
Habitat choice of Grevy's zebras (*Equus grevyi*) in Laikipia, Kenya

Siva R. Sundaresan^{1,2,3*}, Ilya R. Fischhoff^{1,2}, Helen M. Hartung¹, Patrick Akilong² and Daniel I. Rubenstein^{1,2}

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, U.S.A., ²Mpala Research Center, PO Box 155, Nanyuki, Kenya and ³Department of Conservation Biology, Denver Zoological Foundation, Denver, CO 80205, U.S.A.

Abstract

Characterizing habitat choice is essential for endangered species conservation. For the endangered Grevy's zebra (*Equus grevyi*), as with many widely ranging vertebrates, human activities may be an important factor affecting space use. Grevy's zebras are grazing ungulates inhabiting the savannahs of central-northern Kenya and Ethiopia. Past research on their social organization indicates that reproductive status shapes associations and movements. Here, we examine how habitat use varies across four reproductive classes: lactating and nonlactating females, bachelors and territorial males. We also test whether Grevy's zebra avoid locations close to active livestock corrals, or *bomas*. We find that forage quality, forage quantity and habitat openness of locations used by Grevy's zebra vary significantly depending on individual reproductive state. Lactating females and bachelors use areas with green, short grass and medium-dense bush more frequently than nonlactating females or territorial males. We hypothesize that lactating females trade off forage quantity and safety to access nutrients in growing grass. Across reproductive classes, Grevy's zebra choose locations further from active *bomas* than if they used the area randomly. Our results suggest that Grevy's zebra may require a range of vegetation characteristics for different reproductive classes. Further, they may need areas free from competition or disturbance by livestock.

Key words: endangered species, equid, habitat use, livestock, range management, savannah

Résumé

Bien caractériser le choix de l'habitat est essentiel pour la conservation des espèces en danger. Pour le zèbre de Grévy (*Equus grevyi*), comme pour de nombreux vertébrés qui ont un grand domaine vital, les activités humaines peuvent être un facteur qui affecte beaucoup l'utilisation de l'espace. Les zèbres de Grévy sont des ongulés brouteurs qui habitent les savanes du centre-nord du Kenya et l'Éthiopie. Les recherches antérieures sur leur organisation sociale indiquent que c'est le statut de reproduction qui détermine les associations et les déplacements. Nous examinons ici comment l'utilisation de l'habitat varie entre quatre classes reproductives: les femelles allaitantes ou non, les mâles célibataires et les mâles territoriaux. Nous avons aussi regardé si les zèbres de Grévy évitaient les endroits situés près des enclos actifs de bétail, ou *bomas*. Nous avons trouvé que la qualité et la quantité du fourrage et le caractère plus ou moins ouvert des endroits fréquentés par les zèbres de Grévy varient significativement en fonction du statut reproductif des individus. Les femelles allaitantes et les célibataires fréquentent les zones d'herbes vertes et courtes et les buissons moyennement denses plus souvent que les femelles non allaitantes et les mâles territoriaux. Nous faisons l'hypothèse que les femelles allaitantes compensent la quantité et la sécurité de la source alimentaire par l'accès aux nutriments de l'herbe nouvelle. Dans toutes les classes de reproduction, les zèbres de Grévy choisissent des endroits plus éloignés des *bomas* actives que s'ils utilisaient le territoire au hasard. Nos résultats suggèrent que les zèbres de Grévy pourraient rechercher dans la végétation une gamme de caractéristiques différentes selon les classes reproductives. De plus, ils pourraient avoir besoin de zones où il n'y a ni compétition, ni perturbations dues au bétail.

*Correspondence: E-mail: ssundare@princeton.edu

Introduction

Central to the conservation of many species is our understanding of habitat use. Most large-bodied vertebrates range widely, thereby encountering diverse habitats. Overlying the natural fluctuations and trends in the environment, human land use decisions affect resources directly and may also disturb wildlife. Grevy's zebra in Laikipia exemplify many endangered species facing these challenges. To craft better conservation plans for these species, we must characterize their habitat use patterns. By identifying how their preferences overlap with human land uses, we can determine the potential for conflict, and suggest possible solutions.

