Dartmouth in Namibia

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Herbivory Impacts on !Nara

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Introduction

Herbivory is a biotic interaction which potentially limits plant fitness, survival, and biomass production. This interaction can have adverse effects on many species and even humans, especially if the plant involved is a keystone species. Herbivory pressure on keystone species can have a cascading effect on other taxa if they rely on the plant's resources or services (Klopatek & Stock, 1992). Therefore, it is necessary to understand the factors limiting the success of keystone species in order to gain a greater understanding of an ecosystem as a whole. Exclosure experiments have proven to be useful in examining long term effects of herbivory on flora (Goheen & Palmer, 2010; Pringle et al, 2011; Young et al, 2003; McCauley et al, 2008; King & Caylor 2010). The prohibition of access by herbivores to plants allows researchers to monitor the change in induced responses to herbivory. One theory regarding plant responses is the growth rate model, which predicts greater induced defenses due to more stressful conditions (Wise & Abrahamson, 2006). While the definition of stressors is broad, it could represent the degree of herbivore activity around a plant. Within the framework of an exclosure experiment, a researcher would be able to test this theory and hopefully draw conclusions that further overall understanding of herbivorous interactions.

!Nara (*Acanthosicyos horridus*) is a dioecious keystone species of the Cucurbitaceae family and endemic to the Namib Desert (Berry, 2003). Every year since 2013, students from Dartmouth College have conducted monitoring experiments on !nara along the Kuiseb River and areas surrounding the Gobabeb Research and Training Centre. The student research groups have collected baseline data and formulated methods for future data collection (McLaughlin et al, 2013). Research shows !nara invest in defense mechanisms against herbivory through the production of sharp spines that are about 2-3cm long (Young et al., 2003). However, there may exist additional defense mechanisms on the microscopic level. Typical of other Cucurbitaceae species, !nara have a network of trichomes spread across the epidermis (Metcalfe & Chalke, 1972). These structures are covered with a waxy layer about 5µm thick. This feature likely reduces the intensity of incoming radiation to keep the surface temperature low and overall humidity around the stomata higher (Hebeler, 2000). However, for many tropical Cucurbitaceae species, the combination of trichomes and waxy structure act as a deterrent to herbivores and fungal damage (Mohammed & Guma, 2015). It is unknown if this feature acts as a form of defense for !nara as well (Hebeler, 2000).

Major !nara herbivores include donkey, oryx, springbok, giraffe, and jackals. Within this group, donkeys and jackals are the most significant influences of herbivory. Jackals do not completely chew and destroy !nara seeds when consuming the fruit. A study looking at !nara seeds in herbivore faeces found that jackal scat contained both broken and intact seeds (Henschel et al., 2004). Jackals excrete undamaged seeds as they wander far distances, often at the base of dunes, and their faeces provide a nutritional foundation for the seedling to grow in an otherwise nutrient-scarce environment (Henschel et al., 2004). Jackal distribution also overlaps with that of the !nara; jackals are considered to be the main seed dispersal agent for !nara and crucial for the persistence of healthy populations of the plant (Henschel et al., 2004). Donkeys, on the other hand, do not differentiate between ripe and unripe fruit; studies on their scat revealed that all !nara seeds were broken or damaged and did not contain any viable seed embryos (Henschel et al, 2004). Donkeys are considered to be a major contributor to !nara herbivory and plant damage.

Donkeys can strip entire !nara plants of fruit and prevent any seed recruitment. They also pose a substantial threat to fruit production. It has been noted that female !nara not frequented by donkeys can produce up to 5 to 10 times more fruit than plants that experience intense herbivory (Henschel et al, 2004). Furthermore, !nara plants are a critical component of local Topnaar communities' livelihoods. They have been harvesting the fruit for 6000-8000 years (Henschel et al, 2004). The plants act as fodder for livestock, while their melons are an important part of community member's diets and can even be used to create products for commercial sale (Botelle & Kowalski, 1995). Therefore, the Topnaar people, together with ecological communities that depend on the !nara plant, may be negatively impacted by herbivory.

Effects of herbivory extend beyond the !nara plant itself since it is a major keystone species within the Namib Desert ecology (Henschel et al, 2004). !Nara provides nutrition, water, and shelter for a wide range of species (Henschel et al, 2004; Klopatek, 1992). Lizards and insects have been shown to benefit from large mammal herbivory. They consume juices released from the tips of !nara branches, which have been broken by livestock feeding (Berry, 1991). Many species, such as the skoog lizard (*Angolosaurus skoogi)*, rely completely on !nara juices as their sole source of water in a hyperarid climate (Nagy et al., 1991). In our own experiment, we noted such liquid secretions from recent livestock herbivory. Occasionally, !nara may exhibit symptoms of a disease or deformation in the form of flattened stems and aberrant spine distribution. Unfortunately, there is very little known about !nara disease and no current research being done on it- it is even unclear whether it is carried by viruses or pathogens.

Exclosures are used as a method to study the extent to which large mammalian herbivores (LMH) - in our case donkeys and cattle - influence plant communities in the long term. Exclusion treatments are large-scale manipulations of LMH presence and make it easier to single out response variables for examination, along with factors that affect the health of the species in question. In addition to our work on herbivory data collection, we assisted with the establishment of ten !nara exclosures within the vicinity of the Gobabeb Research and Training Centre. Such experiments have allowed researchers to examine the long term effects of herbivory on specific plant species (Goheen & Palmer, 2010; Pringle et al, 2011; Young et al, 2003; McCauley et al, 2008; King & Caylor 2010). Those effects may indirectly propagate throughout food webs, having significant effects on insects and smaller animals (Goheen et al, 2013). For example, Henschen et al. predict at least a 10% increase in fruit production among !nara within livestock exclosures. Such an outcome could have significant effects on various ecosystem levels.
In this year's experiment, we focused primarily on observing !nara's induced responses to herbivory damage. Our methods focus on researching herbivory damage caused exclusively by livestock animals, in particular donkeys and cattle. Generally, livestock have free reign to graze any !nara hummocks within Gobabeb Valley. However, Berry (2003) noted that livestock more readily visit !nara within close proximity to the Kuiseb River as opposed to the populations further off in the sand dunes. In addition to damage caused by feeding, livestock can easily damage young stems by trampling over areas where they feed, and thus speed up the accumulation of dead biomass (Berry, 2003). Such disturbances have been found to affect the densities of plants and small consumers; the strength of these indirect effects varies depending on context (Pringle et al, 2010). The exclosures constructed for this project will prevent local livestock from reaching certain !nara hummocks, but do not necessarily keep out game animals, which can still enter by jumping over the fences or weaving through its wires (Henschel et al,

2004). The exclosure design, which consists of strung wire rather than chicken wire mesh, specifically allows black-backed jackals (*Canis mesomelas)* to enter, as they can dig holes underneath the fencing wires and access the !nara.

By establishing a long-term exclosure study and a standardized methodology to monitor the plants for changes, it will be possible to determine how livestock herbivory affects the survival, fitness and estimated biomass production of !nara.

Hypotheses:

Variables that Affect Herbivory Patterns

1. The level of herbivory may be positively correlated with the frequency at which livestock visit hummocks. The activity level can be determined by assessing the presence of livestock scat around the hummock- scat serves as a proxy for livestock presence by hummock. Animals may visit a hummock and defecate but not browse on the plant, or they may browse on the plant but produce scat elsewhere. We want to determine whether scat presence can be used as an indicator of the herbivory level of !nara plants. Differentiating between different livestock, specifically donkeys and cattle, may discern which animals have a greater impact on !nara. If plants have higher livestock activity levels, then there will be higher instances of herbivory.
2. Livestock tend to graze close to the riverbed since the vegetation and trees growing there provide shade. The ephemeral Kuiseb River is also a source of water at certain points throughout the year. As a result, livestock will be more likely to browse on !nara plants in this area. Plants further away from the riverbed that are along the dunes may not be as worthwhile for livestock to frequent from an energy efficiency point of view. If nara plants are growing closer to the riverbed, then there will be increased levels of herbivory. Similarly, !nara growing near the riverbed may develop higher spine densities in response to increased herbivory. Therefore, if nara plants are growing closer to the riverbed, then there will be higher spine densities on branches.
3. Livestock may be more likely to browse on patches of !nara on the edges of hummocks- the outer clusters are more accessible and would require less energy from grazers. If the radial distance from the center of the plant increases, then there will be heightened levels of herbivory. Consequently, radial distance may have an impact on density of spines as clusters increase in distance from the center of the hummock to areas of increased herbivory. If the radial distance from the center of the plant increases, then there will be an increase in the density of spines on !nara branches.

Herbivory Affecting Patterns in Other Variables

4. Increased herbivory could cause plants to divert energy from general expansion and fruit production to boosting its defense mechanisms. Research on *Acacia drepanolobium* in East Africa showed herbivory to induce greater defense in those acacia species, as indicated by increased spine length (Young et al, 2002). We believe that herbivory on !nara plants may also stimulate a defense response, but in the form of increased spine

density to deter potential grazers. If plants have heightened herbivory, then they will have a higher spine density.

5. Fruit production is an energy-intensive endeavor for !nara, especially in hyperarid environments such as the Namib Desert. !Nara plants have been found to produce up to 500 melons ranging in size from 10 to 20 cm in diameter that weigh between 0.5 and 1.0 kg, each containing up to 300 seeds (Henshel et al., 2004). However, should there be heightened herbivory and thus harm to the plants, !nara may divert energy from fruit production to strengthening defense mechanisms. If plants have higher levels of herbivory, then they will have lower fruit density.
6. Plants may direct energy into better defending itself as opposed to increasing the overall extent of above-surface live plant when predated upon. Livestock disrupt and inhibit plant growth when they trample existing live vegetation and feed on growing meristems, thus inhibiting the overall sprawl of live vegetation. If plants have heightened herbivory, then they will have less above-surface live biomass.

   Similarly, livestock browsing on live biomass may trample existing dead above-surface biomass, compressing dead !nara matter. Intense herbivory may also act as a way of pruning vegetation that will eventually die off, and decrease the overall amount of dead plant material. If plants have heightened herbivory, then they will have less above-surface dead biomass. Alternatively, increased herbivory could increase above-surface biomass by killing off extended parts of a plant, and trampling could have less of an impact on dead vegetation than expected.
7. Increased presence of livestock at a !nara hummock could lead to disturbances that inhibit organisms such as scorpions and gerbils from creating burrows. Livestock could trample and destroy burrows as they forage on vegetation, while disturbances in the sand may prevent certain species from forming additional burrows. If plants have heightened herbivory, then there will be less animal and arthropod burrows around the hummock.
8. Some !nara show symptoms of a disease or malformity that results in a flattening of stems and an abnormal increase in spines, with three or more spines growing rather than the normal pairs of spines. Affected !nara plants sometimes resemble cactus nopales (pads). It is unclear what causes these malformations, as there is no existing literature on !nara diseases. However, !nara plants that regularly experience herbivory may be more susceptible to pathogens or other foreign bodies entering the plant due to open entry points where vegetation was predated upon. Livestock may not necessarily be transmitters of !nara disease, but weaken plants, making them more vulnerable to disease. Herbivory will increase with radial distance from the center of the plant.

Methods

Site selection

We studied 21 female !nara hummocks within Gobabeb Valley (Table 1, Appendix 1). All are located within a few kilometers of Gobabeb Research and Training Centre for easy accessibility. Additionally, these plants were selected as they will now be used in a long-term study on the effect of exclosures on !nara ecology. Although Nara Valley contains many more individual !nara, the local communities would not allow exclosures to be built there. Furthermore, due to its proximity to the Gobabeb Research and Training Centre, future researchers can easily visit our 21 subjects frequently. All 21 subjects varied in size, approximate age, and distance from the Kuiseb River, with the farthest located about five kilometers away. Within the subject group, ten females were chosen to be exclosed. The remaining eleven females will remain open to livestock herbivory, and have been paired with similarly sized, aged, and spatially located exclosed subjects to be compared against in the future. The exclosures are all different sized polygons depending on the size of the hummock (Table 1). Five strands of wire are secured between fence posts for the purpose of keeping out large livestock. We designed our data collection methods with the objective of observing the impacts of herbivory on all twenty-one plants from October 29 to November 6, 2016. In the future, data from the exclosed and control groups can be compared to study !nara responses to the long-term impacts of herbivory.

Table 1. !Nara study plant location and size information

Plant ID	Sex	Latitude	Longitude	Surface Area (m^2)	Volume (m^3)
GB1	f	-23.5644	15.0361	263.751	98.9833
GB4	f	-23.5645	15.035	1135.74	1171.26
KE1	f	-23.5634	15.0366	1282.1	1864.82
KE7	f	-23.5655	15.0382	860.6	1021.95
PX201	f	-23.5687	15.0407	54.242	13.3599
PX101	f	-23.571	15.0411	27.2906	6.2996
PX100	f	-23.5727	15.0415	211.294	155.754
PC201	f	-23.5861	15.0514	206.064	99.1671
PC202	f	-23.5848	15.0509	223.453	104.207
PC205	f	-23.5887	15.0518	206.174	134.633
GB12	f	-23.5885	15.0511	38.7456	2.75668
PC03	f	-23.5893	15.0504	418.573	259.936
PC05	f	-23.5901	15.0511	75.9161	25.6487
PC08	f	-23.5902	15.0519	92.4603	37.1025
PC09	f	-23.5908	15.0519	661.795	116.533
PC11	f	-23.592	15.0515	86.3658	27.4709
PC100	f	-23.588	15.04897	661.868	703.295
PC102	f	-23.5878	15.048	308.323	150.669
PC103	f	-23.5877	15.04818	115.546	50.8338
200LowDune	f	-23.5677	15.0405	56.0727	13.2408
200Dune	f	-23.568	15.0399	n/a	n/a

Transects and radial distance

Using the “wagon wheel” transect method (McLaughlin, 2013), !nara hummocks were divided into eight sections using a compass. Flags were placed at the base of the N, NE, E, SE, S, SW, W, and NW directions from the center of the hummock. The radial distance of each cluster to the center of the hummock was then measured. !Nara clusters that crossed the transect lines were used for all measurements.

Livestock activity levels (scat count)
Livestock activity was measured based on the presence or absence of scat in each of the eight transect sections. Only the scat of large livestock (donkey and cow) were recorded. Observations of livestock frequency around the hummock and where scat was spatially positioned, such as on the periphery or within the hummock were also noted.

Spine density and percent herbivory
A stem from each marked cluster on a transect was randomly chosen. The length of the first five branches from the tip of the stem were measured and the number of spines on each of the five branches were counted. The total number of branches on the whole stem were then counted, including the tip. Of this total number of branches, it was noted how many showed signs of herbivory, which would provide a total percent herbivory for a stem on a particular cluster.

Fruit count
The total number of fruit on the hummock were counted. Only fruits that were larger than 1 cm^2 were recorded. Using the surface area and volume of a hummock, fruit density per square meter could then be calculated.

Aboveground biomass proxy
We measured !nara heights with a meter stick from the base of a live plant to the height of the bush (McLaughlin et al., 2013). We visualized a plank or other object being placed on top of each cluster, thus providing an average height of the clump. The heights of each marked cluster were then averaged, and combined with the surface area of live biomass found using aerial drone photography to determine the approximate aboveground live plant volume. This measurement was then used as a proxy for aboveground live biomass.

Number of burrows
The total number of burrows observed on each hummock was counted. A burrow was determined to be any noticeable hole or opening on the side of the hummock or at the base of a clump of !nara.

Disease/plant deformities
We noted whether each hummock had plants with malformed stems, which indicated the presence of a !nara disease or other ailment. We only noted the presence of this malformity and did not count the actual number of malformed stems on a hummock.

Distance from river
Distance to the river was calculated with the Measure tool in ArcMap v. 10.4.1 by visually selecting the shortest straight line distance between each focal hummock and the edge of the vegetation-free Kuiseb River channel without crossing over any large dunes. Dune, river edge, and hummock locations were visually interpreted from a 2010 Worldview pan-sharpened (0.5 m pixel) satellite image.

Unmanned aerial vehicle
A 3DR Iris+ quadcopter equipped with a Canon S100 digital camera was used in conjunction with open source Mission Planner software to systematically gather aerial imagery over focal hummocks. Georeferenced orthomosaics and digital elevation models were generated from the raw aerial imagery using standard workflows in Agisoft Photoscan Pro (Appendix 1). Total hummock surface area and volume were calculated from the dense point cloud in Photoscan Pro. Hummock orthomosaics were exported from Photoscan Pro and then georeferenced and classified using a supervised maximum likelihood approach in ArcMap v10.1. Class designations were: live !nara, non-living !nara, and non-vegetated (sand) surface areas for each hummock (Appendix 1: workflow).

Analytical methods
JMP 12.1.0 was used for all of our statistical analyses. Linear regression models were used to analyze the data for a majority of our hypotheses (hypotheses 1, 2, 3, 4, 6, 8, and 9). For analyses that yielded a significant relationship between variables, residuals were plotted to test to see if they were randomly distributed with no pattern present. For variables in which there was no discernible relationship between variables, no further analyses were done. For hypotheses 5 and 7, the distribution of total number of burrows and fruit density was not normal, so a Poisson regression model with a log link was used to analyze the relationship between variables.

Results

Scat counts, used as a proxy for herbivore activity at a !nara hummock, were determined from the presence of donkey and cattle dung scattered between the eight cardinal and intercardinal directions around the plant. Average herbivory was determined based on the percent of predated branches on a randomly chosen stem on each cluster along the transects. The average percent of herbivory on !nara hummocks increased with the presence of donkey and cattle scat combined (Fig 1; $n = 20$, $df = 19$, $p = 0.0016$), and individually donkey scat (Fig 2; $n = 20$, $df = 19$, $p = 0.0014$) and cattle scat (Appendix 2; $n = 20$, $df = 19$, $p = 0.0494$).

We found no significant relationship between the distance of hummocks from the riverbed and the level of herbivory on the !nara (Appendix 3; $n = 20$, $df = 19$, $p = 0.3296$). However, there was a positive, significant relationship between the spine density of !nara branches and the distance of the plant from the riverbed (Fig. 3; $n = 20$, $df = 19$, $p = 0.0203$).

Radial distance from the center of a hummock was calculated for !nara clusters on each of the eight cardinal and intercardinal directions, with clusters divided from the outer plant in their respective transect. The average number of spines was calculated from the number of spines per cm on each of five branches studied on each !nara cluster along our transects. There is no significant relationship between the radial distance to the edge of a hummock and the level of herbivory on the !nara (Appendix 4; $n = 20$, $df = 19$, $p = 0.8233$). There is no significant relationship between the radial distance to the edge of a hummock and the average number of spines per centimeter on each branch of a !nara stem (Appendix 4; $n = 20$, $df = 19$, $p = 0.3450$).

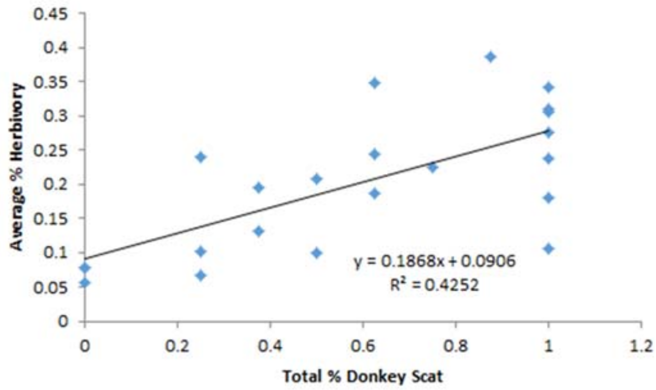

Fig. 2. Average percent of herbivory on a !nara plant as a factor of the total percent of donkey scat around a hummock. Results from a linear regression model showed a positive, statistically significant relationship (n= 20, df= 19, p= 0.0014).

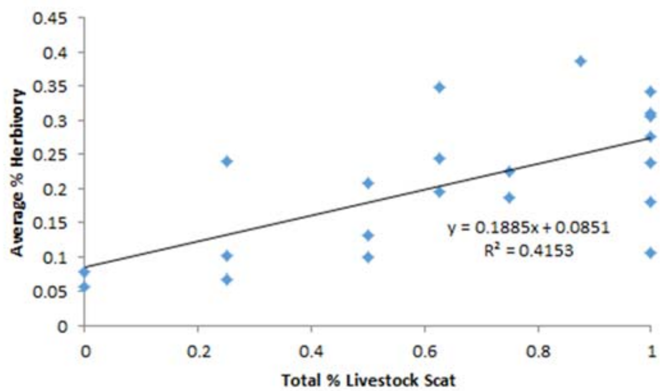

Fig. 1. Average percent of herbivory on a !nara plant as a factor of the total percent of livestock (cow and donkey) scat around a hummock. Results from a linear regression model showed a positive, statistically significant relationship (n= 20, df= 19, p= 0.0016).

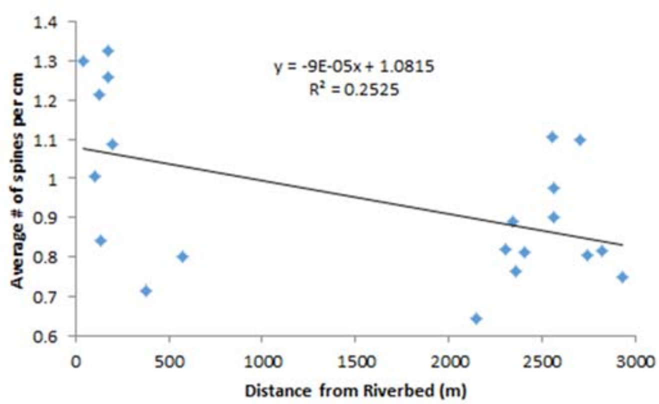

Fig. 3. Average number of spines per cm on a !nara branch as a function of distance of hummock from the riverbed in meters. Results from a linear regression model showed a negative, statistically significant relationship (n= 20, df= 19, p= 0.0203).

There was no significant relationship between the percentage of !nara branches predated on and the average number of spines per cm for each branch (Fig 4; n= 20, df= 19, p= 0.9572). We found no significant relationship between average percentage herbivory and fruit density in terms of surface area (Appendix 5; n= 20, df= 19, p= 0.4019) or volume (Appendix 5; n= 20, df= 19, p= 0.2312).

There was a positive, significant relationship between average percentage of herbivory and the surface area m^2 of aboveground live vegetation (Fig. 5; n= 20, df= 19, p= 0.0244). There was a positive, significant relationship between the average percentage of herbivory and the volume m^3 of aboveground live vegetation (Appendix 6; n= 20, df= 19, p= 0.0264). We found no significant relationship between average percentage of herbivory and the surface area of aboveground dead plant matter (Appendix 7; n= 20, df= 19, p= 0.4538).

There was a positive, significant relationship between the average percent of herbivory and the total number of burrows on a hummock; more burrows are associated with places that experience a high frequency of herbivory (Fig 4; n= 20, df= 19, p= <0.0001). We found no relationship between the presence of disease/stem malformities and average percent of herbivory on !nara plants (Appendix 8; n= 20, df= 19, p= 0.8006).

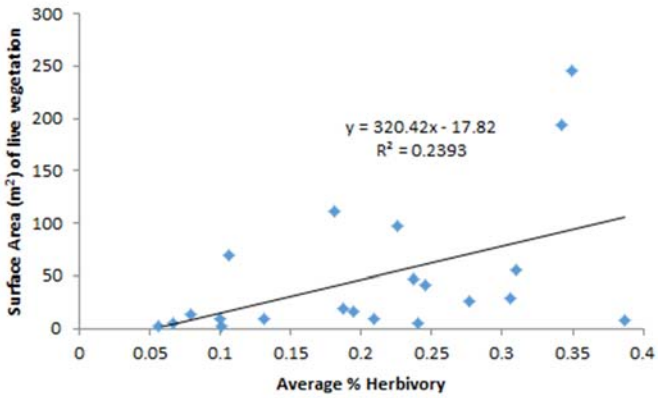

Fig. 5. Surface area (m^2) of live vegetation on a !nara hummock as a function of average percent of herbivory on the plant. Results from a linear regression model showed a positive, statistically significant relationship (n= 20, df= 19, p= 0.0244).

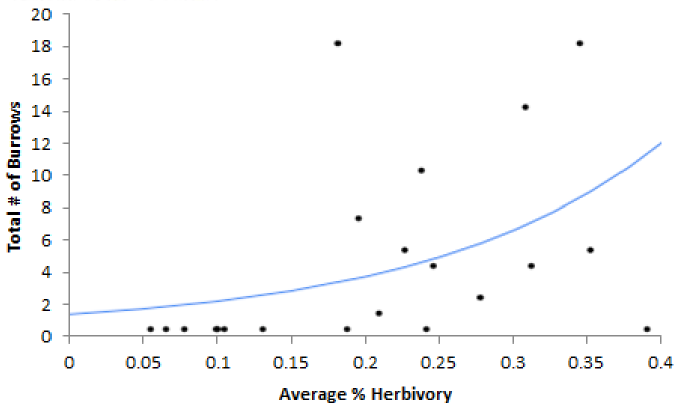

Fig. 6. Total number of burrows on a hummock as a function of the average percent of herbivory on a !nara plant. Results from a poisson regression model showed a positive, statistically significant relationship (n=20, df= 19, p= <0.0001).

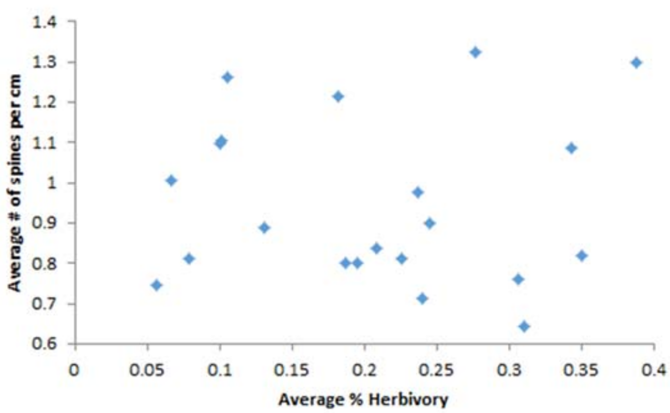

Fig. 4. Average number of spines per cm on a !nara branch as a factor of the average percent of herbivory on the plant. Results from a linear regression model showed no significant relationship (n=20, df= 19, p= 0.9572).

Discussion

The relationship between overall scat count (both donkey and cattle) and herbivory supports our hypothesis that herbivory increases with livestock visitation. These results indicate that scat count is an appropriate proxy for livestock activity levels, and therefore a reasonable gauge of herbivory around !nara hummocks. On the other hand, we did not find that radial distance from the center of a !nara hummock had an impact on either average herbivory or spine density. This may be because spine density does not vary too much from one cluster to another on each hummock, and if spine density was to increase in one cluster, spine densities on the hummock as a whole could increase since the clusters are essentially all part of the same plant. Livestock may also randomly browse on !nara hummocks rather than focusing on the periphery. Future studies could further tease apart the feeding habits of livestock on a hummock and how this relates to radial distribution of !nara clusters.

