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Variations in Elephant (Loxodanta africana) Diet Along a Rainfall Gradient: The Effect of Latitude, Grass Reserves, and Proximity to Water

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Abstract

Global climate change is predicted to bring longer dry seasons and changing rainfall patterns to equatorial Africa, causing range reductions for species such as elephants, whose diets are constrained by water availability. Elephants are facultative grazers whose diets are seasonal, with woody proportion of diet increasing in the dry season. In this study, we sought to identify the factors that predict woody percentage of elephant diet along a rainfall gradient at the Mpala Research Centre in central Kenya. We used elephant dung as a means to analyze the woody content of elephant diet. We found that grass biomass and distance to the nearest river explained the most variability in elephant diet, while latitude was a less influential predictor. Because these local factors were more important determinants of elephant diet differences than rainfall along a gradient, we conclude that climate change will likely affect elephant populations through elongated dry seasons, which may limit availability of nearby water sources.

1. Introduction

Global climate change is predicted to bring longer dry seasons and changing rainfall patterns to equatorial Africa, causing range reductions for many species whose diets are constrained by water availability (Global Biodiversity Outlook 3, 2010). Elephants (*Loxodonta africana*) are one such species, as their diets are indirectly determined by rainfall and seasonality (Laws 1970, Barnes 1982, Birkett and Stevens-Wood 2005, Loarie et al. 2009). Elephants are facultative browsers that increase the woody proportion of their food intake when grass availability is low (Napier and Sheldrick 1963, Laws 1970, Barnes 1982, Birkett and Stevens-Wood 2005). In turn, grass availability depends on a variety of biotic and abiotic factors, including rainfall, soil nutrient content, and grazing pressure (Sankaran et al. 2013, Augustine 2003, and Higgins et al. 2000). Grass availability is expected to vary predictably along a rainfall gradient, with grass reserves accumulating where rainfall is relatively high (Sankaran et al. 2013). However, soil nutrients and grazing pressure may vary along a gradient, interacting with rainfall to produce more complex patterns of grass availability (Augustine 2003). Previous work tracking elephant diet preferences along a rainfall gradient has indicated that elephants actively seek green forage throughout the year (Loarie et al. 2009). Because of the various factors controlling food availability, this green-seeking behavior results in heterogeneous feeding preferences: in the wet season, elephants increase grass consumption while its nutritional value is high and grass biomass is widely available (Barnes 1982, Loarie et al. 2009), whereas in the dry season, they increase consumption of woody species (Barnes 1982). Additionally, elephant family groups are limited by the minimized mobility of young individuals, who must also consume a greater proportion of grass than wood to meet metabolic requirements (Laws 1970).

Although rainfall ultimately determines forage abundance on large scales, permanent water sources have also been demonstrated to influence elephant feeding habits on more local scales (Laws 1970, Ihwagi et al. 2009). Elephants frequently migrate to and congregate near permanent water sources, especially in the dry season (Laws 1970, Leuthold and Sale 1973). In contrast to the larger scale determinants discussed above, nearness to permanent water sources may prove more important in structuring elephant diet than rainfall along a gradient. Additionally, if elephants' ranges are restricted by proximity to water (Laws 1970, Leuthold and Sale 1973), local grass reserve may become a more important predictor of elephant diet than gradual changes in biomass along a gradient.

In this study, we explored whether elephant diet in the dry season changes along a rainfall gradient and, if so, what predictive variables governed these changes. We expected that at more northern latitudes, reduced rainfall would diminish grass reserves, causing the woody component of elephant diet to increase. Likewise, we hypothesized that, because family groups with young individuals will be located nearer to a permanent water source (here, a river or rivers), the woody component of elephant diet would decrease with increased proximity to a river. Finally, we expected that when we observed high grass biomass at a site, elephant diet at that site would exhibit a higher proportion of grassy components than woody components.

2. Methods

2.1 Study Sites

This study was conducted along a rainfall gradient at the Mpala Research Centre (MRC) (0°17'N, 37°52' E) in Laikipia, Kenya. The northernmost portion of MRC receives approximately 350mm of rainfall annually, while the southernmost portion receives between 550-600mm annually. We chose five sites approximately evenly spaced along this gradient: Site 1, 0°30'52.1"N, 36°51'38.9" E, 1650m above sea level; Site 2, 0°27'05.4"N, 36°51'55.3" E, 1684m above sea level; Site 3, 0°24'49.7"N, 36°54'05.3" E, 1640m above sea level; Site 4, 0°20'36.3"N, 36°54'41.7"

E, 1654m above sea level; Site 5, 0°17'45.7"N, 36°54'17.1" E, 1672m above sea level (see *Figure 1*). All sites were located on the red clay soil.

2.2 Field Methods

At each site, we collected 10 samples of elephant dung within 75m of the road. As termite damage indicates greater than one year of decay and prevents analysis of dung content, we avoided samples showing signs of termite damage (surface of sample intact, but internal contents consisting of soil and pockmarked with holes). To speed the drying-out process for our samples, we chose dung that was mostly dried.