Grevy's zebra are large-bodied (350–450 kg.), grazing ungulates living in rangelands of central-northern Kenya and Ethiopia. The species numbers 3000 globally, and has undergone a 75% decline since the 1970s. Grevy's zebra have their last remaining stronghold in the Laikipia–Samburu Ecosystems of central Kenya (Williams, 2002). Laikipia is a 10,000 sq. km. area characterized by semi-arid bushed grassland, with diverse human land uses and attitudes towards wildlife. The majority of Laikipia is large commercial livestock ranches, some of which are also engaged in ecotourism. Little is known about Grevy's zebra ecology in Laikipia. The species expanded its range into Laikipia beginning in the 1970s (Williams, 2002). Its population has grown in this area, while it has declined in most other parts of its range. Past studies of Grevy's zebra ecology have been outside Laikipia (Williams, 1998). This research concluded that Grevy's zebra and cattle competed over waterholes. Other studies have focused on social organization (Ginsberg, 1988; Ginsberg & Rubenstein, 1990; Rowen, 1992; Sundaresan *et al.*, 2007). Females form unstable groups, moving among male territories. Bachelor males wander. From past studies, we know that lactation strongly influences water and energy needs of females. Physiology underlies differences between lactating and nonlactating females in movements and assortative female associations by reproductive state.

In this study, we examine habitat characteristics of locations used by Grevy's zebra in a 200 sq km area spanning two adjacent ranches, Mpala and El Karama. On these ranches, as in most of their range where the species coexists with people, Grevy's zebra must choose among locations that vary in their vegetation characteristics and proximity to human activities. Vegetation features important to zebras include forage quantity and

quality, and habitat openness. Bush density affects visibility, which in turn may influence Grevy's zebras' ability to detect predators. Grevy's zebra may avoid areas close to humans and their livestock because of direct disturbance, or due to indirect competition with domestic ungulates over forage.

First, we determine how habitat use varies among individuals in different reproductive classes: lactating and nonlactating females, bachelors and territorial males. We hypothesize that lactating females prefer higher-quality grass because of their more specific nutrient needs (Ginsberg, 1988). Secondly, we ask how Grevy's zebra respond to the presence of active livestock corrals. In our study area, as in most of Laikipia, people house livestock in camps called bomas, the location of which moves every few weeks or months. We hypothesize that Grevy's zebra avoid areas close to bomas because of potential competition with livestock (Williams, 1998).

Materials and methods

Study site and field data

Since 2003, we have gathered data by driving census loops through Mpala Ranch and El Karama. The ranches are in central Laikipia (36°53'E, 0°17'N). Annual rainfall is approximately 500 mm. The habitat is a bushed grassland. The woody vegetation is dominated by *Acacia* species. Grasses are primarily of the genera *Themeda*, *Cynodon* and *Pennisetum*. On both ranches, wildlife conservation is a management goal. Wildlife is free to move among the ranches.

The data presented here were collected between June 2003 and August 2005. During our loops, we record the date, time and GPS location of all Grevy's groups sighted. We record the reproductive status of all individuals in each group. We categorize adults as lactating or nonlactating females, or bachelors or territorial males. For the analysis presented here, we consider each individual sighting independent. Although Grevy's zebra are often found in groups, there are no long-term bonds; thus each individual is free to choose his or her location (Ginsberg, 1988). Only adult sightings are included here; we assume that infants and juveniles follow their mothers.

For each sighting, we record the grass colour, grass height and bush density of the surrounding habitat. Grass colour and height reflect quality and quantity of forage. We categorize grass colour as brown (>75% brown leaves

or stems), brown-green (50–75% brown), green-brown (50–75% green), or green (>75% green). Grass height categories are relative to the typical adult Grevy's zebra: less than hoof height, less than hock, or less than belly. We measure bush density using the Bitterlich stick method in which we count the number of bushes wider than the arc subtended by a 10 cm. object held 1 m away from the eyes (Grosenbaugh, 1952). From this count, we categorize an area as open (zero to one bushes), light bush (two to six), medium bush (seven to eleven) and dense bush (12+).

From June to August 2005, we recorded the location of all active bomas and noted the dates on which livestock are moved to a different boma or a boma is abandoned. Each boma is approximately 100 m in diameter. A boma houses about ten people and 200–400 head of livestock, including cattle, donkeys and camels.