There is no significant relationship between the total percentage herbivory and each !nara hummocks' distance from the riverbed. It is worthwhile to consider how the four-year drought currently afflicting Namibia affects the grazing patterns of livestock, and whether our data is representative of cattle and donkeys' usual choice for grazing. However, there is a significant relationship between spine density and !nara distance from the river, but we cannot conclusively state the reason for this phenomenon. Moreover, this project essentially occurs during a single, short time period so there is no time scale taken into consideration. Some responses of the !nara plant may occur over a long time period, so future tests regarding river-distance and spine density may provide insight into this interesting relationship.

Our findings on the impact that level of herbivory has on the number of burrows around a hummock was unexpected, as we believed that small mammals and arthropods would not favor constructing burrows in places frequented by livestock. Our results show that the number of burrows increases with herbivory, though there may be a confounding variable that is the true reason for why total number of burrows increases. Plotting the response of burrow number to both the surface area and volume of hummocks reveals a strong positive relationship for both predictor variables (Appendix 9; n=20, df=19, p= 0.0014 and n=20, df=19, p= 0.0014). However, when the density of burrows per m^2 is plotted against the average level of herbivory, there is no significant relationship (Appendix 10; n=20, df=19, p= 0.1232). Burrow number may therefore be determined by the size of each hummock, only coincidentally increasing as the level of herbivory changes due to some other factor, such as distance from the riverbed.

We did not find evidence that increased levels of herbivory negatively impacted fruit production. However, there are several factors that affect fruit production which we did not take into account in plotting herbivory against fruit density, such as the age of each hummock. We did find that hummocks tend to produce either a substantial crop of fruit or very little to none at all, but we can draw no conclusions based on our data on why that is the case. Sustained monitoring is required to better understand the drivers of fruit production in relation to livestock herbivory.

The lack of relationship between the average number of spines and instances of herbivory fails to support our hypothesis that plants with heightened herbivory will have a higher spine density in an attempt to boost its defense system. However, patterns may become apparent as the plants are monitored and the experiment progresses. Alternatively, plants with higher spine densities may experience less herbivory because the plants are unappealing and more risky to eat to animals. As !nara plants increase their spine densities in response to increased levels of herbivory, herbivores may be tempted to visit other clusters on the same plant or other plants entirely that still have a favorable, lower spine density that makes it less risky and easier to feed on branches. Therefore, animals may favor plants with lower spine densities and travel around finding plants that have these lower densities.

Our results show a significant relationship between live surface area and volume in comparison to herbivory. This finding contradicts our hypothesis that plants experiencing heightened herbivory will have less live above-surface biomass than plants that are predated on less. However, we are not drawing any conclusions from these results since a variety of factors could be at play, such as age, hummock size, or distance from the riverbed. The exclosure experiment will better determine a pattern, should there be one, between these variables by seeing how exclosed !nara plants adjust in the absence of herbivory. Significant changes in biomass may indicate herbivory's role as a factor that influences biomass growth. Should biomass levels decrease, our hypothesis would be validated. However, if biomass levels increase more in protected plants than control plants, this would suggest that current herbivory limits their growth. According to the growth rate model, herbivory acts as a positive stimulant to plant growth: plants divert more energy to creating additional live biomass to make up material that has been consumed or damaged by grazers (Wise & Abrahamson, 2006). There is, however, no significant relationship between dead plant surface area and the average percent of herbivory. This indicates that the effects of livestock trampling was less severe than we expected and did not contribute to decreasing the surface area of dead !nara biomass. Livestock herbivory may also not have been intense enough to contribute to an increase in dead biomass coverage.

There is no significant relationship between total percentage herbivory and the presence of !nara disease. This does not support our hypothesis that predated plants will be more susceptible to the branch or spine deformities that depict disease. In the future, experiments could be carried out to more fully understand !nara disease. Beyond physical malformations, it would be interesting to see if the disease inhibits fruit production or adversely affects the lifespan of hummocks. Understanding the cause, carriers, and effects of the disease that cause some !nara to become deformed would be a good opportunity for upcoming research.

It is important to consider the effect exclosures will have on the subjects of this experiment. We expect there to be a substantial increase in herbivory pressure on unprotected control plants once the ten !nara plants are exclosed since it limits feeding options for local livestock. Based on our observations, we extrapolate that the control plants may experience a higher percentage of predated stems per branch, fruit loss, and increased trampling due to condensed livestock activity. Furthermore, the previously mentioned long-term exclosure experiment in Kenya on acacia trees found that a lack of disturbances from the absence of large herbivores induced marked shifts in the demographics of symbiotic insect populations (Palmer et al., 2008). It is possible that exclosing !nara hummocks will produce similar shifts in insect populations. Analyzing exclosure impacts on insect populations of various taxa is not the focus of our research, but nonetheless an important consideration for future !nara research. There are some insect taxa such as the !nara cricket (*Acanthoproctus diadematus*) that exclusively are found on the !nara. It is important to understand how these range-restricted and specialized species may be impacted by variations in levels of herbivory. Research has also been conducted on small scale herbivores such as lizards and gerbils (Berry, 1991; Nagy et al., 1991), but much remains to be seen regarding insect influences on !nara herbivory. It would be beneficial for such an experiment to develop a comprehensive method of insect identification and population calculation.

Going forward, it may be interesting to expand the project across spatial scales to see how that would affect plant-herbivore interactions. Experiments have been conducted in Sandwich Harbor, Visnara, and !Nara Valley in addition to the Kuiseb River and sand dunes surrounding Gobabeb Research and Training Centre (Henschel et al., 2004). These spatial differences not only provide a greater sample size but also greater input on herbivory-induced plant responses. For example, Berry (2003) found that Sandwich Harbor does not consist of any domestic livestock and the !nara there produced significantly more fruit than !nara surrounding the Gobabeb Research and Training Centre. Greater understanding can be established from replicating similar experiments with the specific focus of observing herbivory induced plant responses.

As we have learned, the act of herbivory influences !nara responses in various ways. Through the establishment of exclosure plots, much work can be done to expand our knowledge regarding !nara's induced responses due to herbivory. As a keystone species, many aspects of the Namib Desert ecosystem are dependent on the presence of healthy !nara populations. Klopatek & Stock (1992) state that "a complex of nara plants in the dunes of the Namib can be compared to a coral reef. They provide micro-ecosystems of biological diversity relative to the area that surrounds them." This coupled with the utilization of the !nara by the Topnaar community stresses the importance in understanding how herbivory from livestock impacts these plants and the potential for addressing such herbivory to ensure the long term vitality of the !nara plant for many communities for years to come.

Acknowledgements

We would like to thank Flora Krivak-Tetley, Jeff Kerby, Michael Butler Brown, Doug Bolger, Gillian Maggs-Kolling, André, Julian Fennessy, Fred the Rock and the Gobabeb staff for their assistance, time and thoughtful comments throughout the planning and implementation of our research and analyses.

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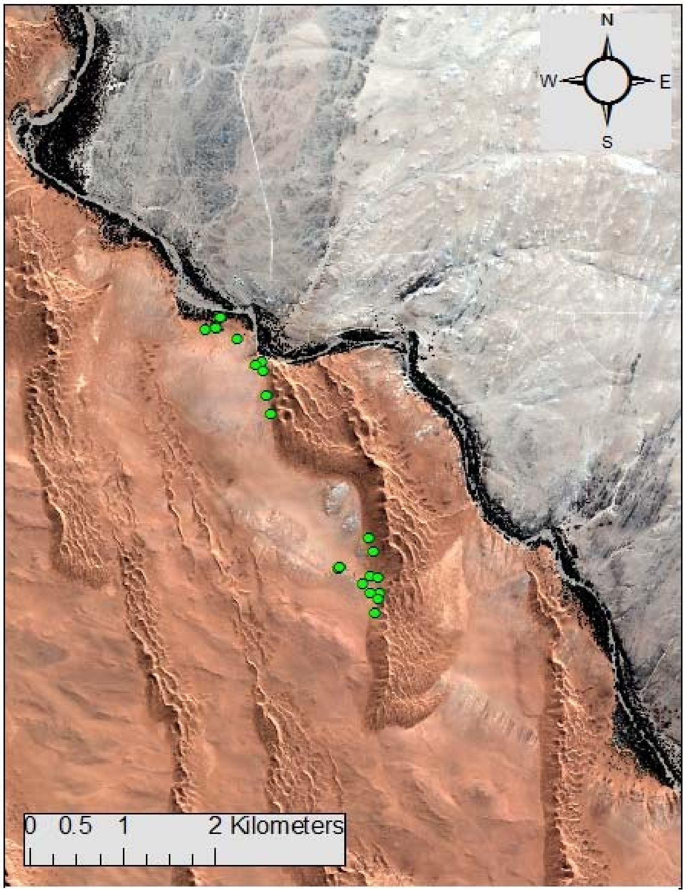
Appendices

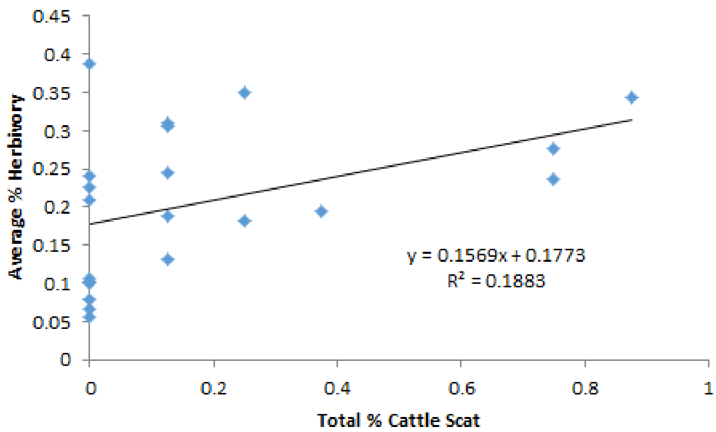
Appendix 1: Map of !Nara and Unmanned Aerial Vehicle (*Jeff and Flora will provide details*)



App. 1. GIS map of the !nara plants near Gobabeb Research and Training Center chosen for our study and for the long-term exclosure experiment. There are 21 total female plants.

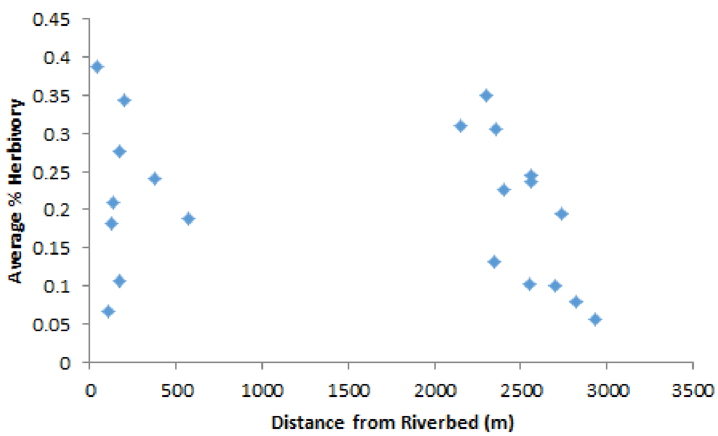
(Unmanned Aerial Vehicle Stuff Here)

Appendix 2: Cattle Scat



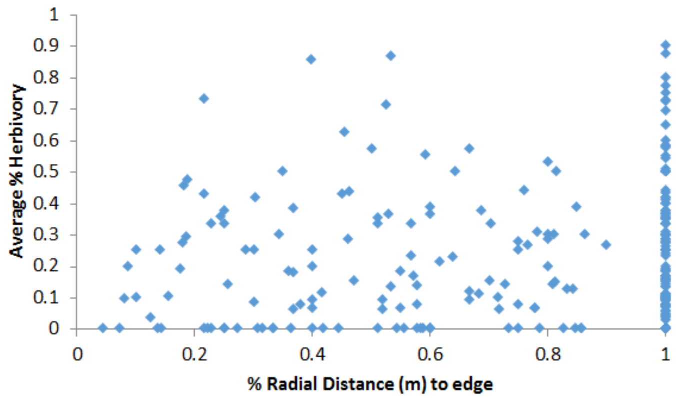
App. 2. Average percent of herbivory on a !nara plant as a factor of the total percent of cattle scat around a hummock. Results from a linear regression model showed a positive, statistically significant relationship (n=20, df= 19, p= 0.0494).

Appendix 3: Distance from Riverbed

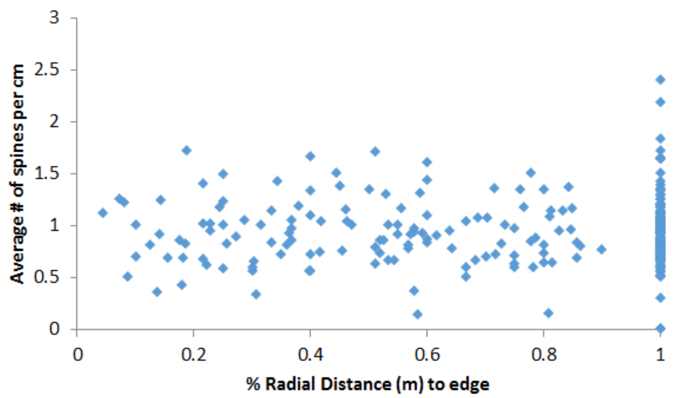


App. 3. Average percent of herbivory on !nara as a function of distance from the riverbed in meters. Results from a linear regression model showed no significant relationship (n=20, df= 19, p= 0.3296).

Appendix 4: Radial Distance

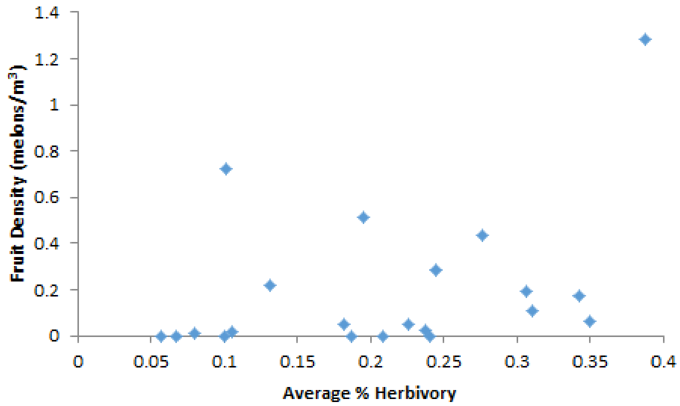


App. 4. Average percent herbivory on a !nara branch as a function of the percent radial distance outwards from the center of a hummock. Results from a linear regression model showed no significant relationship (n= 20, df= 19, p= 0.3450).

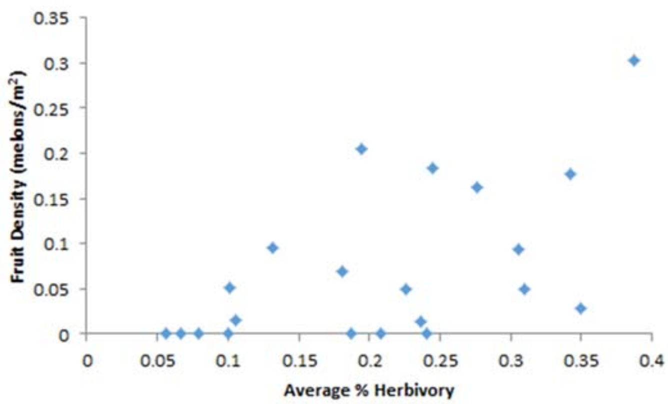


App. 4. Average number of spines per cm on a !nara branch as a function of the percent radial distance outwards from the center of a hummock. Results from a linear regression model showed no significant relationship (n= 20, df= 19, p= 0.8233).

Appendix 5: Fruit Density

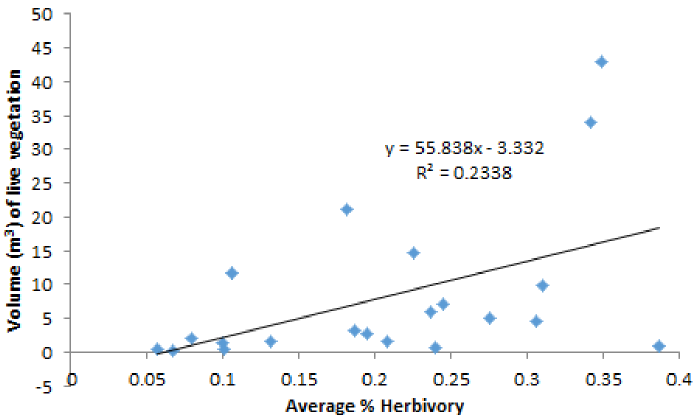


App. 5. Fruit density in terms of volume of a !nara hummock as a factor of the average percent of herbivory on the plant. Results from a poisson regression model did show any statistically significant relationship (n=20, df= 19, p= 0.2312).



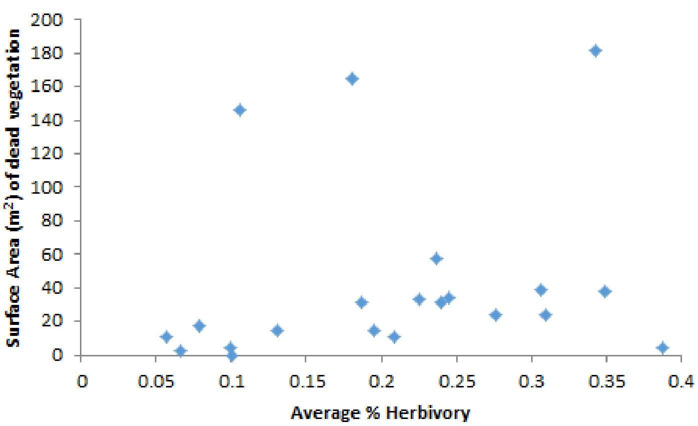
App. 5. Fruit density in terms of surface area of a !nara hummock as a factor of the average percent of herbivory on the plant. Results from a poisson regression model did show any statistically significant relationship (n=20, df= 19, p= 0.4019).

Appendix 6: Volume of Live Vegetation



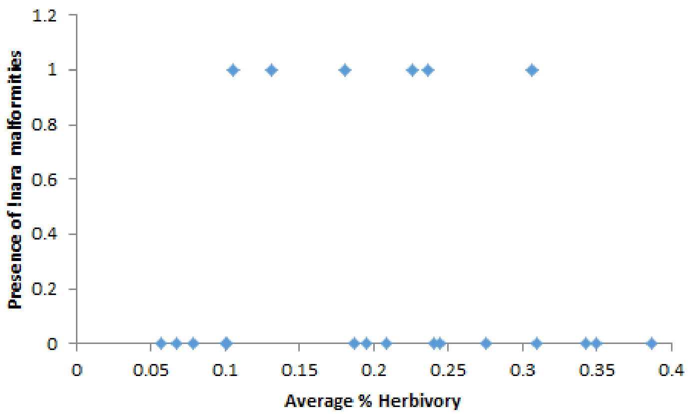
App. 6. Volume in (m^3) of live vegetation on a !nara hummock as a function of average percent of herbivory on the plant. Results from a linear regression model showed a positive, statistically significant relationship (n= 20, df= 19, p= 0.0264).

Appendix 7: Surface Area of Dead Vegetation



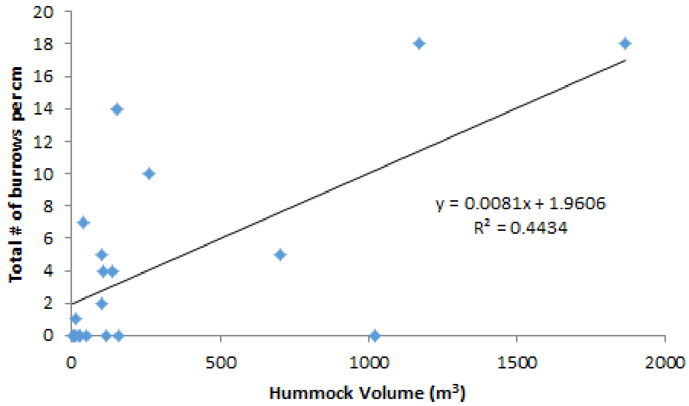
App. 7. Surface (m^2) of dead vegetation on a !nara hummock as a function of average percent of herbivory on the plant. Results from a linear regression model showed no statistically significant relationship (n=20, df= 19, p= 0.4538).

Appendix 8: Stem Malformations/ Disease

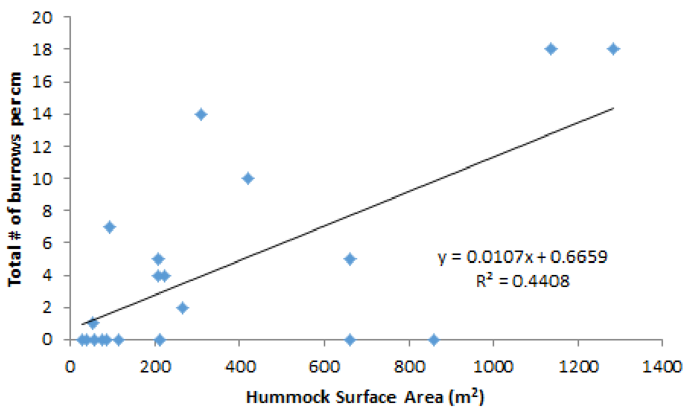


App. 8. Presence of !nara stem malformities as a function of the average percent of herbivory on the plant. Plants with no malformities present have a 0 score, while those with the condition have a value of 1. Results from a logistic regression model showed no statistically significant relationship (n=20, df=19, p=0.8006).

Appendix 9: Surface Area & Volume with Number of Burrows

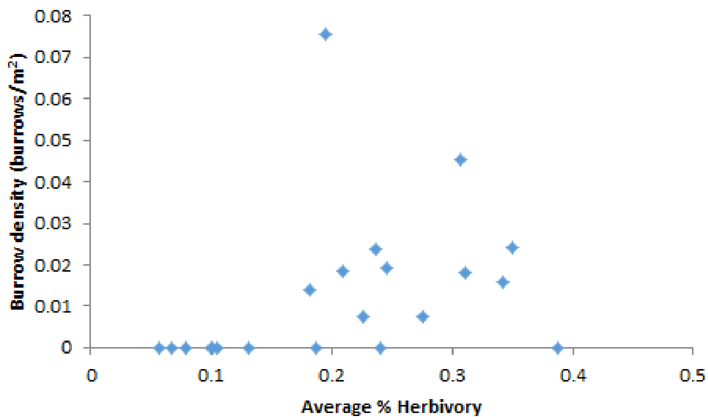


App. 9. Total number of burrows per cm as a function of hummock volume. Results from a linear regression model showed a positive, significant relationship (n=20, df=19, p= 0.0014).



App. 9. Total number of burrows per cm as a function of hummock surface area. Results from a linear regression model showed a positive, significant relationship (n=20, df=19, p= 0.0014).

Appendix 10: Burrow density



App. 10. Burrow density in terms of surface area of a hummock (m^2) as a function of average percent of herbivory on !nara plants. Results from a linear regression model showed no signficant relationship (n=20, df=19, p= 0.1232).

Perceptions of Livelihoods and Tourism Opportunities within the Topnaar Community

November 11, 2016

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Abstract

Using the results from a livelihood survey conducted at ten Topnaar settlements in the Erongo Region of Namibia, this paper analyzes community members' perceptions of current and alternative livelihood sources, particularly in tourism. The data collected demonstrate that Topnaar community members have diverse livelihoods and that there are significant differences in predominant livelihoods between upstream and downstream settlements. Pensions, !nara, and livestock were the sources of livelihood chosen as most important by respondents. The livelihood source for which they most wanted outside assistance was livestock, and the tradition of farming livestock was shown to be of importance to the Topnaar community. Findings also reveal a clear interest in the expansion of tourism activities in the region. Concerns regarding the use of a top down implementation strategy are considered, and a small scale, locally driven tourism initiative is proposed.

Introduction

Foundations of livelihood amongst the Namibian Topnaar community have a complex history due to the community's remote location and the unique landscape of the Erongo Region. The Namib Desert of central Namibia, although almost entirely uninhabited by humans, is home to the Topnaar Nama community. The Namib, meaning "vast place" in Nama, stretches inland from the Atlantic Ocean covering over 806,000 km2 (WWF 2016). In 2013, the Namib Sand Sea, a major feature of the Namib Desert, was inscribed as a World Heritage Site. This declaration, while restricting further landscape development within the region, has provided opportunity for potentially beneficial alternative livelihood sources for the Topnaar people.

Traditionally dependent on hunting and herding livestock, the livelihoods of the Topnaar have been greatly influenced by legislation affecting the ways they utilize their land and native natural resources. Particularly, the Topnaar were greatly influenced by the 1907 declaration of the Namib-Nauhluft Park. This establishment prevented community members from herding and hunting outside of the Kuiseb riverbed region. Years later in 1963, the South African Odendaal Plan attempted to create specific homelands for each ethnic group within Namibia as a method of promoting development (Botha 2016). As part of this plan, the government attempted to relocate the Topnaar, but the Topnaar refused to leave and claimed the land as their own because of their historic presence in the area. Heavy debate transpired between the Topnaar and local agencies over their reluctance to relocate and thus the community failed to receive financial assistance for the development of their land.

Today the Topnaar are amongst the most marginalized groups within the Erongo Region. According to a 2004 census, the Topnaar were socioeconomically categorized as poor along with 41% of Namibians. However, the Erongo Region where the Topnaar reside is considered the second wealthiest area in Namibia, largely a result of its situation between two major cities, Swakopmund and Walvis Bay (LEAD 2013). Topnaar settlements face high levels of unemployment, and proper education is scarce given their remote location and limited access to transportation, contributing to high dropout rates. These factors combined with limited historical interaction with the outside world means that the Topnaar community face development challenges distinct from communities more robustly connected to urban areas and centers of tourism.

Although tourism is not yet an established industry along the Kuiseb, given its close proximity to Swakopmund, Walvis Bay, and the C14, a major highway traveled by tourists, its tourism potential is no secret. Nyabunu and Ndiovu (2010) found that one of the principal reasons for the lack of tourism expansion is the fear of tourism activities interfering with household responsibilities, thus impacting the effectiveness of already significant livelihood sources. Additionally, the Topnaar community has historically had difficulty seeking support in terms of funds, training, and tangible resources necessary to expand the limited tourism practices currently in the Erongo Region. Because of a general lack of knowledge of the industry, the practicalities of tourism are relatively unfamiliar to the Topnaar. Even with a lack of public opposition for the expansion of tourism in the area, given the lack of adequate knowledge, the inherent need for strict management, and the extensive planning associated with tourism development in a safeguarded region, Topnaar have yet to solidify a tourism industry within the Kuiseb River area.

The Ministry of Environment and Tourism recently released the 2015 Tourist Statistical Report which highlights the visitor increase seen in Namibia since 2010. For illustration, in 2010 984,099 individuals traveled through Namibia, compared with 1,387,773 visitors in 2015; an increase in tourism by over 40%. Given this increase in visitor interest, the Topnaar people have recently been granted two tourism concessions by the Namibian government, the Kuiseb Development Trust and the Topnaar Concession Trust, which grant them the right to develop tourism practices within the protected area.

