared at Mpala Research Centre where they co-occur. I hypothesize that Grevy's zebras will eat primarily C₄ grass material in areas with low grazing pressure from livestock, and will have a mixed diet with a higher proportion of C₃ grass in areas with heavy livestock grazing pressure. Additionally, I hypothesize that Grevy's and Plains zebras will exhibit some difference in diet composition, indicating that they resource partition when co-occurring.

Materials and Methods

This study was conducted in collaboration with Siva Sundaesan at Princeton University and the Equid Research and Conservation Project at the Denver Zoological Foundation. Samples of *Equus grevyi* and *Equus quagga* tail hair were collected by collaborative researchers at Mpala Research Centre and Wildlife Foundation, Lewa Wildlife Conservancy, and nearby Westgate community land in the Laikipia region of central Kenya (Fig. 1). Samples were collected between October 2005 and February 2010 from individuals captured or found dead for a variety of reasons, including being killed by predators or captured for trial vaccines or GPS collar attachment. The sample size for each species and location was as follows: 5 Plains and 7 Grevy's individuals at Mpala, 7 Grevy's at Lewa, and 3 Grevy's at Westgate. Because lactating zebra

females are known to have unique dietary preferences, only non-lactating females and territorial males were used for this study (Sundaesan *et al.* 2007).

Because equine species tend to grow their tails about 2 mm per month (Dunnett 2001), approximately 2 cm of hair was clipped from the base, middle, and tip of the tail of each study animal in order to get samples that represent diet during different times throughout the year. The samples were homogenized and weighed to between 0.70 – 0.80 mg. Samples were sent to the stable isotope laboratory at the University of Santa Cruz (<http://es.ucsc.edu/~silab/index.php>) for analysis to obtain values for the C^{13}/C^{12} ($\delta^{13}C$) ratio and N^{15}/N^{14} ($\delta^{15}N$) ratio in the hair samples.

Resulting $\delta^{13}C$ and $\delta^{15}N$ values were analyzed using the SIAR model (Stable Isotope Analysis in R) (Parnell *et al.* 2010) to obtain the proportions of C_4 , C_3 fixing and C_3 non-fixing plants in the diet of each sample. $\delta^{13}C$ and $\delta^{15}N$ values from each hair clipping were treated as separate samples, meaning that each individual zebra was represented three times in the sample (as the base, middle, and tip of the tail). This is justified by the fact that different parts of the tail represent different periods of time throughout the year, and since diet of most savannah herbivores varies temporally, each tail clipping should represent a distinct diet composition (Dunnett 2001; Cerling *et al.* 2009).

A one-way ANOVA was performed to test for significant difference between the proportion of C_4 grass in the diets of Grevy's and Plains zebras at Mpala Research Centre using the bottom 5% error margin of the proportions yielded by the SIAR model. Similarly, a one-way ANOVA (also using the bottom 5% error margin of proportions from SIAR) was performed to test for a significant difference in proportion of C_4 in the diets of Grevy's zebras across three areas with varying livestock grazing pressure: Lewa Wildlife Conservancy (no livestock), Mpala

Research Centre and Wildlife Foundation (managed livestock farming), and Westgate community land (heavy and unmanaged livestock farming).

Results

Interaction of Grevy's and Plains zebras at Mpala Research Centre and Wildlife Foundation

At Mpala Research Centre and Wildlife Foundation, both Grevy's and Plains zebras ate primarily C₄ grass (greater than 80%) and very little C₃ browse (Fig. 2, 4). However, Plains zebra diet contained a significantly higher proportion of C₄ grass than Grevy's zebra diet (Fig. 2, 3, 4; One-way ANOVA; $F_{1,11}=56.234$, $P<0.001$). Additionally, while Plains zebras all had high $\delta^{13}\text{C}$ of a narrow range in between -10 and -11.5, Grevy's zebras had a significantly higher variance of $\delta^{13}\text{C}$ values between -10 and -14.5. (Fig. 3; Levene's test of equal variances: $P<0.001$).