Habitat use analysis

Vegetation characteristics. We test whether vegetation characteristics of Grevy's zebra locations vary by reproductive state. For each reproductive class, we tally the number of individual observations in each category of grass colour. We then use a chi-squared contingency test to evaluate whether counts in each grass colour category are independent of reproductive state. We compute analogous chi-squared tests of independence between reproductive state and number of observations for each category of grass height and bush density. Further, for each contingency test, we examine if particular reproductive classes deviate strongly from their expected use of a habitat type, by analysing the standardized residuals of each cell in the contingency table (Sheskin, 2004). Standardized residuals are computed as the difference between the observed and expected values for the cell, divided by the square root of the expected value for the cell. If a cell has an absolute value of the residual greater than two, this indicates that the observed frequency for that cell deviates significantly from its expected frequency at the $P < 0.05$ significance level. A negative residual shows that the observed frequency is less than expected, while a positive value indicates that observed frequency is greater than expected (Sheskin, 2004).

Response to bomas. We examine how Grevy's zebra respond to the presence of active bomas. We compared the mean distance to the closest boma of the observed Grevy's

zebra locations to the mean distance to the closest bomas for random points in the area used by Grevy's zebra. The number of random points used is the same as the number of individual Grevy's zebra observations. For this analysis, we define the area of use as the minimum convex polygon that encompasses all our sightings. We only drop random points within this polygon because we only observe Grevy's zebra within this region. Within our study site on the two ranches, there are areas where we have never observed Grevy's zebra. By assuming that only locations in the minimum convex polygon are available to Grevy's zebra, we are excluding from our analysis areas that Grevy's zebra apparently avoid.

To randomize the data, we changed every observed zebra location to that of a point chosen randomly within the minimum convex polygon of Grevy's zebra locations. The date of the observation is kept constant. We computed the distance of all these random points to the closest active bomas for their respective dates. By repeating this randomization 1000 times, we generated a null distribution of mean distance to closest boma. We computed a P -value to test the hypothesis that Grevy's choose to avoid active bomas. The P -value is equal to the fraction of randomizations for which the observed mean distance is greater than the mean from the randomization.

We next tested whether distance to closest boma varied depending on reproductive state. We used a one-way ANOVA with reproductive state as the factor.

Results and discussion

Habitat use: vegetation characteristics

Grass colour. We find that the grass colour of locations used by Grevy's zebra differs depending on an individual's reproductive state (Fig. 1; $\chi^2 = 121.3$, d.f. = 9, $P < 0.001$). We had 1602 total observations including 391 for lactating females, 687 for nonlactating females, 258 for bachelors and 266 for territorial males. Across all reproductive classes, most sightings are green grass locations. As apparent from visual examination of the figure (Fig. 1), the most striking difference among reproductive classes is the greater use of green grass (standardized residual = 5.5) and avoidance of brown (standardized residual = -4.0) and brown-green (standardized residual = -5.5) areas by bachelor males. There also appears a tendency for nonlactating females (standardized residual = -2.2) or territorial

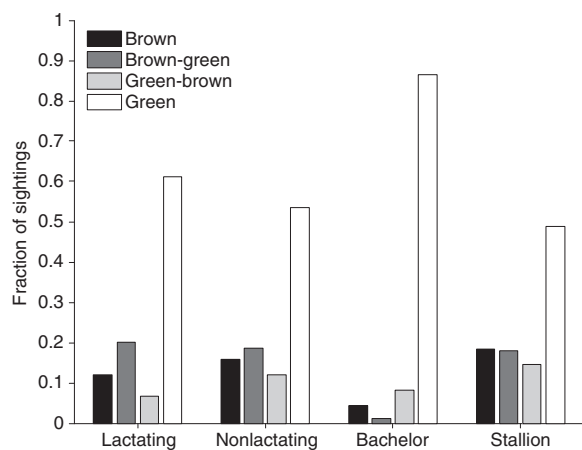


Fig 1 Proportion of Grevy's zebra sightings in locations of varying forage quality (grass colour) for individuals in the four reproductive classes: lactating females, nonlactating females, bachelor males and territorial males

males (standardized residual = -2.3) to be less frequently observed in areas with green grass. Overall, we conclude based on the contingency table that Grevy's zebra preferences for forage quality vary with reproductive state.