A 2016 report by students from Worchester Polytechnic Institute (WPI) aimed to identify employment opportunities that interest the Topnaar and potential tourism products (WPI 2016). The researchers conducted interviews with Topnaar people from Utuseb, tour guides, and with tourists. Based on responses to their surveys, the WPI report concluded that: 1) the Topnaar community is interested in developing community-based tourism, 2) there is a lack of communication and trust between the Topnaar and tour operators, and 3) the creation of a Topnaar tourism association would enable the development of community-based tourism by facilitating trust and communication with tour operators (WPI 2016). While this study contributes valuable knowledge towards the development of tourism among the Topnaar community, it lacks a strong community-based perspective. For illustration, while their survey prompted discussion of the community's opinions regarding various tourism practices, the survey did not provide an opportunity for respondents to give answers other than three listed response options. Tourism initiatives that lack a strong foundation in community desires have the potential to perpetuate a history of Topnaar development attempts defined and driven by outside actors.

Gobabeb Research and Training Center (GRTC) has historically shown involvement with the Topnaar community, conducting research as well as facilitating the expansion of community development projects. Founded in 1962 by Dr. Charles Koch, Gobabeb is an internationally recognized facility for training and research practices. Gobabeb is situated south-east of Walvis Bay in the Namib Desert at the site of an abandoned Topnaar settlement. Since 1998, GRTC has been a joint Venture between the Ministry of Environment and Tourism (MET) and the Desert Research Foundation Namibia (DRFN) (Gobabeb 2016). Given Gobabeb's mission as a scientific research center, they have no staff with a primary background in community development, however Gobabeb is presently involved in several livelihood projects within the surrounding Topnaar community. Throughout this study we worked with Gobabeb and members of the Topnaar community to attain a complex data set representative of the current and potential livelihoods of the Topnaar people. Building upon previous research and Gobabeb's past experiences with the Topnaar people, we constructed an in depth evaluation of interest in alternative sources of livelihood and their perceived potential within the Namibian Topnaar community.

Within the Topnaar community, numerous attempts to initiate tourism initiatives by outside organizations have been predominantly unsuccessful. There is extensive literature addressing the need for context-appropriate livelihood schemes, community interest and leadership in livelihood development schemes, and the potential negative implications of poorly managed community based tourism (CBT). Toner & Franks (2006) explain that livelihood sources depend on the availability of capital assets (i.e. human, social, physical, financial and natural), which limits their availability within different contexts. However, when a community embraces their available natural resources and uses them to their advantage, they can successfully develop alternative sustainable livelihood sources strengthen their resilience as a community.

Enchantment and Disenchantment: The Role of Community in Natural Resource Conservation by Agrawal and Gibson provides a theoretical framework delineating the importance of local community involvement in interactions with external institutions. While their paper focuses on community natural resource conservation, the lessons from Agrawal and Gibson about communities working collectively and interacting with external organizations to better their livelihood options apply equally to context of community tourism. Local community members are crucial to the success of development efforts as resident actors understand community values and directly control the daily use of surrounding natural resources (Agrawal & Gibson 1999). The authors emphasize the need to take into consideration both internal and external factors that affect communities, their level of motivation directed towards development, and the interactions that transpire during decision-making processes (Agrawal & Gibson 1999). Top down, externally driven approaches to development have limited potential for success without community buy-in. "The past several decades of planned development and top-down conservation practices have made one fact amply clear: [a community's] capacity to coerce their citizens into unpopular development and conservation programs is limited" (Agrawal & Gibson 1999).

The decentralization of local authority is important to any community development as it fosters the use of community driven approaches, where the community members themselves are the main perpetuates of change and transformation. In addition, the possession of shared norms between neighboring communities often propagates collective action efforts that bolster larger scale development while still prioritizing a bottom up approach. If all empowered, multiple local actors have the ability to collaborate and promote future development and change collectively. Common community interest and inspiration also play a large role in realization of such collective action (Agrawal & Gibson 1999). In our analysis of Topnaar livelihoods and the feasibility and desirability of tourism as an alternative livelihood source, we prioritized the individual voices of community members and the various opinions of additional local actors. We specifically formulated a survey using Agrawal and Gibson's bottom up framework as a foundation so that local opinions were prioritized moving forward. As previously mentioned, past plans for tourism development within the Erongo Region failed to blossom into an established, sustainable tourism industry that community members are eager to take part in.

Noel Salazar's *Community-based cultural tourism: issues, threats and opportunities* addresses risks associated with the development of a tourism industry, specifically pertaining to the preservation of traditional culture. Salazar warns local communities of the threat of major industry development to local actors. He writes, "Because of the communicative power of tourism, representations of destinations have direct and potentially significant influences on people who are being presented, represented and misrepresented" (Salazar 2012). He expresses that local control in management is key to ensuring that locals are able to directly benefit from tourism and thus will remain interested and enthusiastic about further development within the industry. The only way for a community to overcome a diminished sense of local power when developing community based tourism practices is to take into account the operational, structural, and cultural limits to community participation so that external actors do not assume unequal authority.

Salazar highlights three major failings of CBT: 1) it tends to take a functional approach to community involvement, 2) it tends to treat the host community as a homogeneous bloc and 3) it neglects the structural constraints on local control of tourism industries. Salazar contends that successful CBT suggests a symbiotic or mutual relationship where the tourist is not given central priority but becomes an equal part of the system, highlighting that power imbalances often act as significant barriers to productive interactions between locals and tourists (Salazar 2012).

Erik Cohen's *Authenticity and Commoditization in Tourism* further expands upon on the risks associated with community based tourism practices by exploring the potential of tourism to transform cultural practices and values. He asserts that tourism implies the commoditization of culture, which can destroy the authenticity of local cultural products and human relations and warp tourists' genuine desire for authentic experiences (Cohen 1988). In other words, he warns of the ability of tourism industry development to perpetuate cultural change that diminishes the traditional significance of cultural practices.

Community based tourism has the potential to contribute to economic development within communities while simultaneously conserving a community's natural surroundings. While this form of tourism can bolster economic stability within a community, the literature shows that unequal distribution of power between various actors has the potential to disadvantage local communities and influence traditional culture and values. Our research contributes to this literature in that we explore the interest of Topnaar community members in developing tourism as compared with other livelihood options as well as the extent to which Topnaar community members are aware of the potential impacts of tourism on their culture.

Methods

Survey design

The objective of this study was to gain a deeper understanding of Topnaar livelihoods, livestock management as a key livelihood, and their perceptions of tourism opportunities within their community. Data were obtained by interviewing Topnaar community members from various villages along the Kuiseb Riverbed. After meeting with Chief Seth Kooitjie to obtain his permission to conduct research among the Topnaar people, surveys were designed following the guidelines of OECD 2012 and Valentine 2001. Survey questions were kept concise and used simple language to ensure consistent and easy translation into respondents' target language (OECD 2012). Some questions used a Likert Scale, which allows respondents to choose a response from a five point scale (McLeod 2008). The final survey was divided into five sections and included questions on demographic information, livelihood sources, relative importance of livelihood sources, livestock management practices, interest in tourism, and perceived implications of tourism for the Topnaar community (Appendix 1). Livelihood sources included in the survey were livestock, !nara, government pensions, migrant labor, tourism related activities, employment, and an additional category for other sources of livelihood.

Data collection

We interviewed 25 people from ten settlements over four days. Settlements were in four main clusters and broadly divided into an upstream region and downstream region. The downstream region, consisting of settlements between Aramstraat and Utuseb, was chosen because it is the area with the most potential for tourism, and the upstream region, consisting of Homeb, Natab, and Soutrivier, was chosen because that area has historically been known for a greater dependence on livestock (Henschel et al. 2004). These settlements span about 100km along the Kuiseb Riverbed. Respondents were interviewed from households where people were present, available, and willing to be interviewed. With their permission participants' names were recorded, although within this report all specific responses or quotes are kept anonymous. With few exceptions where the respondent was proficient in English, questions and responses were translated by a translator from the Topnaar community. Each survey took 30 minutes to an hour to conduct. Notes were taken on paper copies of the survey, and interviews were also digitally recorded as a form of backup in case any of the written answers require further clarification. Digital recordings will not be retained after analysis, but the filled out paper surveys and a spreadsheet of compiled responses will be kept at Gobabeb for further reference.

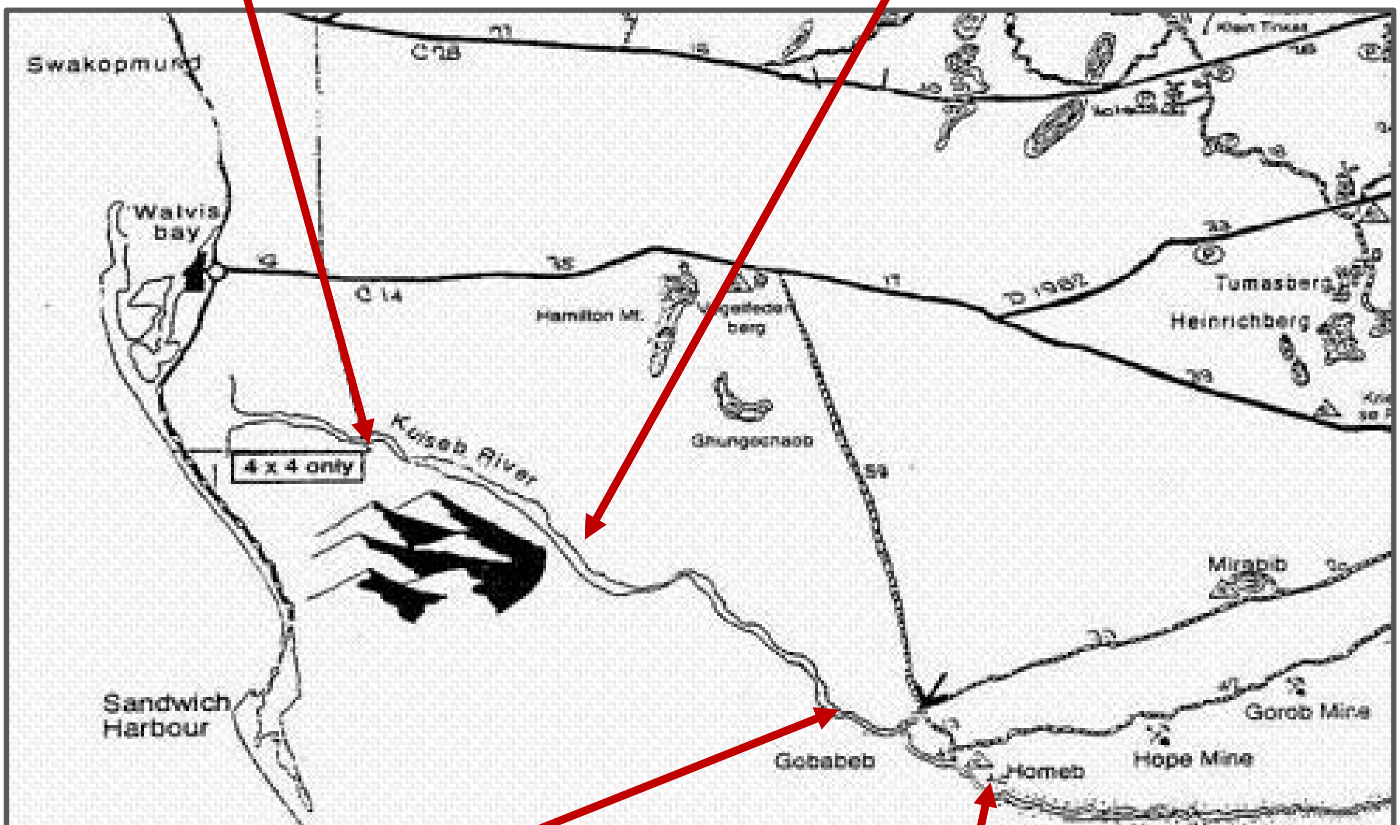
Data analysis

We compiled the results of the quantitative aspects of our survey into descriptive statistics such as averages and frequencies. We analyzed open-ended questions by identifying categorized by recurrent themes in the data, such as types of tourism activities that respondents were interested in. Where useful, we quantified the text responses into descriptive statistics as well. Observed frequencies of livelihoods were compared with expected frequencies, calculated assuming equal likelihood of each livelihood option using a chi-square test. Using contingency tables, we compared observed and expected frequencies of livelihoods and livelihood development priorities between upstream and downstream regions and between households that receive pensions and households that do not.

Topnaar Settlement Respondents

Aramstraat Settlement Averages (N = 9)
Household Size: 4.2 people
Age: 46 years old
Male: 2 (22% of respondents)
Female: 7 (78% of respondents)
Main Livelihood Source: !Nara

Uteseb Settlement Averages (N = 10)
Household Size: 4.5 people
Age: 47 years old
Male: 1 (10% of respondents)
Female: 9 (90% of respondents)
Main Livelihood Source: Pensions



Soutrivier Settlement Averages (N = 2)
Household Size: 5 people
Age: 49 years old
Male: 0 (0% of respondents)
Female: 2 (100% of respondents)
Main Livelihood Source: Pensions

Natab & Homeb Settlement Averages (N = 4)
Household Size: 3.75 people
Age: 40 years old
Male: 4 (100% of respondents)
Female: 0 (0% of respondents)
Main Livelihood Source: Livestock

Results

Chief Kooitjie

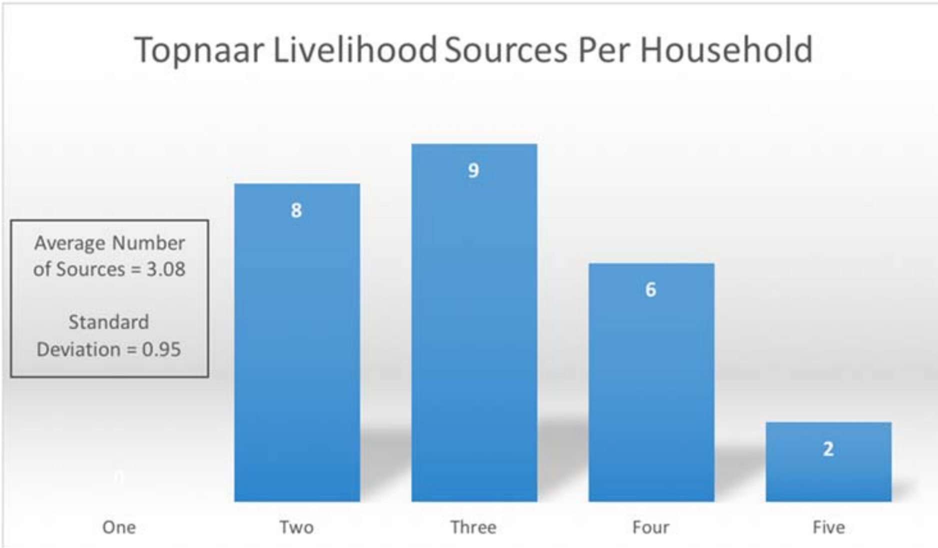
In our meeting with Chief Seth Kooitjie, he indicated that he sees great potential for development among the Topnaar community through community-based tourism. For him, the community's location within a national park is ideal because the natural environment has many features that attract tourists. He is eager for an expansion of tourism, saying, "Tourism for us is priority number one" (S. Kooitje, personal communication, October 31, 2016). At the same time, he emphasized that community involvement in any development project is essential. He reported that the Topnaar people have had negative experiences with economic development plans designed by outside professionals who had no understanding of Topnaar culture, traditions, and history. Because of this, he feels strongly that the community must be included in decision-making around tourism and other development initiatives. In addition, Chief Kooitjie believes that community based tourism will encourage young people to engage with Topnaar traditional culture, rather than moving to urban areas and losing touch with their roots (S. Kooitje, personal communication, October 31, 2016).

Demographics

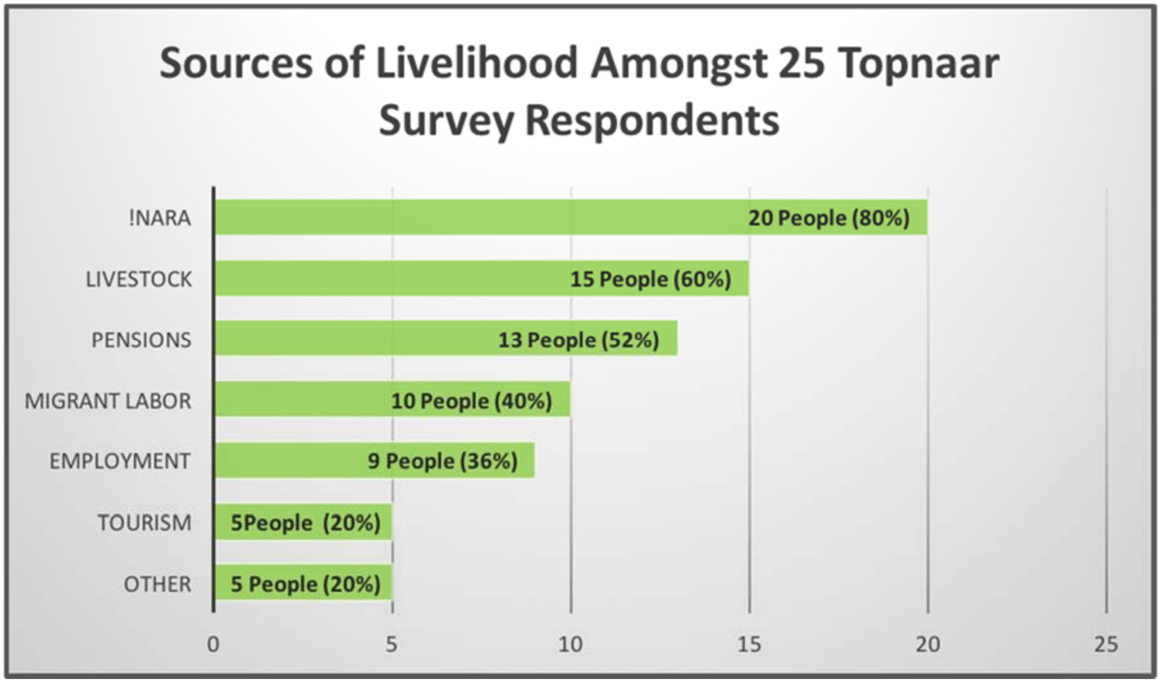
We interviewed individuals from twenty-five households in ten settlements. We surveyed eighteen females and seven males. Their average age was 46, with the youngest respondent being 20 years old and the oldest 86 years old. The average household size was 4.3, with 10 being the largest and one being the smallest. While we gathered demographic data of the primary interviewee, often multiple people from the household contributed to the survey responses.

Livelihoods

Our results show that Topnaar livelihoods are diversified. All households surveyed had at least two sources of livelihood, and 68% of households had three or more. This distribution of number of livelihood sources was significantly different from all numbers of livelihood sources (one through five) being equally likely (chi square = 12.0, df = 4, p-value = .02).



!Nara was a source of livelihood for 80% of households, making it the most common livelihood source in our sample. Forty-eight percent of these households harvest !nara themselves and 48% sell !nara or !nara products. Those who included !nara as a livelihood source but did not harvest themselves were given !nara by friends or family. Livestock was the next most common source of livelihood. Of those who included livestock as a source of livelihood, 40% cared for only livestock they owned themselves, 27% cared only for livestock owned by other people, and 33% owned livestock and cared for livestock owned by other people. The next most common source of livelihood was pensions (either old-age or disability), followed by support from family members in urban areas (migrant labor), employment, tourism related activities, and other sources of livelihood (e.g. vegetable gardens or selling firewood).



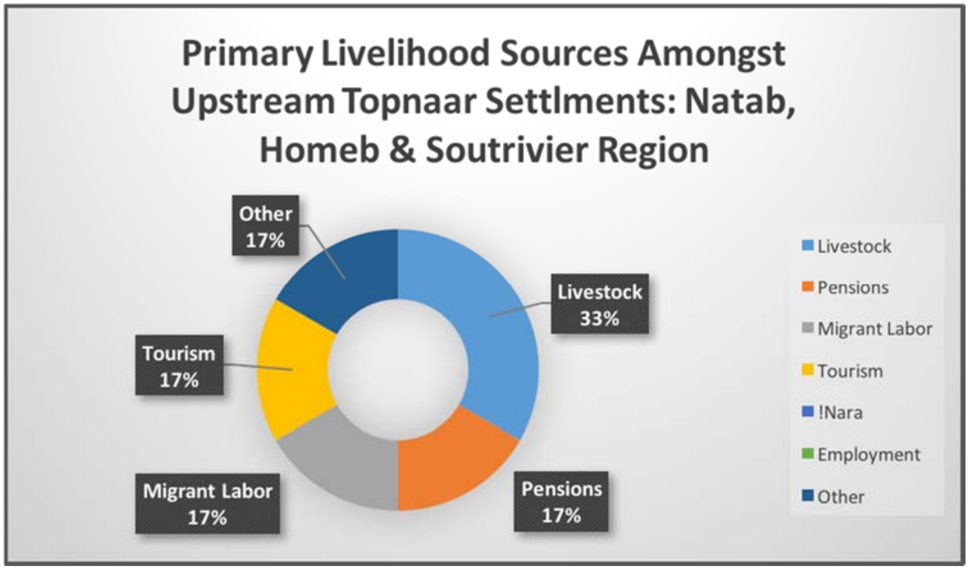
When asked to rank their livelihood sources from least important to most important, nine of the 25 (36%) chose pensions as their most important source of livelihood, making pensions the most common primary source of livelihood. The next most common primary source of livelihood was !nara with seven respondents (28%) choosing it as their most important source. Four households chose livestock as their most important source of livelihood, one chose support from family in urban areas, one chose income from tourism related activities, and one chose another livelihood source (income from her boyfriend). We found that this distribution of primary livelihoods was statistically significant different from all sources being equally likely (chi square = 17.84, df = 6, p-value < .01). For their least important source of livelihood, the most common answer was !nara, followed by migrant labor, tourism related activities, livestock, employment, and an other livelihood source. This was a statistically significant difference from all sources being equally likely at the 10% level (chi square = 11.68, df = 6, p-value = .07). This shows that there are significant trends in the importance of various livelihood options in the Topnaar community.

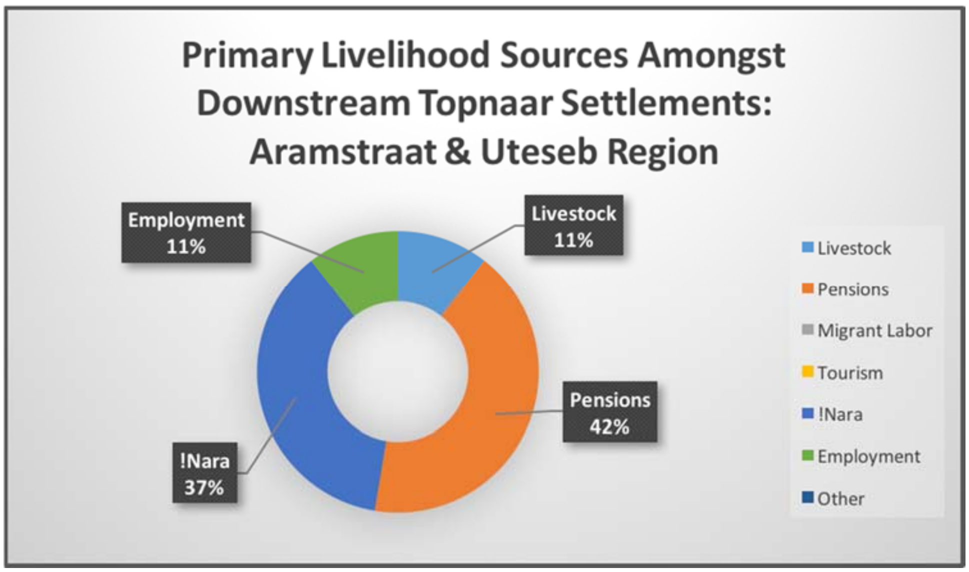
Self Identified Most Important Sources of Livelihood, N = 25	
Livelihood Source	**Frequency**
Pensions	9
!Nara	7
Livestock	4
Employment	2
Migrant labor	1
Tourism	1
Other	1

Self Identified Least Important Sources of Livelihood, N = 25	
Livelihood Source	**Frequency**
!Nara	8
Migrant labor	6
Livestock	3
Employment	3
Tourism	3
Other	2

We examined the difference between primary livelihood sources in two regions: upstream settlements (Natab, Homeb, and Soutrivier) and downstream settlements (Aramstraat and Utuseb region). We interviewed seven households in the upstream region and eighteen households in the downstream region. In the upstream region, the most common primary source of livelihood was livestock, while downstream the most common primary livelihood source was pensions, closely followed by !nara. A contingency table showed that the difference in selected primary livelihoods between upstream and downstream regions was statistically significant (chi square = 14.64, df = 6, p-value = .02), meaning that there is a relationship between the type of livelihood source selected as the primary source and the location. We found no significant difference between upstream and downstream regions in terms of livelihood development preferences (chi square = .89, df = 6, p-value = .83) or total number of livelihood sources (chi square = 1.93, df = 3, p-value = .59).

Contingency Table of Selected Primary Livelihood Sources by Region (Chi Square = 14.64)								
Observed Primary Livelihood Sources								
	!Nara	Livestock	Pensions	Employment	Migrant labor	Tourism	Other	Total
Upstream	0	2	1	0	1	1	1	6
Downstream	7	2	8	2	0	0	0	19
Total	7	4	9	2	1	1	1	25
Expected Primary Livelihood Sources								
Upstream	1.68	0.96	2.16	0.48	0.24	0.24	0.24	6
Downstream	5.32	3.04	6.84	1.52	0.76	0.76	0.76	19
Total	7	4	9	2	1	1	1	25





When asked what they believed the main source of livelihood among all Topnaar people was, 21 people said !nara, 10 people said livestock, two people said tourism, one person said pensions, and one person said employment. There are more than 25 responses because some people answered with more than one livelihood source. We also asked people to choose which aspect of their livelihood they would want help with if an outside organization were to offer assistance. The most common livelihood choice was livestock, followed by tourism. Assistance establishing a garden was also a common response, and four people said another livelihood option: a salon, a music studio, assistance for a school, and assistance becoming a builder. Both of these questions yielded results that were statistically different from all responses being equally likely (chi square = 70.56, df = 6, p-value < .01; chi square = 46.89, df = 6, p-value < .01). This shows that there is a significant trend in the perception of main livelihood and in livelihood development priorities among Topnaar community members.