Impact of livestock on Grevy's zebra foraging ecology

In the absence of livestock at Lewa Wildlife Conservancy, Grevy's zebra diet was almost entirely made up of C₄ grasses (Fig. 5, 6, 7). At Mpala Research Centre in the presence of light managed livestock, 90% of their diet still consisted of C₄ grass but they ate a slightly higher proportion of C₃ browse than they did at Lewa (Fig. 5, 6, 7). In the Westgate community land in the presence of high levels of unmanaged livestock, Grevy's zebras ate approximately half C₄ grass and half C₃ browse (Fig. 5, 6, 7). Grevy's zebras ate significantly less C₄ grass with increasing livestock presence (One-way ANOVA: $F=6.148$, $P<0.005$).

Discussion

Grevy's zebra diet composition

This study shows that while Grevy's zebras (*Equus grevyi*) in Laikipia prefer to eat grass, they also eat browse material, and under certain conditions will eat a fairly high proportion of browse (Fig. 5, 6, 7). This is the first geochemical evidence that this species browses at all, which is to some extent surprising since until recently this species has been assumed to be an exclusive hyper-grazer eating almost exclusively grass. However, previous studies of Grevy's zebra habitat preference in Laikipia have indicated that even in areas such as Mpala Research Centre and Wildlife Foundation with plenty of lush grassland, they do tend to spend some time in shrubland as well as grassland (Sundaresan *et al.* 2007). Thus, the fact that they eat some browse material is not entirely unexpected.

Sundaresan *et al.* (2007) also showed that use of shrubland versus grassland differed with reproductive class among Grevy's zebras, with non-lactating females and territorial males spending more time in shrubland than lactating females and bachelors. Most likely, this trend was due to non-lactating females and territorial males sacrificing the higher nutrient quality of forage in grassland for the safety afforded by crypsis in shrubland (Sundaresan *et al.* 2007). The present study analyzed only territorial males and non-lactating females, and the results likely show a higher proportion of browse in diet than if all reproductive classes had been used. While the present analysis of non-lactating females and territorial males is probably the most generally informative sample within Grevy's zebra demography, it is also important to understand the foraging ecology of lactating females because of their importance for recruitment. Therefore, it may be useful in the future to repeat the analyses of this study for lactating females. Additionally, this analysis should be repeated with a larger sample size of Grevy's individuals.

Interaction of Grevy's & Plains zebras at Mpala Research Centre & Wildlife Foundation

The results of this study show that Plains zebras (*Equus quagga*) eat significantly more C₄ grass than Grevy's zebras (*Equus grevyi*) when the two species co-occur as in Mpala Research Centre and Wildlife Foundation in Laikipia (Fig. 2, 4). This is the first geochemical evidence of resource partitioning between these two species. This confirms our hypothesis that there are subtle but significant differences in the diet between these species, which is expected for several reasons. One is that evolutionarily, it is highly unusual for two reproductively isolated species such as Plains and Grevy's zebras to share a range and to also exhibit identical feeding patterns. Additionally, because Grevy's zebras are highly endangered while Plains zebras are not, it seems likely that their differential success in the same range must reflect some difference in ecology that makes Grevy's zebras more sensitive than Plains zebras to environmental change.

As discussed above, recent studies have indicated that Grevy's zebras may eat browse material due to their occasional use of shrubland for safety purposes (Sundaresan *et al.* 2007). However, Plains zebras are also known to spend time in shrubland in order to avoid predation by lions (Fischhoff *et al.* 2007). However, Plains zebras are generally only found in woodland areas at night, when they are less likely to be feeding than during the day (Fischhoff *et al.* 2007). The study examining Grevy's zebra habitat use did not indicate the time of day at which Grevy's were more likely to be found in shrubland (Sundaresan *et al.* 2007). Since it was not otherwise specified, presumably the study took place during the day. In this case, we can conclude from these studies that while both species use shrubland at times, Plains zebras only use it for safety at night and likely feed very little there, while Grevy's zebras use it during the day as well and likely do feed there. While further study is needed to confirm this pattern of nighttime versus

daytime habitat choice between the two species, it could help to explain the resource partitioning indicated by the present study. Additionally, it could indicate other environmental conditions that make it necessary for Grevy's, but not Plains, zebra to sacrifice high quality grass forage for the safety of shrubland during the day.