Grass height. Grass height of Grevy's zebra locations also varies significantly with reproductive class (Fig. 2; $\chi^2 = 183.6$, d.f. = 6, $P < 0.001$). Out of a total of 1624 observations, we had 393 lactating female records, 697 nonlactating sightings, 258 for bachelors and 276 for

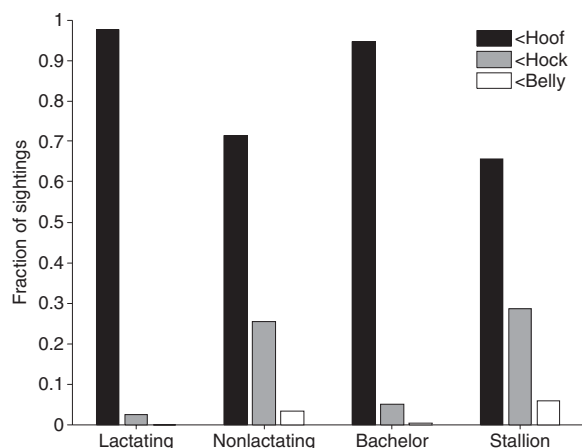


Fig 2 Proportion of Grevy's zebra sightings in locations of varying forage quantity (grass height) for individuals in the four reproductive classes: lactating females, nonlactating females, bachelor males and territorial males

territorial males. All reproductive classes primarily use locations with short grass. Among reproductive classes, we find similarity in choices about grass height between bachelors and lactating females, and between territorial males and nonlactating females. Bachelors are more frequently observed in short grass areas (standardized residual = 2.6). Lactating females also follow a similar pattern (standardized residual = 3.8). On the other hand, both territorial males and nonlactating females are observed less frequently than expected in short grass areas (standardized residual = -2.8 and -2.7 respectively). The results indicate that reproductive state modifies preferences for forage quantity as well as quality.

Bush density. Our data show that reproductive state affects choices about the visibility of locations as measured by bush density (Fig. 3; $\chi^2 = 97.3$, d.f. = 9, $P < 0.001$). We have 1608 observations including 390 lactating female records, 688 for nonlactating females, 257 for bachelors and 273 for territorial males. Except for lactating females, individuals of all reproductive classes appear to avoid locations of dense bush. Lactating females are observed less frequently in open areas (standardized residual = -3.0) than in areas of dense bush (standardized residual = 6.0). Bachelors are also observed rarely in open habitat (standardized residual = -2.7) and more frequently in medium bush (standardized residual = 3.5). As with grass colour and height, territorial males and nonlactating females have

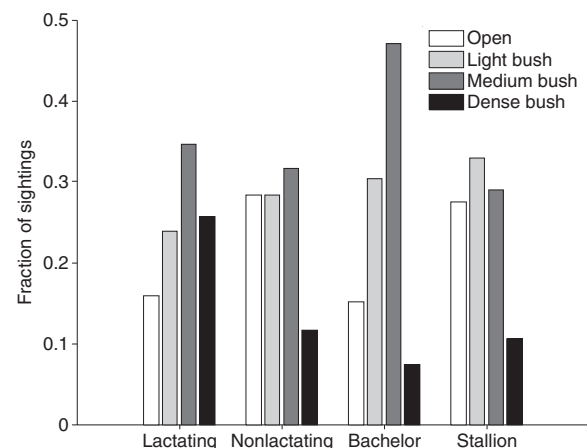


Fig 3 Proportion of Grevy's zebra sightings in locations of varying habitat openness (bush density) for individuals in the four reproductive classes: lactating females, nonlactating females, bachelor males and territorial males

