

**FORAGING ECOLOGIES OF GIRAFFE AND CAMELS IN NORTHERN
KENYA: EFFECTS OF HABITAT STRUCTURE AND POSSIBILITIES FOR
COMPETITION?**

By

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ABSTRACT

Domestic camels (*Camelus dromedarius*) have become increasingly popular livestock in arid regions of sub-Saharan Africa. However, little is known about the environmental impacts of these animals, and concern has been mounting about possible competition with wild native ungulates. Unlike the more traditional pastoralist livestock species, camels are large-bodied, long-necked browsers which increases the potential to overlap with wild giraffe foraging, especially as the space available for browsing decreases. Giraffe ecology and social dynamics are poorly understood; it is believed that reticulated giraffe (*Giraffa camelopardalis reticulata*) population is in decline, and the effects of introducing a new potential competitor could be an added stressor. This study examines the foraging ecologies of reticulated giraffe and domestic camels in the Laikipia District of Kenya, an area where these two species have not been sympatric until very recently.

Both wild giraffe and domestic camel foraging heights and food species were quantified using multi-metric observations. Using repeated two-minute group scans I recorded feeding height categories and plant food preferences. Transects were used to sample the vegetation in areas in which foraging observations were recorded.

The results indicate that domestic camels do not overlap with giraffe in feeding heights. Not only do camels feed below giraffe, the two species also do not overlap in plant food preferences. Giraffes do not exhibit sexual dichotomies in plant food preferences. However, giraffes do exhibit sexual dichotomy in foraging heights, with females feeding at lower elevations than males. Habitat type has an effect on foraging ecologies of both giraffe sexes, but it is most pronounced in males; in contrast, habitat did not influence camel foraging. Such differences may be driven by local habitat structure and plant densities rather than by differing preferences between camels and giraffe. In addition, camel herder husbandry techniques also influence the dynamics of camel foraging by determining where and for how long camels browsed. These results have implications for the conservation and management of both species and the wider ecosystem if the twin goals of wildlife conservation and livestock production are to be achieved.

Keywords: Reticulated giraffe, camel, foraging ecology, pastoralist, conservation, Laikipia, Kenya

INTRODUCTION

Eastern Africa's semi-arid ecosystems exhibit dynamic interactions between pastoralist cultures, wildlife, complex rainfall patterns and soil types (Kjekshus 1996). Within this region, the existing balance between the two most important habitats, grasslands and *Acacia* dominated bush/woodlands, is particularly shaped by the interactions between herbivorous livestock and wildlife.

The East African savanna biome includes about 46 extant free-ranging ungulate species (Owen-Smith and Cumming 1993), as well as three dominant livestock species: cattle (*Bos* spp.) goats (*Capra hircus*) and sheep (*Ovis aries*), the latter two often grouped under the umbrella term 'shoats'. African herbivores are typically categorized into a browsing and a grazing guild (du Toit 1995); within each guild coexisting species tend to have differing body sizes and feeding strategies (Woolnough & du Toit 2001). This in turn leads to a central question: how are shared food resources partitioned among coexisting species (Sinclair 1979, Butt & Turner 2012)?

Competition between different herbivores depends on numerous factors: population densities relative to available resources, as well as habitat and feeding preferences (Du Toit 1990). African ungulate guilds are thought to partition existing plant resources along temporal and spatial axes (McNaughton & Georgiadis 1986, du Toit 1990). Considering the spatial axis, browser species optimize their foraging to maximize nutritional and energetic intake by focusing their feeding on different heights of vegetation (Pellew 1984a, McNaughton & Georgiadis 1986, du Toit 1990, Cameron & du Toit 2007). Although there is clear stratification in feeding preferences, overlap does exist in the feeding heights of different species, especially among the medium- to small-sized ruminants, for example between kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), and steenbok (*Raphicerus campestris*) (du Toit 1990). Such overlap in resource usage sets the stage for possible competition for browse resources (see Prins and Fritz (2008) for a comprehensive list of ungulate feeding overlap examples).

Pastoralism livestock systems occur across much of the Eastern African savanna, with livestock herds often overlapping spatially with wild herbivores, and utilizing the same resources. In areas where such livestock grazing occurs, it represents an added layer of pressure on the vegetation available for wild herbivores. Though still under investigation,

livestock feeding and husbandry could have significant knock-on effects on the functioning and structure of the savanna system, as well as on the availability of browse (Butt & Turner 2012). With varying degrees of habitat and dietary overlap between pastoralist livestock and wildlife (Odadi *et al.* 2007), it has long been assumed that competition for food resources exists between livestock and wildlife (Prins 1992, Voeten and Prins 1999, Awerbeck *et al.* 2009, Butt 2010). However such views may be overly simplistic, with the interactive effects between wildlife and livestock being more complex, and ranging from facilitative to competitive between the two groups (Odadi *et al.* 2011, Butt & Turner 2012), and well as on vegetation (Du Toit & Cummings 1999).

However, a species that exists alongside pastoralists and wild ungulates - the giraffe – has long been thought to escape such resource overlap with either wildlife or livestock (Ciofalo & Le Pendu 2002). This is primarily due to giraffe's capacity to feed on vegetation out of reach of other ruminants, and its ability to travel long distances in search of forage (du Toit 1990, Young & Isbell 1991, Bond & Loffell 2001, Woolnough & du Toit 2001, Parker & Bernard 2005).

Researchers have referred to giraffe as the “Forgotten Megafauna”, and until very recently they have been surprisingly understudied when compared to other African savanna species according to the Giraffe Conservation Foundation (Tutchings *et al.* 2013). Giraffe physiology is comparatively well understood, many other questions around giraffe ecology are still debated, including herd and social interactions, its effect on its habitat, foraging dynamics, etc. Even giraffe phylogeny and taxonomy are only now becoming clarified (Brown *et al.* 2007), with consensus growing that there are 9 extant giraffe subspecies (Seeber *et al.* 2012, GCF 2013).

Getting a better understanding of giraffe ecology is ever more important as many of the subspecies are experiencing sharp declines as a result of increased hunting pressures, habitat loss and changing cultural practices (Seeber *et al.* 2012). For example, the reticulated giraffe's (*Giraffa camelopardalis reticulata*) estimated wild population has declined sharply over the past 15 years from 28,000 to about 5,000 today (GCF 2013, Tutchings *et al.* 2013).

Pastoralist herders try to manage their livestock in accord with prevailing environmental conditions (Ellis and Galvin 1994, Galvin 1992, Galvin *et al.* 1994). When

other social, economic and zoonotic risks are added, pastoralists must balance their herd sizes, composition, and grazing patterns in response to these pressures to remain profitable (Homewood 2008). Although climatic analyses foresee differential impacts of climate change in East Africa, the models predict that regions of Eastern Africa are likely to experience long-term increases in temperatures, and some areas will be drier, while others will experience greater rainfall, occurring in heavier, more unpredictable events. (Bates *et al.* 2008, McSweeney *et al.* 2008, Thornton *et al.* 2002).

Droughts represent a particularly serious challenge to African pastoralists (Butt 2010a, Davies and Bennett 2007, Kiage 2013). One way pastoralists have dealt with increased aridity is to change herd composition, away from traditionally cattle-dominated groups to including more, or completely switching, to shoats or even camels. Domestic camels (*Camelus dromedarius*) are more drought-tolerant than cattle, performing well in adverse conditions, and have lower energy requirements (Faird 1995, Maloiy *et al.* 2009).

Such changes in herd composition can have important implications for overall livestock productivity, animal nutritional requirements, as well as milk production (Little *et al.* 2008, Ericksen *et al.* 2013). Milk is often the prime source of income for pastoralists. While camels are more expensive to acquire initially, they have the potential to generate more income through the production of more, and higher priced, milk relative to other East African livestock taxa (Baars 2000). In addition, they produce well in both wet and dry seasons, yielding more milk than cattle, especially over the dry season (Bekele *et al.* 2002).

Like giraffe, camel foraging is little studied, especially compared to other livestock species (Dereje & Uden 2005). Few studies exist currently on the effects of introduced camels on ecosystem function and the resident herbivore communities. Camel browsing may affect forage availability, vegetation composition or structure. One particularly important relationship could exist between domestic camels and reticulated giraffe. Both are large ungulate browsers, with the ability to feed across a large vertical spectrum, and camels can stretch into higher vegetation zones than other livestock, thus reaching into giraffe feeding levels.

This research explores the foraging preferences of domestic camels and wild reticulated giraffe. Using field observations of both species and by gathering multi-metric vegetation and spatial data, we investigate the following questions:

- i) Is there overlap between camel and giraffe feeding heights and preferred plant food species?
- ii) Are there differences between adult female and adult male giraffe foraging ecologies across habitat types?
- iii) Do giraffe exploit their presumed competitive advantage by always eating the tallest and most common plant species in the landscape?

METHODS

Study Area

In order to collect data on co-existing giraffe and camel in an East African savanna setting, this research was conducted at the Mpala Research Centre (MRC) in Laikipia Province (north central Kenya). Situated at elevations between 1,700-2,000m asl, MRC encompasses 19,873 ha of savanna and dry woodland habitats and contains diverse, abundant wildlife communities that includes 22 species of native wild mammalian herbivores (Goheen *et al.* 2013). Herds of cattle and shoats are also kept at Mpala in a quasi-pastoralist fashion, with livestock herded during the day, and returning each evening to *bomas* (temporary animal enclosures built either of cut acacia branches or of mobile metal fencing).

Camel herding is increasing in popularity as are camel stocking levels in Laikipia (Kinnaird and O'Brien *pers. comm.*, Kinnaird & O'Brien 2012), encouraged by the establishment of a camel milk processing facility in the area, providing a local outlet for camel products. Recently, camels started to be stocked at Mpala, providing the opportunity to compare camel and giraffe foraging ecologies. These camels are kept in largely sexually segregated herds, composed either of all-male animals or of majority female and immature young, with a handful of mature bulls.

Because of its location within the rainshadow of Mount Kenya Mpala receives only 640 mm of rain annually. There is a pronounced north to south increase of rainfall across

Mpala resulting in more luxuriant vegetation in the southern sector (Goheen *et al.* 2013). Adding to this, Mpala contains two different soil types that result in two strikingly different vegetation types and structure (see Figures 1 & 2).

Western Mpala is composed of topographically flat, “black cotton” vertisol (clay) soils, resulting in an open, low diversity savanna dotted by small trees. Tree communities are dominated by ant-acacia (*Acacia drepanolobium*), which accounts for more than 97% of the overstory cover, while ground cover is composed to 90% of only five grass species and two forbs (Young *et al.* 1997, 1998). This low vegetation diversity is in part caused by the extreme shrink-swell movements of black cotton clays, that destroy the roots of most plant species (Pringle *et al.* 2010).

Eastern and northern Mpala is composed of infertile red sandy loams (alfisols; locally termed ‘red soil’). This soil type supports a diverse, structurally variable bushland habitat with a patchy understory of perennial grasses and a canopy cover dominated by prickly thorn (*Acacia brevispica*), wait-a-bit thorn (*Acacia mellifera*), and mgunga (*Acacia etbaica*) (Augustine & McNaughton. 2004, Kinnaird & O’Brien 2012).

Between the black cotton and red soil areas is a transition zone, which supports a savanna dominated by perennial grasses with widely spaced trees and shrubs (Kinnaird & O’Brien 2012) and which includes species from both the black cotton and red soil habitats. These three soil types produce vegetation types that are very different in species richness, and result in distinct habitat structures, allowing for comparison in herbivore foraging ecology across these three ‘zones’.

Field data were gathered between May and August 2011. Appendix 1 summarizes the methods relied upon to collect data for each of the research questions

Behavioral Observations

In order to determine overlap in feeding height and plant food species preferences between giraffe and camels, geo-located behavioral observations were used to record frequency of feeding at different height categories, as well as the frequency of feeding on different plant species.

Reticulated Giraffe Surveys & Observations

Mpala was divided into six sectors to allow for even distribution of sampling effort and timing (Figure 3). Giraffe were surveyed in the 6:30am -11:00am period and again from 3:00pm to sunset, to avoid the heat of the day when the animals are least active. Observations were vehicle-based for safety, and because giraffe were generally more accustomed the vehicles.

Once a giraffe, or group of giraffe, were encountered the vehicle was pulled to the side of the track, and the engine switched off. The number and sex of visible giraffe were recorded (Figure 4), and a group of giraffe was defined as any giraffe within 100m of others (Shorrocks & Croft 2009). Giraffe separated by more than 100m, were considered to be individuals, or part of a separate group. Other visible ungulate species were also counted and recorded [except dik-dik (*Madoqua kirkii*) which were presumed not to interact with giraffe].

To place each encounter in space, a GPS waypoint was taken using a hand held GPS unit (Garmin etrex VistaTM). The distance to the most central giraffe in the group was measured by a laser rangefinder (Nikon Prostaff 550), and the bearing angle to the most central giraffe was also taken using a handheld compass (Brunton Classic). This allowed for exact positioning of the giraffe in the landscape using GIS trigonometry functions (Figure 5). Likewise, the distance and angle to other species present were also noted, to record their exact positions relative to giraffe. When the encounter ended (and a new waypoint taken if the vehicle was moved during observations), the distance to the animal's last location and the corresponding compass bearing were also recorded. This allowed for a later vectoring using GIS, of the giraffe group's browsing movement through the landscape.

Because of the fission-fusion nature of giraffe groups (Bercovitch & Berry 2013), the size of each giraffe group was determined in the evening, and was based on the size of the group at its most numerous.

Giraffe in this region are comparatively more vigilant and skittish (Kinnaird pers.comm.), making observation challenging. As such, all behavioral observations were vehicle-based to minimize disturbance to the animals. Giraffe observations were made

through Nikon binoculars using 2-minute group scans (Altmann 1974, Bøving & Post 1997, Hamel & Cote 2008, Treydte et al. 2011). Group instantaneous scan sampling was chosen over focal animal observations, because initial field testing revealed that the presence of dense bushes prevented sustained following of an individual. However, for cases of solitary animals, or for smaller groups where individual giraffe could be tracked with confidence, the same group scan method was still used, but observations were coded to identify individual giraffe.

The same observer (DOC) made all observations. The observation logistics and data recorded are detailed in Figure 6. Although observations were spread across all of MRC to avoid recording an individual more than once, this possibility cannot be excluded with confidence, as giraffes could not be marked individually.

To quantify giraffe feeding heights, four feeding height categories were assigned based on the angle subtended between the neck and forelegs (Figure 7): feed high 180°, feed medium 135°, feed level 90°, and feed below 45° (see du Toit 1990). Actual measurements of each of these height categories were made on focal male and female adult giraffe feeding heights on plants in the field (du Toit *pers. comm.*). After recording a clearly visible giraffe feeding at one of the neck angle categories on a plant, the same plant was visited after the giraffe's departure and the corresponding bite mark located (previously recorded with a camera). The height of the bite mark above ground level was then measured using wooden poles marked in 50cm increments. Thus the height of feeding represented by each neck angle category was measured. To ensure an accurate representation, each of the four neck angle categories were measured for approximately 15 giraffe of each of the sexes.

While feeding and behavioral data were recorded for juvenile giraffe, they are not part of this study since they are still growing, and thus their feeding heights are hard quantify. Only adult giraffe data were used for statistical analyses.