Another trend found by this study was that Grevy's zebras had a significantly more variable diet between individuals than Plains zebras did (Fig. 3). The reasons for this trend are unclear. It is possible that Grevy's zebras are more capable of digesting a wider range of plant material than Plains zebras, which could actually be an advantage in a situation in which grass is limiting. However, because Plains populations are more stable than Grevy's, this seems unlikely. More probably, this difference in variation of diet composition reflects that Grevy's zebras are more affected by changes in environmental conditions throughout their range and throughout the year than are Plains zebras. Therefore, Grevy's zebras may be more likely to resort to eating browse material under adverse conditions.

This analysis should be repeated and expanded with a larger sample size of both zebra species. Additionally, in order to understand whether Plains and Grevy's zebras are differently affected by livestock grazing pressure, it would be useful to compare Plains zebra diet across locations with varying livestock presence as was done in this study with Grevy's zebras. Furthermore, the comparison of diet composition of Plains and Grevy's zebras should be repeated in an area with no livestock (such as Lewa Wildlife Conservancy) to see whether resource partitioning is as strong as at Mpala Research Centre. Combining these results with those of future research efforts may provide much insight into the reasons behind the differential conservation status of Plains and Grevy's zebras in Laikipia and other parts of East Africa.

Impact of livestock on Grevy's zebra foraging ecology

This study showed that Grevy's zebras eat significantly less grass (and therefore more browse) in areas with a greater livestock presence (Fig 5, 6, 7). This is likely due to the difference in grazing pressure from livestock across these areas resulting in different amounts of available grass. Lewa Wildlife Conservancy is a very lush area with lots of available grass, and in this area Grevy's zebras ate almost entirely grass. Westgate community lands, on the other hand, is heavily overgrazed, and in this area Grevy's zebras diet was made up of only about 50% grass. At Mpala Research Centre, which contains some managed livestock but still has lush grasslands, Grevy's zebras ate somewhat less graze than at Lewa, but still very little browse compared to Westgate (Fig. 5, 6, 7).

We can conclude from these results that heavy, unmanaged livestock presence has a negative impact on Grevy's zebra diet. These findings are reinforced by other studies which indicate that Grevy's zebras avoid areas containing livestock whenever possible (Young *et al.* 2005; Sundaresan *et al.* 2007). Additionally, Williams (1998) showed that Grevy's zebras compete with cattle for access to waterholes, which could be an additional way not addressed by the present study that livestock negatively impact this endangered species. Because of this competition with livestock, in such overgrazed areas as Westgate, Grevy's zebras are probably not getting as high quality of nutrients as they do when they eat their preferred diet of mostly grass. This reduction in nutrition could be a factor contributing to the decline of this species. This strongly suggests that continued overgrazing by livestock in East Africa may facilitate further Grevy's zebra population decline.

Awareness of Grevy's zebra conservation in Kenya has notably increased during the past decade, and some conservation efforts have begun to form (Kenya Wildlife Service 2009; Low *et*

al. 2009). Strategies thus far have included the establishment of protected areas, and attempting to strengthen community infrastructure within the Grevy's range in order to enable projects such as construction of new water sources to decrease competition with livestock (Kenya Wildlife Service 2009). Additionally, inclusion of community members within Laikipia in monitoring studies can help to increase local awareness and economic interest in conservation efforts (Low *et al.* 2009).