Perception of Most Important Source of Livelihood Among Topnaar	
Livelihood Source	**Frequency (% of respondents)**
!Nara	21 (84%)
Livestock	10 (40%)
Tourism	2 (8%)
Pensions	1 (4%)
Employment	1 (4%)
Gardening	1 (4%)

Livelihood Priority for Outside Help	
Livelihood Source	**Frequency (% of respondents)**
Livestock	14 (56%)
Tourism	5 (20%)
Gardening	4 (16%)
Other	4 (16%)

Livestock
Fifteen of the households surveyed included livestock as a source of livelihood. All fifteen households had at least one goat, four owned donkeys, three had cows and sheep, and one had horses. The average number of livestock owned was 23, with a minimum of one and a maximum of 111+. When asked why their livestock were important to them, seven people gave reasons strictly related to their present-day livelihoods, e.g. "I eat and drink from them" (respondent 1605). Four gave reasons that included consideration for their future livelihoods, e.g. "When I retire, I'll live from my livestock" (respondent 1625). Three gave reasons that included a love for their livestock or a tradition of farming livestock, e.g. "I grew up with livestock. I do it for the love of it and to sustain myself" (respondent 1603). Fourteen of the fifteen said yes when asked whether it was important to them to continue their family tradition of owning livestock.

Average Number of Livestock					
	Goats	**Donkeys**	**Cows**	**Sheep**	**Horses**
Mean	16.3	5.2	10.3	12.6	2
Std. Dev.	24.9	4.1	4.9	9.1	N/A
N	15	6	3	3	1

With the exception of one man who was hired to care for the chief's son's livestock and did not benefit from the livestock in any other way, they all reported using their livestock for meat and/or milk. Twelve of the fifteen also sell their livestock. Of these, ten people said that they sell to men who come to their settlement, and some specified that they come from Walvis Bay or Swakopmund. Reports of how frequently people come to buy livestock ranged from once or twice per month to two to three times per year. Two people said they take their livestock to Walvis Bay to sell them. When asked about barriers to selling livestock, two people cited lack of transportation as a barrier to getting their livestock to market, but six people indicated that they were happy with how frequently the buyers came to their settlement and so were not interested in taking their livestock into town to sell.

As for how they take care of their livestock, most people explained that they let their livestock out in the morning and that they roam freely. No respondents differentiated between types of livestock when describing their management practices. Twenty-four respondents said that their livestock return home every evening. One woman said that her cows only come back to the kraal about every four weeks. Four people indicated that the young ones stay in the kraal all day, although this was not specifically asked about so it is possible that other respondents simply did not mention that they keep their young livestock in the kraal. Five people said they herd their livestock, three people said they herd sometimes, and seven people said they do not herd, although two of those employ herders. Two people said that a dog goes out with their livestock, one said that a dog sometimes goes, and twelve people said that no dog goes with their livestock. Six of the fifteen said that their livestock go to surrounding settlements for water. Responses to how far their livestock go ranged from staying in the riverbed just by their settlement to traveling 5km away.

When asked how the drought has impacted them and their livestock, fourteen of the fifteen indicated that they had been seriously negatively impacted. Eleven people mentioned that livestock have died, and other impacts included that their livestock are thinner, that they are unable to sell because of the bad condition of their livestock, that their livestock did not give birth at all in the last year, that they do not produce enough milk for their young, and that they are more easily killed by jackals. Eight households have adopted strategies to mitigate the effects of the drought. Three families have taken up collecting food to supplement their livestock's forage, and one woman said that she now must work harder to collect enough food for her young livestock. Other strategies included letting the livestock out earlier in the day so they have more time to feed, moving the kraal to a better location, and changing where livestock are herded. Seven people said that they have not changed how they take care of their livestock at all because of the drought. Only one respondent said they have purposely reduced their number of livestock because of the drought, which they did by slaughtering them to eat.

We asked participants to identify the main reasons their livestock die. Nine people said food scarcity was the leading cause of death, five said predation, four said disease, one said ticks, and one did not know. Fourteen of the fifteen said that jackals prey on their livestock, ten people mentioned an animal that our translator identified as "wolves", two people said hyena, one person said dogs, and one person said she has no predators. When asked about differences in livestock behavior between rainy season and dry season, some people indicated that during rainy season their livestock sometimes stay out overnight and that they stay closer to the kraal because there is enough forage close by.

Tourism

We wanted to explore respondents' opinions on developing community based tourism initiatives. Twenty-two of the 25 respondents said they were interested in seeing tourism expanded in the Topnaar community. Respondents who were not interested in tourism believed that they would not benefit from tourism or said that they were not knowledgeable about tourism, e.g. "What can tourism do for me?" (Respondent 1610), or "I don't know anything about tourism" (respondent 1620). Among those positive about tourism, activities that they were interested in included donkey cart rides, walking trails, campsites/accommodation, stalls or a center to sell handicrafts, bicycle trails, and horse riding. Aspects of Topnaar culture that they suggested sharing with tourists included traditional dance, !nara harvesting and processing, traditional foods, singing, handicrafts, traditional attire, traditional medicine, storytelling, the marriage process, cosmetics, information about the Kuiseb river, how to make fire, how to ride a donkey cart, how to slaughter a goat, and how to build a traditional house.

What type of tourism activities would you want?	
Tourism activity	**Frequency (% of respondents)**
Donkey cart rides	12 (48%)
Walking trails	11 (44%)
Campsite/accommodation	4 (16%)
Stall/center to sell handicrafts	3 (12%)
Bicycle trails	2 (8%)
Horse riding	2 (8%)
!Nara demonstrations	1 (4%)
4x4 trails	1 (4%)

What about Topnaar culture would you want shared?	
Aspect of culture	**Frequency (% of respondents)**
Traditional dance	13 (52%)
!Nara harvesting and processing	9 (36%)
Traditional foods	5 (20%)
Singing	3 (12%)
Handicrafts	3 (12%)
Traditional attire	3 (12%)
Traditional medicine	2 (8%)
Other	9 (36%)

When asked what would need to happen to make these tourism initiatives possible, the most frequent response was cooperation and planning among the community, followed by education and training, road signs/advertisement, transportation, startup supplies/funding, a change in mindset and attitude, and better roads. For who should lead these tourism initiatives, nine people volunteered themselves or their family members, six people said the Topnaar Traditional Authority, four people said young people from the community, and three people said community members in general.

Twenty people said they would like Gobabeb to be involved in tourism projects and two people said they would not. When asked to identify ways that Gobabeb could help, responses included offering education and training, advertising and sending tourists from the Center to the community, providing funding, helping to implement the project and running it with the community, and helping with transportation. The two people who thought Gobabeb should not be involved said that Gobabeb has not followed through on their promises in the past and that Gobabeb would not be invested in the project for the long-term.

How would you like Gobabeb to be involved?	
Involvement	**Frequency (% of respondents)**
Training/education	8 (36%)
Advertising/sending tourists	5 (23%)
Funding	2 (9%)
Running the project with the community	2 (9%)
Transportation	1 (5%)

Only two people said they thought tourism would affect traditional culture. One of these specified that tourists driving around in the !nara fields would damage !nara plants. Nineteen people said that tourism would not affect their current sources of livelihood. Some of these respondents explained that tourism and their current sources of livelihood could complement each other, for example because !nara harvesting is seasonal, or because other livelihood activities could occur after normal business hours. Only two people said that tourism might affect their current livelihoods. Three people said that tourism would affect the traditional livelihoods that the Topnaar currently practice, and all three specified that tourism would increase the number of Topnaar interested in practicing traditional livelihoods. Two of those said that there would be an increase in !nara production and the third said that there would be an increase in production of traditional handicrafts. Eighteen people said there would be no effect on traditional livelihoods, with some specifying that tourism would only boost income but not interfere with their other livelihood sources.

We also wanted to test the influence of pensions on total number of livelihood sources and interest in tourism. However, we found no significant relationship between pensions and either of those results (chi square = 6.7, df = 4, p-value = .15; p-value = .22).

Discussion

We found that an overwhelming majority of respondents were interested in an expansion of tourism within the Topnaar community. Those who said that they were not interested in tourism clarified that they felt they would not personally benefit from tourism, and not that they were against any tourism initiatives in their community. Community members believe that there is potential for tourism to be a viable source of income. Respondents focused on the positive implications of tourism, i.e. increased income for them and their family. As Agrawal and Gibson discuss, common community interest is necessary for successful collective community action that can lead to larger scale development while remaining bottom-up. This mutual interest in tourism could promote successful collaboration between Topnaar individuals and settlements and, thus, foster the establishment of tourism practices with potential for a future tourism industry in the area.

Respondents were not concerned with potential negative implications of tourism. Most people felt that tourism would not affect their current sources of livelihood, the traditional livelihoods that the Topnaar currently practice, or Topnaar traditional culture. This is in contrast to the findings of a report by Nyakunu and Ndiovu which found fear of tourism interfering with current livelihood activities as a main barrier to the expansion of tourism. Perhaps this difference is because our study focused on tourism initiatives identified by community members themselves, whereas Nyakunu and Ndiovu's report proposed larger scale tourism projects. It is possible, however, that the Topnaar community is simply unaware of the potential negative impacts of regular tourism activities in their communities, having only experienced an infrequent and low volume of tourism thus far (Nyakunu & Ndiovu 2010). Consideration should be given to exploring potential consequences of tourism activities with community members during the development of tourism initiatives. This would allow community members to understand a range of implications of tourism, both positive and negative.

Everyone we interviewed suggested that tourism projects should be led by either community members or the Topnaar Traditional Authority. This suggests that Topnaar feel strongly that responsibility for tourism initiatives should be maintained by the Topnaar community rather than external actors. This aligns with Salazar's discussion of local level participation in tourism development. Solid community ownership and leadership could protect against a power imbalance between external tour operators and community members that Salazar warns of. However, the tensions that exist currently between the Topnaar Traditional Authority, community members, and tour operators will need to be overcome for any tourism activities to take place. Focusing on small-scale tourism activities acceptable to both community members and the Traditional Authority could build leadership capacity and social capital between particular community members and tour operators.

While the community was supportive of developing tourism, we found that livestock was the livelihood source for which the community was most interested in receiving outside help. This shows that successfully farming livestock is a top priority for many Topnaar. This is supported by the result that it was important to nearly all livestock owners to continue their family tradition of farming livestock, which could indicate that many Topnaar consider livestock farming to be an important part of their identity. This should be a consideration in the development of projects aiming to improve Topnaar livelihoods. Unlike most tourism activities, the Topnaar community already has the capacity to farm livestock, but there is perhaps potential to increase their productivity in this area. With livestock being such a high priority among Topnaar community members, it is interesting that there has not been more discussion of livestock development in the area. It is possible that the Ministry of Environment and Tourism is opposed to an increase in the number of livestock within the park where the Topnaar are located.

The livelihood source respondents most commonly chose as their most important source of livelihood was pensions. This aligns with Chief Kooitjie's impression that many Topnaar young people have migrated to urban areas, leaving predominantly children and the elderly in settlements. Our finding that households that collect pensions do not have significantly less diversified livelihoods than households without pensions suggests that households do not give up alternative livelihoods as members of the household become eligible for pensions. Households that received pensions were also not significantly less likely to be interested in an expansion of tourism. These results show that, despite the perception of Topnaar settlements comprising mostly children and the elderly, Topnaar community members are still able to maintain alternative livelihood sources and are interested in participating in new livelihood ventures.

The livelihood source that respondents most commonly chose as their least important livelihood source was !nara. However, !nara was the most common source of livelihood among our sample, respondents overwhelmingly perceived !nara to be the most important livelihood source among the entire Topnaar community. While our sample may have underrepresented households that are primarily reliant on !nara because many individuals may have been in the !nara fields harvesting during the time we conducted interviews, our results show that there is great variety in the extent to which Topnaar households depend on !nara as a source of livelihood. These findings show that, even though !nara is often an insignificant livelihood source, it is still a central part of Topnaar culture. This is confirmed by the community's interest in sharing !nara practices with tourists, the viability of which has been proven by successful examples !nara-based tourism activities.

We also found a significant difference in livelihood sources between upstream and downstream settlements. This could be a result of the geomorphological differences between the upstream and downstream regions discussed by Henschel et al. (2004). Communities situated further upstream, closer to the Khomas Highlands have historically been known for a more significant dependence on livestock because the greater forage availability. On the other hand, Topnaar villages situated closer to Walvis Bay in the lower Kuiseb River and Delta have been known for heavy reliance on !Nara fields. While we did not find any statistically significant difference in livelihood development priorities between the upstream and downstream regions, it is possible that we simply did not have a large enough sample to confirm any difference. Regardless, differences between upstream and downstream communities should be taken into account in the design of any livelihood development schemes for the Topnaar community, perhaps allowing for different priorities upstream and downstream and varying interest in tourism or types of tourism activities.

Conclusion and Recommendations

Based on Topnaar respondents' overwhelmingly positive interest in the development of tourism as an alternative source of livelihood, we propose that small scale tourism initiatives are viable in these communities. Currently, the limited training opportunities, resources and economic support, means that a large scale initiative would most likely lack a solid, community-based foundation. Without a strong, locally-focused foundation, a large scale tourism initiative would likely fall to external actors attempting. A reliance on external actors, as Cohen and Salazar argue, often leads to unanticipated cultural change and a lack of local community interest in industry development.

When asked about the cultural aspects they would share with tourists, respondents were interested in !nara related activities, traditional dance demonstrations, and well as the sale of handicrafts. Any development plan should prioritize the consideration of activities that the Topnaar themselves mentioned or are amenable to. Activities such as !nara processing demonstrations and cultural dance displays would not only allow tourists to experience and better understand Topnaar culture, but would also facilitate the development of a profitable, durable industry as a form of livelihood.

While the Topnaar we interviewed expressed a clear desire for the expansion of tourism as an alternative livelihood source, they strongly emphasized their desire for additional livestock management support. From this, we concluded that a livestock support project could bolster the productivity of livestock farming in addition to tourism expansion. The goal of such a project would be to allow for the collaboration of outside organizations with locals. Through this interaction we hope that external organizations will be able to provide local Topnaar with livestock related guidance they desire without taking on an authoritative role and thus perpetuating a history of externally driven initiatives within Topnaar settlements. Further research could reveal specific areas of livestock assistance that could most benefit the Topnaar people.

Finally, our theoretical foundation and data support the encouragement of community driven initiatives with local values and traditions at the core of industry development. If community interests are not considered or used as a development platform, locals will not be drawn to join the industry development effort consequently, tourism and other niches will not expand as viable alternative livelihood sources.

Recommendations for Further Research

- Survey urban Topnaar community members on livelihoods, tourism, and relationship with Topnaar settlements along the Kuiseb Riverbed
- Conduct a study on the geomorphological features differentiating upstream and downstream settlements and their effects on livelihoods
- Investigate types of livestock assistance desired by Topnaar community members
- Evaluate the effectiveness of the Fund for Local Cooperation in livelihood and tourism development among the Topnaar community

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Appendices

Appendix 1: Survey

Perceptions of Livelihoods among the Topnaar Community

<u>Demographics:</u>

1. Name (First, Last): ____________________
2. Age

Age	0-5	6-10	11-15	16-18	19-29	30-39	40-49	50-59	60-69	70+
Number										

3. Gender: Male Female
4. Highest Level of Education Completed: ____________________
5. Settlement: ____________________
6. Household Size: ____________________
7. Age composition of household

Age	0-5	6-10	11-15	16-18	19-29	30-39	40-49	50-59	60-69	70+
Number										

<u>Current Livelihoods:</u>

Livestock:

1. Do you own any livestock? Y N
2. Do you take care of any livestock that do not belong to you? Y N

   a. Who do they belong to? ____________________
   b. Chart:

Cows	Sheep	Goats	Donkeys	Horses	Other

   If other, what kind? ____________________

3. Why are your livestock important to you? ____________________
4. How long has your family owned livestock? ____________________
   a. Is it important to you to continue your family tradition of owning livestock? Y N
5. What do you use your livestock for? ____________________
   a. If sell, what do you use the money for? ____________________
   b. If saving, what do you save for? ____________________
6. If sell, where do you sell? ____________________
   a. If someone comes to village to buy, how often do they come? ____________________
      i. Do you wish they came more often? Y N
   b. Do you wish you could take your livestock to market? Y N

7. What are the constraints you face getting your livestock to market? ________________
8. Can you explain how you take care of your livestock ____________________________
9. Do you herd your livestock? Y N
10. Do you employ herders? Y N
11. Does a dog go out with them? Y N
12. Do you know where they eat? Y N
    a. If yes, where? ____
13. How far do they go from the kraal? ______________________________________
14. How often do they come home? ____
15. Do they go to surrounding settlements for water? Y N
    a. If yes, where? ____
16. How has the drought impacted you and your livestock? _________________________
    a. Have you changed how you take care of your livestock because of the drought?
        i. Have you tried to reduce the number of livestock you have? Y N
        ii. If yes, how do you reduce the number? __________________________
17. Have you noticed any change in the availability of forage over the last 5 years? Y N
    a. If yes, what changes? ____
18. What are the main reasons your livestock die? ________________________________
19. What are the main predators of your livestock? _______________________________
20. How is the behavior of your livestock different in dry season and rainy season? ________

Pensions:

1. Does anyone in your household receive a pension from the government? Y N
    a. If yes, what type of pension? ____
    b. How many grants does your household receive? ___________________________
    c. Is this your main source of income? Y N
    d. Do you have any other sources of income? ______________________________
    e. To what extent do pensions contribute to your livelihood?

       1 → Not a source of livelihood

       2 → Somewhat contributes to livelihood

       3 → Contributes to livelihood

       4 → Main source of livelihood

       5 → Only source of livelihood

Migrant Labor:

1. Do you have family members who live in urban areas? Y N
    a. How are they related to you?____
    b. Are they employed? Y N
        i. If yes, where are they employed? ______________________________

c. Do they support you financially? Y N
d. Is this your main source of income? Y N
e. Do you have any other sources of income? ________________________________
f. To what extent does this money contribute to your livelihood?

1 → Not a source of livelihood

2 → Somewhat contributes to livelihood

3 → Contributes to livelihood

4 → Main source of livelihood

5 → Only source of livelihood

Tourism:

1. Do you currently get any income from tourism related activities? Y N
   a. If yes, what type of tourism? ____
   b. Is this your main source of income? Y N
   c. Do you have any other sources of income? ________________________________
   d. To what extent does this money contribute to your livelihood?

      1 → Not a source of livelihood

      2 → Somewhat contributes to livelihood

      3 → Contributes to livelihood

      4 → Main source of livelihood

      5 → Only source of livelihood

!Nara:

1. Do you eat !nara? Y N
2. Do you harvest !nara? Y N
   a. If don't harvest yourself, how do you get it? _______________________________
3. Do you sell !nara or !nara products? Y N
   a. If yes, what kinds of products? ____
   b. Where do you sell these products? ______________________________________
   c. Is this your main source of income? Y N
   d. Do you have any other sources of income? ________________________________
4. Besides those already mentioned, do you use !nara for anything else? ________________

5. To what extent does !nara contribute to your livelihood?

    1 → Not a source of livelihood

    2 → Somewhat contributes to livelihood

    3 → Contributes to livelihood

    4 → Main source of livelihood

    5 → Only source of livelihood

Employment:

1. Is anyone in your household employed? Y N
    a. Who? ____
    b. Where are they employed? ______________________________
    c. How long have they had this job? __________________________
    d. Have they had other jobs before this one? Y N
        i. If yes, what jobs? ______________________________
2. To what extent does the income from this job contribute to your livelihood?

    1 → Not a source of livelihood

    2 → Somewhat contributes to livelihood

    3 → Contributes to livelihood

    4 → Main source of livelihood

    5 → Only source of livelihood

Other sources of livelihood:

1. Besides the ones previously mentioned (livestock, pensions, migrant labor, tourism, !nara), do you have any other sources of livelihood? Y N
    a. If yes, what? ____________________________________
    b. To what extent does this contribute to your livelihood?

        1 → Not a source of livelihood

        2 → Somewhat contributes to livelihood

        3 → Contributes to livelihood

        4 → Main source of livelihood

        5 → Only source of livelihood

Using these pictures, please rank the different aspects of your livelihood from the smallest part of your livelihood to the largest part of your livelihood:

Smallest ____Largest

If an outside organization were to help with one aspect of your livelihood, which aspect would you choose? This can include things you don't currently have. _______________________

a. Why this? ____

Community:

1. Who do you consider to be your community? ____________________________
2. What is the main source of livelihood among the Topnaar community? _____________

Tourism:

Entire community:

1. Are you interested in seeing tourism expanded in the Topnaar community? Y N
   a. Why? ____

2. To what extent do you think tourism has the potential to benefit the entire Topnaar community?

      1. Not at all
      2. Slightly
      3. Moderately
      4. Very much
      5. Extremely

   a. Explain your answer: ____
3. What are the main barriers to successful tourism in your community? ____________
4. What kind of tourism activities do you want in your community? ________________
5. What do you think would need to happen for these to begin? ___________________
   a. Who should lead these projects? _________________________________
   b. What outside help would you need? ______________________________
   c. Would you like Gobabeb to be involved? Y N Why? _______________

      i. If yes, how? ____

Individual interest:

1. Could you see yourself getting involved within the tourism industry in your community? Y N
   a. How would you want to be involved? ______________________________________

2. How do you think tourism in this community would benefit you and your family? ______
3. Do you think tourism could become your main source of livelihood? Y N
4. Do you think introducing tourism into your community would affect your current sources of livelihood? Y N
   a. If yes, how? ____
5. Do you think tourism would affect Topnaar traditional culture? Y N
   a. If yes, in what ways? ____

6. Not about tourism but just you personally, to what extent do you value preserving traditional culture?

   1. Not at all
   2. Slightly
   3. Moderately
   4. Very much
   5. Extremely

   a. Explain your answer: ____

7. Do you think tourism would affect how much you value preserving your culture? Y N
   a. Why? ____
8. Do you think tourism will make young people less likely to move to urban areas? Y N
   a. Why? ____
9. With tourism in the community, what do you think would happen to the traditional livelihoods that the Topnaar currently practice? ___________________________________

Portrayal of Culture:

1. What about Topnaar culture do you want to be shared with tourists? __________________
2. Are you interested in having a model village for tourists to learn about the Topnaar and your culture? Y N
   a. Why does this sound like a good idea or not? _______________________________

Effects of Temperature Variation and Vegetation Heterogeneity on Topnaar Livestock Selection of Resources and Space Use

November 11, 2016

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Introduction

Availability of food and thermal resources are critical in determining the survival of all organisms. Changes in the availability of these resources cause stress in individuals. Fluctuations in temperature, rainfall, and floods slowly alter vegetation communities, affecting resource distribution and thus animal movement and survival. In this report we explore the potential ways in which climate and vegetation variation impacts the condition of livestock. In order to adapt to projected climate change scenarios, livestock owners must understand how their local ecosystems will respond to unpredictable weather patterns and shifting vegetation compositions. This is especially critical in extremely hot, dry regions, where food resources are limited.

This study focuses on the livestock of the Topnaar people of the Kuiseb River catchment. The Topnaar are highly vulnerable to these changes--their livelihoods depend heavily on livestock and their home in the Namib Desert is classified as a hyper-desert, one of the hottest, driest ecosystems in the world (Desert Research Foundation of Namibia 2015). Hyperarid regions have at least 12 consecutive months without rainfall and lack a seasonal cycle of rainfall. They receive less than 25mm of rainfall. Arid regions receive between 25 and 200mm of rainfall (Laity 2009). The Topnaar have successfully farmed livestock in the Namib for over 800 years (Desert Research Foundation of Namibia 2015). In order to sustain this practice, they have requested information about the effects of climate on their environment and livestock. As of yet, no work has been done to examine the effect of temperature variation and resource distribution on movement and body condition of livestock in the Namib Desert.

Movement and spatial ecology

Movement ecology is a relatively new field which studies the movement of organisms by considering the internal state of organisms, their motion capacity, and their navigation capacities. It also includes external factors influencing movement (Nathan et al. 2008). Internal state refers to the physiological and psychological state of an individual and examines their possible goals for movement. Motion capacity concerns an individual's ability to move in various ways, while navigation capacity refers to the direction, position, invitation, and cessation of movement. Exploring the motivations of animals, such as livestock, to move and how they must expend its energy in order to optimize their resource use can shed light on important behavioral patterns and choices.

Dynamic optimization methods refer to the trade-offs individuals make between food gains and other resources and risks. Optimality assessments consist of cost/benefit analyses of an identified activity, the location of that activity, and benefits derived from that activity. These trade-offs may depend on the current body state of the individual and availability of resources. The primary influence on home range occupation patterns of large herbivores is the spatial-temporal availability of resources. Thus, there are a variety of patterns of behavior that can be derived from knowledge of resource availability across seasons: if resources are predictably found at different places depending on season, animals will have seasonally disparate home ranges. However, if resource availability is unpredictable, animals will appear nomadic (Mueller et al. 2011). If resources are scarce, they will travel further.

The way in which animals optimize their energy-resource trade-offs is further explored through optimal foraging theory, which considers how animals behave when they are searching for food. Foraging theory includes how animals choose where to search for food, when to feed, which types of food to consume, and when to stop feeding and move on. Decisions to move to another patch occur when the current patch contains less food and a farther one contains more, even when accounting for energy expenditure while traveling to the new patch (Charnov 1976). Herbivores usually feed at clusters, with browsers spending 65-80% of foraging time feeding and grazers spending 80-90% of foraging time feeding (Owen-Smith et al. 2010). Foraging usually happens at dawn-early morning and late afternoon-evening, while animals rest during the heat of midday and most of the night. Food is an important resource that drives livestock movement, and understanding the foraging habits of livestock is key behavior considering other resources they might seek within or without their home range.

An animal's home range is structured so as to ensure that an individual is able access all necessary resources as efficiently as possible. Home range selection is also influenced by individuals' previous knowledge as well as physical constraints (age, sex, breeding status, etc). Bartlam-Brooks et al.'s research on zebra movements in Zimbabwe indicates that home ranges contain lower density patches with less shade complexity in drier areas, compared to high densities and high shape complexity in wetter areas. Additionally, loss of seasonal ranges forced zebras to expand their home ranges. This leads to increased competition with other species for key resource, and results in population declines (Bartlam-Brooks et al. 2013). In this report we look further at the home ranges of livestock in the Namib Desert, looking at resource availability and movement in particular relation to temperature.

Ecology of thermal stress

Little is known about the specific temperatures at which livestock experience thermal stress, and how this relates to the desert-adapted cows and donkeys in the Kuiseb catchment. Dalcin et al. showed that dairy cattle in Brazil tend to experience moderate heat stress--at which point they struggle to regulate their body temperatures--above 28 degrees Celsius, and extreme heat stress above 30 degrees (Grotz et al. 2015). These temperature constraints may be applicable to Topnaar cattle, but additional parameters such as humidity, diet, and water availability must all be considered along with raw ambient temperature. The Namib Desert is drier than the area in Dalcin et al.'s study, and food resources are both scarcer and less nutritious, suggesting that Topnaar livestock might experience thermal stress at lower temperatures. It is known that, as temperature rises, livestock are less able to regulate their body temperatures to normal levels. Additionally, livestock lose more water through sweating and panting as temperature increases in order to regulate internal temperatures. Blood pressure also decreases due to vasodilation (the dilation of blood vessels due to thermal expansion). Together, these effects mean that food intake and digestion are less efficient at high temperatures (Thompson 2010).