Camel Surveys & Observations

All foraging observations on camel were taken from the same herd of animals. The herd consisted almost exclusively of females, and all observations reported here were

made on adult female camels. While male giraffes are slightly larger than females, these data also provide broad insights on male foraging behaviors.

Camel observations were made on foot on 5 days spread over the study period, with the observer (DOC) walking with the herders across the landscape. Observations were spread over the whole course of the day while camels were foraging across the savanna. The observer tracked his own movements throughout the day via GPS.

As with giraffe, camel observations were collected via two-minute long group scans (Altmann 1974, Bøving & Post 1997, Hamel & Cote 2008, Treydte *et al.* 2011). These were conducted during 1h long sessions, at the end of which a break was taken to avoid observer fatigue. At the beginning and end of each of the hour-long observation periods, a GPS waypoint was taken. This allowed for vectoring of the movement of the camel herd during the observation periods, as was done with the giraffe encounters. However, since the observer walked within the camel herd the waypoint was not adjusted with GIS.

For each two-minute group scans, observations were recorded of the first twenty adult camels seen, though after the first three days of observations, this number was reduced to 15 camels, due to the difficulty of recording 20 camels at a time when they were spread out and foraging. This was the maximum number of camels from which behavior could be recorded during each two-minute group scan. Observations were not made during periods of active herding, when the herders were pushing the herd onward to new areas or back to the boma.

To record camel activity budgets (see Appendix 4), during each scan we recorded the following behavioral categories: standing, walking, running, laying, aggression (visibly engaged in fighting), and feeding. In a similar fashion to giraffe, to gather foraging data, we recorded the feeding height category, as well as the species of plant being fed upon. The feeding height categories are based on the angle subtended between the neck and forelegs (Figure 8): feed high 135° , feed level 90° , feed below 45° and feed ground (grazing).

To measure the height of each of the feeding height categories, I measured were made of 15 adult female camel heads when held at the body level approximately at middle of each category (head held high, shoulder-level and knee-level) while in the boma (du Toit *pers. comm.*).

Camel GPS Collar

In order to record camel foraging movements over the course of the day, I employed a similar methodology that has been used for pastoralist livestock tracking (Butt *et al.* 2009, Butt 2010a,b). A GPS (Garmin Forerunner 301™), at its default settings was attached to an adult female camel's neck. The unit's stopwatch function (time and distance) was set to track the camel's movements while foraging in the bush (Figure 9). A small plastic cover, taped over the start/stop button prevented the unit from switching off during the day. The GPS unit was attached before an animal left the boma in the morning and was then collected after it returned to the boma in the evening.

Initially the GPS unit was attached using a rope, but this set-up was modified, so that the GPS unit was enclosed in a Ziploc bag and placed into a protective canvas pouch attached around the camel's neck with a canvas leash (Butt *pers.comm.*, Butt *et al.* 2009, Butt 2010a,b). After a unit was attached in the boma, we observed the camel's interactions with the rest of the herd to evaluate possible effects of the unit on animal behavior and social effects. These observations revealed that after some initial curiosity from other camels, and as the unit absorbed the smell of the herd over time, there was little, to no, additional attention by other animals. The unit did not cause distress or impede movements or feeding of the camel to which it was attached.

For those few situations where the camel GPS collar had to be affixed or removed from the animal while the animal was enclosed and resting in the boma, the GPS data were edited to the time the animal actually departed from, and returned to, the boma.

All methods used were conducted in full accordance with the relevant institutional animal care guidelines (University of Michigan UCUCA permit 10553-1).

Vegetation Transects

To measure how giraffe and camel foraging and feeding heights related to the vertical structure and relative density of plant species in the landscape, 33 multi-metric vegetation transects were conducted along observed browsing paths of giraffe and camels (Figure 10). Point-centered quarter method samples were taken at every 25m along a transect line (Pellew 1983, Young and Isabell 1991, Cornelissen *et al.* 2003, Mitchell 2010). At each

of the point-centered quarter sample points, the landscape was divided into four quarters by the crossing perpendicular east-west and north-south compass lines. Within each of the quarters, the distance to the branch end of the nearest woody plant taller than 0.8m was measured using a 100m tape measure. The height of the plant was also measured to the end of its highest branch using a fiberglass telescoping tree measurement pole.

To ensure sampling power, each transect had a minimum length of 250m. In more open habitat where shrubs were separated by long distances, some transects had to be longer (to a maximum of 500m) to avoid double-counting the same plant in subsequent point-centered samples. Regardless of total length, there were 10 point-centered samples per transects. Using the previously gathered GPS and distance data, these transects lines followed the direction of movement (vector) of an encounter of a giraffe or camel group from which feeding was observed. The close proximity allows for sampling of vegetation and structure of the habitat the animals were browsing in, and enabled the pairing of these feeding observations to vegetation structure.

In addition, at these 25m intervals, percent ground cover was estimated using a 1m² quadrat frame. Every 50m along the transect line bush density was categorized using a Bitterlich stick (Grosenbaugh 1952, Sundaresan *et al.* 2008). This method involves counting the number of bushes wider than the arc subtended by a 10 cm rectangle held 1m away from the eyes.

Only plants that were alive were measured. This included damaged or elephant-pushed over plants that were still alive.

GIS Analysis

All GPS data were imported into ArcGIS 10 using Garmin BaseCamp. Giraffe encounter waypoints were moved/projected in ArcGIS using the distance and angle data to the actual position of the giraffe in the landscape.

Statistical Analysis

All statistical analyses were completed using both R and R Commander software (R Foundation for Statistical Computing), after first being organized in Microsoft Excel. Data were tested for normality using the Shapiro-Wilk test for normality. Where data

were normal or could be successfully transformed (using standard methods such as logarithmic or square root transformations), parametric tests were used. Non-parametric tests were used for non-normal data (e.g. plant heights, un-pooled feeding heights).

For comparison of feeding heights within and between species, the possibility of non-independence of observations was minimized by pooling and then averaging each animal's feeding height data over the observation period. This would result in an averaged feed height measure for each animal. For encounters with large herds, where observations were not tracked to individuals - the aforementioned 'animals' may not have been the same individual, and in such cases they were categorized as composite animals (Appendix 3).

To examine the foraging overlap between camel and giraffe, un-averaged feeding height data were used to analyze the feeding heights of camels and giraffe on plant species (Tables 4,7). As such, those results should be interpreted with caution due to the possibility that the data aren't independent.

The feeding heights of camels and giraffe on plant species were analyzed using Mann-Whitney U tests. Multiway ANOVAs and Tukey's HSD pairwise comparisons were used to determine the influence of habitat type and sex on the feeding heights of giraffe, using summarized data. Linear regression analyses were used to investigate paired giraffe browsing vectors and vegetation structure (Appendix 1).

RESULTS

Giraffe occurrence & feeding height categories

A total of 657 giraffe* were seen during the study period of 30 days, with behavioral observations made on 563 giraffe* across 85 encounters. Over 290 hours, 8,696 observation points were recorded for giraffe (a point being a single observation from the two-minute group scans). Feeding height data were recorded for 337 adult giraffe (Appendix 2). Note however that these may not all be unique individuals, as a given giraffe may have been repeatedly sighted on different days.

* This number may include some repeat encounters with the same giraffe on different days

Table 1 (see also Figure 7) shows the results of the giraffe feeding category measurements, with feeding height observation being categorized as either feeding high, feeding medium, feeding level or feeding below.

Camel occurrence & feeding height categories

Camel herd size varied between 62 and 78 individuals over the study period. Our survey produced 10,324 observation points, of which 7,340 were feeding data (Appendix 4).

Table 2 (Figure 8) shows the results of the domestic camel feeding category measurements, and each feeding height observation was categorized as either feeding high, feeding level, feeding below or feeding ground.

Influence of habitat type and sex on adult giraffe foraging

Based on data from 337 adult giraffe with averaged feeding height observations (Appendix 3), giraffe exhibit a significant difference in feeding heights between males and females, with males feeding on average at 3.7m while females feed at 2.5m (ANOVA $F_{1,331} = 254.7$, $p < 0.001$). To determine whether this trend remained the same across all three habitat types, and to account for differing vegetation structure biasing this result, average male and female feeding heights were compared separately for each of the three habitat types (Table 3, Figure 11). Indeed, for each of the three habitat types, adult male average feeding heights were significantly higher than adult female (Black Cotton: ANOVA $F_{1,51} = 48.0$, $p < 0.001$; Red Soil: ANOVA $F_{1,199} = 135.3$, $p < 0.001$; Transition Soil: ANOVA $F_{1,81} = 102.1$, $p < 0.001$).

Average adult giraffe feeding heights were compared between habitat types. Habitat had a significant effect on feeding (ANOVA $F_{2,331} = 90.3$, $p < 0.001$). The median heights of vegetation in each habitat (Table 3) were significantly different (Kruskal-Wallis $H = 79.6$, p -value < 0.001).

Adult males exhibited significant differences in their average feeding heights across all three habitat types (ANOVA $F_{2,151} = 44.8$, $p < 0.001$). Adult females also showed the same significant differences (ANOVA $F_{2,180} = 46.9$, $p < 0.001$), however Tukey's HSD revealed that there was not a significant difference between adult female feeding heights

in the black cotton and red soil habitats ($p=0.09$), but that they were significantly lower in transition soil ($p<0.001$) (Figure 11).

Giraffe food plants

Adult giraffe observations of feeding height and plant species are summarized in Table 4. Adult giraffe fed on 8 identified plant species across Mpala, whereas plant transects recorded 15 species of woody plants (Appendix 5).

The four food plant species with the most feeding observations (*Acacia mellifera*, *A. drepanolobium*, *A. etbaica* and *Boscia albitrunca*) were selected for further analysis, as the sample sizes for the other species were too small to obtain sufficient statistical power. The average heights and absolute density of the four plant species were summarized by habitat type (Table 5). Giraffe feeding heights on those four species, and the average heights of the plants as determined from the vegetation transects are shown in Figure 12. Male giraffe consistently feed significantly above the median height of the plant for *A. drepanolobium* (Mann-Whitney U, $U = 17371$, $p<0.001$), but not significantly so for *A. etbaica* ($p=0.1$) or *Boscia albitrunca* ($p=0.052$).

In contrast, female giraffe with the exception of *Boscia albitrunca*, feed below the median height of a tree. Thus, female giraffe feed significantly below the median heights of *A. drepanolobium* (Mann-Whitney U, $U = 106765.5$, $p<0.001$) and *A. etbaica* ($U = 20153$, $p<0.001$), but not for *Boscia albitrunca* ($p=0.4$).

Only *Acacia mellifera* was found in all three habitat types, and showed a significant difference in its median height across habitats (Kruskal-Wallis $H = 20.4$, $p\text{-value} <0.001$). The strongest difference was between the red soil and transition soil ($p\text{-value} <0.001$), followed by black cotton and red soil ($p\text{-value} <0.01$), whereas the differences between plant heights in black cotton and transition soil were not significant ($p\text{-value} = 0.3$).

Overall giraffe feed at a height different to the median height of *Acacia mellifera* (Mann-Whitney U, $U = 212797.5$, $p < 0.05$). Females feed significantly lower (Mann-Whitney U, $U = 164377$, $p<0.001$), while males feed significantly higher (Mann-Whitney U, $U = 48420.5$, $p<0.001$) than the median height of the plant.

The situation may be more nuanced though, especially for females in different habitat types (Figure 13). In the black cotton soil, females do not feed higher than the median

and mean height of the plant (Mann-Whitney U, $U = 224$, $p=0.09$), but there is a small sample size here (plant height $n=15$, feeding height observations $n=45$). In the red soils females feed significantly above the median plant height, but the height difference is small (Mann-Whitney U, $U = 16593$, $p<0.001$). While in the transition soils, females feed significantly below the height of the plant (Mann-Whitney U, $U = 46101.5$, $p<0.01$). Males on the other hand feed significantly higher than *Acacia mellifera*'s median height in all habitats (Black Cotton: $U = 10$; Red Soil: $U = 13837$; Transition Soil: $U = 8807$, all $p<0.001$).

Paired Giraffe feeding observations and plant transects

The data from the plant transects ($n=28$) that traced the direction of movement (vector) of observed giraffe feeding groups, enabled the pairing of feeding observations to vegetation structure (Figure 10). The overall average height of the plants measured in each transect was calculated, as was the overall average feeding height for the observed giraffe group. The relationship between plant height and feeding height was further explored using linear regression ($r^2 = 0.3516$, $p<0.001$), and overall plant height showed a significant influence on average giraffe feeding heights (Figure 14).

Camel browsing orbits

Tracks of both the camel GPS collars and the human observer can be seen in Figure 15. The tracks of the human observer were used in instances when a camel GPS collar failed, as a proxy to the herd's movement. Camels browsed in both the red soil and transitional soil, travelling a straight line distance up to 2.2km from the boma.

A circle drawn around the furthest extent of the camel's browsing orbits (white circle in Figures 1 & 15), encompasses an area of 1,004 hectares. Using just the GPS collar data, and discarding the browsing orbits with only partial GPS recordings, the average camel orbit is 6km over 7h 31mins ($n = 9$, see Table 6 details).

Camel food plants

Observations of feeding height and plant species consumed adult female camel are summarized in Table 7. Recordings of feeding at ground level were removed for analysis of feeding height levels due to their zero height value. Camels fed on 7 identified species. Categories denoted as “*Acacia* spp.” and “*Euclea* spp.” were not identified to plant species level. Mean plant heights for each plant category are given in Table 7.

The four most frequently fed upon plant species were analyzed further. Camels fed significantly below the heights of *A. brevispica* (Mann-Whitney U, $U = 462318$, $p < 0.001$), *A. mellifera* ($U = 80223$, $p < 0.001$), *A. etbaica* ($U = 16005$, $p < 0.001$), and *B. albitrunca* ($U = 4525$, $p < 0.001$).

Paired camel feeding observations and plant transects

Using a similar approach as was used for giraffe, we paired camel feeding observations to vegetation structure by using the plant transects ($n=5$) that traced the camel browsing vector tracks ($n=5$) (Figure 10). Although a small sample size, we found no significant relationship between plant height and camel feeding height ($r^2 = 0.3601$, $p = 0.3$). Overall plant height did not appear to influence average camel feeding heights, unlike the case for giraffe. Instead the heights of the plants fed upon by camels closely matched the heights of the same species measured across Mpala. However the density of the plant species in the area in which the camels fed differ to the densities of these species across Mpala (Table 8). In the areas where camels browsed, *A. brevispica* was much more dense, while the other three species were less dense when compared to the rest of Mpala.

Giraffe and Camel feeding height comparison

Average feeding height data were compared between giraffe ($n=337$, individual average feed height $\bar{x} = 3.0\text{m}$) and camels ($n=340$, individual average feed height $\bar{x} = 1.36\text{m}$). Camels fed significantly lower than giraffe (Mann-Whitney U, $U = 2567$, $p < 0.001$) (Figure 16). The difference remained significant ($U = 2538.5$, $p < 0.001$) even

after the giraffe observations from black cotton habitat were removed (giraffe $n=284$, median individual average feed height = 2.93m).

When camel feed heights were separately compared to male ($n=129$) and to female giraffe feeding heights ($n=155$), camels still feed significantly lower than male giraffe ($U = 34.5$, $p<0.001$) as well as significantly lower than female giraffe ($U = 2504$, $p<0.001$) (Figure 17).