However, the benefits of some of these efforts may be reaching only a very small portion of the Grevy's zebra population. For instance, only 0.5% of Grevy's zebras live within protected areas (Moehlman *et al.* 2009). The results of this study show that the interaction between Grevy's zebras and livestock overgrazing may be highly significant in terms of Grevy's zebra conservation. I recommend redirecting the focus of future management efforts toward the development of sustainable livestock farming practices, which could potentially greatly benefit Grevy's zebras in Laikipia and other areas of East Africa.

Figures and Tables

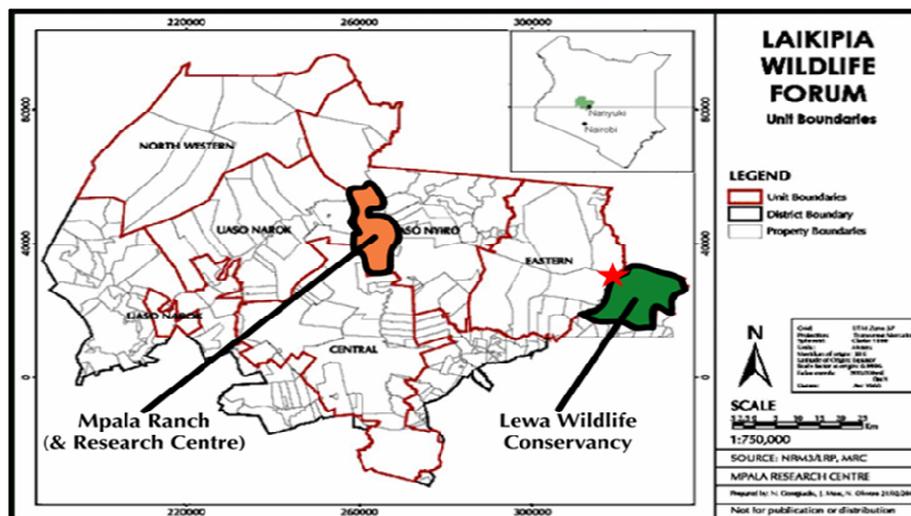


Figure 1. Map of Laikipia region of Kenya. Locations of Mpala Research Centre and Wildlife Foundation and Lewa Wildlife Conservancy are highlighted in orange and green, respectively. Red star indicates the approximate location of the Westgate community land outside of Lewa Wildlife Conservancy. Figure modified from <http://www.mpala.org/Maps.php>.