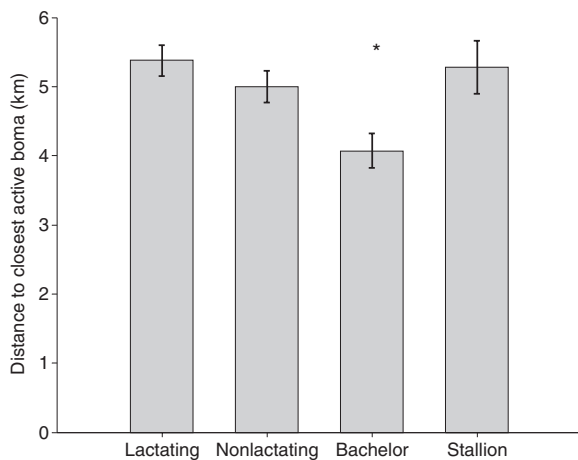


Fig 4 Distance to closest active livestock corral (mean \pm standard error) for each adult reproductive class. Multiple comparisons reveal a significant difference between bachelor males and all other classes

similar distributions. Here again, we conclude that reproductive state influences Grevy's zebra choices of open versus bushy habitats.

Habitat use: response to bomas

There is a mean distance of 4.90 km between Grevy's zebra locations and the closest active boma, averaged over 749 individual sightings. The mean distance for the random points is 4.08 km, averaged across 1000 random runs, with a standard error of the mean of 0.07 km. Our randomization test shows that Grevy's zebra are significantly further away from bomas than they would be if they chose locations randomly ($P < 0.001$). Our data suggest that Grevy's zebra avoid areas close to active livestock corrals.

Our data on observed distances from active bomas reveals that reproductive class has a significant effect on distance to closest boma (Fig. 4; ANOVA, $F_{3,745} = 5.6$, $P = 0.0008$). The data used in the ANOVA include 235 observations of lactating females, 230 for nonlactating females, 199 for bachelors and 85 for territorial males. Multiple comparisons, using Tukey–Kramer HSD, indicate a significant difference between bachelors and the other three reproductive classes. Bachelors tend to be closer to bomas.

Discussion

We have shown that reproductive state mediates Grevy's zebra responses to ecological features, including human

disturbance. Overall, we tend to observe Grevy's zebra in areas of short, green grass. As grazers, we would expect Grevy's zebra to seek out areas with high-quality forage. Our data indicate that lactating females and bachelors tend to use areas with greener but shorter grass. In choosing these areas, we hypothesize that lactating females and bachelors are seeking higher-quality forage at the cost of reduced quantity. For females with foals, specific nutrient demands of lactation may drive this choice (NRC 1989). We can posit three possible explanations for bachelor use of these habitats. They may be attracted to these areas because of the presence of lactating females, which come into predictable oestrus (Ginsberg, 1988; Rubenstein, 1994). Secondly, bachelors may require higher nutrient content because many are still growing and therefore need particular micronutrients more abundant in growing grass. Finally, bachelors may be avoiding areas used by territorial males who harass bachelors (DIR, SRS, personal observations). In using areas with lower-quality, higher-bulk forage, nonlactating females and territorial males may be pursuing a strategy of gaining weight.

Our data show that lactating females are more often seen in dense woody vegetation. This is a surprising result because such low visibility areas are thought to be relatively unsafe, as they provide cover for lions. Given the vulnerability of foals to predation, we may have expected lactating females to choose more open areas. Foal survival is approximately 50% in our study area, suggesting that predation may pose a major risk (Rubenstein, unpublished data). The use of denser bush by lactating females suggests that they are trading off the risk of predation for other benefits of these areas, such as proximity to water or high-quality forage. We hypothesize that bachelors' greater use of medium bush areas is due to their avoiding territorial males.

We have shown effects of active cattle corrals on Grevy's zebra space use. One hypothesis for the closer proximity of bachelors to active bomas is that they are driven there by agonistic encounters with stallions. Across all reproductive classes, Grevy's zebra avoidance of bomas may mean that from a Grevy's zebra's perspective, part of the landscape is unavailable. People change the locations of cattle corrals over time, resulting in a shifting mosaic of preferred habitat. We do not yet know the specific factors associated with livestock corrals that are causing Grevy's zebra to stay away from them. They may be responding to human presence, cattle presence, or the effects of competition for forage or water. Each day, herders graze the livestock on a

path several kilometres from the corral that includes water shared by Grevy's zebra. To understand how livestock and Grevy's zebra interact throughout the day, we would need finer-scale data on movements of both.

We do not know whether Grevy's zebra avoidance of boma sites translates into decreased survival or reproductive rates. By comparing vital rates across ranches with a range of livestock densities, we can determine whether vital rates correlate with land use intensity.