To investigate whether differing habitat structure might explain these differences, the plant transects taken along giraffe browsing paths (transect $n=22$, plant $n=968$) from red soil and transition soil habitat were compared to the plant transects taken along camel browsing vectors (transect $n=5$, plant $n=220$). The median height of the vegetation along camel browsing vectors ($\theta = 1.75\text{m}$) was significantly lower than for giraffe browsing paths ($\theta = 2.18\text{m}$) using Mann-Whitney U ($U = 81296.5$, $p<0.001$).

DISCUSSION

This study investigated (i.) whether there is overlap between camel and giraffe feeding heights and preferred plant food species, (ii.) whether there are differences between female and male giraffe foraging ecologies across habitat types; and lastly, it explored (iii.) whether giraffe exploit a competitive advantage by always eating the tallest and most common plant species in the landscape.

Camel and giraffe foraging overlap

The results of this investigation find that there is no direct overlap in the feeding heights of adult female camels and adult giraffe of either sex (Figures 16 & 17). This lack of overlap remains even after the exclusion of either (i.) camel ground level feeding data, or (ii.) giraffe black cotton habitat observations.

Giraffe and camel do overlap in their consumption of six plant species. However, of the four most frequent species eaten by each, overlap only occurs with *A. mellifera* (Tables 4 & 7). *A. mellifera* makes up 44% of a giraffe's foraging compared to 6% of a camel's (Appendix 2 & 4). Using frequency as an indicator of preference, giraffe and

camel prefer two very different plant palettes, with feeding further concentrated at different heights.

A second explanation for the observed differences in giraffe and camel food preferences is that vegetation densities are different at the particular locations where camels foraged compared to the broader Mpala landscape where giraffe foraged (Table 8). The overall height of vegetation that camels fed upon was significantly lower than the height of vegetation fed on by giraffe. The relative and absolute densities of plant species in the areas in which camels were feeding also differed to densities of plants in areas where giraffe were feeding. As such vegetation structure may be driving the dynamics of camel foraging could explain the observed differences in preference between camels and giraffe rather than preference.

Even so, earlier research from Ethiopia has shown similar camel plant food preference results to those we found at Mpala. They found that during the wet season *Acacia brevispica* is the camel's favorite food item (22% of diet), while *A. mellifera* is less favored (8%), and *Boscia* spp. (< 1%) is rarely eaten (Dereje & Uden 2005). This mirrors our results that show camels favor *Acacia brevispica*, making up 50% of their diet, while *A. mellifera* accounts for only 6% and *Boscia albitrunca* is less than 1% (Appendix 4). Therefore the camel food plant species preferences in these results could be widespread across camels in general, and not a peculiarity of the plant densities in which the camels were feeding at Mpala.

Human management practices dictate a large part of the foraging dynamics of camels (Dereje and Uden 2005, Gallacher and Hill 2005, Farah *et.al.* 2004) through the selection of the enclosure location and movement schedule. Camel bomas are relocated periodically once the surrounding vegetation is deemed to be exhausted by livestock managers. If a boma is moved to a location with vastly different habitat structure in order to accommodate foraging needs, then that may alter the camels foraging ecology. Examining the foraging response of camels to a changed boma location could shed light on whether camel's preferences are hardwired or whether the animals are just responding to the vegetation structure and densities of their habitat.

A further factor in which husbandry may affect foraging patterns is through the provision of supplemental feeding. If camels receive supplemental feed such as salt,

molasses, etc. this potentially could affect the types of plants and nutrients they are seeking (Nyariki *pers. comm.*).

Foraging by camels has been shown to impact both plant species diversity and community composition (El-Keblawy *et al.* 2009), and when stocked heavily, camels can drive a shift from *Acacia* savanna to low dwarf scrub (Gallacher and Hill 2006). How the plant community at Mpala will respond to recently introduced camel browsing is unknown, as is the extent of any knock-on effects on giraffe and other wild herbivore communities.

Interest is growing among pastoralist communities to raise camels as livestock to diversify and hedge their herds against uncertainties, to adapt to changing rangeland ecology and to maximize livestock production (Desta and Coppock 2000, Kinnaird and O'Brien *pers. comm.*, Young *et al.* 2013). For instance, camels are the best animals for milk production under the pastoral conditions in southern Ethiopia (Megersa *et al.* 2008). As such, herd composition could shift gradually from cattle and shoats to just camels or camels and shoats, resulting in an increase in camel populations. Understanding the effects of increased camel populations on arid rangelands is a prerequisite for effective management, as well as for continued sustainable livestock-wildlife interactions (Retzer, 2006).

Comparing camel browsing orbits to cattle grazing orbits provides an alternative explanation for differences between cattle and camel foraging. Cattle grazing orbits last about 11 hours covering 8-11km, covering a straight-line distance of between 2.8-4.6km (Butt 2010b) from the boma. Camels traveled only 2.2km from the boma, covering an average distance of 6km and browsing for 7.5 hours. Such differences in cattle and camel orbit footprints, could have differential impacts the wildlife and environment in which these livestock are herded.

While no direct evidence was found for overlap in camels and giraffe, there are a number of additional and complicating factors that need to be considered to better understand the drivers of feeding heights and plant food preferences for both species, and how preferences change under different habitat structures. In addition, there are a number of potential temporal overlaps such as the herbivore pressure of the camel's lower

feeding level on the ability of vegetation to grow into the feeding heights of giraffe that were not examined and are hard to predict.

Understanding the interactions between browsing camels, their environment, giraffe and other wild ungulate populations is important in order to identify areas of competition for shared resources. This is a prerequisite in order to develop strategies that allow for continued co-existence of the two species, as well as to improve camel production. Browse plants are an important resource and must be managed effectively both for camel, as well as for giraffe and other wild ungulate consumption. Understanding these trade-offs is particularly critical today as many wildlife populations are in decline (GCF, 2013), and the impacts of large herbivores on this ecosystem are complex and counterintuitive (Pringle *et al.* 2011).

Female and male adult giraffe foraging patterns and plant food preferences

The clearest difference between male and female foraging heights is that females feed on average 1.2m lower than males. The difference is greater than what would be expected based the females' smaller body size (a consistent 0.6m lower in each feeding category). This indicates that giraffe sexes diverge in their foraging heights, perhaps to avoid intraspecific competition, and more so than what body size differences would indicate. This indicates that males consistently feed at higher feeding levels, or, given that males can only stretch so much, that females feed lower that is expected for their height.

The general pattern of females feeding disproportionately lower than males is well documented in giraffe (du Toit 1990, Ciofolo & Le Pendu 2002). Furthermore, for the three most frequently eaten plant species (*A. drepanolobium*, *A. etbaica*, and *A. mellifera*), males feed higher than the average plant heights, while females feed below the average plant heights, with the most pronounced difference seen on *A. drepanolobium*. However this result may be caused in part by female proclivity for feeding on *A. drepanolobium* plants found in the 'low drep' areas of transition soil, where the plants growth is stunted (Kinnaird *pers. comm.*). In contrast males foraged more frequently in the 'high drep' black cotton habitat where *A. drepanolobium* grows to 5+ meters (Young and Okello 1998).

Habitat type has a stronger influence on male rather than female feeding heights. With females feeding lower in the canopy, they are less strongly affected by fluctuating habitat structures across the landscape, whereas males, feeding above the canopy level are driven up and down as the plant heights change.

While it is not clear whether it is habitat structure or preference that explain male giraffe feeding heights. Females do seem to exhibit preferences for lower foraging. As indicated by the foraging patterns on *A. mellifera*. Thus across all habitat types male giraffe followed a familiar pattern of consistently feeding high, while females showed a more nuanced approach altering their feeding heights across habitat types and average plants heights. Such complexity also indicates that, at least below the very highest feeding levels, female's shorter neck and smaller body size is not the primary cause of these differences.

No consensus exists currently on the reason for these inter-sex feeding height differences. Several theories have been put forth to try to explain the differences between male and female giraffe foraging including inter-sex body size differences, males striving to access the nutritious browse found in plant higher parts, and males driven to the higher parts of the plants by competitive browsing from below by females or from other species (du Toit 1990, Ginnet & Demment 1997, Woolnough & du Toit 2001). It has been suggested that lower feeding heights of females could negatively impact their browse intake because (i.) lower elevation leaves are of lower nutritional quality (Woolnough & du Toit 2001) and (ii.) there is increased potential for resource overlap with other wild or domesticated browsers (Cameron & du Toit 2007).

However, most ruminants over 25kg exhibit some degree of sexual body-size dimorphism (Owen-Smith 1992). As such, giraffe feeding height differences may be just a reflection of a broader pattern seen in all sexually dimorphic ungulates, rather than the result of a giraffe-specific sex-based feeding strategy. Unraveling the causes of intraspecific variation in giraffe browsing behaviors can help advance behavioral and ecological foraging theory, as well as improve understanding of resource utilization in all species, all of which are also of relevance for giraffe conservation.

In contrast to feeding height preferences, female and male giraffe are more closely matched in their feeding plant choice (Appendix 2). Indeed their foraging seemed to

closely reflect (with the exception of *A. brevispica*) the plants species availability in the habitat (Table 4). Interestingly, giraffe in this study feed on a very limited number of species compared to other studies, where giraffe have been known to feed on 20 or 30+ species (Pellew 1984b, Parker & Bernard 2005). As with giraffe elsewhere, woody acacias were the preferred food type. It is unknown whether this dichotomy is due to the existence of a limited plant species palate at Mpala or to the limitations of this study.

Study Limitations

As a result of the study's short duration, there are some limitations on these results. For example findings are based only on observations of adult female camels and adult giraffe. The extent to which foraging habits of juvenile giraffe and camels, as well as adult male camels, may result in more or less overlap in foraging between the two species remains to be explored. The low-diversity diet we documented for giraffe could be attributed to this study's short timeframe and not recording giraffe foraging over all the seasons (Table 4, Appendix 2).

The camel research was conducted at a single boma location. Gathering data from different camel herds at several boma locations would allow for a better understanding of the effects husbandry techniques have on camel foraging, and thus provide a clearer picture on overlap with giraffe. Obtaining comparative habitat structure and relative plant density data from the areas foraged by giraffe and areas foraged by camels would further clarify differences in camel and giraffe foraging (Table 8).

Given the preliminary nature of this study, our results should be interpreted with caution. For logistical reasons there were several factors that could not be considered in this study. Several factors that may affect foraging ecology such as giraffe herd size, age and sex-ratios (Young & Isbell 1991), presence of other herbivore species, vigilance trade-offs, social dynamics, etc., could not be considered for logistical reasons in this study. Further long-term collection of data is needed to provide a more complete picture.

Conclusion

Is there overlap between camel and giraffe feeding heights and preferred plant food species?

Distinct variations occur in the nutritional values of plant species between season, between species and between different plant parts (Senft *et al.* 1987). To compensate for these variations, herbivores adapt their foraging behavior to achieve the daily nutrient and energy requirements needed for reproduction and maintenance (Pellew 1984a). Such adaptations include the choice of foraging habitat, the plant species and plant parts they feed on, and the time allocated to feeding (Johnson 1980, Pellew 1984a), all which combined form a herbivore's optimal foraging strategy. It can be argued - perhaps more so than for any other ungulates - that giraffe have more opportunity to optimize such decisions due to their large (>3m) vertical feeding arc (Table 1). Camels are offset vertically from giraffe, but they have a similarly sized 3m feeding arc (Table 2) allowing for similar opportunities for foraging optimization. Thus, these two species have a wide vertical choice when foraging, and these results show an absence of foraging height overlap with each other. More data are needed to determine whether these differences are the result of passive or active optimization. There is pressing need for further research, especially if pastoralist and ranching management trends continue to bring these two large, iconic, and fascinatingly complex ungulates together.

Are there differences between female and male giraffe foraging ecologies across habitat types?

Do giraffe exploit their competitive advantage by always eating the tallest and most common plant species in the landscape?

My results show that the relationships between habitat structure and male and female foraging ecologies are complex and nuanced. Habitat structure and plant heights evoke differing responses from males and females, even though they pursue very closely aligned plant food species preferences.

However, my results are in line with the general trend of earlier studies (du Toit 1990, Ciofolo & Le Pendu 2002) in suggesting that female giraffe feed at lower levels than males across all habitat types. Male giraffe also exhibit the strongest exploitation of their

competitive foraging height advantage with their consistently elevated feeding. Females did not exhibit this. The reason for these divergences has not been satisfactorily answered since difference in body size can provide only partial explanation.

In some aspects of foraging, the sexes almost behave as if they are different herbivore species, with different optimal foraging strategies. Unraveling these differences is important to effectively understand giraffe ecology, resource utilization, and for developing reticulated giraffe conservation strategies.