This research examines how Topnaar livestock navigate a complicated landscape of forage resources (including seed pods and grasses) and thermal refugia (such as shade). The higher the ambient temperature, the more energy is required to forage and find food, and the less livestock gain from each bite of fodder. At the same time, digestion is less efficient at higher temperatures, with greater food mass required to maintain neutral condition on hot days. Current available habitat for free-range Topnaar livestock include the Kuiseb riverbed, which has seed pods and shade available. Additionally, the inter-dune areas of the Namib Desert, which periodically contains grasses during green flashes but has no shade trees. Use of these habitats will vary based on rains, seasons, and daily temperatures, and little is known about livestock preferences based on these parameters. Understanding these preferences is crucial in predicting the animals' responses rising temperatures, and in making recommendations for Topnaar communities adapting to climate change.

How theories may be influenced by climate change

A major challenge associated with climate change is the variability of its effects across space and time, and the associated unpredictability of climatic events. Some parts of the world will see decreased temperatures and higher rainfall, while others will experience the opposite extremes. In general, climates will trend toward higher extremes and greater unpredictability. Higher rainfalls would initially increase foliage levels, providing more fodder for livestock. However, an over-abundance of flood events and heavy rains can lead to waterlogging, nitrogen leaching, fungal infections, and the drowning of flood-intolerant plant species (Mendelsohn 2006). By the same token, higher temperatures and drier weather can lead to increased dry matter production in the short term, which would benefit desert-adapted livestock accustomed to consuming dry seed pods. However, in the long term, higher temperatures will increase thermal stress on livestock and favor vectors like mosquitoes, midges, flies, and ticks. Pathogens like anthrax and Foot and Mouth disease have also been shown to develop faster at higher temperatures (Thornton 2009).

A major challenge associated with climate change is the variability of its effects across space and time, and the associated unpredictability of climatic events. Some parts of the world are projected to experience decreased temperatures and higher rainfall, while others will experience the opposite extremes. In general, it is believed that climates will trend toward higher extremes and greater unpredictability. Higher rainfalls would initially increase foliage levels, providing more fodder for livestock. However, an over-abundance of flood events and heavy rains can lead to waterlogging, nitrogen leaching, fungal infections, and the drowning of flood-intolerant plant species (Mendelsohn 2006). By the same token, higher temperatures and drier weather can lead to increased dry matter production in the short term, which would benefit desert-adapted livestock accustomed to consuming dry seed pods. However, in the long term, higher temperatures will increase thermal stress on livestock and favor vectors like mosquitoes, midges, flies, and ticks. Pathogens like anthrax and Foot and Mouth disease have also been shown to develop faster at higher temperatures (Thornton 2009).

Most relevant to this study, vegetation communities will shift with changes in temperature, rainfall, and atmospheric carbon levels. Globally, atmospheric carbon dioxide has passed the threshold of 400 parts per million--scientists have repeatedly warned that atmospheric carbon levels over 350 parts per million will cause irreparable damage to the Earth's most vulnerable ecosystems, including the Arctic and arid regions in Sub-Saharan Africa (Hoffert et al. 2002). For example, woody plants with quick growth responses to atmospheric carbon dioxide are flourishing under current conditions, causing vegetation communities will lose the resilience that comes with high herbaceous biodiversity (Polley 1997). The International Panel on Climate Change (IPCC) has predicted that an increase in global mean temperatures of just 2.5 degrees

Celsius will cause Southern Africa to lose 41-51% of its endemic plant species. Rising temperatures have already threatened to drive 20-30% of these species to extinction. These endemics are slowly being outcompeted by alien species, and higher temperatures favor legumes over grasses (Thornton 2009). These changes impact livestock diets through the availability of nutrients. If vegetation shifts faster than livestock can adjust, animals will experience increased food stress and malnutrition.

Finally, rising temperatures may restrict seasonal migrations through which livestock distribute their resource use, dunging, and urination throughout the landscape. These migrations are dictated by resource availability and they naturally spread the symbiotic processes of grazing over a large area. Grasses and fodder plants rely on livestock just as much as the animals need the plants, so a disruption in livestock migration can damage vegetation through under-utilization, and thus less fodder is available for the animals (Savory 2008). As temperatures rise, travel becomes more energy-intensive, and thus optimal grazing patterns may encourage animals to opt for lower quality vegetation closer to their home range rather than higher quality farther away. This would ultimately lead to a stressed food supply due to overuse and degradation of their home range.

Relation of movement ecology and climate change to livestock in the Lower Kuiseb

For the past 11,000 years, agriculture has shaped environmental and social systems in Namibia (Mendelsohn 2006). Agricultural systems range from highly resilient combinations of livestock and grain farming, to intensive plant-based agriculture, to free-range livestock ranching (Mendelsohn 2006). Livestock, especially cattle, goats, and donkeys, represent the main agricultural focus for 70% of the country, and they account for 89% of agriculture's contribution to its GDP (Desert Research Foundation of Namibia 2015). Communities relying mainly on livestock are less resilient to climate change as they have low diversity of resources to utilize if any one resource is no longer feasible. This is especially in dry areas where raising crops is not viable. This is particularly true for resettled, previously disadvantaged ranchers; Since Namibian independence in 1990, a gradual process of land reform has endeavored to return valuable arable land to black farmers who were disenfranchised during the apartheid regime. The reforms are critical for addressing socio-economic inequality in the country, but many previously disadvantaged farmers and ranchers do not have the knowledge or experience to adapt land management to the complex and unpredictable challenges of climate change. Researchers at Gobabeb Research and Training Centre relayed that the local Topnaar communities with free-range livestock often do not see their animals for weeks at a time. Due to this limited supervision, the livestock owners have expressed interest in gathering knowledge of what factors drive livestock movements and feeding patterns. These gaps in knowledge represent significant threats to the livelihoods of farmers and ranchers who depend on the wellbeing of their animals. Thus there is a significant need throughout the country to discover and disseminate information about the preferences and needs of livestock, and how climate change will impact those needs.

Climate change in the Kuiseb River catchment

The Namib Desert and Kuiseb catchment are projected to get hotter and drier as atmospheric carbon levels continue to increase (Midgley et al. 2005). The region has recorded a decadal temperature increase of 0.2 degrees Celsius over the past 60 years (Midgley et al. 2005). Mean temperatures in the summer and winter months are expected to rise, resulting in climate-sensitive tree species such as *Acacia erioloba* and *Faidherbia albida* experiencing increased difficulty establishing new seedlings. Thus, total leaf cover area is projected to fall, with less canopy to shade life on the ground (Midgley et al. 2005).

All long-term weather stations in Namibia have showed a steady decline in water balance (a composite metric of temperature, humidity, and rainfall which indicates the water available to plants). It is projected that the Benguela current will continue to make the landscape more arid, evaporation rates will rise linearly with temperature, and flooding events are predicted become more irregular and intense on the Kuiseb (Midgley et al. 2005). Together these effects decrease water supply for vegetation along the Kuiseb riverbed (Midgley et al. 2005).

Rainfall events will also likely become more extreme, with a projected 30% increase in year-to-year variability. Thus, it is possible that the Kuiseb catchment will see fewer, but more intense, rain events (Hulme et al. 2001). This change in rainfall and rainfall intensity causes a wide variety of environmental impacts, such as higher vulnerability to erosion, lower water tables, and fewer green flashes of inter-dune grass growth. All these effects spell uncertainty for Topnaar livestock management.

Hypotheses

In this study, we ask: *How does spatiotemporal vegetation heterogeneity and thermal stress impact livestock food and thermal resource selection and choices?* We examined the space use of Topnaar cattle and donkeys, both daily and seasonally. While there are additional livestock species in the Topnaar communities, only cattle and donkeys were observed in order to simplify data analysis. Additionally, goats are usually kept near settlements and are guarded by dogs, while horses are in relatively low abundance and of little importance to the subsistence of the Topnaar people. Given that donkeys and cattle have free range with relatively few limiting factors aside from watering holes and that they are economically very important to the Topnaar people, we felt that exploring their movement patterns would be the most worthwhile to pursue.

In the landscape surrounding the Homeb community, we were interested in what characteristics of the livestock habitat make it preferable to other areas, and how variable temperature might change those preferences.

We hypothesize that:

1. With increasing temperatures, the total distance traveled by livestock per hour decreases, to decrease energy expenditure and thermal stress.
2. With increasing temperatures within a day, the intensity of the activities performed by livestock decreases, since they try to reduce energy expenditure and thermal stress.
3. Individuals will tend to cluster in habitats with food resources dominated by *Faidherbia albida* and *Acacia erioloba* pods.
4. However, as temperature increases due to seasonal changes, individuals will utilize areas with relatively more shade resources.

5. As temperature increases due to seasonal changes, the total displacement within this period increases, as livestock cover a larger area to utilize more sparse vegetation.
    a. Alternatively, as temperatures increase due to seasonal change, the total displacement and dispersion of livestock might reduce, as they are limited to areas close to water holes needed to reduce increasing thermal stress.

Methods

Field methods

Vegetation mapping: Sampling spatial heterogeneity in transects (SSHIT) method

In order to assess vegetation distribution and livestock utilization along the Kuiseb River, we employed the SSHIT method, established during Dartmouth's research in 2015. We divided approximately 20km of the lower Kuiseb riverbed into sections, conducting vegetation and livestock dung transects at 2 km intervals to analyze resource distribution, livestock use, and cattle migration (Grotz et al. 2015). Starting at 0km, we traveled 10km from camp both upstream and downstream (Figure 1). At each of the 11 points, two transects were studied on either side of the river, in order to account for potential variations in the vegetation community and livestock use in relation to distance from the primary river channel. Data were collected from a 50x2m transect of the riverbed behind the first tree line (A) and at a parallel 50x2m transect located 20m further inland from the center of the river (B) (Figure 2). Thus, for each cross-section of the river, four transects were studied. The locations of each transect were recorded with GPS (Appendix A).

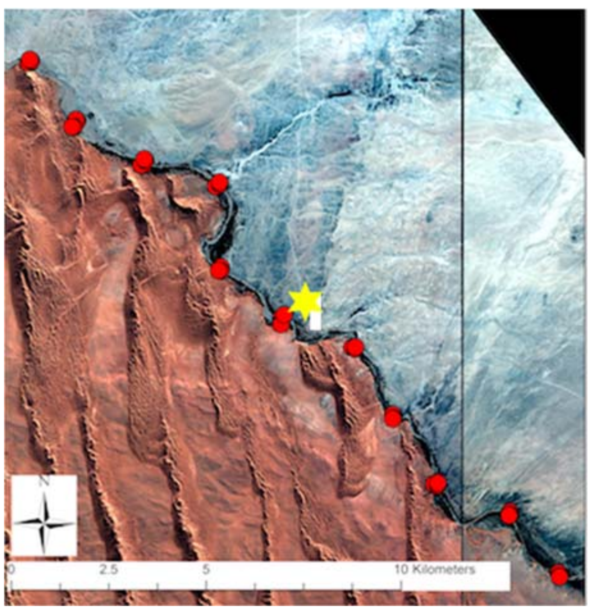


Figure 1. Map indicating point where transects were measured along lower Kuiseb River. Red points indicate where we conducted SSHITs to map the Kuiseb River vegetation. The yellow star represents the Gobabeb Research Center and demarcates our starting (0km) point.

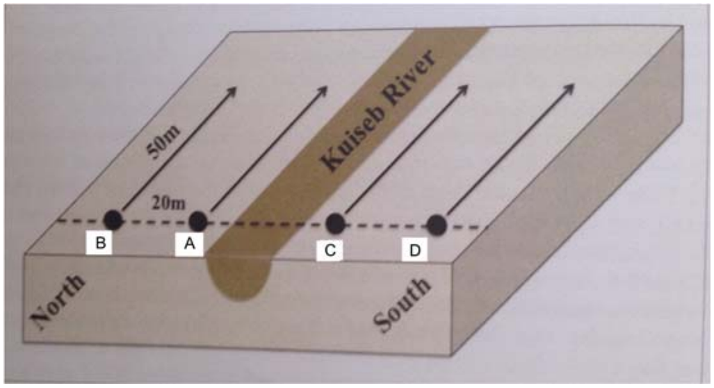


Figure 2. A diagram showing transect labeling and position relative to the Kuiseb River (Grotz et al. 2015). A and C were placed at the first tree line, and B and D were measured 20 meters further inland.

Throughout each 50x2 meter transect, we collected data on cattle and donkey dung, canopy coverage, vegetation cover, and seed pod numbers distributions. Cattle and donkey dung deposits were estimated based on quantities of dung in a defecation event, rather than individual pieces. We also counted *A. erioloba* and *F. albida* seed pods. We targeted these types of pods as they have been identified as a primary food source of livestock (Grotz et al. 2015). Additionally, at 5m and 45m along the transect we identified and measured vegetation within a 5m radius. We took the circumference of tree trunks when applicable and the area of grasses and shrubs. To assess canopy coverage and ground vegetation, we utilized a cardboard of 47x28cm with 15 holes (radius of 2.5cm). There were 3 rows of 5 holes, with 10cm separating the center of adjacent holes. Every 10 meters of our transect, we placed this cardboard on the ground and counted how many holes contained leaf litter. We used the same method to count how many holes had visible canopy coverage, holding the cardboard over our heads. We also measured the air temperature at every 10-meter point.

When our path was blocked by dense bushes (i.e. *Salvadora persica*), we estimated leaf litter, canopy coverage, and temperature from the closest point parallel to our transect. We were able to look through the bushes to estimate dung and seed pod counts and identify vegetation. Thus, these cross-sections of the river showed the spatial distribution of vegetation and utilization.

Livestock observations

We performed focal follow behavioral observations on individuals to gather data on the sequence of livestock behavior and to gain insight into how livestock respond to temperature changes, with the ultimate hopes of drawing parallels between patterns observed on the ground and those from the collar data. Following a single animal allows the observer to focus on an individual despite group formation and separation. Focal follows occurred with observers at a distance that did not appear to disturb observed individuals. We chose to observe individual animals on an ad libitum basis. It is important to note the inherent bias in this method, as ad libitum sampling only counts conspicuous animals (Altman 1973). Our focal follows involved either following the activities of one individual for one hour, and recording information at 10 minute intervals, or alternatively observing an individual for a half hour, and recording information at 5-minute intervals.

To gather data on animal behavior, particularly with regard to how the intensity of the activities performed by livestock varies at different temperatures, we used instantaneous, or scan, sampling methods. In instantaneous sampling, the total group size is recorded and quick notes are taken on the entire herd (Altmann 1974). The observer does not follow the herd or an individual. The behaviors noted ought to be easily recognizable in order to make the sampling quick. Our instantaneous scans involved observing the activities and condition of individuals and recording the surface temperature of each animal using a handheld thermal sensor.

Recorded information during instantaneous sampling included surface temperatures of individual, whether they were in shaded or sunny areas, their exhibited behavior (standing, lying down, etc.), whether they were moving or stationary, body condition (using the method identified in Grotz et al. 2015), the air temperature, and the location of the individual. During focal follows, all of the same information was recorded aside from surface temperature. Surface temperatures of the individuals were recorded solely the end of the observation period of a focal follow, so that there would be minimal change in the animal’s behavior and that data would not be compromised.

We created an ethogram (Table 1) to describe the activities that livestock were engaged in and rate the relative intensity associated with each activity, following the methods described in Dobman et al. (2008). The higher the score, the higher is the intensity of that activity. These scores are helpful to synthesize the animal observation data we collected in the field to simplify statistical analysis while investigating the influence of body and air temperature on the intensity of livestock activity, thus trying to quantify the impact of thermal stress.

Score	Activity
1	Lying down
2	Lying down and ruminating
3	Drinking water
4	Standing
5	Standing and ruminating
6	Foraging
7	Walking

Table 1. An ethogram rating the relative intensity of livestock activities. We ranked activities according to intensity, to simplify synthesis of data.

Instantaneously scanned individuals were not used for focal follows, as recording the animal’s surface temperature required close proximity to the animal and thus generally disturbed the animals’ natural trajectory of behavior.

Spatial analysis methods

Telemetry data

Selected livestock along the lower Kuiseb region were outfitted with global positioning system (GPS) collars to monitor movement behaviors as part of a pilot project on livestock space use. Initially, six collars were deployed on several livestock species including cattle (2 collars), goats (2 collars) and donkeys (2 collars). All cattle were initially collared in close proximity to Homeb, donkeys were collared near Tsaobabis and goats were collared near Natab. Collars were supplied by African Wildlife Tracking (AWT) and are reported to have an estimated spatial precision of 10 meters. Initially, collars were programmed to record coordinate fixes at hour or two hourly intervals, but have since been reprogrammed in mid-April, 2016 to record coordinate fixes at 10 minute intervals. Location data are stored onboard the collar unit and are downloaded in the field via a UHF transceiver for subsequent analyses. The authors of this paper were not involved in the initial design or implementation of the collaring or data collection protocol. To limit the effect of irregular sampling regimes and to minimize the effects of temporal gaps in data, this study was limited to telemetry data that were collected between May 1, 2016 and October 15, 2016. Collar analyses were limited to cattle and the one continuously monitored donkey.

Collar data transect mapping and utilization distributions

We chose to look at the utilization distribution of collared individuals in three time periods: hot/dry, cool/dry, and cool/post-rain. We chose these periods based on the seasonal variations present in the area. The specific dates chosen for CD and HD are considered to be at the height of each season, while the dates for CDR were chosen based on the rainfall events occurring in 2016. For both of these seasons, we identified locations of high use and no use.

To examine seasonal variation in habitat use, we first generated seasonal utilization distributions for 2 GPS-collared cattle in the Homeb area (describe location). The Namib deserts sees two main season through the year, with both the hot dry season, characterized by high temperature We then temporally partitioned collar data to reflect seasonal transitions between cool dry periods and hot dry periods. We additionally examined a period immediately following an abnormally-timed rain event.

Transects were taken in areas that were considered high-use during three periods of the year. The cool dry season with rain dates (CDR) (data from June 9, 2016-July 9 2016) had high use areas that overlapped with no-use areas from the hot dry (HD) season (data from September 1, 2016 - October 15, 2016). The high use data from HD season also overlapped with the no-use area for the CDR season. These locations were in the Kuiseb riverbed, thus necessitating transects that paralleled the bank. In many locations, there was no ability to map transects located transect perpendicular to the bank, so this method was not used. Cool dry (July 15-August 14).

Because of gaps in the collar dataset, efforts were made to control for overall sample size while maintaining relatively uniform temporal extent of seasons. Using coordinate fixes from these seasons, we calculated seasonal utilization distributions using kernel density estimates (KDEs) with reference bandwidth for R statistical package with AdehabitatHR extension (Calenge 2006). KDEs are a method of outlining landscapes to produce utilization distribution, creating a value representing an animal's relative spatial usage (Worton 1989).

We defined seasonal high use areas as the 40% KDE isopleth. Polygons representing these seasonal high use contours were projected and visually inspected for areas of overlap (Figure 3). In all instances the corresponding seasonal utilization for both cattle demonstrated area of overlap. We then randomly selected a GPS collar coordinate fix from the area of overlap for the two cattle to serve as the location for vegetation transects.

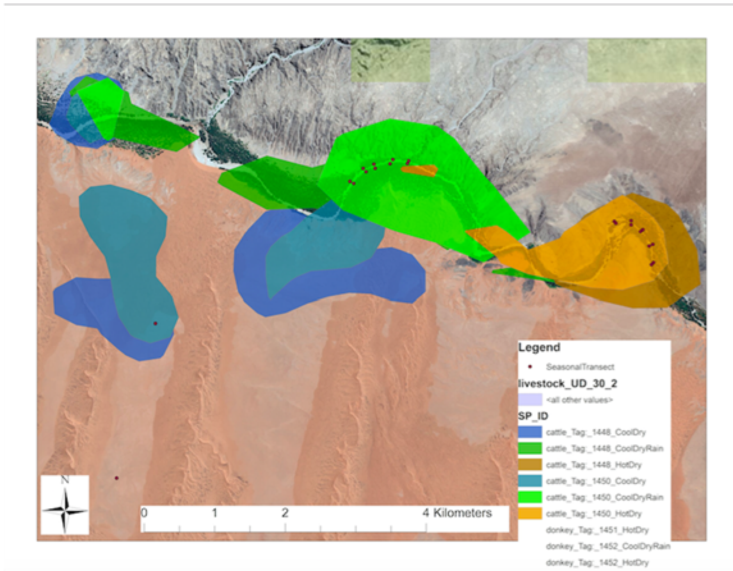


Figure 3. The polygons represent the seasonal utilization distribution for the cattle. Blues represent high KDEs in the cool dry period, greens represent the cool dry post-rain period, and tans represent the hot dry season. The points show where we measured transects.

In these high use overlap areas, 10 transects were taken at each seasonal site. Two transects were taken every 200 meters, with one on the north bank and a parallel transect on the south bank. GPS points were taken at the beginning and end points of each transect for future reference (Appendix 1). Transect were measured out with 50 steps, stopping every 10 steps to measure percent of canopy cover and leaf litter on the ground. At each interval, we recorded plant species comprising canopy cover and the species that was the “nearest neighbor” to that location. Topography of the area (slope, soil classification and compactness), and presence of shade cover were also noted. The number of cow and donkey dung, as well as the number of *F. albida* and *A. erioloba* pods were counted in a two-meter wide area along the transect.

We also conducted modified transects at the high-use and no-use areas for the cool dry season with no rain (CD). These areas were located in a valley, allowing for four transects radiating from a center point. The first degree was chosen randomly, and each of the other three transects were taken by adding 90 degrees to the last number. Each transect was 500 meters in length. The counts of soil classification and vegetation count were taken by recording what was present along the transect every five steps to give a picture of the overall proportion of each plant species, and their relative density in the landscape.

To evaluate the effect of temperature on movement behaviors, we used the telemetry data to calculate the step length between all consecutive coordinate fixes for each individual. We then calculated the cumulative distance travelled during each hour for each individual as the sum of all step lengths that occurred within each hour. Using average hourly temperature data collected at Gobabeb Research Centre, we associated each cumulative hourly distance travelled with a corresponding temperature. We aggregated the data on the basis of species (cow and donkey), and tested for a significant effect of temperature on cumulative hourly distance travelled using a Poisson regression to account for non-normal distribution of the response variable.

Enhanced vegetation index:

Through the telemetry data, we are able to get a spatiotemporal view of livestock movement and sites they choose throughout a period of time. However, our river transects through the SSHIT method only look at the present characteristics and availability of vegetation resources. This only gives us a narrow window, which makes it difficult for us to compare cattle movement since April 2016 with vegetation distribution on Hence, we used

The Enhanced Vegetation Index (EVI) is a vegetation index optimized to remotely capture vegetation signals while removing the effects of canopy background, in this case, soil/sand (Huete et al 2002). EVI is sensitive to variation in leaf area index, canopy architecture, and is widely used to quantify plant phenological dynamics (Huete et al. 2002).

EVI time-series from NASA's MOD13Q1 product (16 day peak value composite) were obtained using the Google Earth Engine API spanning dates from 01 Jan 2016 to 30 Oct 2016. EVI was captured at 250m resolution pixels that correspond to the centroids of the high and no use interdune areas.

Statistical analyses methods

The data collected from our field methods of transects and animal behavior observations were analyzed statistically to identify how factors like vegetation density and heterogeneity, food resources, temperature and shade resources impacted livestock activity, presence in and use of certain habitats and vegetation areas. These relationships were statistically generated through appropriate regression models and tests described below.

Chi-squared tests

Chi-squared tests are tests of "independence and homogeneity of variance" between different sets of data (Christie et al. 2012). It is often used to test the null hypothesis that two or more different distributions of data are not different. In our study, we use the chi-squared test to test whether the vegetation, food and thermal resource distribution between high and low cattle use areas during particular seasons is significantly different, thus trying to pinpoint what sort of resources that exist in a particular area could be driving a difference in cattle usage, as shown by the collar data.

Logistic regressions

Logistic regressions are used to look at how the specified continuous predictor variables influence categorical response variables (yes/no, present/absent, etc.). The result is interpreted as a probability: with unit change in the predictor variable, the probability of the response variable changes by a certain amount predicted by the model. A lot of our data and the variables we are interested in are categorical variables, such as animal presence, whether or not something is a high cattle use area, etc. The regressions were performed using JMP 12.

Zero inflated Poisson model:
Due to an excess of zeros in count data for animal number and cattle dung, zero inflated Poisson generalized regression, its adaptive static net estimation, and AICc model validation was performed with JMP Pro 10.4.1 for analyses with these responses variables (Zuur 2009).

Results

Vegetation mapping

River transects
Our river transects revealed statistically significant relationships with *F. albida* pods, *A. erioloba* pods, leaf litter, and canopy cover as predictors on livestock presence. Higher concentrations of pods and leaf litter made us more likely to see animals in the area (Figure 4), and we used canopy cover and dung as proxies for the amount of shade in the transect and animal use, respectively.

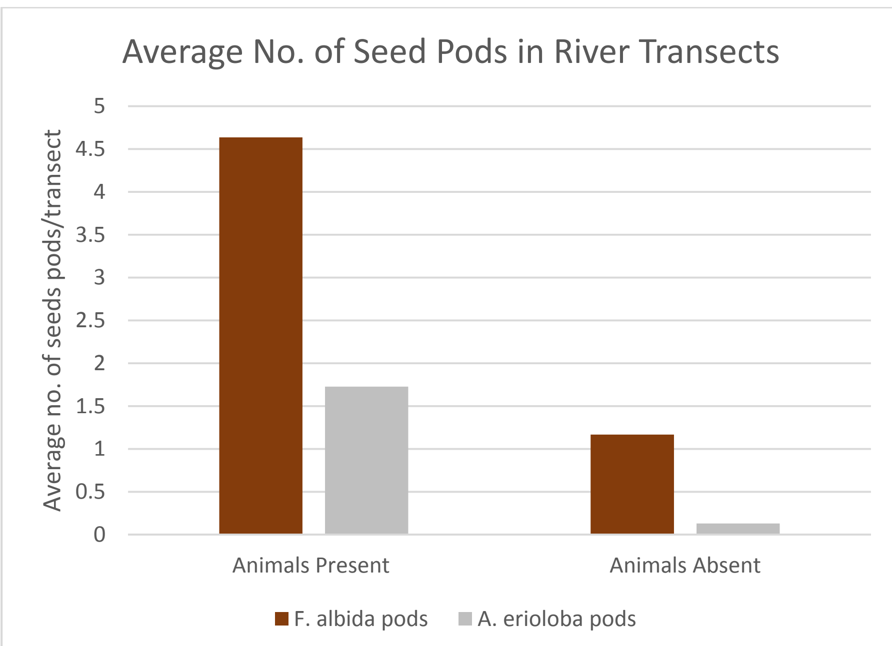


Figure 4: Comparison of the average number of *F. albida* and *A. erioloba* seed pods in transects with and without animals. We observed a higher average number of seed pods in transects where animals were present, compared to transects where animals were not present.