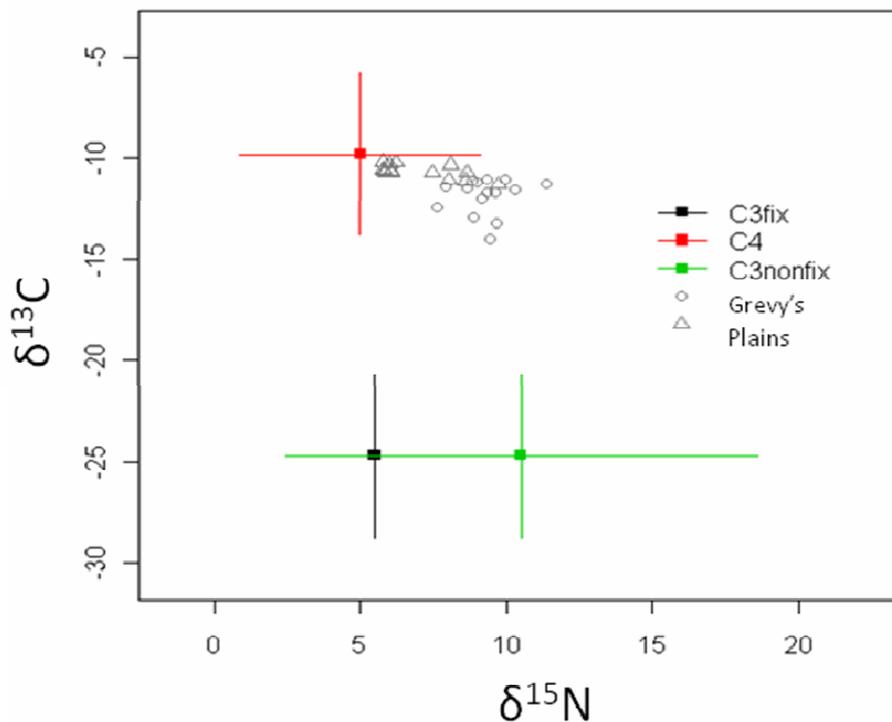


Figure 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicating proportions of C_4 , C_3 N_2 fixing, and C_3 non-fixing plants in Plains and Grevy's zebra diet.

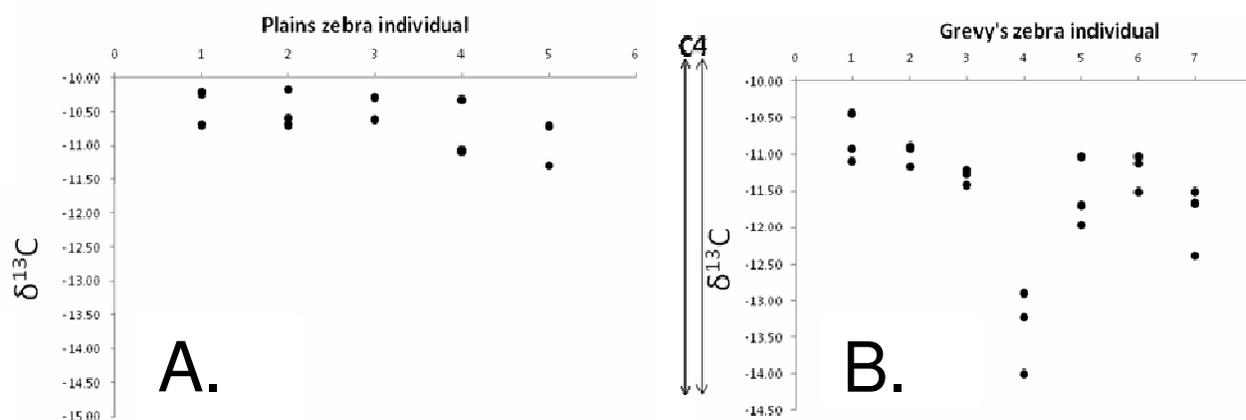


Figure 3. $\delta^{13}\text{C}$ values of (A) Plains and (B) Grevy's zebras. Each individual represents three tail samples (tip, mid, and base). Plains zebra diet is less variable, and has a significantly higher proportion of C_4 grass in their diet than Grevy's zebra diet (calculated using SIAR, Levene's test of equal variances: $P < 0.001$, one-way ANOVA; $F_{1,11} = 56.234$, $P < 0.001$).