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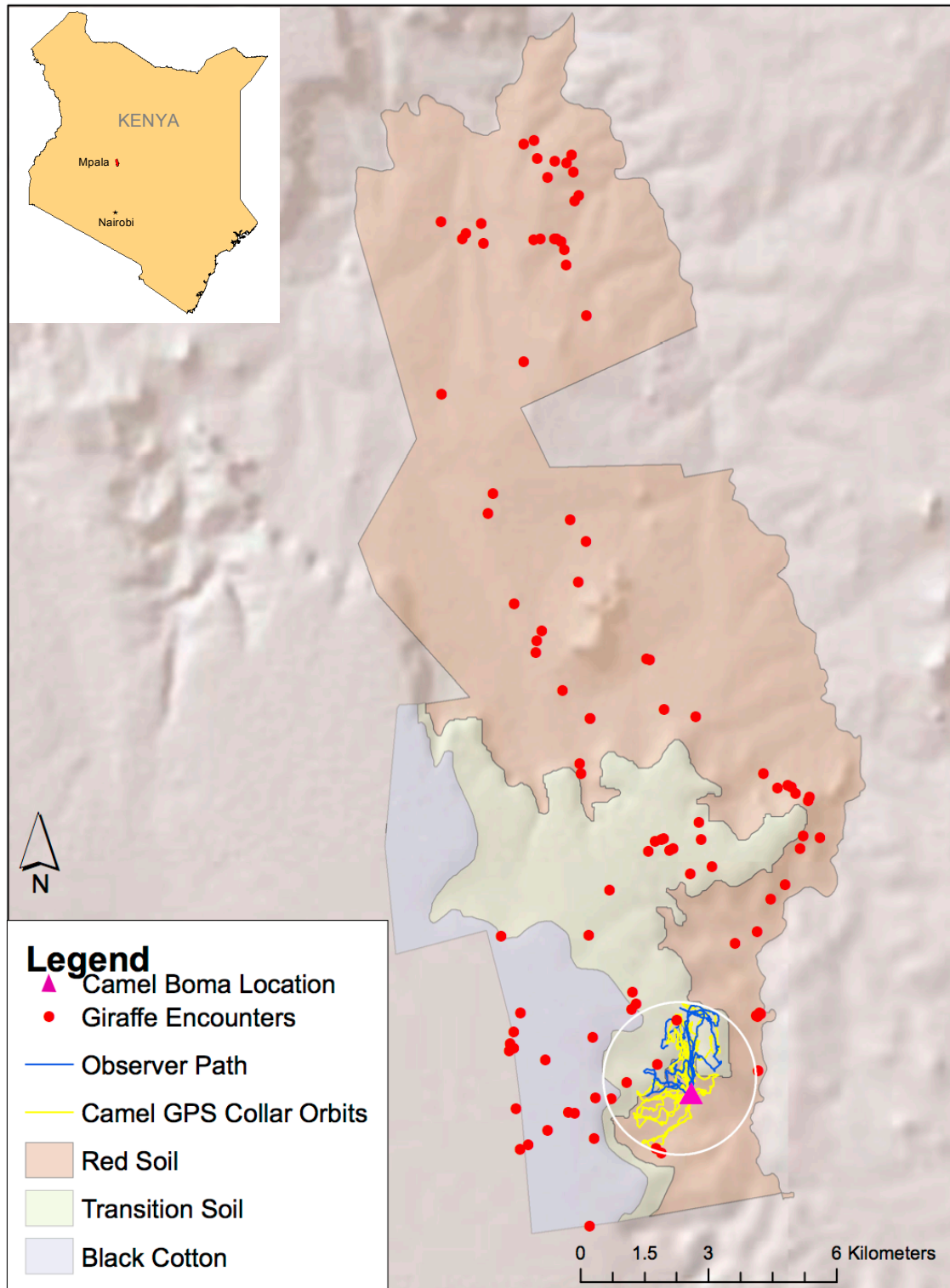
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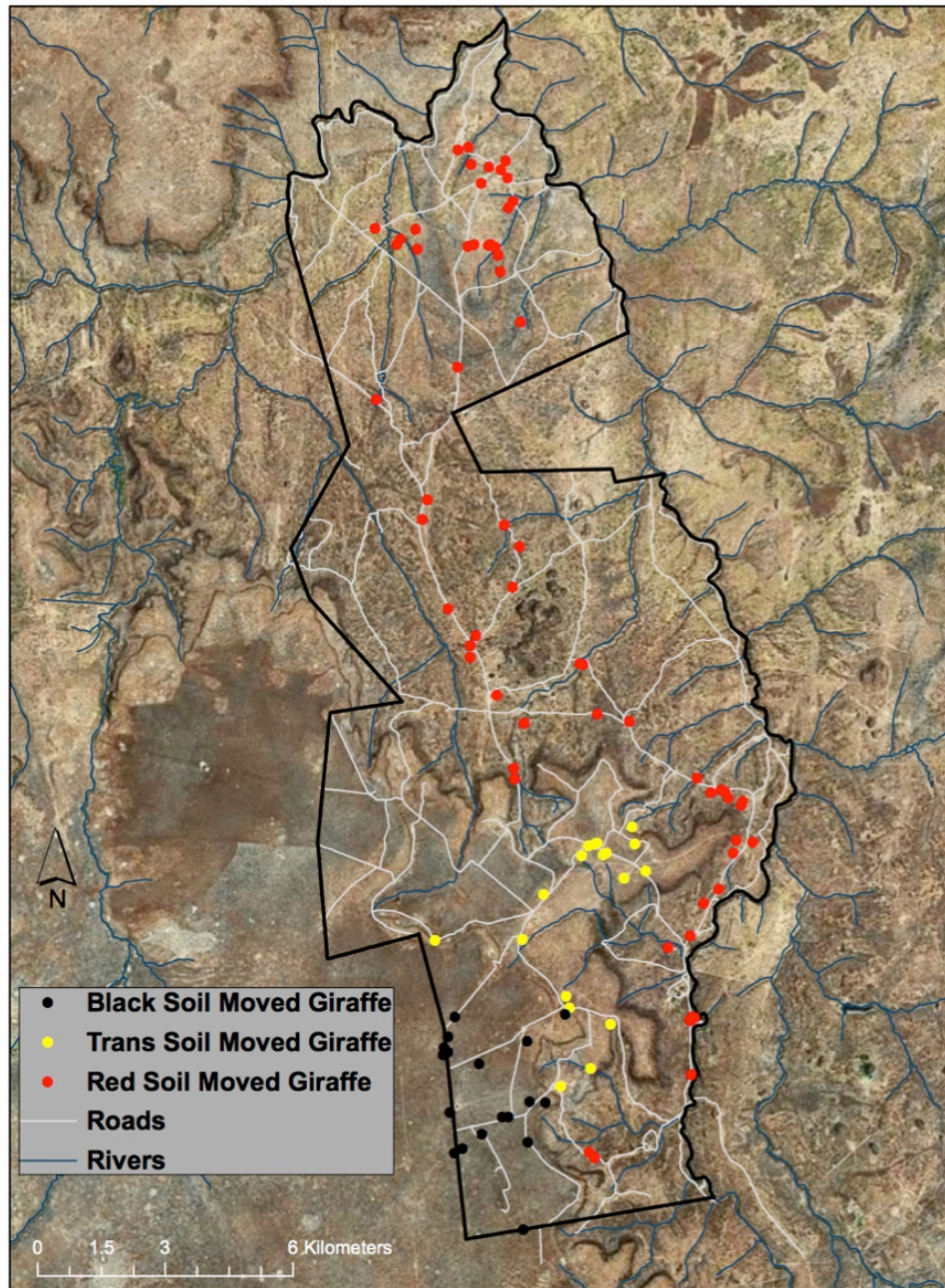
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Projection: USGS 1984 UTM 37N
 Source: The Mpala Research Centre, Nanyuki Kenya (boundary), Bing Maps Aerial (2010)

Figure 1: Map of study area, showing soil habitat types, reticulated giraffe encounters and domestic camel browsing orbits.

Mpala Reserve Giraffe by Soil Type



Projection: USGS 1984 UTM 37N
Source: The Mpala Research Centre, Nanyuki Kenya (Boundary), Bing Maps Aerial

Figure 2: Map of study area, showing giraffe encounters coded by soil/habitat type.

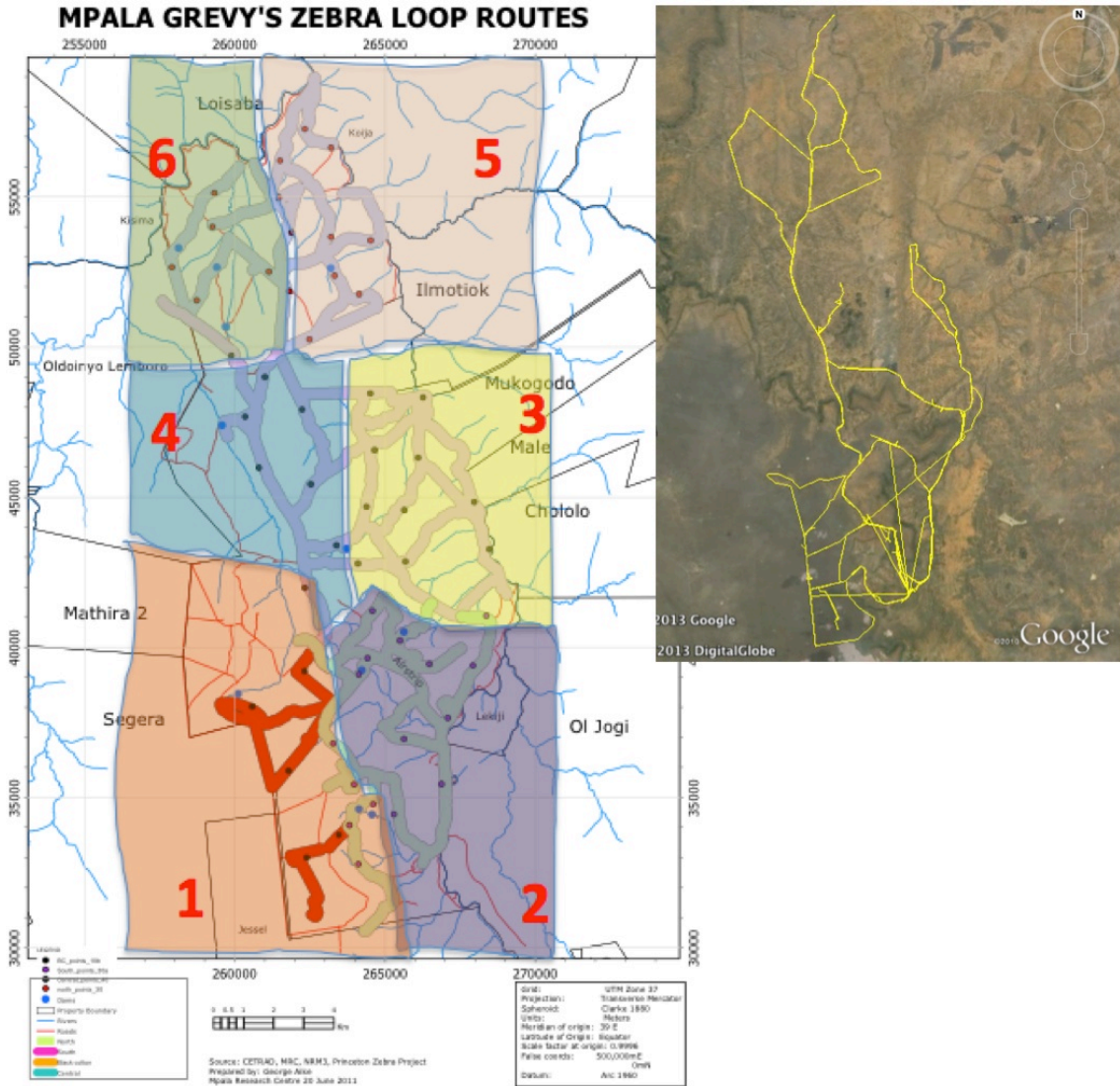
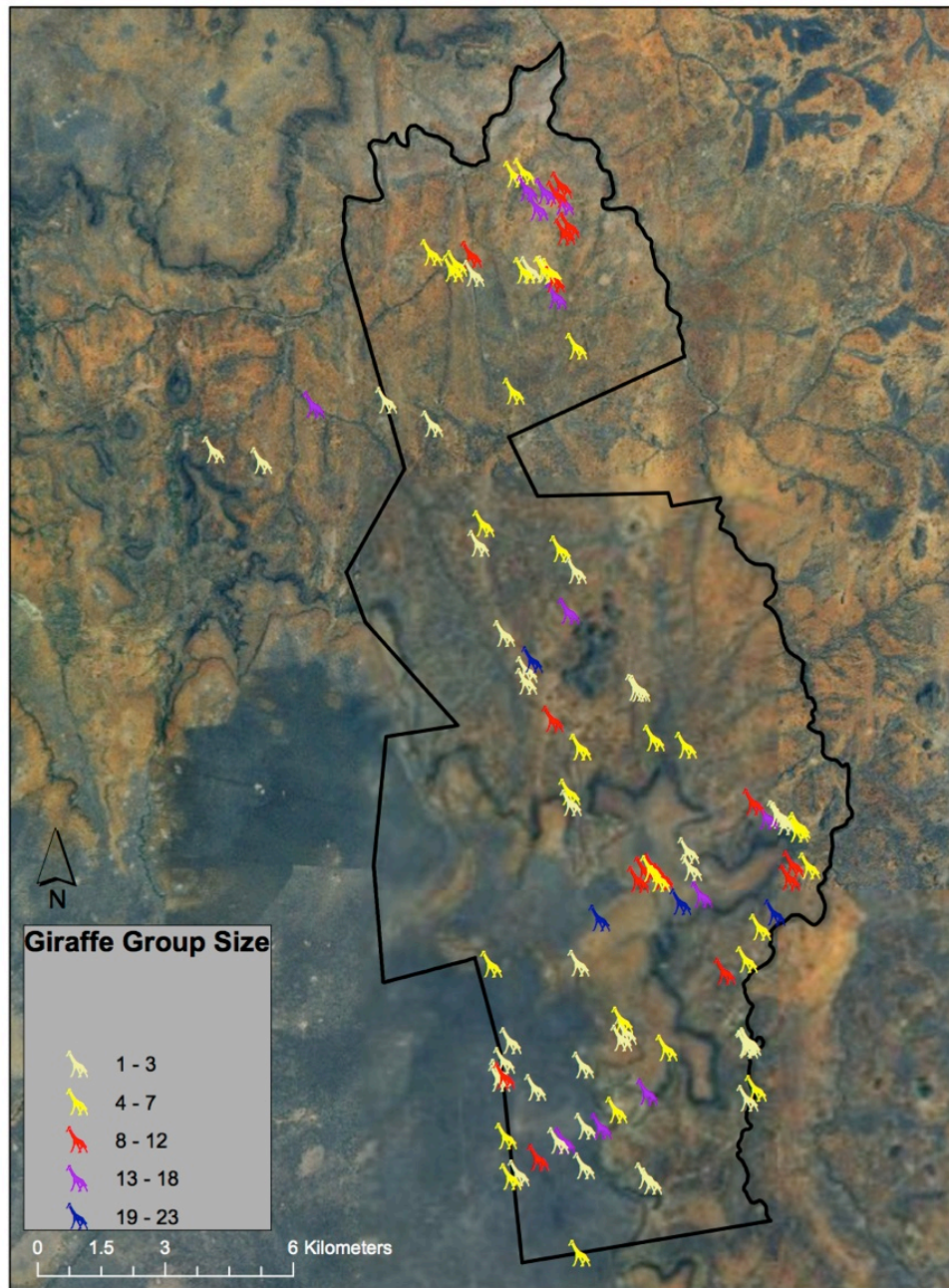


Figure 3: Left - Map showing six driving survey zones (adjusted from *Grevy's Zebra Project*). **Right** - Google Earth map showing GPS tracks of a portion of routes driven to survey giraffe (some areas were impassable/inaccessible due to the terrain or rains)

Mpala Reserve Giraffe Group Size



Projection: USGS 1984 UTM 37N
Source: The Mpala Research Centre, Nanyuki Kenya (Boundary), ESRI World Imagery