Predictor	Effect	Response	Sample Size	Chi Squared	p value
F. albida pods on ground	Strong Positive	Number of animals on transect	74	5.79	0.0161
A.erioloba pods on ground	Weak Positive	Number of animals on transect	74	3.61	0.1070
Cumulative leaf litter across transect	Strong Positive	Number of animals on transect	74	4.07	0.0492
Cumulative canopy cover across transect	Strong Positive	Total donkey and cow dung	74	5.57	0.0183
Average canopy cover in transect	Strong Positive	Total donkey and cow dung	74	4.76	0.0291

Table 2. Results of Zero-Inflated Poisson tests on the effects of environmental variables on habitat use in river transects. Dung counts, seed pods, and number of animals seen were all highly zero-inflated and rough Poisson distributed, necessitating a zero-inflated Poisson regression. We used linear fits to determine whether the relationship was positive or negative.

Seasonal high- and low-use transects

We found through GPS telemetry that high-use areas in the hot dry season overlapped as a no-use area during the cool, dry season. The opposite was true as well, with the high-use areas in the cool dry season being no-use areas on the hot dry season.

Vegetation composition (seasons). We tested the relationship between composition of plant species and high and low-use areas of the cool dry period. Our null hypothesis was that there was no relationship between plant species composition and utilization levels. We calculated observed and expected values for different plants in these locations (Table 3, Table 4).

Observed	Sand	Stip. annual	tip. perennial	Glauca	Seelyae	Kohautia	Dune Grass	Total
High	410.4	133.4	19.2	60.7	23.7	2	2.7	652.1
Low	441	150	20	18	4	0	0	633
Total	851.4	283.4	39.2	78.7	27.7	2	2.7	1285.1

Table 3. Observed density and composition of plant species in high-use and low-use areas during cool dry period.

Expected	Sand	Stip. annual	Stip. perennial	Glauca	Seelyae	Kohautia	Dune Grass
High	432.03	143.81	19.89	39.93	14.06	1.01	1.37
Low	419.37	139.59	19.31	38.77	13.64	0.99	1.33

Table 4. Expected density and composition of plant species in high-use and low-use areas during cool dry period.

We used a chi-square test over these 1285 observations and found a chi square value of 43.69 and a p value less than 0.0001. Thus, we rejected our null hypothesis that there is no difference between plant species composition at high-use and low-use sites within the cool dry season.

Leaf litter. *W*e tested whether there was a significant difference in leaf litter type on the high use and no-use areas during the cool dry rainy period and hot dry periods. Our null hypothesis was that there was no difference in leaf litter composition in these two utilization areas. We calculated observed and expected values for a variety of plant types in both types of utilization areas (Table 5, Table 6).

Observed	leaf_faid	leaf_acacia	eaf_euclea	eaf_tamarix	eaf_mustard	eaf_tobacco	Total
CDR	494.5	202.5	194	219.5	435.5	429	1975
HD	473	0	12	0	0	0	485
Total	967.5	202.5	206	219.5	435.5	429	2460

Table 5. Observed area of leaf litter in high use and no-use areas during the cool dry rainy period and hot dry periods. Units are the cumulative number of cardboard holes covered by each type of leaf.

Expected	leaf_faid	leaf_acacia	leaf_euclea	leaf_tamarix	leaf_mustard	leaf_tobacco
CDR	776.75	162.58	165.39	176.22	349.64	344.42
HD	190.75	39.92	40.61	43.28	85.86	84.58

Table 6. Expected area of leaf litter in high use and no-use areas during the cool dry rainy period and hot dry periods.

A chi square test performed on these 2460 leaf litter observations revealed a chi square value of 861.26 and a p value less than 0.0001. Thus, we were able to reject the null hypothesis that there is no difference in the leaf litter across cool dry seasonal high use areas and hot dry seasonal high use areas.

Canopy coverage. Similarly, we tested whether there was a significant difference in the composition of canopy coverage in the high use and no-use areas during the cool dry rainy period and hot dry periods. Our null hypothesis was that there was no difference in canopy coverage composition in these two utilization areas. We calculated observed and expected values for canopy coverage types in both types of utilization areas (Table 7, Table 8).

Observed	Canopy cum faidherbia	Canopy cum acacia	Canopy cum euclea	Canopy cum tamarix	Canopy cum mustard	Canopy cum nicotina	Total
CDR	276	97.5	8.5	49.5	86	44.5	562
HD	2414	0	15	0	0	0	2429
Total	2690	97.5	23.5	49.5	86	44.5	2991

Table 7. Observed species making up canopy cover in high use and no-use areas during the cool dry rainy period and hot dry periods. The units are the number of cardboard holes covered relatively by different plants.

Expected	Canopy cum. faidherbia	Canopy cum. acacia	Canopy cum. euclea	Canopy cum. tamarix	Canopy cum. mustard	Canopy cum. nicotina
CDR	505.44	18.32	4.42	9.30	16.16	8.36
HD	2184.56	79.18	19.08	40.20	69.84	36.14

Table 8. Expected species making up canopy cover in high use and no-use areas during the cool dry rainy period and hot dry periods.

Our chi-square test on these 2991 observations of canopy cover returned a chi square value of 1332 and a p value less than 0.0001. Thus, we were able to reject the null hypothesis that there is no difference in thermal resources as quantified by canopy cover across cool dry seasonal high use areas and hot dry seasonal high use areas.

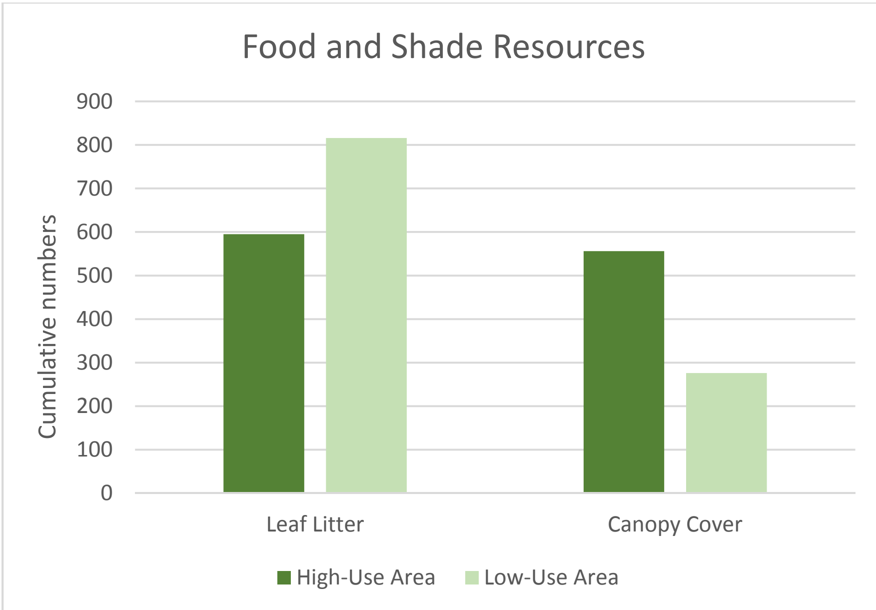


Fig 5: Comparison of food and shade resources in the high-use and low-use area during the hot dry season.

Seed pod coverage. Finally, we tested whether there was a significant difference in the present seed types in the high use and no-use areas during the cool dry rainy period and hot dry periods. Our null hypothesis was that there was no difference in the numbers of types of seed pods in these two utilization areas. We calculated observed and expected values for seed pods in both types of utilization areas (Table 9, Table 10).

Observed	f_pods	a_pods	Total
CDR	101	26	127
HD	4148	2	4150
Total	4249	28	4277

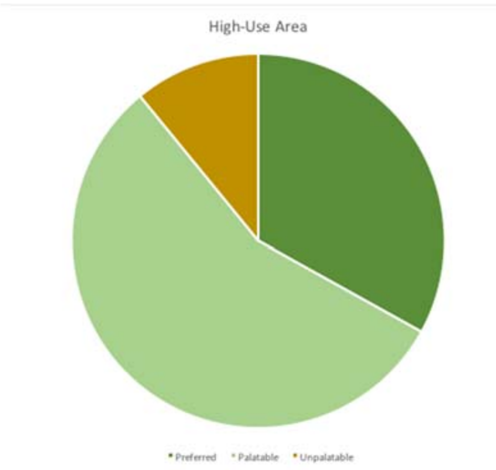
Table 9. Observed counts of *A. erioloba* and *F. albida* pods in high use and no-use areas during the cool dry rainy period and hot dry periods.

Expected	f_pods	a_pods
CDR (low use 11/2016)	126.17	0.83
HD (high use 11/2016)	4122.83	27.17

Table 10. Expected count of *A. erioloba* and *F. albida* pods in high-use and no-use areas during cool dry rainy periods and hot dry periods.

The chi square test on seed pods used a sample size of 4277 and returned a chi square value of 790.38 and a p value less than 0.0001. We were able to reject our null hypothesis that there is no relationship between intensity of usage and seed pod distribution.

Palatability in seasonal transects. The food in the high-use area of the cool dry season was found to contain more highly palatable, preferred food, such as *Centropodia glauca*, along with more unpalatable food (Figure 6).



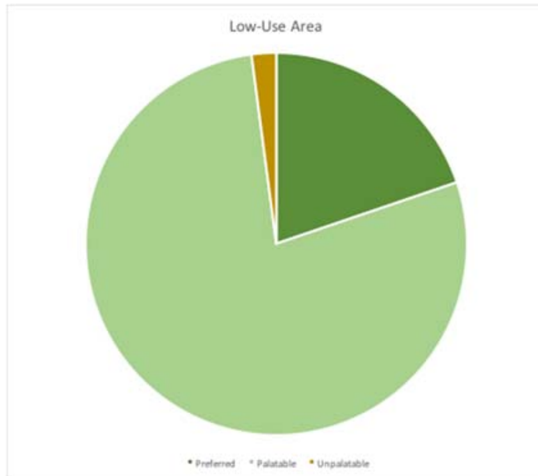


Figure 6. Pie Chart showing relative abundance of palatable, preferred and unpalatable plants. These charts compare palatability of food in the high and low use areas.

Predictor	Relationship	Response	Sample Size	Chi Squared	p value
Proportion of vegetation consisting of faidherbia	Very Strong positive	Being a high use area during the hot dry season	20	14.35	0.0002
Proportion of vegetation consisting of acacia	Very Strong positive	Being a high use area during the hot dry season	20	10.97	0.0009
Cumulative leaf litter	Strong positive	Being a high use area during the hot dry season	20	7.59	0.0059
Cumulative acacia leaf litter	Very Strong positive	Being a high use area during the hot dry season	20	10.97	0.0009
Cumulative canopy provided by Faidherbia	Very Strong positive	Being a high use area during the hot dry season	20	10.98	0.0009
No. of Faidherbia Pods	Very Strong positive	Being a high use area during the hot dry season	20	12.19	0.0005
No. of Acacia pods	Strong positive	Being a high use area during the hot dry season	20	4.29	0.0384
Total cow dung	Weak Positive	Being a high use area during the hot dry season	20	2.89	0.0899

Table 11. Table of Results from zero-inflated Poisson tests. This shows all examined the predictors against the levels of habitat use, either high or low, in the hot dry season. The 20 samples represent our seasonal transects in the hot dry use and non-use areas.

Direct livestock observations

We found several statistically significant relationships using air temperature and animal surface temperature as predictors for different behaviors. In general, animals were more likely to engage in less intense behaviors as temperatures rose, preferring to lie down or ruminate rather than forage or walk about in high temperatures. In addition, animals were more likely to seek shade in higher temperatures, and this tendency was statistically significant.

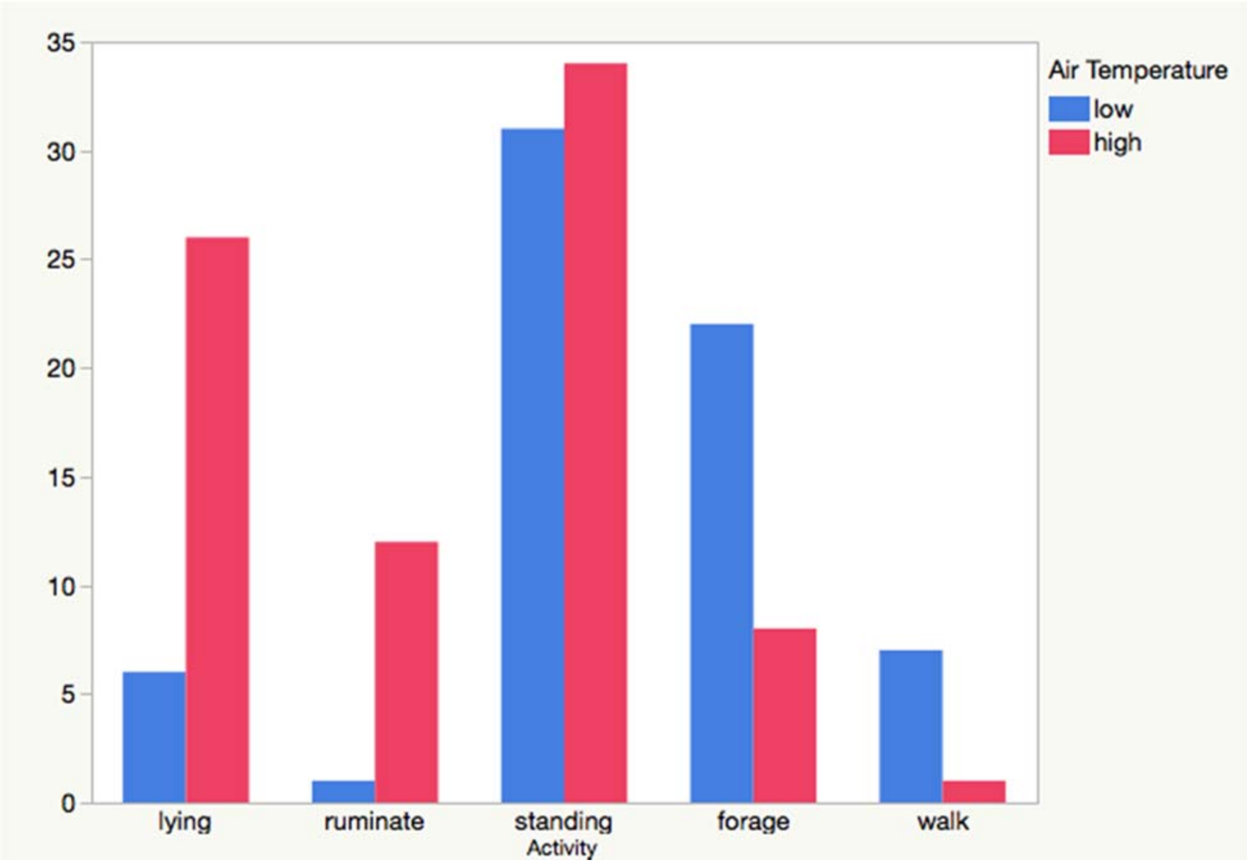


Figure 7. Relative of observations of behavior of livestock individuals at high and low air temperatures. Description: Low temperatures ranged from 22.0-31.7, below the median of temperature recordings. High temperatures ranged from 31.7-41.1, above the median. Observations came from both instantaneous and focal follow samples. The number of instances of each behavior observed is recorded on the y-axis.

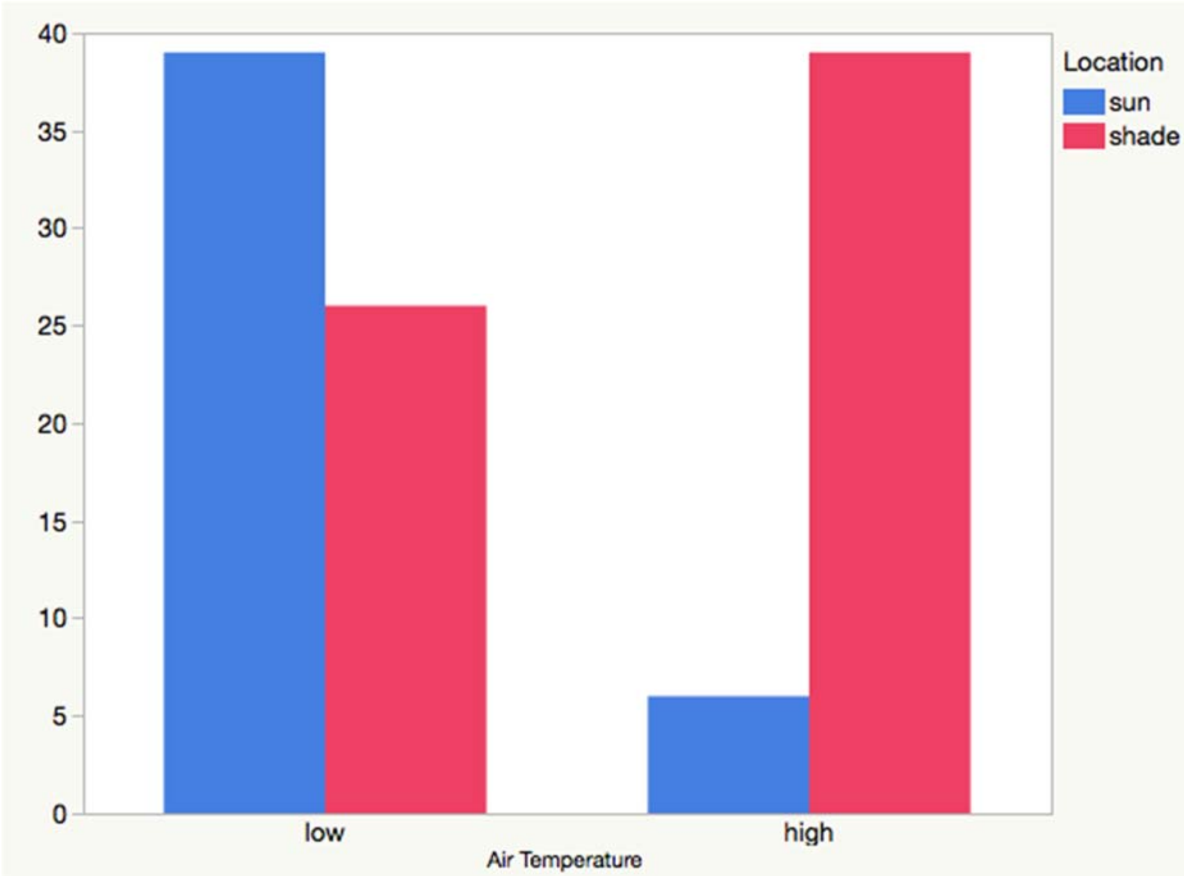


Figure 8. Low and high temperatures were divided at the median (see Figure 7). Number of instances livestock were observed in the sun or shade is recorded on the y-axis.

Predictor	Correlation	Response	Sample Size	Chi Squared	p value
Animal's Surface Temperature	Strong Negative	Foraging Behavior	92	6.47	0.0109
Animal's Surface Temperature	Strong Positive	Ruminating Behavior	92	6.51	0.0108
Animal's Surface Temperature	Strong Positive	Lying Down	92	14.68	0.0001
Animal's Surface Temperature	Weak Positive	Walking	92	1.60	0.0878
Air Temperature	Strong Positive	In Shade	110	19.81	0.0001

Table 12. Results of Logistic regressions on temperature data as it predicts animal behavior.

Sample size is slightly smaller for Surface Temperature than for Air Temperature because some individuals were observed at too great a distance to reliably use the infrared gun, or they were startled and behavior changed by our presence. For shade-seeking behavior, we used air temperature rather than the animal's surface temperature, since we saw shade-seeking as a reaction to ambient temperature, and the animal's surface temperature is expected to decrease as duration of time in shade increases. With our instantaneous scans, had no way of knowing how long an animal had been lying in the shade.

Spatial analyses results

Seasonal area coverage

We found that in the 40% and 60% isopleth areas cattle covered almost double the area in the cool dry and cool dry rain seasons than the hot dry season (Table 13, Figure 9).

40% Isopleth Area (km^2)			
	Cool Dry	Cool Dry Rain	Hot Dry
Tag_1448	4.9	4.3	2.6
Tag_1450	3.8	4	2.11
60% Isopleth Area (km^2)			
	Cool Dry	Cool Dry Rain	Hot Dry
Tag_1448	9.1	9.8	5.4
Tag_1450	7	9.2	4.6

Table 13. Areas calculated by KDEs for cattle by season

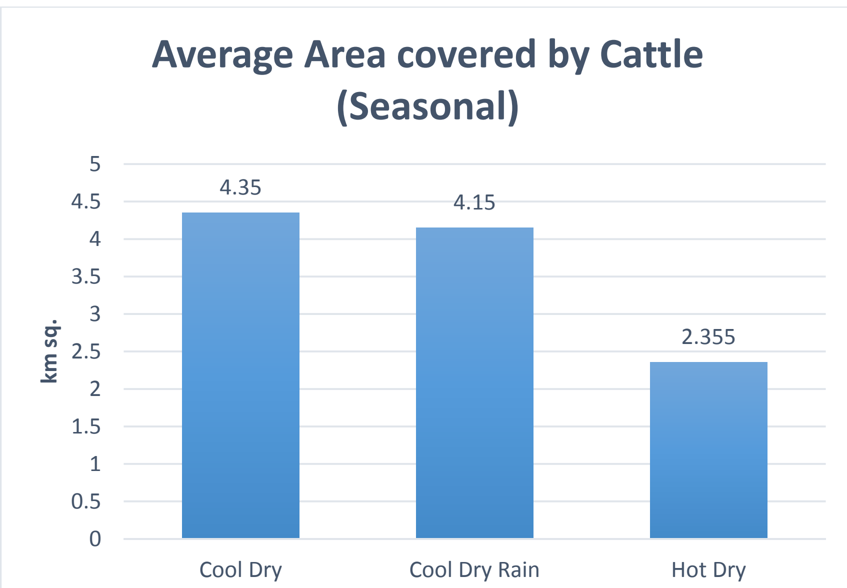


Figure 9: Bar graph displaying average area covered by cattle by season. We found that cattle cover less area in the hot dry season than during the cool dry and cool dry rain season, with average area nearly halved.

EVI results

Results from a preliminary analysis of Enhanced Vegetation Index (EVI) data showed a dramatic increase in correlates of vegetation productivity (Figure 10). These EVI values were calculated at the inter-dune area approximately 60 days after the rainfall occurring June 5 and 6, 2016. This pattern closely corresponds to the data from the collared livestock showing increased use of this area at this time.

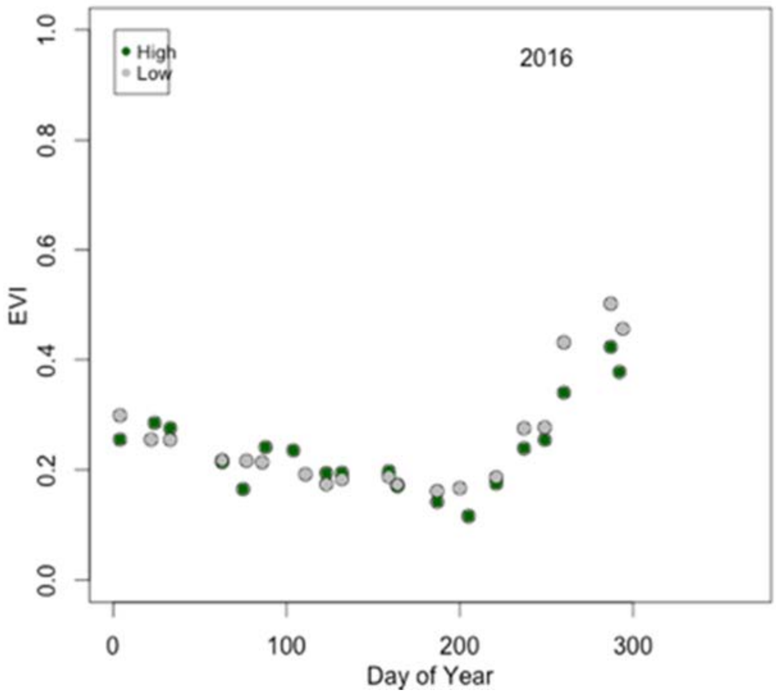


Figure 10. Enhanced Vegetation Index over time in 2016. We found that vegetation dramatically increased in both high and no use areas, approximately six weeks after the rain fall occurring in June 2016.

However, the vegetation increase in the area showing high use (by collared cattle) is similar to the increase in the no use area. The vegetation in the inter-dune area continued to increase going into the hot dry season.

The effect of temperature on hourly cumulative distance travelled

In examining the relationship between ambient temperature and movement parameters, we found a small, significant positive effect of hourly temperature on cattle hourly cumulative distance travelled (Figure 11, Figure 12).