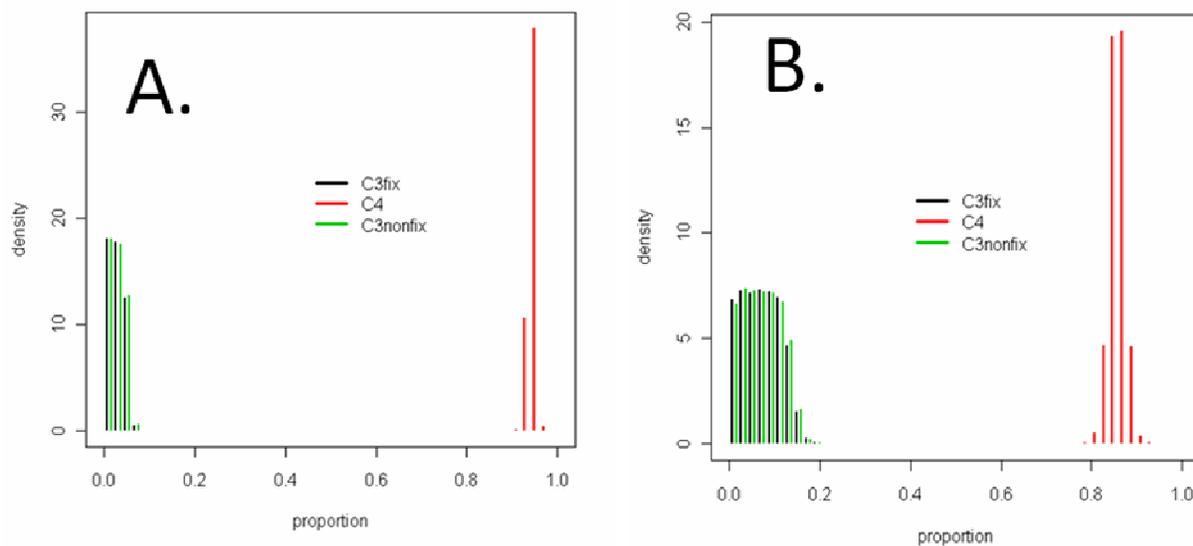


Figure 4. Proportions of C_4 , C_3 fixing and C_3 non-fixing plants in the diets of Plains (A) and Grevy's (B) zebras.

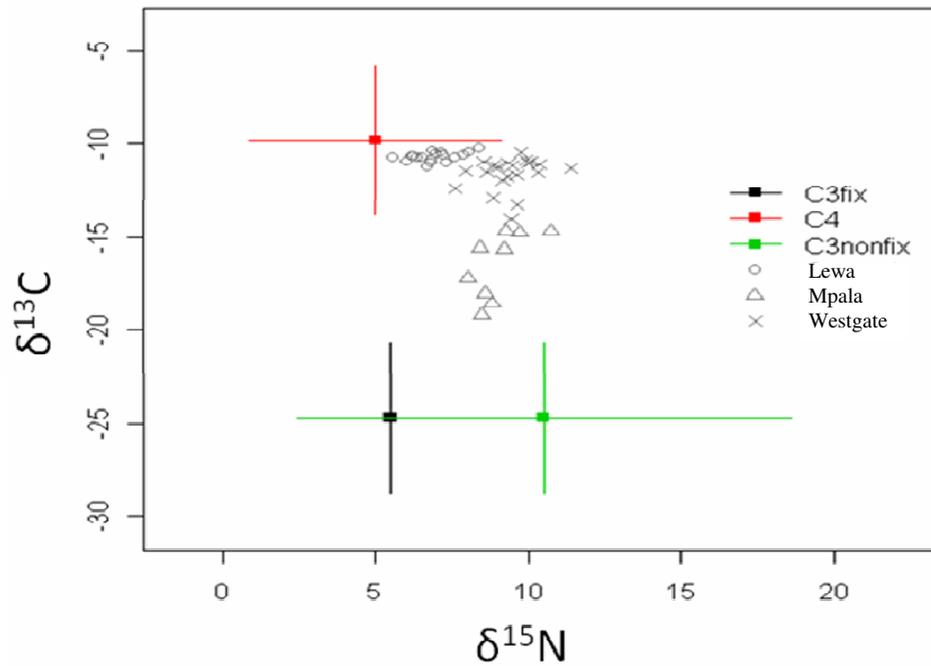


Figure 5. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicating proportions of C_4 , $\text{C}_3 \text{N}_2$ fixing, and C_3 non-fixing plants in the diets of Grevy's zebras at Lewa Wildlife Conservancy (no livestock), Mpala Research Centre and Wildlife Foundation (some managed livestock), and Westgate community land (heavy, unmanaged livestock).