Figure 4: Map showing locations of giraffe encounters and group size

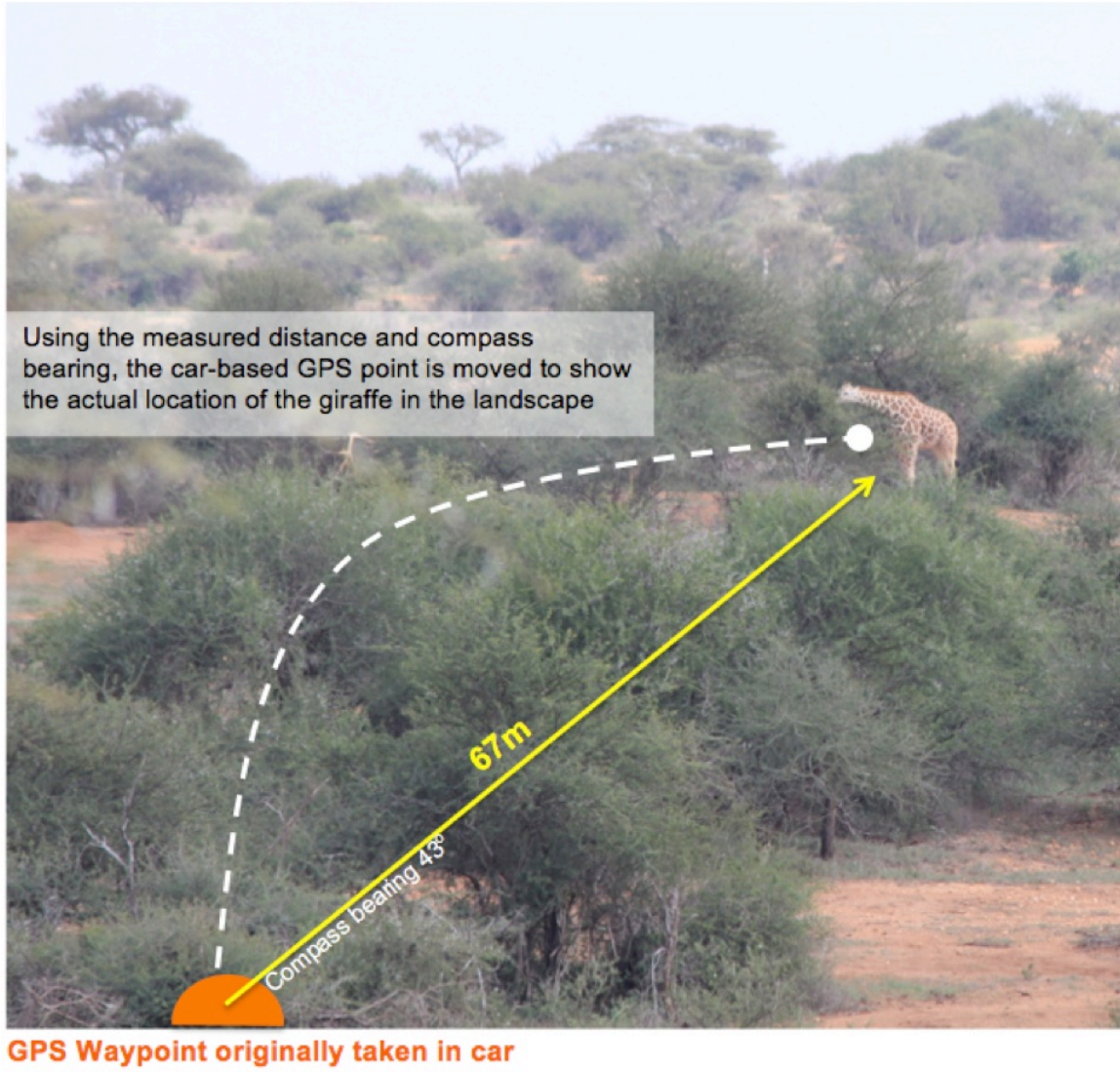


Figure 5: Photo illustration of how the car-based GPS waypoints of giraffe encounters were moved using field metadata and ArcGIS trigonometry to represent the real location of the giraffe in space.

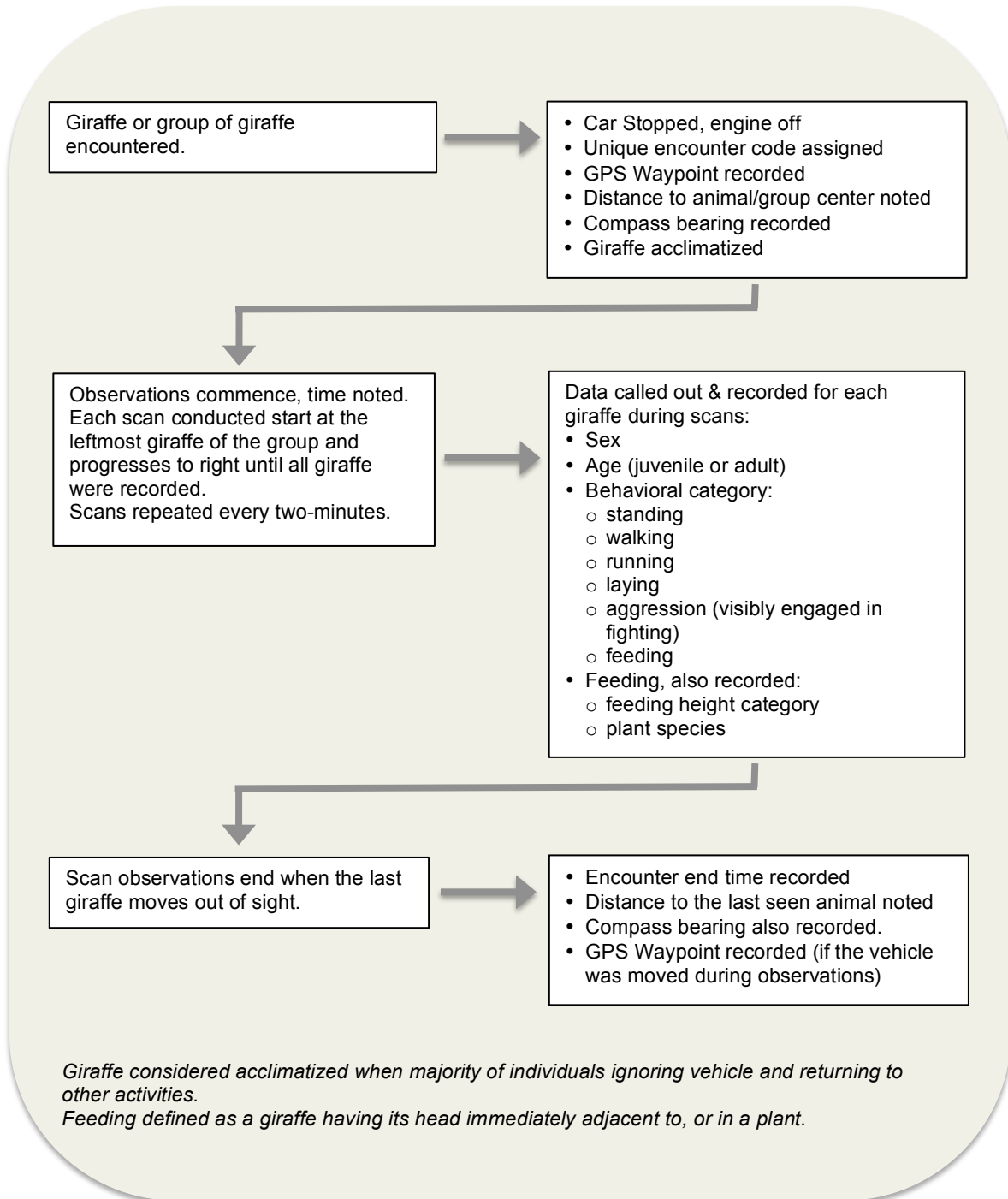


Figure 6: Flow chart detailing the method and data recorded during giraffe behavioral observations.

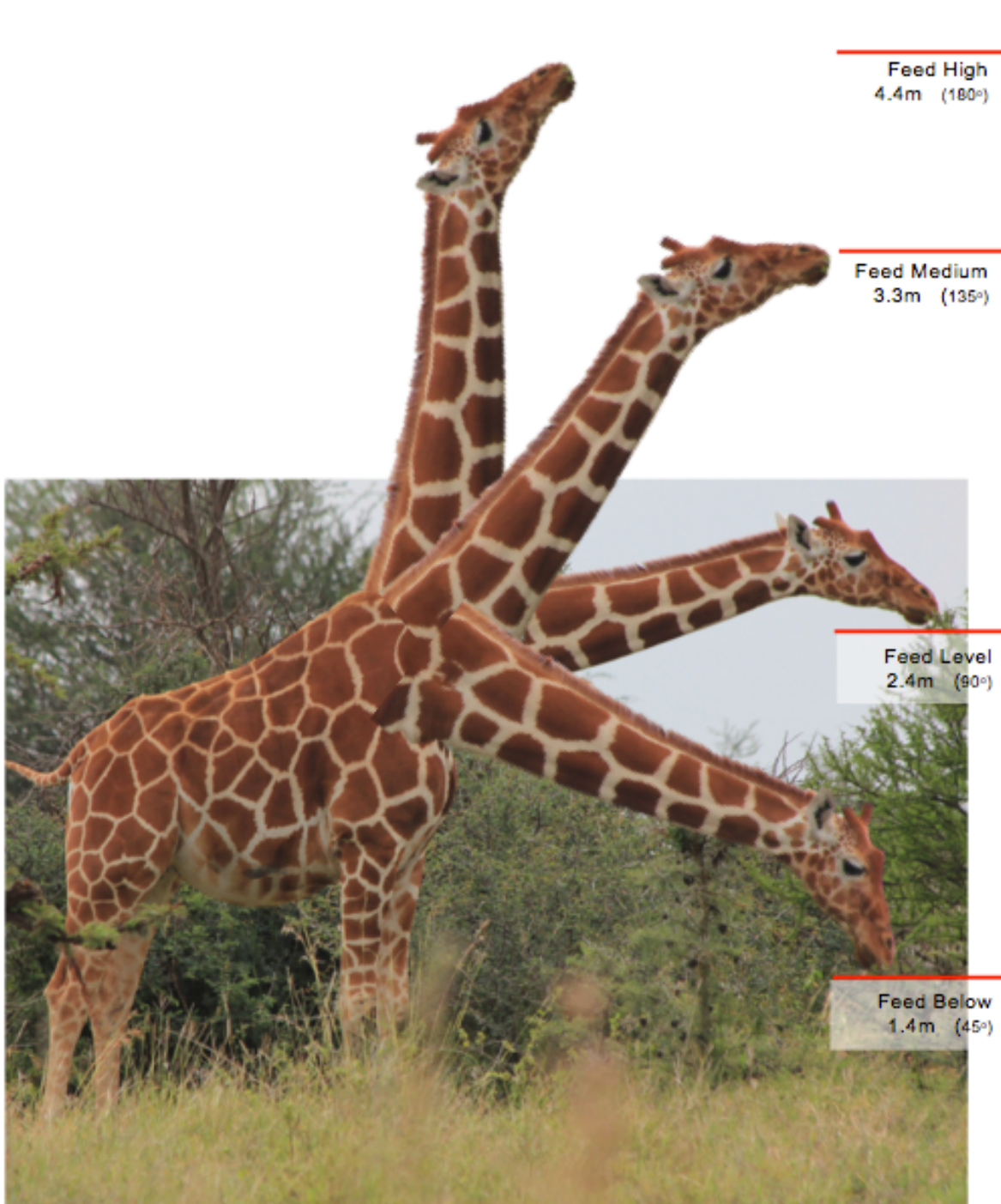


Figure 7: Photo illustration showing the reticulated giraffe pooled feeding height categories and neck angles
(Giraffe in photo illustration is based on an image of an adult female reticulated giraffe)

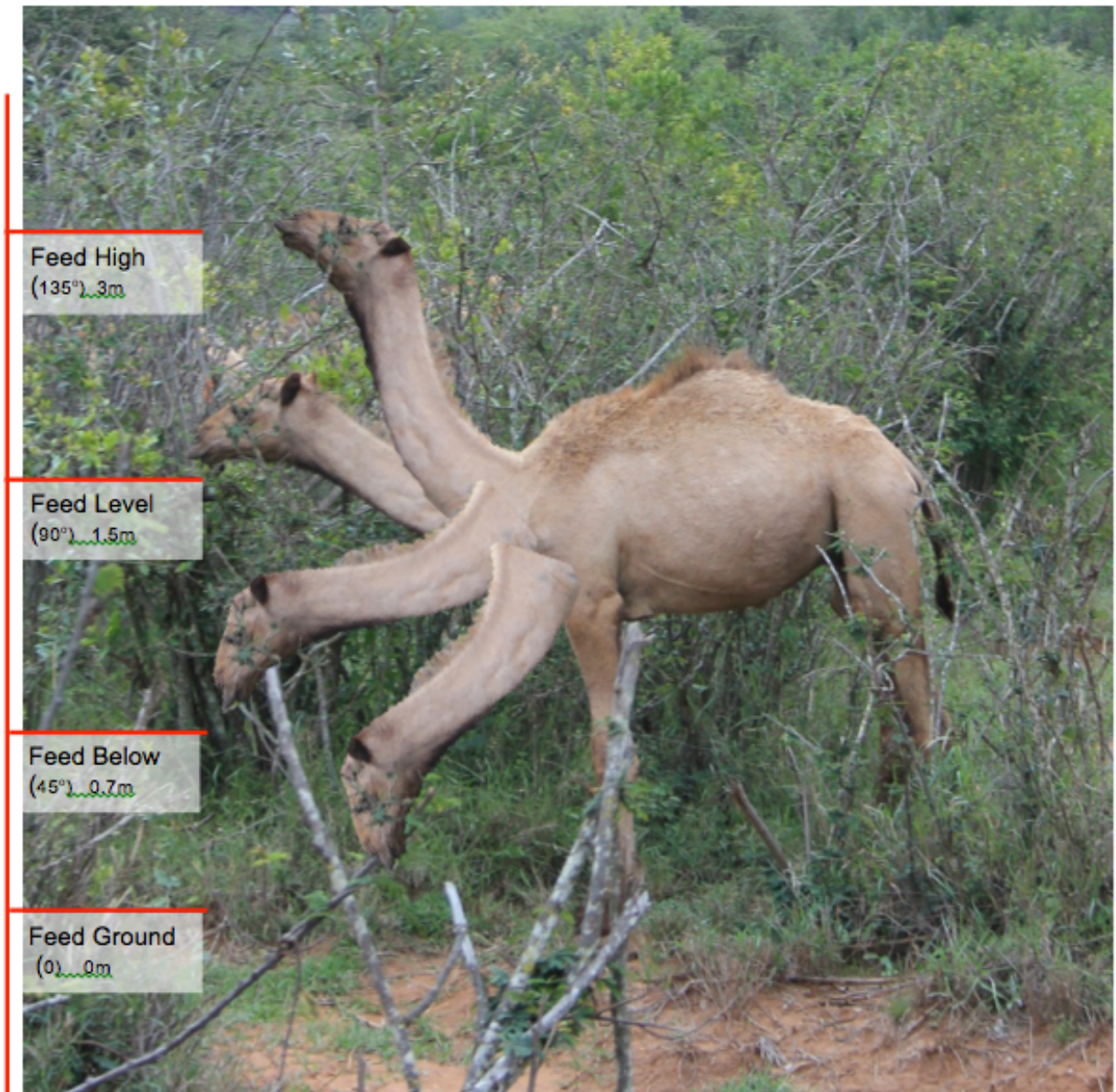
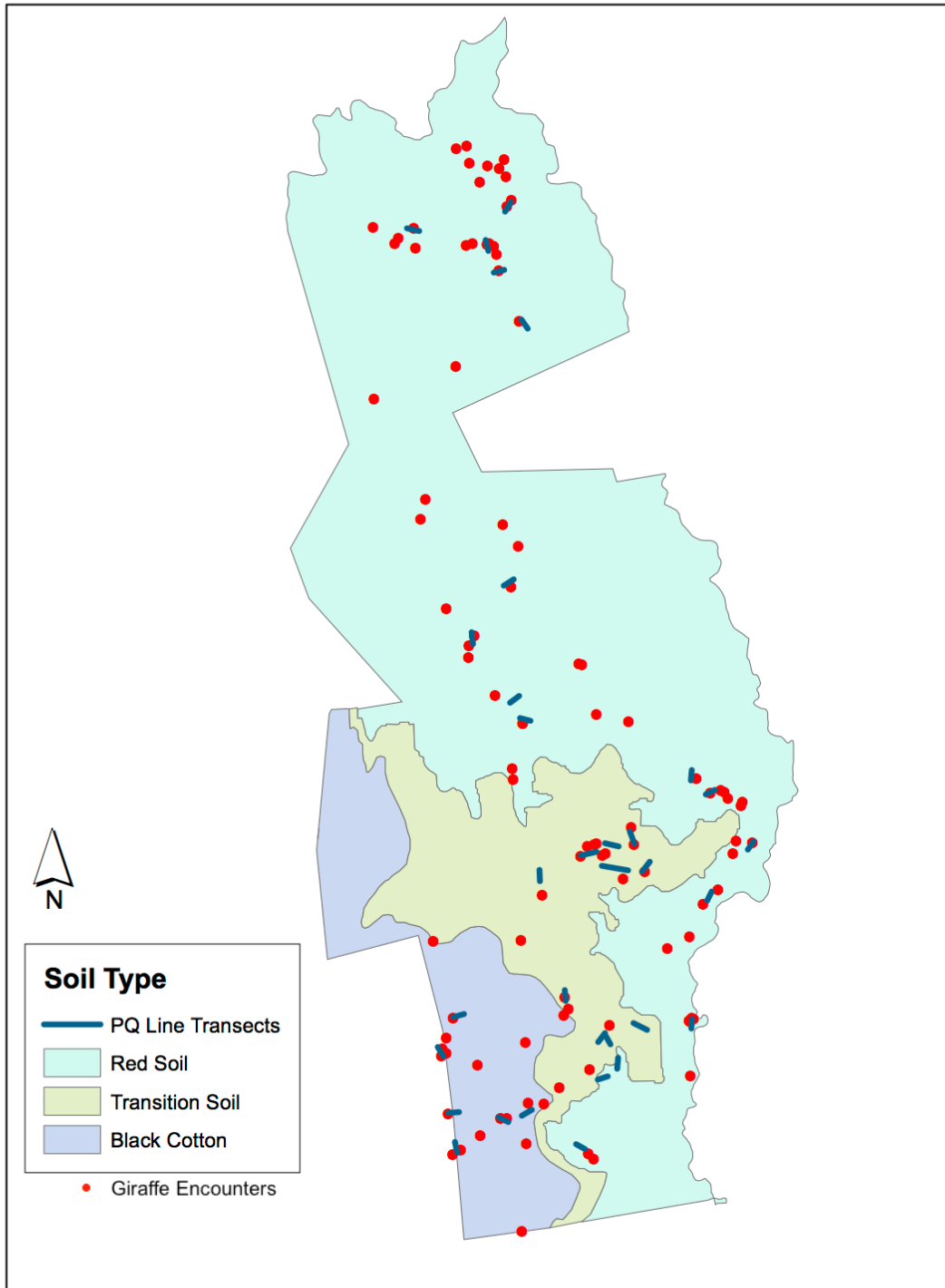