In order to determine the amount of grass available for forage at the respective sites, we took grass biomass measurements using a Disk Pasture Meter (DPM). We paced off approximately 25m from the road and then took DPM measurements every 2m along a 50m walking transect. When possible, we used one walking transect on either side of the road. In cases where our site abutted private property, we used two walking transects 20m apart on one side of the road. Raw DPM measurements were converted to grass biomass values using the equation calibrated grass biomass value in kg/ha = $-3019+2260\sqrt{\text{raw DPM measurement}}$.

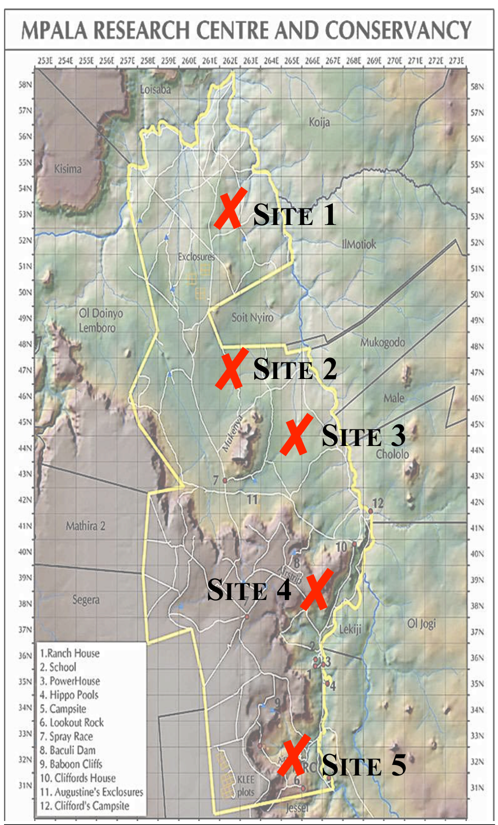

Figure 1: Our study sites were areas located along a 200 mm rainfall gradient at the MRC. Assuming a gradual gradient, Site 1 receives approximately 350 mm rainfall annually, Site 2 receives 390 mm, Site 3 receives 430 mm, Site 4 receives 470 mm, and Site 5 receives 510 mm.

2.3 Analysis of Dung for Woody Components

After collection, we allowed our samples to dry in full sun for approximately six hours. We then weighed the samples for total dry mass. Subsequently we sifted through each sample, identifying woody components by eye and collecting them. Grass components were distinguished from woody components by their hollow structure, yellow color, and shiny cuticle. We then weighed the woody components and divided this mass by the total mass to obtain a percentage of dung that was woody.

2.4 Statistical Analyses

All statistical analyses were performed using JMP Pro 10. We conducted regression analyses comparing woody percentage of dung against three factors: latitude, grass biomass (kg/ha), and distance to nearest river (m). To assess which of these three factors explained the highest proportion of variance in elephant diet, we constructed a model using grass biomass and distance to river as the primary predictor variables. Grass biomass and distance to the nearest river did not co-vary. We were therefore able to include them in a single model.

3. Results

We found that as latitude increased, the woody percentage of dung increased (r^2 = 0.40, N=5, P=0.25; See Figure 1). Although this trend was not significant, latitude still explained 40% of the variance in elephant diet. This relationship supported our initial expectation that elephant diet would exhibit a higher proportion of wood at the northern end of the MRC, where annual rainfall is lowest. We also found that as grass biomass increased, the woody percentage of dung decreased (r^2 = 0.28, N=5, P=0.36). As with latitude, the inverse relationship between grass biomass and the woody percentage of dung was not significant, but the trend explained 28% of the variance in elephant diet and supported our hypothesis that the proportion of wood in elephant diet would be negatively related to grass biomass (See Figure 2). We found that as distance to the nearest river increased, the woody percentage of dung increased (r^2=0.87, N=5, P=0.02). This significant relationship explained 87% of the variation in elephant diet and supported our expectation that there would be a positive correlation between distance to the nearest permanent water source and woody component of elephant diet (See Figure 3). We constructed a model incorporating distance to a river and grass biomass as the two primary explanatory variables of elephant diet (r^2 = 0.96, N=5, P=0.04). Together, these variables explained 96% of the variation in elephant diet, indicating that local-scale determinants of water and food availability have greater impacts on elephant diet than do overall rainfall patterns.

3. Discussion

We found that the percentage of woody content in elephant diet during the dry season at Mpala was significantly correlated with collection-site grass biomass and proximity to a water source. Based on these results, we conclude that food availability is not the sole predictor of elephant diet, and that social dynamics influencing elephant movement also play an important role in structuring elephant diet. While our model shows that distance from a river and collection-site grass biomass in an area are more predictive of woody content than latitude in explaining elephant diet at Mpala, the effects of latitude may operate at a larger spatial scale than was examined in this study, especially given the large distances over which elephants are capable of migrating in short periods (Leuthold and Sale 1973, Barnes 1982). Additionally, because elephants may travel large distances between consumption and defecation, the contents of dung at a site may not be representative of what an elephant consumed at that site. Furthermore, the mean annual precipitation between an elephant's consumption point and the point of dung collection may differ substantially, resulting in potentially misleading associations with rainfall (Barnes 1982). Finally, because we did not control for dung age during this study, our samples represented elephant diet beyond the dry season. Future work would benefit from considerations of elephant mobility and dung age.