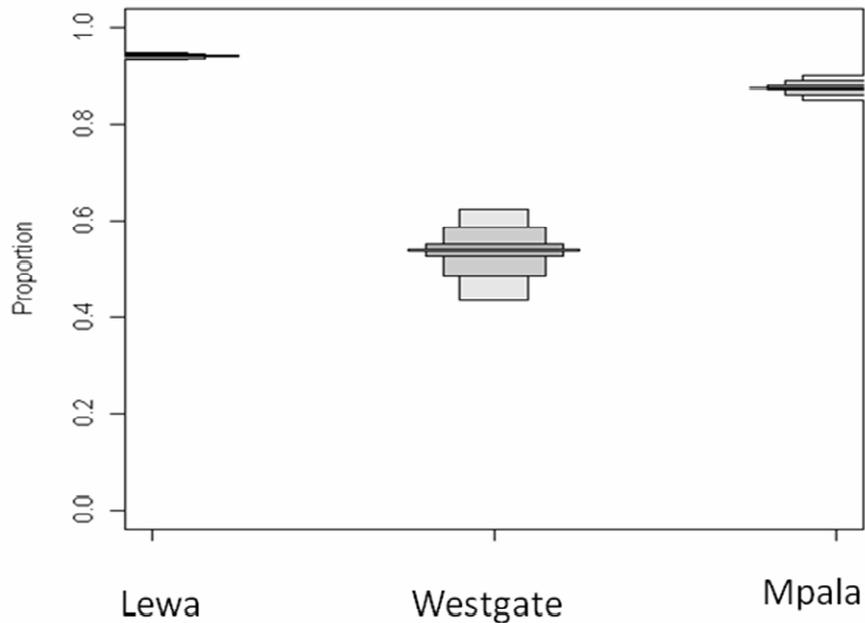


Figure 6. Proportion of C_4 grass material in Grevy's zebra diet at Lewa Wildlife Conservancy (no livestock), Westgate community land (lots of unmanaged livestock) and Mpala Research Centre and Wildlife Foundation (some managed livestock).

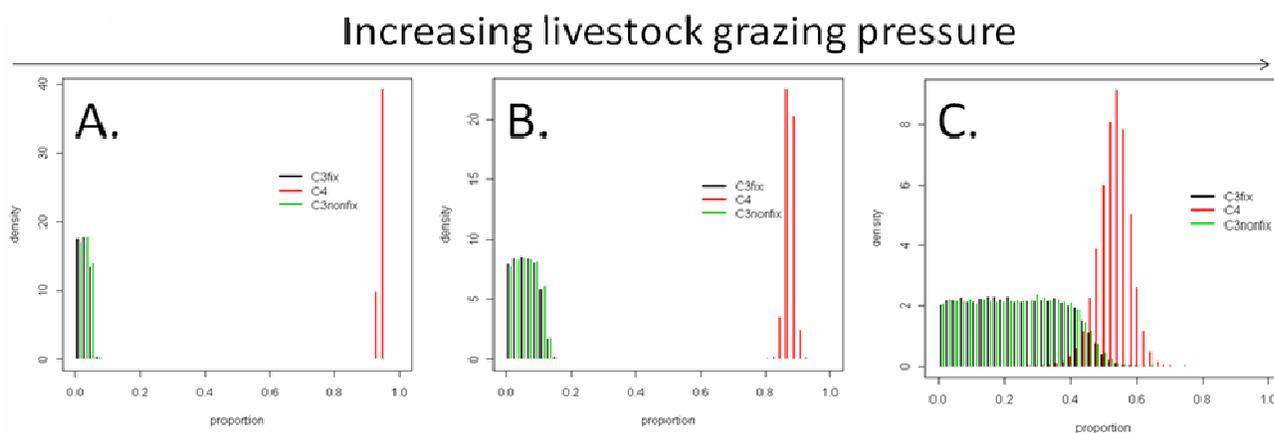


Figure 7. Proportions of plant type in Grevy's zebras by location: A) Lewa (no livestock), B) Mpala (some livestock) and C) Westgate (lots of livestock). Grevy's eat almost entirely C₄ when no livestock are present (A) and significantly less at locations with more cattle (B,C) (one-way ANOVA: $F=6.148$, $P<0.005$)

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