Figure 8: Photo illustration showing the adult female feeding height categories and neck angles



Figure 9: Photos showing the Garmin Forerunner 301 GPS unit used to measure camel browsing orbits (top right), in it's early iteration (left) and the protective canvas pouch used later (bottom right)

Plant Transect Locations



Projection: USGS 1984 UTM 37N
Source: The Mpala Research Centre, Nanyuki Kenya (Boundary).

Figure 10: Map showing the location of 33 plant transect lines, giraffe encounters and soil/habitat types

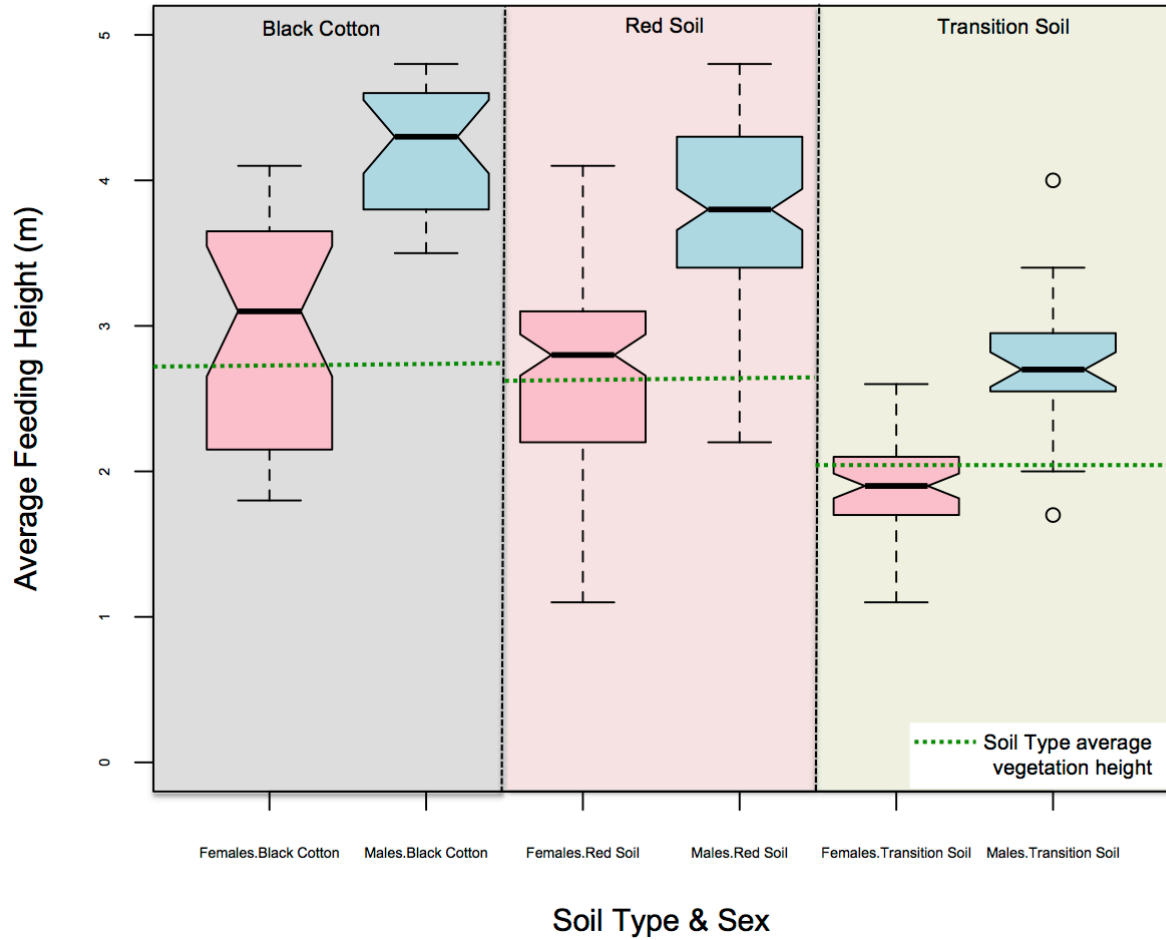


Figure 11: Composite average individual giraffe feeding heights across three habitat types. Male average feeding heights are significantly higher than female (ANOVA - Black Cotton: $F_{1,51} = 48.0$; Red Soil: $F_{1,199} = 135.3$; Transition Soil: $F_{1,81} = 102.1$, all $p < 0.001$).

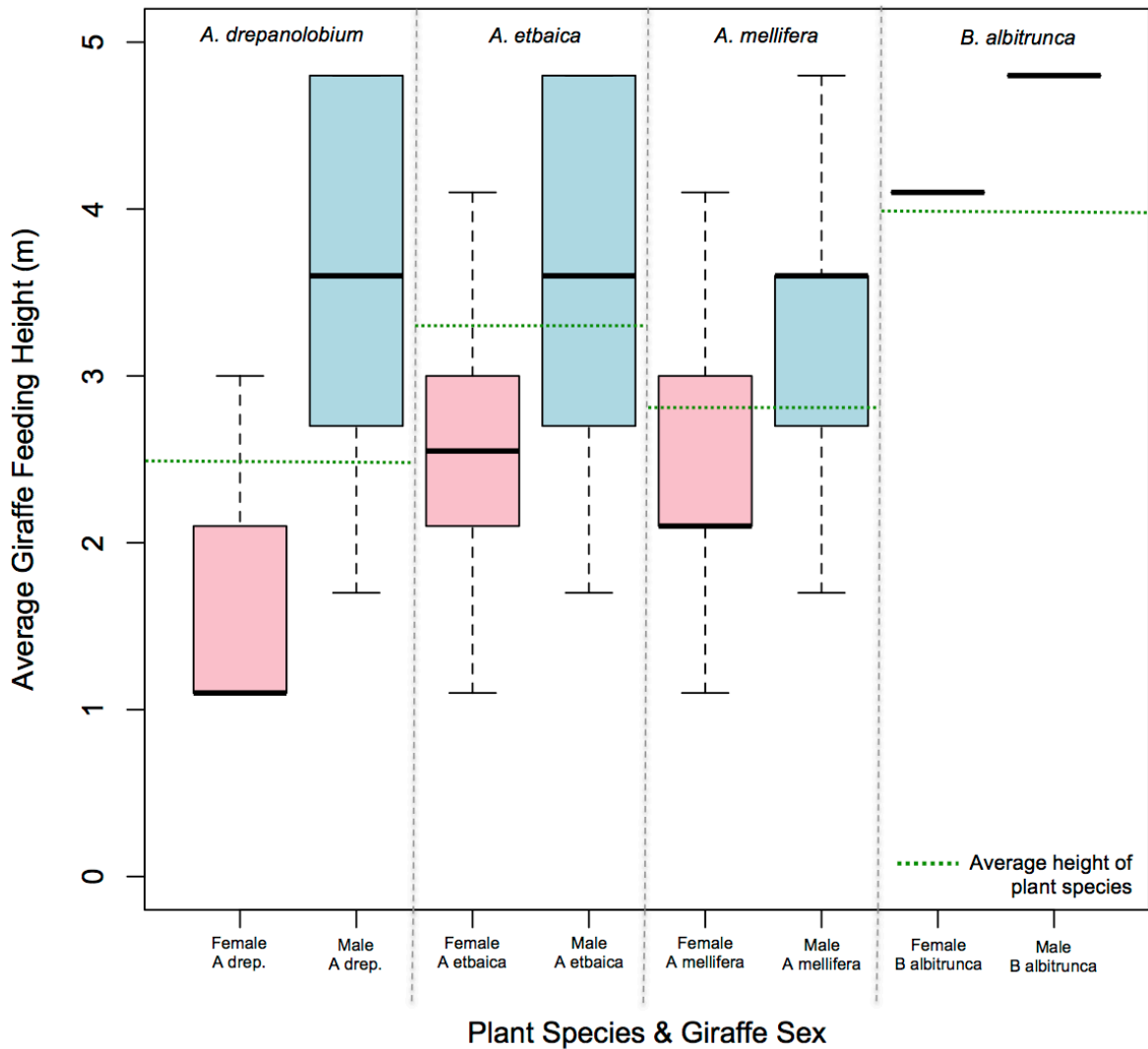


Figure 12: Giraffe feeding heights on the four most frequent plant food species. Males fed consistently above the median heights of *A. drepanolobium* (Mann-Whitney U, $U = 17371$, $p < 0.001$), but not of *A. etbaica* ($p = 0.1$), or *B. albitrunca* ($p = 0.052$). Females fed significantly below the median heights of *A. drepanolobium* ($U = 106765.5$, $p < 0.001$), *A. etbaica* ($U = 20153$, $p < 0.001$), but not significantly different to the median height of *B. albitrunca* ($p = 0.4$).

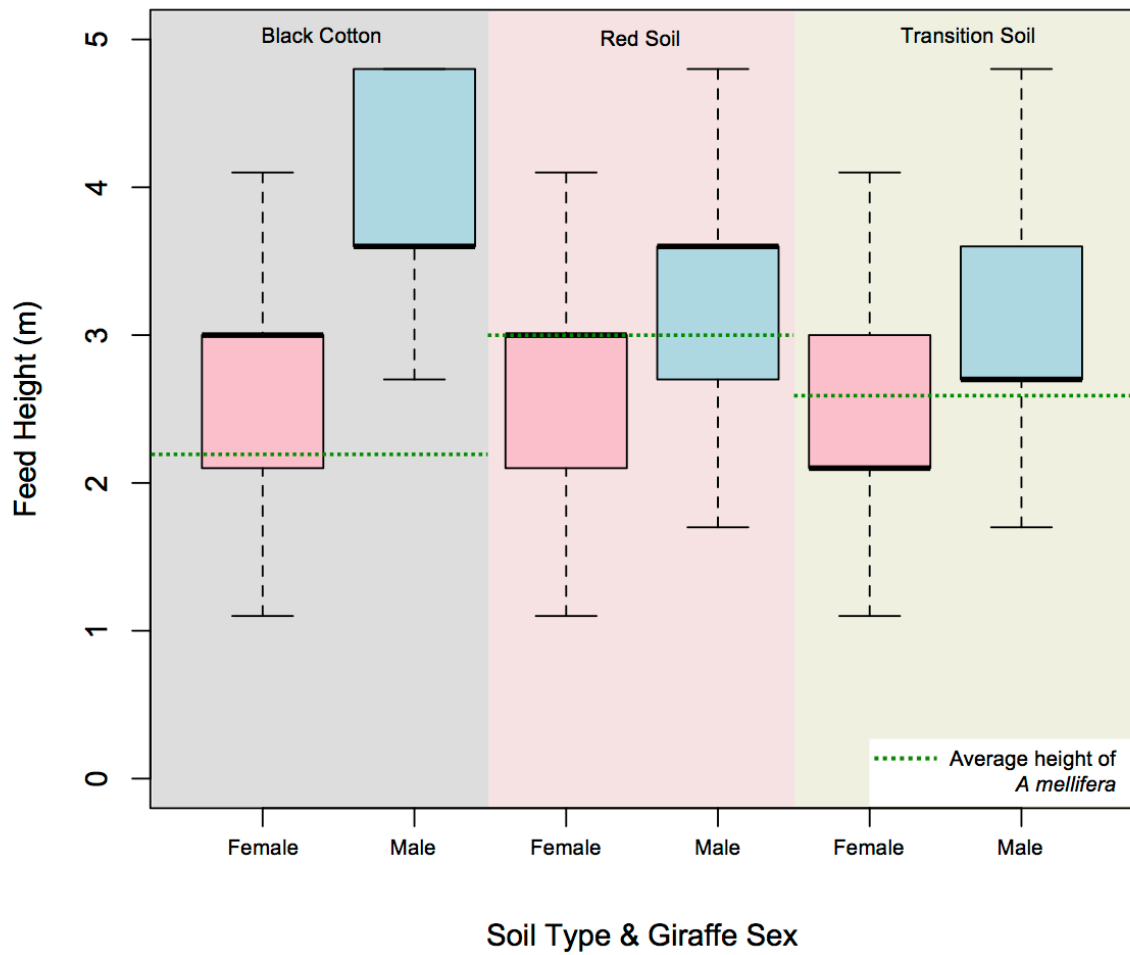


Figure 13: Giraffe feeding heights on *A. mellifera* across three habitat types. plant food species.

Males fed significantly higher than *A. mellifera*'s median height in all habitats (Mann-Whitney U test: Black Cotton: $U = 10$; Red Soil: $U = 13837$; Transition Soil: $U = 8807$, all $p < 0.001$).

Females fed significantly higher than the height of the plants in red soils ($U = 16593$, $p < 0.001$), and significantly below in transition soils ($U = 46101.5$, $p < 0.01$). There was no difference in the black cotton soil ($p = 0.09$).