Despite the confounding effects of elephant movement and dung age, the high predictive power of our model indicates that the relationship between elephant diet, collection-site grass biomass, and distance to the nearest river is robust. During the dry season, local water availability more accurately determines the percentage of woody content in elephant diet than regional mean annual rainfall. This relationship can be applied in assessing how interannual changes in rainfall, which controls available grass biomass, and distance from a river or rivers will affect the movement and behavior of elephant populations at the MRC and across East Africa. More broadly, global climate change is predicted to bring longer dry seasons to equatorial Africa, which may correspond to the drying up of rivers (Global Biodiversity Outlook 3, 2010). Given our findings on the significance of distance to the nearest river in elephant diet, these changes may prevent elephants from meeting grass intake needs, leading to range reductions and population decreases.

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Figures

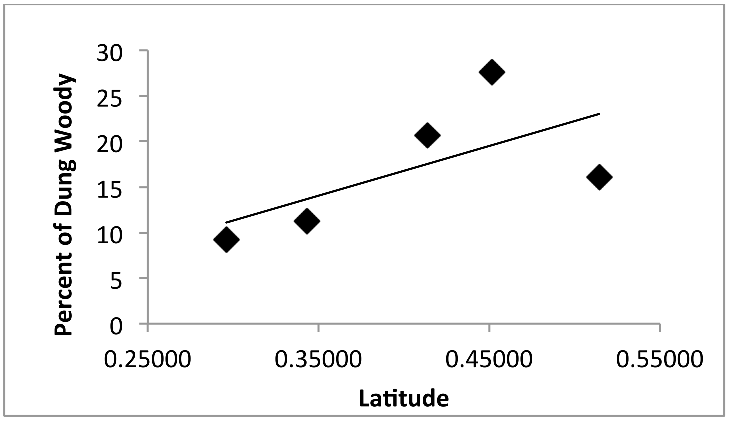

Figure 1: Response of dung woody fraction to latitude. Error bars represent one standard error from the mean percent woody dung in each site. r^2 = 0.40, N=5, P=0.25.

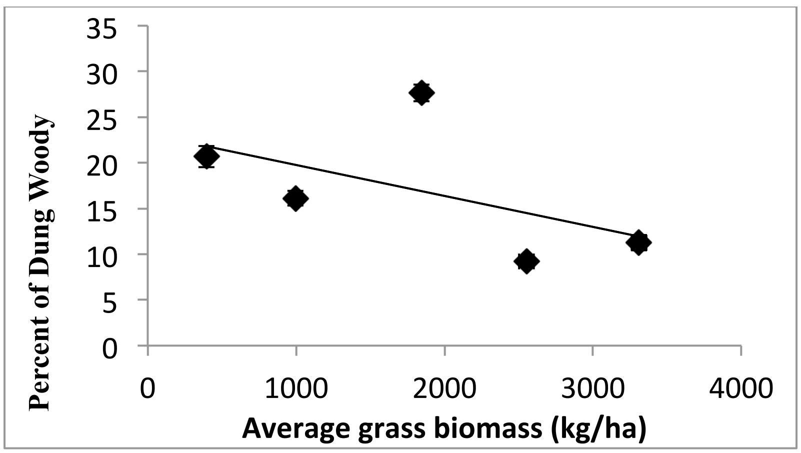

Figure 2: Response of dung woody fraction to grass biomass. Error bars represent one standard error from the mean percent woody dung in each site. r^2 = 0.28, N=5, P=0.36.

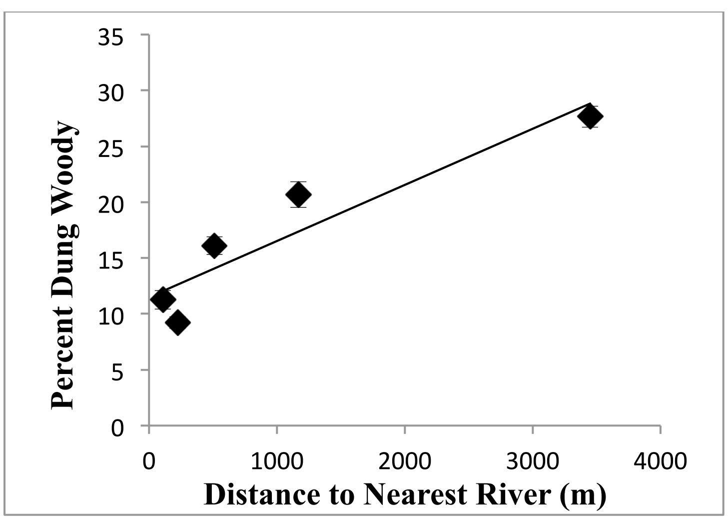

Figure 3: Response of dung woody fraction to distance to the nearest river. Error bars represent one standard error from the mean percent woody dung in each site. r^2=0.87, N=5, P=0.02.