Our findings are relevant for Grevy's zebra conservation. We have demonstrated that habitat use varies by reproductive state. To support all phenotypes in the population, it may be necessary for Grevy's zebra habitat to include a certain range of variation in forage quality and quantity, and openness. The implication that Grevy's zebra move away from livestock corrals indicates that ranching affects Grevy's zebra behaviour, even on properties such as these with relatively low stocking levels and conservation goals. Over almost all their current range, Grevy's zebra must coexist with livestock. One suggestion for mitigating any potential effects on Grevy's zebra vital rates is to avoid situating livestock corrals in 'nursery' areas that are habitually used by Grevy's zebra lactating females (Ginsberg, 1988; Rowen, 1992). Williams (1998) hypothesized that competition over waterholes forced Grevy's zebra to drink at times and places that heightened their risk of predation.

The data we have allow us to characterize broad patterns and form hypotheses about behavioural mechanisms. However, to determine the bases for movement choices within and across habitats, we must sample an individual's daily routes, over the course of multiple days. Future studies should include finer-scale data on movements of Grevy's zebra and livestock, and landscape variation in vegetation characteristics. By characterizing how movements relate to ecological features, we can better predict population-level responses to land use change.

Acknowledgements

We dedicate this paper to the memory of Patrick Akilong (1977–2006). We thank the Ministry of Education, Government of Kenya for permission to work in Kenya. We are grateful to the Mpala Research Center, Mpala Ranch and their staff for logistical field support. Guy Grant gave us

permission and field support for study on his property, El Karama. We thank Dr Jon Lovett and one anonymous review for comments on an earlier version of the manuscript. For funding we thank Lincoln Park Zoo Conservation Funds; National Science Foundation grants CNS-025214 (IRF, HMM, DIR), IOB-9874523 (DIR) and IBN-0309233 (SRS, DIR); Princeton University Department of Ecology & Evolutionary Biology (SRS, IRF, HMM, DIR); Pew Charitable Trusts award 2000-0002558 'Program in Biocomplexity' to Princeton University Department of Ecology and Evolutionary Biology (IRF, SRS, DIR); and the Teresa Heinz Environmental Scholars program (IRF).

References

- GINSBERG, J.R. (1988) *Social Organization and Mating Strategies of an Arid-adapted Ungulate: the Grevy's Zebra*. Princeton University, Princeton, NJ.
- GINSBERG, J.R. & RUBENSTEIN, D.I. (1990) Sperm competition and variation in zebra mating-behavior. *Behav. Ecol. Sociobiol.* **26**, 427–434.
- GROSENBAUGH, L.R. (1952) Plotless timber estimates—new, fast, easy. *J. Forestry* **50**, 32–37.
- NRC (1989) *Nutrient Requirements of Horses*, 5th edn. National Academy Press.
- ROWEN, M. (1992) *Mother-infant Behavior and Ecology of Grevy's Zebra*. Yale University, New Haven, CT.
- RUBENSTEIN, D.I. (1994) The ecology of female social behavior in horses, zebras, and asses. In: *Animal Societies: Individuals, Interactions, and Organization* (Eds P. JARMAN and A. ROSSITER). Kyoto University Press, Kyoto.
- SHESKIN, D.J. (2004) *Handbook of Parametric and Nonparametric Statistical Procedures*. Chapman & Hall/CRC, Boca Raton.
- SUNDARESAN, S.R., FISCHHOFF, I.R., DUSHOFF, J. & RUBENSTEIN, D.I. (2007) Network metrics reveal differences in social organization between two fission-fusion species, Grevy's zebra and onager. *Oecologia* **151**, 140–149.
- WILLIAMS, S.D. (1998) *Grevy's Zebra: Ecology in a Heterogeneous Environment*. University College London, London.
- WILLIAMS, S.D. (2002) Status and action plan for the Grevy's zebra (*Equus grevyi*). In: *Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan* (Ed. P. D. MOEHLMAN). IUCN/SSC Equid Specialist Group, Gland, Switzerland.

(Manuscript accepted 30 August 2007)

doi: 10.1111/j.1365-2028.2007.00848.x