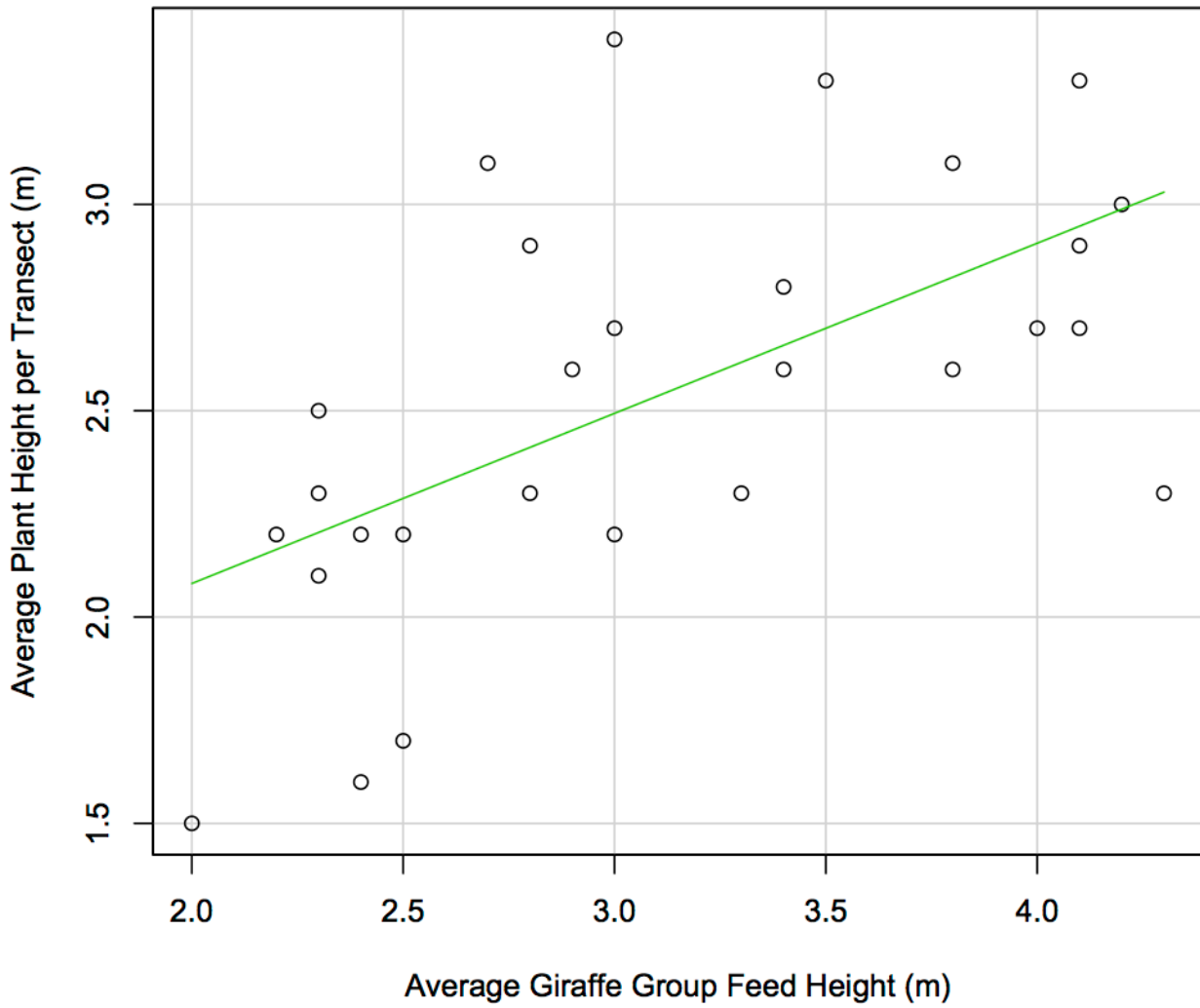
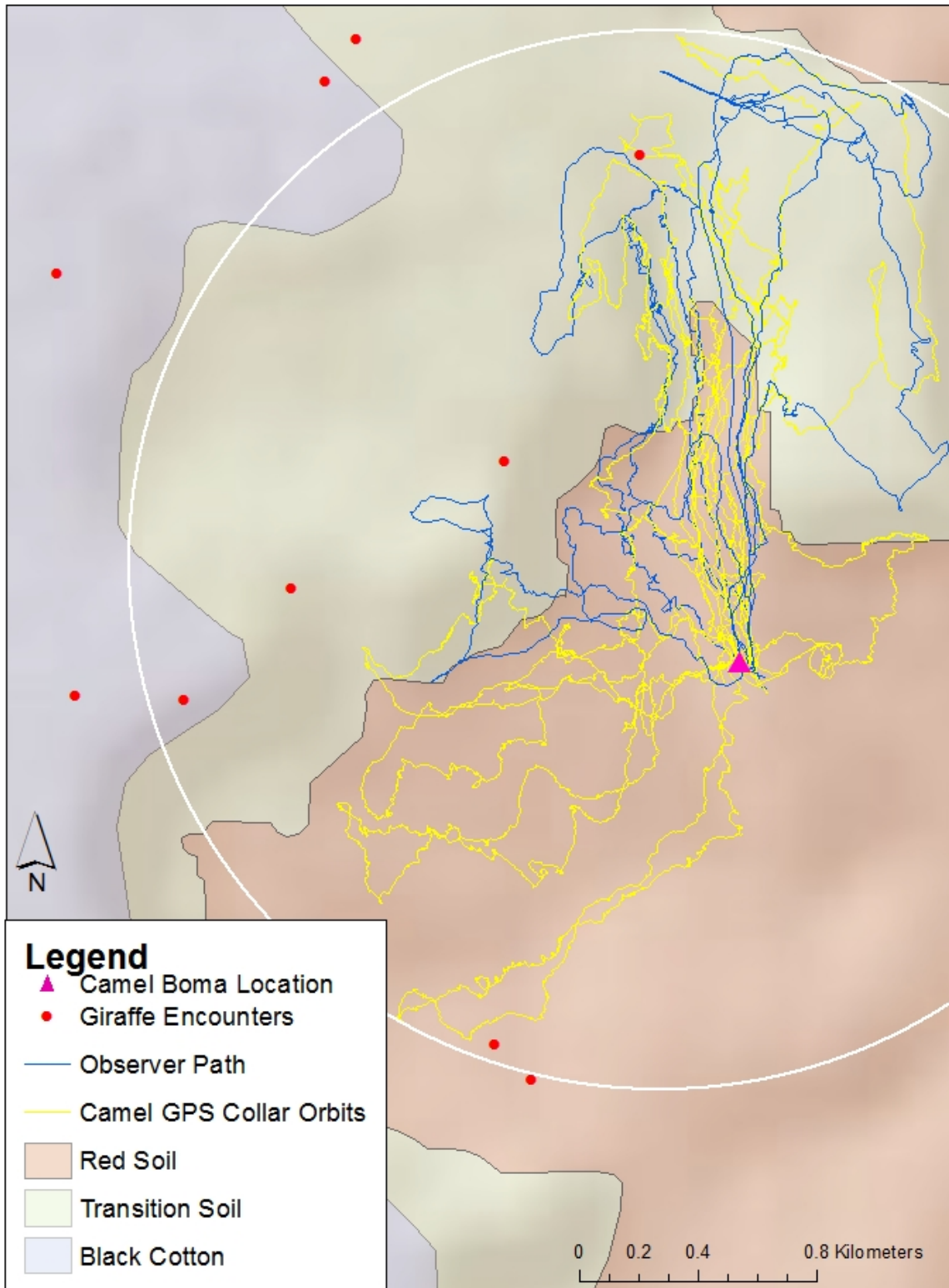


Figure 14: Average group giraffe feeding height versus average shrub height from the corresponding transect. Average shrub height was significantly correlated with average giraffe feeding height ($r^2 = 0.3516$, $p < 0.001$).

Domestic Camel Browsing Orbits - Detail



Projection: USGS 1984 UTM 37N
Source: The Mpala Research Centre, Nanyuki Kenya (soil type), Bing Maps Aerial (2010)

Figure 15: Map showing the GPS tracks of both the camel collars and the human observer measuring the camel browsing orbits

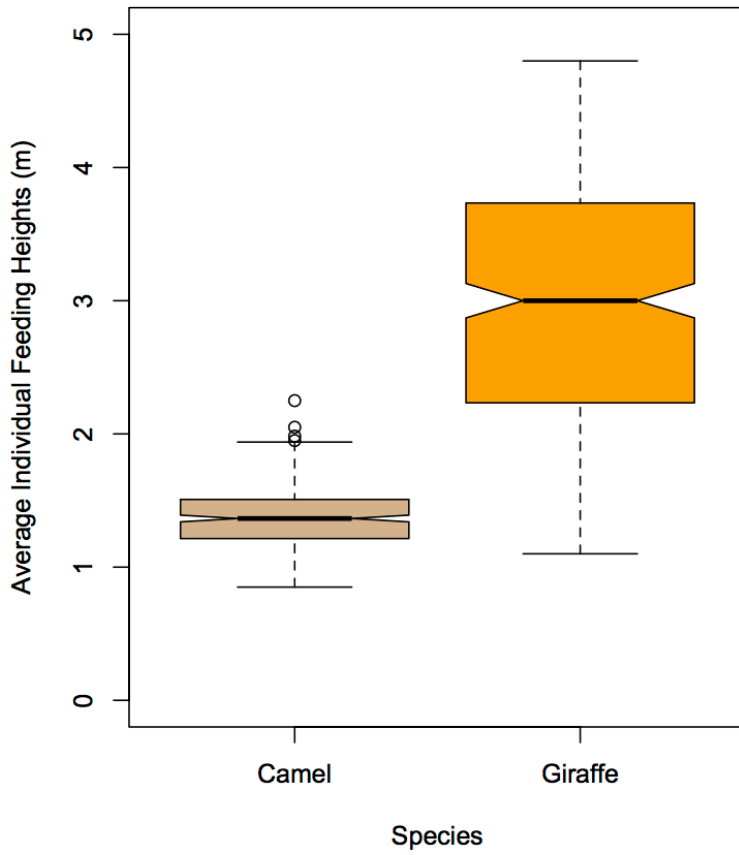


Figure 16: Composite average individual camel and giraffe feeding heights. Camels fed lower than giraffe (Mann-Whitney U, $U = 2567$, $p < 0.001$)

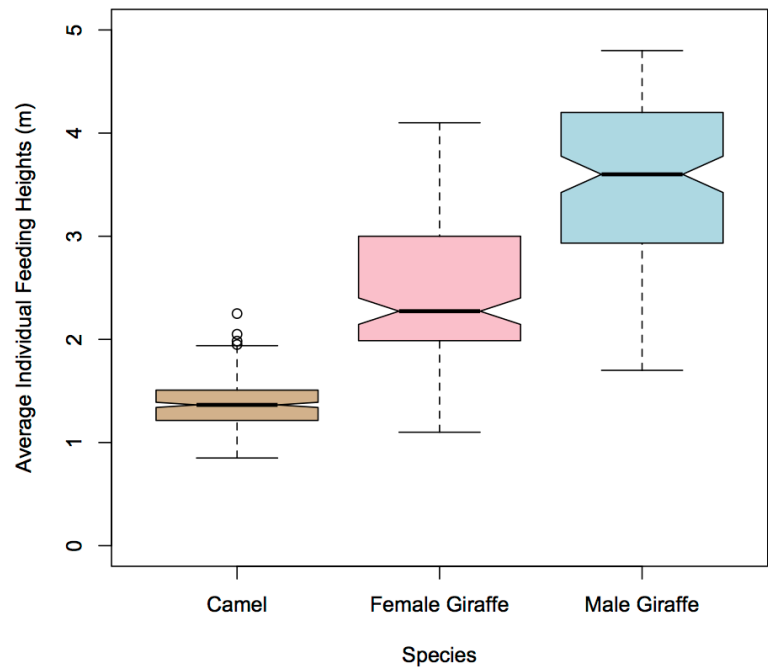


Figure 17: Composite average individual camel and male and female giraffe feeding heights. Camels fed lower than both male ($U = 34.5$, $p < 0.001$) and female giraffe ($U = 2504$, $p < 0.001$)

Table 1: Giraffe feeding height categories and measurements

Giraffe Feeding Height Category	Mature Male +/-SE (n)	Mature Female +/-SE (n)	Pooled +/-SE (n)
Feeding High	4.8m +/-0.11 (15)	4.1m +/-0.03 (15)	4.4m +/-0.09 (30)
Feeding Medium	3.6m +/-0.08 (15)	3.0m +/-0.09 (16)	3.3m +/-0.08 (31)
Feeding Level	2.7m +/-0.10 (16)	2.1m +/-0.05 (18)	2.4m +/-0.07 (34)
Feeding Below	1.7m +/-0.09 (17)	1.1m +/-0.06 (12)	1.4m +/-0.08 (29)

Table 2: Camel feeding height categories and measurements

Camel Feeding Height Category	Mature Female +/-SE (n=15)
Feeding High	3.0m +/-0.07
Feeding Level	1.5m +/-0.05
Feeding Below	0.7m +/-0.03
Feeding Ground	0m

Table 3: Average adult male and female feeding heights and average vegetation height in each habitat

Category	Black Cotton (m)	Red Soil (m)	Transition Soil (m)
Average Male giraffe feed height (+/- SE)	4.2 +/- 0.09 (n=25)	3.8 +/- 0.07 (n=101)	2.8 +/- 0.08 (n=28)
Average Female giraffe feed height (+/- SE)	3.0 +/- 0.15 (n=40)	2.7 +/- 0.06 (n=100)	1.9 +/- 0.04 (n=55)
Average vegetation height (+/- SE)	2.7 +/- 0.07 (n=264)	2.7 +/- 0.05 (n=660)	2.0 +/- 0.06 (n=308)
Median vegetation height	2.6	2.4	1.7

Table 4: (A.) Adult giraffe mean feeding heights* per plant species. (B.) Mean plant species heights from all of Mpala (transect n = 33)

Adult Giraffe Plant Food Species	A.			B.	
	Female Mean Feed Height +/-SE (n)	Male Mean Feed Height +/-SE (n)	Pooled Mean Feed Height +/-SE (n)	Mean Plant Height +/-SE (m)	n
<i>A. brevispica</i>	1.86 +/-0.17 m (26)	2.75 +/-0.27 m (21)	2.26 +/-0.16 m (47)	1.89 +/-0.04	255
<i>A. drepanolobium</i>	1.82 +/-0.04 m (485)	3.63 +/-0.08 m (229)	2.40 +/-0.05 m (714)	2.46 +/-0.07	321
<i>A. etbaica</i>	2.67 +/-0.07 m (182)	3.52 +/-0.08 m (148)	3.05 +/-0.06 m (330)	3.33 +/-0.10	174
<i>A. mellifera</i>	2.29 +/-0.03 m (712)	3.23 +/-0.05 m (355)	2.60 +/-0.03 m (1067)	2.80 +/-0.06	367
<i>A. nilotica</i>	NA	2.03 +/-0.33 m (3)	2.03 +/-0.33 m (3)	2.30 +/-0.16	17
<i>Balanites glabra</i>	NA	3.16 +/-0.38 m (8)	3.16 +/-0.38 m (8)	3.53 +/-0.35	17
<i>Boscia albitrunca</i>	3.84 +/-0.06 m (107)	4.67 +/-0.07 m (27)	4.0 +/-0.06 m (134)	4.05 +/-0.23	24
<i>Croton dichogamous</i>	1.1 +/-0.00 m (1)	NA	1.1 +/-0.00 m (1)	1.73 +/-0.05	146

* Feed height data are the actual observations, not aggregates to individual giraffe, and thus may not be independent.