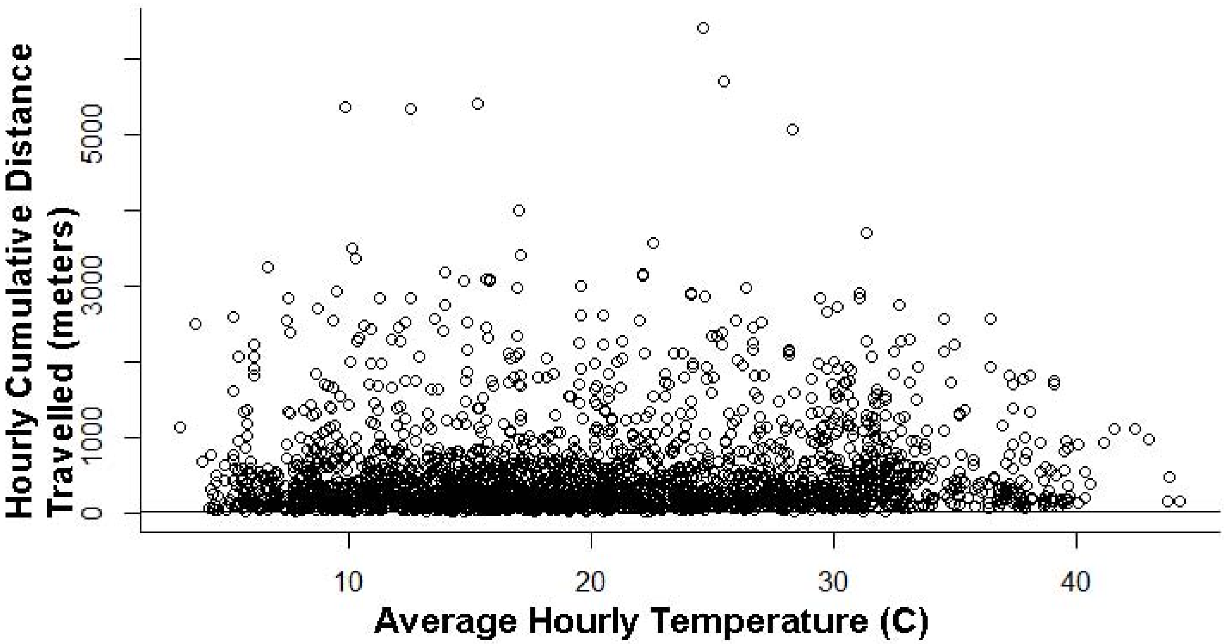


Figure 11. Effect of Hourly Temperature on Cumulative Distance Travelled (Collar 1)

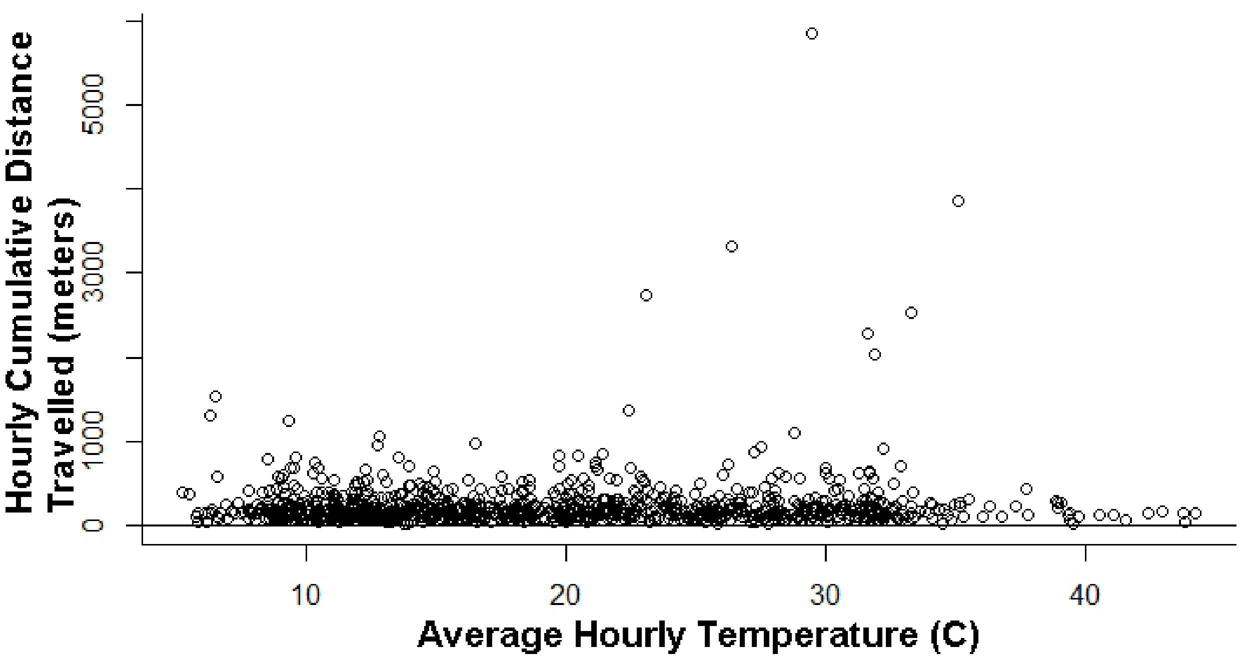


Figure 12. Effect of Hourly Temperature on Hourly Cumulative Distance Travelled (Collar 2)

Discussion

We will discuss our findings as they relate to our 5 hypotheses.

<u>Hypothesis 1:</u> *With increasing temperatures, the total distance traveled by livestock per hour decreases, to decrease energy expenditure and thermal stress.*

We found that as temperatures rose, there was a small but significant increase in the distance traveled by livestock per hour. This was contrary to our hypothesis. This may be due to our sampling method, as we only had GPS telemetry data from four individuals, and so the results are likely biased. Further observation of individuals is necessary, and tracking the movement of more individuals through GPS telemetry would give greater insight into this result. Alternatively, it is also possible that this slight positive influence of temperature on hourly movement is linked to the fact that in the hot dry season, the vegetation is more spread out, forcing cattle to cover more distance despite the heat. In future analysis, one could consider separating the temperatures and hourly distance travelled values based on the season as it could be a confounding factor.

<u>Hypothesis 2:</u> *With increasing temperatures within a day, the intensity of the activities performed by livestock decreases, since they try to reduce energy expenditure and thermal stress*.

Data showed that intensity of movement did decrease as temperatures rose through the day. We found that livestock were more likely to be foraging in low temperatures and more likely to be lying down or ruminating in high temperatures. This is likely to maximize efficiency and nutritional intake from digestion. Thompson (2010) states that food intake and digestive intake both decrease in high temperatures, so livestock get less nutrition from the same amount of food than when digesting in cooler temperatures.

Our findings are consistent with this theory, and thus as temperature rises we expect livestock to become generally more lethargic, with fewer active hours during the daylight hours. This has at least three possible implications for overall livestock health. First, livestock might simply decrease their total energy use by simply spending less time walking between habitats and less time foraging. This adaptation could seriously impact both habitat quality and livestock condition, as food resources may be overused close to the home range, but animals will resist migrating for fresh resources as the heat restricts their movement. Livestock would thus have less access to food and would adapt by spending even less time active, in a positive feedback loop that decreases muscle mass and meat quality (Alfonzo et al. 2016). In this scenario, thus, rising temperatures spell a serious livelihood concern for Topnaar people who rely on the health of their livestock for income and protein.

A second possible response is that livestock will increase food intake as their digestive efficiency drops in high temperatures. This ultimately causes livestock to overuse food in their home ranges in order to find available resources, and ultimately expand their home range (Bartlam-Brooks et al. 2013). Such an expansion requires additional energy expenditure and forces livestock to spend more time in hot conditions, with a resulting decrease in body condition and ability to withstand extreme temperatures (Alfonzo et al. 2016). These two scenarios represent alternate sides of the energy use trade-off for livestock in response to rising temperatures: either sacrifice condition and restrict energy use in order to conserve food resources, or expend excessive energy to secure resources at the risk of not finding enough. Of the two, the second scenario seems the most hopeful, but both still represent a threat to Topnaar livelihoods.

Finally, animals might compensate for inactivity during the day with higher activity at night. If this is presently occurring, and Gobabeb has enough collar data to run a primary analysis on this possibility. A future study could match daily temperatures to cattle displacement during the day versus at night. Then, if a pattern of nocturnal activity develops, observers could conduct focal follows of the same individuals during the day and at night to compare activities. Aside from disturbing the normal diurnal patterns that dictate animal behavior, this strategy seems to be the most promising for livestock to adapt to oppressive temperatures during the day.

<u>Hypothesis 3:</u> *Individuals will tend to cluster in habitats with food resources dominated by* Faidherbia albida *and* Acacia erioloba *pods.*

Analysis of dung counts, as a proxy for livestock use in a particular area, have shown that there is a significant difference in livestock presence in the high-use and no-use areas. This positively correlates with the number of pods counted. However, most pods we found were those of *F. albida*. Additional study is needed to determine if dung counts and *A. erioloba* pods are positively related as well.

Grotz et al. (2015) used dung dissection to suggest that Topnaar cattle use *F. albida* pods as a primary preferred food source, with *A. erioloba* pods as a secondary source. Our results reinforce this conclusion, as both pod types are positively correlated with cattle presence at a transect, but *F. albida* is correlated much more strongly with cattle presence than *A. erioloba.* This could be due to the relative abundance and accessibility of *F. albida* compared to *A. erioloba,* taking seasonality into account, or due to the Topnaar's pod harvesting practices described by Grotz et al 2015.

However, our research has identified a third major food source: *A. erioloba* and *F. albida* leaves, either directly from the tree or as leaf litter on the ground. Looking at animal dung alone for identifying food intake would be biasing the food type analyzed as only seed pods would be clearly visible. Through our focal follows of livestock, we found that *F. albida* and *A. erioloba* leaf litter on the ground was a substantial portion of their food intake. The cumulative leaf litter was correlated strongly with animal presence in a transect—even more so than *A. erioloba* but less than *F. albida*. Thus, should the community harvest *F. albida* pods, should pods drop less, or should *F. albida* trees get further outcompeted by alien invasive species like *Nicotiana glauca*, then livestock may turn to leaf litter as a backup food source. Rising temperatures and greater aridity favor *N. glauca* over *F. albida*, so *N. glauca* will pose a significant threat to cattle diets in the context of climate change in the Kuiseb (Curt and Fernandez 1990). If temperatures rise and *F. albida* becomes less abundant, we expect livestock to forage in denser terrain, farther up the banks of the riverbed. These areas have more of both leaf litter and canopy cover, allowing animals to simultaneously respond to heat stress and a lack of *F. albida* pods. Another implication is that ticks and mites are more abundant in these patches of dense vegetation, thrive in hot climates. Thus, a rise in temperature would represent a significant challenge to livestock due to this shift in the vegetation community (Thornton 2009). One recommendation around this could be that Topnaar people harvest *N. glauca* growing on the riverbed when they harvest *F. albida* and *A. erioloba* pods for fodder. *N. glauca* has high economic value, but more research needs to go into investigating the possibilities for Topnaar to monetize the naturally-occurring *N. glauca* in the area.

<u>Hypothesis 4:</u> *However, as temperature increases due to seasonal changes, individuals will utilize areas with relatively more shade resources.*

In a narrow window of time we identified that there was no significant relationship between surface temperature and an animal's likelihood to be located in the shade. This is likely because we only observed animals on an ad libitum basis. It may be that animals enter shaded areas once they reach a critical internal or external temperature, and that they leave once they have reached a lower temperature. However, we had no way to measure internal temperature and our measure of surface temperature was at times unreliable, since the livestock often became startled and hypervigilant when closely approached with the infrared gun. Additionally, the relationship between surface temperature and animal behavior is still unclear.

However, we did find that livestock tend to use areas with higher canopy cover during the hot dry season. The chi-squared tests testing for significant difference in vegetation distribution, canopy cover and food resources (leaf litter and seed pods) between areas of high-use in the cool dry rain season and the hot dry season show that the difference in each of these three factors are statistically significant. The cool dry area has higher food resources and preferred vegetation, such as *F. albida* and *A. erioloba*, with a smaller amount of canopy cover. In the cool dry season, less canopy is adequate as this is a period of relatively lower temperatures. The data indicates that livestock tend to pick areas with higher quantities of shade resources in the hot dry season. This comes at the cost of less access to the quantity and quality of food available in the cooler season.

This is further exemplified by the livestock usage of inter-dune area during the cool dry period. Through the Enhanced Vegetation Index analysis of the inter-dune areas identified as high-use and low-use during the cool dry season, we found a significant spike in vegetation during the month of August 2016. This correlates with the collar data from the two cows, which started travelling to and utilizing the inter-dune area during the same time, most likely in response to the grass that started sprouting in August 2016 as a consequence of the non-seasonal rain in June 2016.

Interestingly, the vegetation increase in the identified high-use and low-use areas are highly correlated. This can be explained by the significant vegetation differences in the high and low use inter-dune area, as test by the chi-squared test. The high use area has a higher number of very palatable and preferred grasses like *Centropodia glauca*, which could be driving the livestock to this site. The high use area also shows a higher number of unpalatable grasses but this could be because these grasses never sprouted in the low-use area and were not grazed in the high use area. Cattle are primarily, physiologically grazers, though they browse and forage from fallen leaves and pods in the Namib Desert. However, we believe that when nutritious grasses are available, cattle are willing to travel to areas where this is available.

The grassy vegetation in the inter-dune area continued to increase through September-October (the hot-dry season). However, the collar data showed that the cows moved back to the riparian system, which has shade trees like *F. albida and A. erioloba*, close to the settlements and water holes in the hot dry season, despite the presence of grass in the inter-dune area. This points to the idea that cattle, despite primarily being grazers, chose the riparian system which has better shade resources, in the hot dry season.

<u>Hypothesis 5:</u> *As temperature increases due to seasonal changes, the total displacement within this period increases, as livestock cover a larger area to utilize sparser vegetation distribution. Alternatively, as temperatures increase due to seasonal change, the total displacement and dispersion of livestock might reduce, as they are limited to areas close to water holes needed to reduce increasing thermal stress.*

Our findings supported our alternative hypothesis, as we found that total area traveled decreased as temperature rose due to seasonal transitions. However, we were not able to tie this travel decrease to the presence of water holes.

The EVI data comparing the cattle high- and no-use in the inter-dune area showed that vegetation started increasing significantly in August. This corresponds with collar data that shows that cattle moved to this area during this period of booming grass. However, the increase in total vegetation seems to be similar in both the high use and no use areas. The chi-squared test conducted to test the relationship between vegetation in the high and low use areas indicates that the differences in vegetation distribution in the high and the non-use areas are statistically significant. The high use area particularly has a higher number of *Centropodia glauca*, which is a very palatable and nutritious shrub for livestock and wild herbivores (Hoare). According to optimal foraging theory, decision to travel to a farther patch is due to ability to obtain more nutrition and energy at that patch than at a closer one, even with a higher energy expenditure to get there. Thus, the collared livestock likely chose the high-use area because of the food resources made available to them by the rain and the grasses that responded to it two months later. We could safely expand this trend to more individuals than the two collared cattle due to the presence of considerably high count of cattle and donkey dung in the high-use area.

Conclusions & Recommendations

Overall, we found that increase in temperatures have various significant effects on animal behavior and habitat utilization. More extensive transects need to be performed on identified high-use, low-use, and no-use zones from different seasons in order to fully analyze what influences utilization distributions. These transects would help us to investigate how temperature changes influence livestock movement and resource prioritization. Additionally, one can incorporate data available in the Gobabeb Research Center on year-long seed pod availability, to add a temporal dimension to supplement EVI analysis and collar data. Further focal follows would also help us to understand livestock behavior, particularly how it relates to collar data. One way to increase focal follows as well as instantaneous scanning would be to search for animals in all areas rather than on an ad libitum basis. During these follows, the observer would ideally have a non-invasive way to measure the animal's internal temperature. Our observers suffered from the limitations of the infrared gun, which worked only at very close range.

Animals were often startled by our presence, which changed their behavior and could have raised their temperature from stress.

Additionally, it would be useful to study the Topnaar community and their specific views on animal husbandry, in order to make recommendations for management that will work within both their cultural and natural context. As temperatures continue to rise in the near future, livestock owners must work to stay resilient to these changes, and continued research on animal adaptations to thermal stress will help to make this happen.

Acknowledgments

Kyle Kittelberger was one of our most important supporters, providing invaluable equipment along with mental support. We would also like to thank Michael Butler Brown for his boundless enthusiasm and extensive insights into our research. We could not have done it without his energy, knowledge, and willingness to help us at all hours of the day or night. Jeff Kerby and Flora Krivek-Tetley were also critical members of our team with their kindness and support. Thank you to Gobabeb Research and Training Center and all of the staff, particularly Monica, Hannah, and Gillian, for welcoming us with open arms and allowing us to take on this project. Eugene’s dune driving was a skill the likes of which we have never seen before, and Julian’s ability to hunt down donkeys goes unparalleled. Lastly, thank you to Doug and Dartmouth College for the privilege of coming on this trip. Suffice to say we will forever be changed after our foray into the natural sciences.

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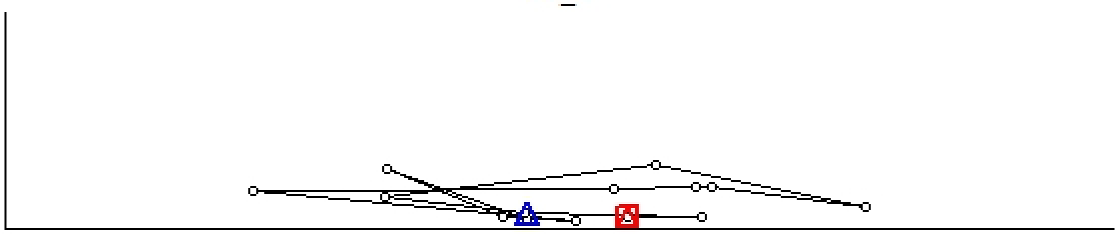
Appendices

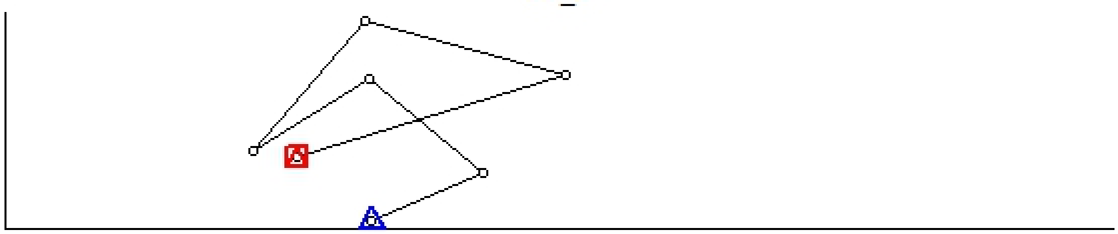
Appendix A: Spatial distribution of activity of animals observed using the focal follow method.

FF_1

FF_2



FF_3



Appendix B: Animal Transect Locations

Waypoint	Latitude	Longitude	y_proj	x_proj	Transect Number	Species	Number in Group
100	-23.588	15.04897	7395464.413	502504.0598	D1	Donkey	1
102	-23.559726	15.035816	7394516.071	503655.17	C1	Cow	4
104	-23.558944	15.035579	7394602.65	503631.0047	C2	Cow	1
106	-23.561943	15.035266	7394270.646	503598.9799	C3	Cow	1
108	-23.559858	15.033371	7394501.518	503405.6443	D2	Donkey	8
110	-23.558064	15.031418	7394700.172	503206.3764	D3	Donkey	3
179	-23.6574	15.241404	7383682.395	524618.0733	C7	Cow	12
1581	-23.655607	15.258045	7383877.929	526315.4676	C4	Cow	8
1589	-23.655714	15.252313	7383867.128	525730.8939	C5	Cow	10
1591	-23.659473	15.243124	7383452.596	524793.0866	C6	Cow	2
1540	-23.517717	14.984508	7399167.145	498418.4756	_-8a_	Cow	2

Appendix C: Location of animal Observations: Instantaneous Scan

Waypoint	Latitude	Longitude	y_proj	x_proj	Transect Number	Species	Number in Group
100	-23.588	15.04897	7395464.413	502504.0598	D1	Donkey	1
102	-23.559726	15.035816	7394516.071	503655.17	C1	Cow	4
104	-23.558944	15.035579	7394602.65	503631.0047	C2	Cow	1
106	-23.561943	15.035266	7394270.646	503598.9799	C3	Cow	1
108	-23.559858	15.033371	7394501.518	503405.6443	D2	Donkey	8
110	-23.558064	15.031418	7394700.172	503206.3764	D3	Donkey	3
133	-23.636452	15.180476	7386010.71	518407.6269		Cow	
135	-23.636256	15.180368	7386032.423	518396.6388		Cow	
153	-23.639503	15.171887	7385674.017	517531.1848		Cow	
154	-23.639373	15.171882	7385688.41	517530.6921		Cow	
161	-23.655456	15.257958	7383894.662	526306.6255		Cow	
176	-23.655739	15.252224	7383864.376	525721.8127		Cow	
177	-23.659504	15.243142	7383449.161	524794.9164		Cow	
179	-23.6574	15.241404	7383682.395	524618.0733	C7	Cow	12
1476	-23.5611	15.036359	7394363.945	503710.5469		Cow	
1477	-23.561101	15.036361	7394363.834	503710.7509		Cow	
1478	-23.559115	15.034757	7394583.74	503547.1111		Cow	
1479	-23.558959	15.034671	7394601.012	503538.3386		Cow	
1480	-23.558959	15.034671	7394601.012	503538.3386		Donkey	
1481	-23.559096	15.035078	7394585.835	503579.8712		Cow	
1482	-23.55865	15.035159	7394635.209	503588.1497		Cow & Donkey	
1484	-23.562027	15.037622	7394261.285	503839.4129		Cow	
1519	-23.550342	15.024179	7395555.199	502467.7415		Donkey	
1520	-23.549567	15.024407	7395640.993	502491.0261		Donkey	

1521	-23.549299	15.023249	7395670.683	502372.8432		Donkey	
1523	-23.560116	15.036289	7394472.883	503703.4307		Cow	
1524	-23.559201	15.03557	7394574.199	503630.0792		Cow	
1525	-23.561956	15.034791	7394269.219	503550.5047		Cow	
1526	-23.55992	15.033154	7394494.659	503383.497		Donkey	
1527	-23.558206	15.031736	7394684.445	503238.8265		Donkey	
1544	-23.517742	14.984427	7399164.377	498410.2069		Cow	
1581	-23.655607	15.258045	7383877.929	526315.4676	C4	Cow	8
1589	-23.655714	15.252313	7383867.128	525730.8939	C5	Cow	10
1591	-23.659473	15.243124	7383452.596	524793.0866	C6	Cow	2
1593	-23.656268	15.240629	7383807.851	524539.2506		Cow	
1594	-23.657284	15.241118	7383695.286	524588.9289		Cow	
1595	-23.646778	15.229311	7384860.384	523386.728		Cow	
1596	-23.645319	15.225957	7385022.454	523044.9181		Cow	

Appendix D: Location of Lower Kuiseb Riverine Transects

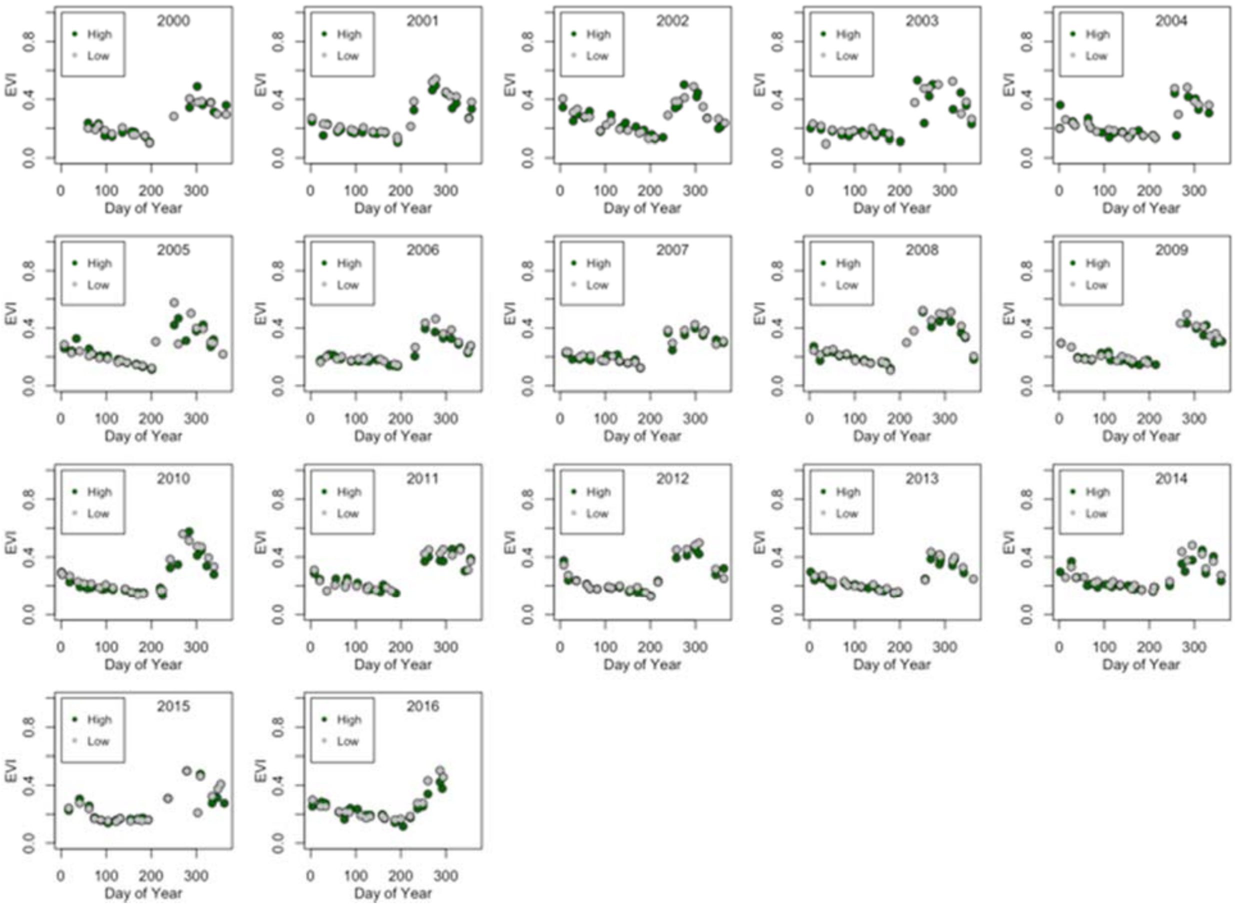
Waypoint	Latitude	Longitude	y_proj	x_proj	Transect Number	Species	Number in Group
70	-23.562019	15.036494	7394262.201	503724.2981	0c		
72	-23.561837	15.036596	7394282.347	503734.7126	0d		
74	-23.562957	15.036543	7394158.356	503729.2722	0a		
76	-23.563385	15.036604	7394110.971	503735.4852	0b		
78	-23.561134	15.037353	7394360.155	503811.9866	2a		
80	-23.56878	15.054403	7393513.126	505551.6697	2b		
82	-23.584563	15.064982	7391765.374	506630.4338	4c		
84	-23.58423	15.064669	7391802.254	506598.5135	4d		
86	-23.60709	15.094309	7389269.786	509621.1706	8c		
88	-23.606692	15.094125	7389313.86	509602.4284	8d		
91	-23.621161	15.106797	7387711.111	510894.0033	10c		
93	-23.620808	15.106413	7387750.22	510854.8618	10d		
95	-23.600711	15.075382	7389977.139	507690.6561	6a		
97	-23.600292	15.075048	7390023.544	507656.605	6b		
112	-23.550259	15.021388	7395564.433	502182.8896	_-2c_		
114	-23.550138	15.021511	7395577.827	502195.4452	_-2d_		
116	-23.531555	15.020591	7397635.115	502101.8439	_-4a_		
118	-23.531452	15.020103	7397646.525	502052.0325	_-4b_		
120	-23.526567	15.001929	7398187.472	500196.9117	_-6a_		
122	-23.526536	15.001385	7398190.904	500141.3804	_-6b_		
124	-23.516397	14.985339	7399313.288	498503.2945	_-8c_		
126	-23.516039	14.985002	7399352.917	498468.8869	_-8d_		
128	-23.502866	14.973526	7400811.09	497297.0583	_-10a_		
130	-23.502865	14.973036	7400811.191	497247.0302	_-10b_		

1497	-23.569061	15.055145	7393481.989	505627.3767	2c		
1499	-23.568625	15.055254	7393530.253	505638.5184	2d		
1501	-23.585032	15.064767	7391713.462	506608.4728	4a		
1503	-23.585187	15.064626	7391696.309	506594.0782	4b		
1506	-23.607355	15.094077	7389240.463	509597.4833	8a		
1508	-23.607521	15.093939	7389222.095	509583.3928	8b		
1510	-23.621523	15.106587	7387671.05	510872.552	10a		
1512	-23.621703	15.106596	7387651.122	510873.4552	10b		
1514	-23.600484	15.075965	7390002.238	507750.1486	6c		
1516	-23.599981	15.076006	7390057.922	507754.3611	6d		
1528	-23.550981	15.021396	7395484.502	502183.6942	_-2a_		
1530	-23.550894	15.020881	7395494.141	502131.1342	_-2b_		
1532	-23.530962	15.021204	7397700.755	502164.4261	_-4c_		
1534	-23.53054	15.02109	7397747.475	502152.7962	_-4d_		
1536	-23.525576	15.002453	7398297.182	500250.4034	_-6c_		
1538	-23.525155	15.00216	7398343.79	500220.4945	_-6d_		
1540	-23.517717	14.984508	7399167.145	498418.4756	_-8a_	Cow	2
1542	-23.517714	14.984004	7399167.472	498367.0239	_-8b_		
1545	-23.502508	14.973785	7400850.728	497323.4944	_-10c_		
1547	-23.502178	14.973401	7400887.254	497284.2819	_-10d_		