Table 5: Mean height (m) and mean absolute density of the four plant species most frequently fed on by giraffe

Soil Type	<i>A. drepanolobium</i> (n=255)		<i>A. etbaica</i> (n=174)		<i>A. mellifera</i> (n=367)		<i>B. albitrunca</i> (n=24)	
	Plant height +/-SE (m)	Plants per ha	Plant height +/-SE (m)	Plants per ha	Plant height +/-SE (m)	Plants per ha	Plant height +/-SE (m)	Plants per ha
Black Cotton	2.8 +/- 0.07	912	NA	0	2.2 +/- 0.37	45	NA	0
Red Soil	NA	0	3.5 +/- 0.11	118	3.0 +/- 0.08	163	4.1 +/- 0.24	17
Transition Soil	1.4 +/- 0.04	809	2.6 +/- 0.26	5	2.6 +/- 0.10	44	3.0 +/- 0.46	2

Table 6: Summary of individual camel GPS collar and observer walk GPS data

Date (year = 2011)	Browsing Orbit Time (hr:mm)	Browsing Orbit Distance (km)	Observer Walking Distance (km)	Camel GPS edited
June 21 [^]	NA	NA	4.71	NA
July 7 [^]	NA	NA	5.36	NA
July 8	7:33	7.88	8.40	No
July 9	6:55	6.31		Yes
July 11	6:52	4.92		Yes
July 13 [^]	NA	NA	6.81	Yes
July 14	8:52	5.61		Yes
July 15	7:26	5.67		Yes
July 16 [`]	5:31	5.44	7.06	Yes
Aug 3 [`]	9:55	3.74		Yes
Aug 5	7:12	5.14		Yes
Aug 6 [`]	0:56	0.25		NA
Aug 7	8:08	6.54		Yes
Aug 11	7:40	6.05		Yes
Aug 12	7:09	5.77		Yes

[^] GPS collar malfunction, and observer GPS data used as a proxy for camel herd movements

[`] Data from these dates were discarded from analysis due either to only partial browsing orbit recording or GPS malfunction.

Table 7: (A.) Adult female camel mean, median and standard deviation of plant species feeding heights*. (B.) Mean plant species heights from all of Mpala (transect n = 33)

A.					B.	
Camel Plant Food Species	Mean Feeding Height (m)	Median Feeding Height (m)	SE Feeding Height (m)	n	Mean Plant Height +/- SE (m)	n
<i>A. brevispica</i>	1.26	0.7	0.01	2337	1.89 +/-0.04	255
<i>A. etbaica</i>	1.79	1.5	0.08	111	3.33 +/-0.10	174
<i>A. mellifera</i>	1.67	1.5	0.05	283	2.80 +/-0.06	367
<i>A. nilotica</i>	1.40	1.5	0.09	46	2.30 +/-0.16	17
<i>Acacia</i> spp.	1.54	1.5	0.12	40	NA	NA
Indeterminate [^]	1.30	0.7	0.02	1324	NA	NA
<i>C. dichogamous</i>	1.13	0.7	0.06	85	1.73 +/-0.05	146
<i>Euclea</i> spp.	1.45	1.5	0.05	267	NA	NA
<i>B. albitrunca</i>	2.13	3.0	0.06	215	4.05 +/-0.23	24

* Feed height data are the actual observations, not aggregates to individual giraffe, and thus may not be independent.

[^]Indeterminate: species indeterminate, most likely either *Croton dichogamous* or *Euclea* spp.

Table 8: Mean height (m) and mean absolute density (plants/hectare) of the plant species most frequently fed upon by camels (A.) in the area in which camels foraged (transect n = 5) compared to (B.) all of Mpala (transect n = 33).

Plant species (camel forage area sample size)	A.		B.	
	Camel Food Plant Height +/-SE (m)	Plants per ha	Mpala- wide plant height +/-SE (m)	Mpala-wide Plants per ha
<i>A. brevispica</i> (n = 72)	2.0 +/-0.07	472	1.89 +/-0.04	305
<i>A. etbaica</i> (n = 16)	3.3 +/-0.41	30	3.33 +/-0.10	78
<i>A. mellifera</i> (n = 14)	2.7 +/-0.31	44	2.80 +/-0.06	108
<i>B. albitrunca</i> (n = 4)	3.5 +/-0.39	33	4.05 +/-0.23	20

APPENDICES

Appendix 1 – Methods and Statistical Test Summary

Methods used to collect data for each research question

Research Question	Behavioral Obs.: Giraffe feed height	Behavioral Obs.: Camel feed height	Point-centered quarter vegetation transects	GIS
1: Is there overlap between camel and giraffe feeding heights and preferred plant food species?	✓	✓	✓	✓
2: Are there differences between adult female and adult male giraffe foraging ecologies across habitat types?	✓	X	✓	✓
3: Do giraffe exploit their presumed competitive advantage by always eating the tallest and most common plant species in the landscape?	✓	X	✓	✓

Statistical tests used to analyze data for each research question

Research Question	Mann-Whitney U	Multiway ANOVA	Tukey's HSD	Linear Regression	Kruskal-Wallis
1: Is there overlap between camel and giraffe feeding heights and preferred plant food species?	✓	X	X	✓	X
2: Are there differences between adult female and adult male giraffe foraging ecologies across habitat types?	✓	✓	✓	X	✓
3: Do giraffe exploit their presumed competitive advantage by always eating the tallest and most common plant species in the landscape?	✓	X	X	✓	X

Appendix 2 – Giraffe Activity and Foraging Data

Activity Summary

7680 entries

[Adult Female 56.85%(4366), Male Adult 43.15% (3314)]

Activity	Records	Percentage
Feeding	3617	47.10%
Stand	2157	28.09%
Walk	1476	19.22%
Lay	239	3.11%
Aggression (males only)	178	2.32%
Head to Ground	12	0.16%
Suckle	1	0.01%

POOLED ADULT GIRAFFE FEEDING HEIGHTS

3617 feeding observations for adults only.

Female n = 2194 (60.66%)

Male n = 1423 (39.34%)

Feeding Level	Records	Percentage
Feed High (4.4m)	801	22.15%
Feed Medium (3.3m)	871	24.08%
Feed Level (2.4m)	1139	31.49%
Feed Below (1.4m)	806	22.28%
Total	3617	

Feeding Level	Female Records	Male Records
Feed High	16.3% (358)	31.1% (443)
Feed Medium	20.9% (458)	29.0% (413)
Feed Level	35.1% (771)	25.9% (368)
Feed Below	27.7% (607)	14.0% (199)
n	2194	1423

POOLED GIRAFFE FOOD SPECIES & FEEDING HEIGHTS

(Inc. sub adult observations)

Plant Species	Feed Height				Total (n)	Total %*
	Feed High	Feed Medium	Feed Level	Feed Below		
<i>A. brevispica</i>	6	8	18	26	58	2%
<i>A. drepanolobium</i>	177	117	197	318	809	33%
<i>A. etbaica</i>	86	105	105	45	341	14%
<i>A. mellifera</i>	88	392	414	198	1092	44%
<i>A. nilotica</i>	0	0	1	2	3	0.1%
<i>B. albitunca</i>	128	16	5	2	151	6%
<i>B. glabra</i>	1	4	1	2	8	0.3%
<i>C. dichogamous</i>	0	0	2	1	3	0.1%
Total	486	642	743	594	2465	

*Totals may not equal 100% due to rounding

FEMALE ADULT GIRAFFE FEED HEIGHTS & SPECIES

Plant Species	Feed Height				Total (n)	Total %*
	Feed High (4.1m)	Feed Medium (3.0m)	Feed Level (2.1m)	Feed Below (1.1m)		
<i>A brevispica</i>	2	1	12	11	26	2%
<i>A. drepanolobium</i>	48	33	144	260	485	32%
<i>A etbaica</i>	44	47	64	27	182	12%
<i>A mellifera</i>	37	236	287	152	712	47%
<i>A nilotica</i>	0	0	0	0	0	0
<i>B albitunca</i>	89	11	5	2	107	7%
<i>B glabra</i>	0	0	0	0	0	0
<i>C dichogamous</i>	0	0	0	1	1	0.1%
Total	220	328	512	453	1513	

*Totals may not equal 100% due to rounding

MALE ADULT GIRAFFE FEED HEIGHTS & SPECIES

Plant Species	Feed Height				Total (n)	Total %*
	Feed High (4.8m)	Feed Medium (3.6m)	Feed Level (2.7)	Feed Below (1.7m)		
<i>A. brevispica</i>	4	3	4	10	21	3%
<i>A. drepanolobium</i>	100	53	31	45	229	29%
<i>A. etbaica</i>	41	57	34	16	148	19%
<i>A. mellifera</i>	50	142	120	43	355	45%
<i>A. nilotica</i>	0	0	1	2	3	0.4%
<i>B. albitunca</i>	24	3	0	0	27	3%
<i>B. glabra</i>	1	4	1	2	8	1%
<i>C. dichogamous</i>	0	0	0	0	0	0
Total	220	262	191	118	791	

*Totals may not equal 100% due to rounding

Appendix 3 – Numbers of tracked and composite giraffe

Total numbers of adult giraffe with feeding height observations from 65 encounters, and breakdown of the numbers of tracked and composite giraffe

Sex	Black Cotton (n)	Red Soil (n)	Transition Soil (n)	Total (n)
Female	28	100	55	183
Male	25	101	28	154
Total	53	201	83	337
Averaging Type				
Tracked Giraffe	13 <i>2 female, 11 male</i>	132 <i>62 female, 70 male</i>	28 <i>17 female, 11 male</i>	173 <i>81 female, 92 male</i>
Composite Giraffe	40 <i>26 female, 14 male</i>	69 <i>38 female, 31 male</i>	55 <i>38 female, 17 male</i>	164 <i>102 female, 62 male</i>
Total	53	201	83	337

Appendix 4 – Camel Activity and Foraging Data

Camel Activity Summary

Number of Observations: 10,324 (Adult Females Only)

Activity	Records	Percentage
Feeding	7340	71.1%
Lay	21	0.2%
Stand	774	7.5%
Walk	2189	21.2%
Total	10,324	

Camel Feeding Heights

Including the "feeding ground" (Adult Females Only)

Number of Observations: 7340

Feeding Level	Records	Percentage
Feed High	1022	13.92%
Feed Level	2377	32.38%
Feed Below	2863	39.01%
Feed Ground	1078	14.69%

Camel Basic Plant Food Analysis (Adult Females Only)

4708 entries of plant food species

Camel Plant Food Species	Records	Percent
<i>A. brevispica</i>	2337	49.64%
<i>A. drepanolobium</i>		
<i>A. etbaica</i>	111	2.36%
<i>A. mellifera</i>	283	6.01%
<i>A. nilotica</i>	46	0.98%
<i>Acacia</i> spp.	40	0.85%
<i>Balanites glabra</i>		
<i>Boscia albitrunca</i>	215	4.57%
<i>C. dichogamous</i>	85	1.81%
Indeterminate*	1324	28.12%
<i>Euclea</i> spp.	215	5.67%
Total		

*species undecipherable, most likely either *C. dichogamous* or *Euclea* spp.

Feeding Heights & Plant Species

Camel Plant Food Species	Feed Below (0.7m)	Feed High (3.0m)	Feed Level (1.5m)
<i>A. brevispica</i>	1241	288	808
<i>A. etbaica</i>	21	33	57
<i>A. mellifera</i>	64	67	152
<i>A. nilotica</i>	13	4	29
<i>Acacia</i> spp.	11	7	22
Indeterminate	669	185	470
<i>C. dichogamous</i>	47	4	34
<i>Euclea</i> spp.	125	57	85
<i>Boscia albitrunca</i>	40	111	64
Total			

Feeding Heights & Plant Species % of Total

Camel Plant Food Species	Feed Below (0.7m)	Feed High (2.62m)	Feed Level (1.5m)	Total
<i>A. brevispica</i>	26.4%	6.1%	17.2%	49.6%
<i>A. etbaica</i>	0.4%	0.7%	1.2%	2.4%
<i>A. mellifera</i>	1.4%	1.4%	3.2%	6.0%
<i>A. nilotica</i>	0.3%	0.1%	0.6%	1.0%
<i>Acacia</i> spp.	0.2%	0.1%	0.5%	0.8%
Indeterminate	14.2%	3.9%	10.0%	28.1%
<i>C. dichogamous</i>	1.0%	0.1%	0.7%	1.8%
<i>Euclea</i> spp.	2.7%	1.2%	1.8%	5.7%
<i>Boscia albitrunca</i>	0.8%	2.4%	1.4%	4.6%
Total	47.4%	16.1%	36.6%	100%

Appendix 5 – Plant Transect Height Summaries

General Observations

Total number of plants measured for height on PQ transects: 1452

15 plant species

Plant Food Species	Records	Percent
<i>A. brevispica</i>	255	17.56%
<i>A. drepanolobium</i>	321	22.11%
<i>A. etbaica</i>	174	11.98%
<i>A. mellifera</i>	367	25.28%
<i>A. nilotica</i>	17	1.17%
<i>A. tortilis</i>	11	0.76%
<i>Balanites glabra</i>	17	1.17%
<i>Boscia albitrunca</i>	24	1.65%
<i>Carissa edulis</i>	19	1.31%
<i>Croton dichogamous</i>	146	10.06%
<i>Euclea</i> spp.	31	2.13%
<i>Hibiscus flavifolious</i>	2	0.14%
<i>Lycium shawii</i> (<i>Lycium</i> spp.)	18	1.24%
<i>Rhus natalensis</i>	4	0.28%
<i>Sido oventor</i> (?) <i>Sida</i> spp.	46	3.17%
Total	1452	

Plant species Mean, Median & SD height (m)

Plant Food Species	n	Mean Height (m)	Median Height (m)	SD Height (m)
<i>A. brevispica</i>	255	1.89	1.77	0.61
<i>A. drepanolobium</i>	321	2.46	2.09	1.19
<i>A. etbaica</i>	174	3.33	3.28	1.33
<i>A. mellifera</i>	367	2.80	2.68	1.17
<i>A. nilotica</i>	17	2.30	2.40	0.65
<i>A. tortilis</i>	11	2.51	2.55	1.12
<i>Balanites glabra</i>	17	3.53	3.20	1.43
<i>Boscia albitrunca</i>	24	4.05	4.04	1.14
<i>Carissa edulis</i>	19	1.94	1.84	0.84
<i>Croton dichogamous</i>	146	1.73	1.57	0.59
<i>Euclea</i> spp.	31	2.01	1.71	0.97
<i>Hibiscus flavifolious</i>	2	1.55	1.55	0.66
<i>Lycium shawii</i> (<i>Lycium</i> spp.)	18	1.46	1.29	0.46
<i>Rhus natalensis</i>	4	1.72	1.63	0.76
<i>Sido oventor</i> (?) <i>Sida</i> spp.	46	1.50	1.40	0.42
Total				