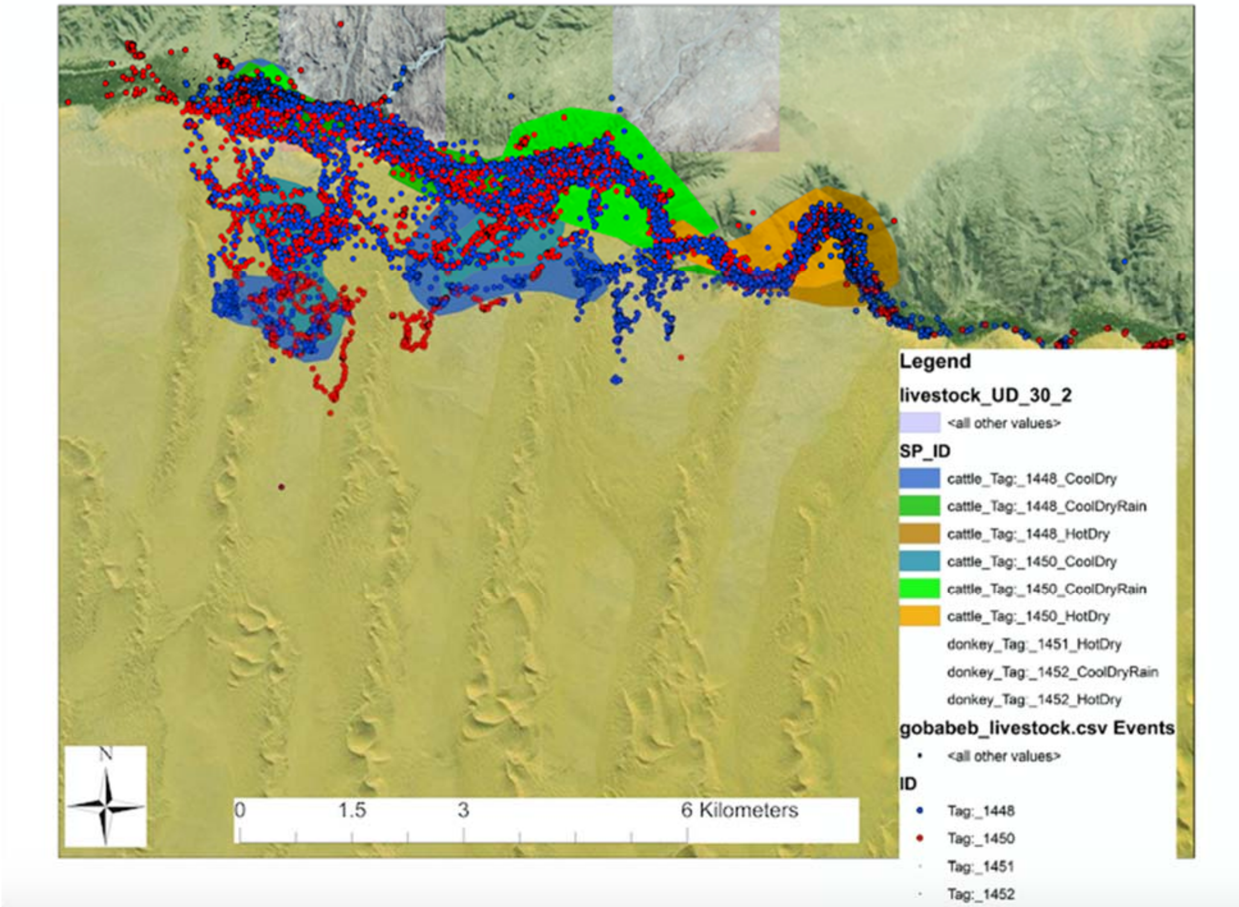
Appendix E: Seasonal Transects

Waypoint	Latitude	Longitude	y_proj	x_proj	Transect Number	Species	Number in Group
138	-23.66537	15.188935	7382808.103	519266.1685	CD_1		
155	-23.644394	15.221903	7385125.508	522631.6161	CDR_S_2		
157	-23.644891	15.223949	7385070.16	522840.1996	CDR_S_4		
159	-23.653569	15.256452	7384103.848	526153.4177	HD_S_0		
163	-23.655211	15.25817	7383921.747	526328.2945	HD_N_2		
166	-23.657543	15.258265	7383663.555	526337.5157	HD_N_4		
172	-23.652702	15.255137	7384200.074	526019.4826	HD_S_-2		
174	-23.652261	15.252793	7384249.322	525780.5212	HD_S_-4		
1556	-23.685207	15.183569	7380612.67	518716.1575	CD_0		
1560	-23.645511	15.21945	7385002.232	522381.2468	CDR_S_0		
1562	-23.644989	15.219284	7385060.049	522364.4055	CDR_N_0		
1564	-23.64745	15.216459	7384788.032	522075.8747	CDR_S_-4		
1566	-23.6472	15.215942	7384815.79	522023.1894	CDR_N_-4		
1568	-23.645956	15.218196	7384953.163	522253.2783	CDR_S_-2		
1570	-23.645534	15.217788	7384999.946	522211.7385	CDR_N_-2		
1573	-23.644927	15.221524	7385066.56	522592.8707	CDR_N_2		
1575	-23.644552	15.224102	7385107.666	522855.8628	CDR_N_4		
1577	-23.653336	15.256766	7384129.586	526185.4865	HD_N_0		
1579	-23.655406	15.257667	7383900.251	526276.9591	HD_S_2		
1583	-23.657803	15.257978	7383634.823	526308.1957	HD_S_4		
1585	-23.652175	15.255141	7384258.417	526019.9948	HD_N_-2		
1587	-23.652512	15.253001	7384221.496	525801.6845	HD_S_-4		

Appendix F: Enhanced Vegetation Index data – 2000 - 2016



Appendix G: Map of GPS points of Collared Livestock with Identified Seasonal Ranges.



!Nara Niche Construction: Understanding Factors that Influence Plant Performance

November 11, 2016

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Background

Niche construction theory

Organisms not only adapt to their surrounding environments but also actively modify biotic and abiotic aspects of their local environments (Brathen and Ravolainen 2015; Laland et al. 2016; Lewontin 1983; Matthews et al. 2014; Odling-Smee et al. 1996; Scott-Phillips et al. 2013). This has strong implications if a niche is considered the sum of all conditions necessary for a species to survive and reproduce or the "set of points in an abstract n-dimensional N space," in which each ecological property is plotted along its own axis (Hutchinson 1957, p. 416). Organisms that actively modify their biotic and abiotic environments are, in essence, changing or constructing their own niche. Niche construction theory (NCT) explores these dynamics and states that the changes species make to their own environments lead to key ecological and evolutionary consequences (Matthews et al. 2014; Scott-Phillips et al. 2013; Zeder 2016).

Within the NCT literature, there are differing perspectives regarding the ecological significance of niche construction. A subset of niche construction theorists uphold that NCT is embedded within evolutionary theory, but that it expands to explain how organisms and environments coevolve (Odling-Smee et al. 2013; Laland and Boogert 2010; Scott-Phillips et al. 2013). These proponents argue that processes of niche construction are of equal explanatory importance to natural selection, and ultimately, that the two cannot occur independent of each other (Kendal et al. 2012; Lewontin 1983; Odling-Smee et al. 1996; Scott-Phillips et al. 2013, p. 1231). In contrast, others do *not* recognize niche construction as a fundamental driver of evolutionary change (Krakauer et al. 2009; Lehmann 2008; Post and Palkovacs 2009). They conceptualize niche construction as an ecological process by which organisms alter their environments, which may or may not have an influence on processes occurring at the time-scale of evolutionary responses (Post and Palkovacs 2009).

Niche construction in desert environments

In desert climates, NCT may provide a useful theoretical framework through which to explore the relationship between plant performance and biotic and abiotic niche factors. Desert soils often contain low soil nutrients, so plants that persist in these environments often change factors related to patterns of nutrient cycling, temperature, humidity, soil fertility, and shade in order to cope with environmental conditions (Srivastava and Jefferies 1996; Willis et al. 1997; Yue et al. 2004). Yue et al. (2004) utilized the tenets of NCT to study how aspects of niche construction affect vegetation cover rate of saksaul (*Haloxylon ammodendron*), a plant found in Badain Jaran Desert of western China. The study found a positive feedback interaction in the niche construction of saksaul, whereby the accumulation of organic matter beneath the plant stems enriches the soil nutrient content, leading to high net growth rate and, subsequently, more organic matter. This case demonstrates how positive feedback at the individual level influences survival of the organism, and thus makes the plant more fit with a larger biomass (Yue et al. 2004, p. 241).

In order to survive in arid, hyper-arid, and desert climates where annual precipitation can be as low as 50mm or less, plants also have physiological adaptations to maintain photosynthetic rates (Hebeler 2000; Kartusch and Kartusch 2008). Desert plant species often have features such as extended root systems, sclerenchymatisation (tough tissue to prevent wilting), succulence (water storing tissue), and microphylly (smaller leaves and leaflets that reduce transpiration) (Gibson 1998; Hebeler 2000; Hebeler et al. 2004). Further, some desert plants may shed their leaves during drought and regrow leaves when rainfall occurs, and others undergo Crassulacean Acid Metabolism (CAM) photosynthesis (Hebeler 2000). These characteristics allow plants to manage levels of radiation, as well as to access and conserve water in conditions of high evaporation.

Niche construction of !Nara, Namib Desert

The hyper-arid Namib Desert is characterized by infrequent, low-intensity rainfall and variably frequent fog events. The average rainfall in the Central Namib is between 5 and18 millimeters per year, and it experiences the highest variability in southern Africa due to its dependence on several transboundary weather phenomena, such as the Angolan Low and Tropical Temperate Troughs. Fog events, unlike rainfall, are of local origin and occur more frequently in some areas of the Namib. The most common type of fog near Gobabeb of the Namib Desert is known as "high fog." It typically commences in the early morning and ends during sunrise. From the coast to the inland "far east" regions, there is a gradient in the occurrence of rainfall and fog events. Annual rainfall increases from 10 mm at the coast to 60 mm 100 km inland (Eckardt et al. 2013). As such, vegetation of the inland region relies more on rain for water provision, whereas vegetation of the coastal region relies more on fog. Gobabeb Research and Training Center is located in the middle of this gradient, receiving an average of 25 mm of rainfall each year since 1962 (Eckardt et al. 2013; Gerber, M., pers. comm., 10/31/2016). Despite the need for water conservation in this arid environment, !nara (*Acanthosicyos horridus),* an endemic species of the Namib Desert, has high rates of transpiration (Hebeler et al. 2004). Relative humidity, expressed as RH or vapor pressure, and temperature are both important factors in the rate of transpiration because they impact the water potential at the surface of leaves, or spines, in the case of !nara. Low temperature and high humidity are associated with reduced transpiration, which is positive for plant performance (Hopkins and Hüner 2009, p.219).

In this study, we focus on the !nara plant because it is an important species in the Kuiseb River Valley for the local Topnaar peoples, who harvest its seeds and melons for sale in nearby cities (Ito 2005; Van Damme and Van Den Eynden 2000; Pendergrast et al. 2013). Within the Topnaar and Gobabeb communities, there is interest in determining how to cultivate !nara because it could bring greater returns to the Topnaar peoples. However, despite numerous attempts, the plant has not yet been successfully cultivated (Maggs-Kölling, G., pers. comm., 10/30/2016). The lack of information on !nara establishment, recruitment, and survival impedes cultivation efforts (Maggs-Kölling, G., pers. comm., 10/30/2016). Prospects for !nara cultivation–-and even sustainable use–-may be limited by environmental conditions and ultimately, by climate change. Water resources within the Kuiseb valley have notably decreased due to increased usage in nearby cities (Victor 2013). Since !nara utilize deep groundwater, a lowered water table may threaten the production of flowers and fruits, thereby limiting reproductive capabilities (Eppley and Wenk 2001; Victor 2013). It is key to understand the conditions under which !nara thrive, as well as its particular adaptations in order to predict how changes in climate and resources will affect its populations in the Namib Desert.

Previous studies have found that the !nara has several features that aid in its survival. !Nara plants have long tap roots (Stix 2003) to uptake water and nutrients from groundwater sources, which can extend between 30-100 meters beneath the surface (Henschel and Moser 2004;

Hebeler 2000; Kartusch and Kartusch 2008; Klopatek and Stock 1994). !Nara also have trichomes, which are fine hairs on the stems and thorns that reduce stem temperature through reflection and absorption of infra-red radiation (Hebeler et al. 2004; Klopatek and Stock 1994). Additionally, !nara have stem-borne adventitious roots, which are thought to take up water from fog events (Henschel and Moser 2004; Kartusch and Kartusch 2008). Klopatek and Stock (1994: 234) state that the distribution of !nara from the western coast to the inland area in the east aligns with the areas where there is fog intrusion. Based on recent data analysis and observations, it is believed that !nara seedlings utilize fog events to grow tap roots that extend deep enough to reach groundwater sources (Gerber, M., pers. comm., 10/30/2016).

The formation of !Nara hummocks, or mounds of sand and biomass, may be a form of niche construction. While there is a lack of information on hummocks made by !nara, there is a more extensive literature on another hummock-forming plant occurring in the Atacama Desert of northern Chile, which may provide insight into !nara niche construction. Within the genus *Tillandsia*, there are several species including *Tillandsia landbeckii*, *Tillandsia marconae*, and *Tillandsia virescens* that form lomas, or mounds (Pinto et al. 2006; Rundel et al. 1997). These same mounds form in bands and create a westward inclination (Latorre et al. 2011; Westbeld et al. 2009). Each mound forms in horizontal layers as wind blows sand, increasing mound volume and thus exposure to oncoming fog (Latorre et al. 2011). Organic matter becomes buried within the compounded layers, which allows the *Tillandsia* sp. plants to sustain growth in the sandy soil. From the perspective of NCT, *Tillandsia* sp. lomas are a type of local environment modification whereby the plant is able to maximize its available resource base for survival and reproduction. Larger *Tillandsia* mounds have increased exposure to moisture via fog absorption and may have richer reserves of soil nutrients. In this way, those plants with larger mounds may be more successful. Dongol et al. (2013) find evidence that larger hummocks have more successful plants because they have a higher percentage of their volume made up of live biomass and a higher volumetric ratio of live to dead !nara. We also may expect that larger hummocks are better protected against herbivory due to the relative inaccessibility of !nara clumps at the top of a large hummock. Slope could be a mediating factor if larger hummocks have steeper slopes that reduce herbivore access to live biomass. In other words, hummock formation may be a strategy to release parts of the plant from herbivory.

In order to study !nara, we consider the factor of proximity to the Kuiseb River, which may be a confounding factor in exploration of abiotic and biotic factors affecting !nara's niche in the local environment. Past research found that herbivore utilization is more intense nearer to the Kuiseb River bed (Grotz et al. 2015). This effect may be balanced by the relative shallowness of water tables in proximity to the Kuiseb River bed, which would allow !nara plants to reach groundwater more easily. Furthermore, we consider hummock aspect. Due to the intensity of solar radiation of the northern side of hummocks, the southern aspect of hummocks may be more amenable to !nara performance (Gerber, M., pers. comm., 11/4/2016). Furthermore, we must consider how abiotic characteristics, such as volume and slope, may influence the microclimates on a hummock. If larger and/or steeper hummocks cast a greater shadow at dawn and dusk, there may be surface temperature and humidity consequences, which could impact plant performance (Appendix 11).

In this study, hummock sizes are used to test for evidence of niche construction. We attempt to quantify the extent to which individual !nara plants in the Namib Desert construct elements of their niches, measured by the volume of their hummocks, and relate this to measures of individual performance. In particular, we focus on three main "axes" of !nara's niche: biotic interactions with herbivores, landscape context, i.e. distance to the Kuiseb River, and hummock microclimates. In doing so, we establish a baseline dataset for understanding the interaction between abiotic factors such as hummock volume, slope, aspect, distance to the Kuiseb River bed, surface air humidity, and surface temperature and biotic factors including !nara photosynthetic efficiency, herbivory, and percent live biomass cover.

We explore 5 specific hypotheses relating to !nara niche construction and !nara's relationship to possible confounding variables in the local environment.

H1: We expect that hummock volume will be positively correlated with measures of plant performance, namely the percent volume of live !nara on hummocks, the volumetric ratio of live to dead !nara, photosynthetic efficiency, fruit density. Hummock volume will be positively correlated with slope. It will be negatively correlated with two proxies for herbivory utilization: the percentage of lateral shoots that have been browsed and spike density.

H2: We hypothesize that increased distance from the Kuiseb River bed will be negatively correlated with photosynthetic efficiency, percentage lateral shoots browsed, and spike density, but will be positively correlated with fruit density. We expect no relationship between distance from the Kuiseb River bed and percent volume of live !nara nor between distance and slope.

H3: Hummock slope will be negatively correlated with the percentage of lateral shoots browsed and spike density, but positively correlated with fruit density. We expect no relationship between hummock slope and photosynthetic efficiency.

H4: Photosynthetic efficiency and the percent volume of live !nara will be higher on the southern side of hummocks. We expect no relationship between aspect (North vs. South) and any of the measurements for herbivory utilization (percentage of lateral shoots browsed and spike density).

H5: We expect that hummock volume will have a positive relationship with surface air humidity and a negative relationship with surface air temperature.

Methodology

Full sample analyses

Site selection.

For the study, !nara hummocks were selected in Gobabeb Valley based on accessibility from the road or camp, distance from the Kuiseb River bed, and relative size. Due to the geographic layout of the interdune area, it was more time-efficient to select hummocks that were easily accessible by foot or by vehicle. When possible, hummocks of varying distances from the Kuiseb River bed were included in study site selection. Further, in order to address one of the primary research questions, obtaining data from hummocks of different sizes was a priority in site selection criteria. Only female plants were selected to control for effect of sex, and because females produce fruits, which can be used to understand a population's fitness trajectory more effectively than flowers on males. At each site, we measured several abiotic and biotic factors that were identified as predictor and response variables in order to understand !nara niche construction (Table 1).

Table 1: Variables Analyzed in the Study

Responses	Predictors
Photosynthetic efficiency (PI)	Hummock volume
Percent volume live !nara	Slope
Herbivory: spike density, % lateral shoots browsed, fruit density (ratio of # of fruits to volume live biomass)	Distance from the Kuiseb River bed
Slope	Aspect

Photosynthetic efficiency

Photosynthetic efficiency (measured as total performance index, PI) was utilized in this study as a proxy for !nara plant performance as it is difficult to directly quantify plant fitness in a short-term study. Total performance index was measured using a Handy PEA device (See Appendix 10). The Handy PEA sensor head is composed of a connection cable and control unit, which has a high intensity LED array to emit infra-red light (peak wavelength of 650 nm) and a photo sensor to receive fluorescence from the plant (Hansatech Instruments Ltd. 2006). For our purposes, we collected photosynthetic efficiency data no earlier than 8:30 pm to allow the plant sample to dark adapt (Gerber, M., pers. comm., 10/31/2016; Stirbet and Govindjee 2011).

Percent volume live !Nara, ratio live to dead !Nara

We also analyze the percent volume of live !nara and the volumetric ratio of live to dead !nara as a possible response to the abiotic predictors. These factors are also used to understand plant performance. With the use of drone data from our collaboration with Jeff Kerby, we obtained volume and surface area data. A Canon S100 digital camera mounted on a 3DR Iris+ quadcopter gathered aerial imagery over the study hummocks. Its route was planned on the open-source Mission Planner software. Applying standard workflows in Agisoft PhotoScan Pro to the resulting aerial imagery, orthomosaics and digital elevation models (DEMs) were created (see Appendix 3). Total hummock surface area and volume were calculated in PhotoScan Pro. Then, the orthomosaics of the hummocks were exported into ArcMap v10.1, where they were georeferenced and classified by vegetation type. A maximum likelihood approach and a supervised class training-set were employed to determine the surface areas of live !nara, dead !nara, and non-vegetated (sand) for each hummock.

Each reclassified hummock image is composed of uniform pixels of equals cell size in a raster file. The ratio of live to dead !nara was computed by dividing the number of live pixels by dead pixels. To find the percent volume of live !nara, first the surface area of live !nara was calculated by multiplying the number of live pixels by the cell size for the particular image. Then, the surface area of live (in cm^2) was multiplied by the average height of the clumps on the hummock (averaged from eight transects on each hummock, from herbivory measurements). This number was divided by 1,000,000 to calculate the volume of live !nara in m^3. Next, the volume of live !nara was divided by the total volume of the hummock and multiplied by 100 to yield the percent volume of live !nara. For the purposes of this study, the percent live !nara cover was analyzed as a continuous variable.

Slope

Hummock slope was identified as both a response to hummock volume and a predictor of the extent of herbivory. Along N, NE, E, SE, S, SW, W, and NW transect lines, we placed a meter stick on the surface of the hummock. Using the iPhone compass application's clinometer function, we placed the phone on the flat edge of the meter stick and recorded the angle. The measurement was repeated twice for a total of three slope measurements at each aspect which were then averaged for the mean slopes. The locations of measurement were selected along non-vegetated sections that would be the more likely path of herbivore movement. Additionally, the N, NW, and NE average slopes were averaged in order to find the average slope on the northern side of the hummock. Similar aggregation was completed for the S, SW, and SE aspects.

Proxies of herbivory

Quantifying the effects of herbivory helped us to understand whether the extent of herbivory (a response) is influenced by !nara niche construction, and in particular, characteristics of its hummock. When plants experience stress, they may allocate more energy into "structural reinforcement," or defense mechanisms, such as toughened leaves, trichomes, and spines (Herms and Mattson 1992, p. 285). Essentially, there is a physiological trade-off in energy allocation between growth and defense, which is impacted by abiotic factors as well as biotic factors such as herbivory (Herms and Mattson 1992). In accordance with this concept, we calculated spine density to examine its relationship to the abiotic factors in question. To quantify herbivory more directly, we collected data to calculate the percentage of lateral shoots bitten on arbitrarily selected stems of !nara clumps on all 8 aspects of hummocks. Lastly, we calculated the density of !nara fruits among live biomass as a response to both abiotic characteristics, such as hummock volume, and the biotic characteristics associated with herbivory.

On each hummock, the N, NE, E, SE, S, SW, W, and NW transect lines were marked. If there were clumps that intersected the transect line, their distance was recorded from the center of the hummock to the approximate center of the clump. At each transect line, one clump was arbitrarily selected for herbivory assessment. Depending on the particular transect line on the hummock, there were different numbers of clumps available for analysis, which impacted clump selection, such as in situations in which there was only one intersecting clump. In the case of multiple intersecting clumps, we attempted to vary the distances of clumps from the center of the hummock for a more representative sample of the hummock's overall herbivory assessment.

To begin herbivory assessment, the height of the clump was recorded, and then a stick was used to arbitrarily select a stem on the clump. On the stem, five lateral shoots were arbitrarily measured for their length and number of spines (to calculate spine density). Then, the number of bitten and non-bitten lateral shoots were recorded on the stem (to calculate the percentage of lateral shoots browsed). Following this, the number of fruits and burrows (for fruit and burrow density) were counted on the entire hummock. We recorded the presence of cow or donkey droppings, as well as insect names or descriptions. Aspect markings from the herbivory protocol was useful for measuring photosynthetic efficiency, herbivory, and slope at these exact locations. The spike density, percent lateral shoots browsed, fruit density, and burrow density were analyzed as continuous variables.

Proximity to the Kuiseb River bed
To quantify distance from the Kuiseb River, the straight line distance from each hummock to the Kuiseb River bed was recorded in meters using GIS data and imagery. In the ArcMap interface, we utilized the “Measure” function to approximate these distances. Direct distances to the river bed were found, but ultimately, we utilized distances along the valley in order to account for the dunes and likely movement paths of herbivores through Gobabeb and !Nara Valleys. The distance from the river along the valley is more meaningful in our study because herbivores would be more likely to walk from the river to the hummocks via this path rather than over the dunes on the side of the valley. These distances were categorized into hummocks near to and far from the river bed. The “near” and “far” groups were then utilized as categorical variables in statistical analyses of these data in addition to distance as a continuous variable.

Statistical analyses
To determine the relationships between the predictor variables and response variables we utilized Analyses of Covariance (ANCOVA) using JMP 12.1.0 software. An ANCOVA test is a linear model similar to a one-way ANOVA test, but the ANCOVA reduces within-group error variance and reduces biases by including a possible confounding variable, known as a covariate (Field 2016). In this case, the ANCOVA tests the effect of the predictor on the response, while controlling for the effect of valley. A primary assumption made in using ANCOVA involves the independence of the covariate and treatment effect (Field 2016). The ANCOVA test assumes that that the covariate does not have different effects across the groups of dependent variables. Another main assumption of ANCOVA has to do with the homogeneity of regression results. This occurs because the ANCOVA first fits a regression line to the data, regardless of the differences between the covariate and treatment variable (Field 2016). This means that the two regression lines have the same slope, but have adjusted y-intercepts, which account for the differential impacts of the covariate and predictor on the response.

Sub-sample microclimate analyses
Site selection
One larger (KE1) and one smaller (GB1) female !nara hummock were selected near the Kuiseb River bed for a sub-sample analysis of microclimate variation and plant performance. Time and available data collection devices limited the ability to expand the microclimate study sample size.

Variables of interest
In addition to the variables measured in the primary study, including photosynthetic efficiency, percent surface area of live biomass, slope, aspect, and hummock volume, other variables related to microclimate were recorded. Through the theoretical framework of niche construction, these factors are of interest because they allow us to compare local scale environments between hummocks. The surface air humidity and temperature were measured on KE1 and GB1 for 2

consecutive days to examine how these factors are influenced by volume and slope and, in turn, influence plant performance. Although we cannot extrapolate to the larger !nara population, this is useful for comparison between KE1 and GB1 to provide preliminary insight into the differences in local environmental conditions between large and small hummocks.

Table 2: Variables Analyzed

Responses	Predictors
Photosynthetic efficiency (PI)	Hummock volume
Surface air humidity	Slope
Surface air temperature	Aspect
	Time of Day

Surface air humidity and temperature
On the North and South sides of KE1 and GB1, HOBO U23 Pro v2 Temperature/Relative Humidity Data Loggers were deployed on November 2 at approximately 12:00pm and retrieved at 12:00pm on November 6. The devices were programmed to record data every 15 minutes. The HOBOs were placed approximately halfway between the center and the edge of the hummock along the respective transect lines. The HOBO U23 Pro v2 device records relative humidity most accurately in the absence of direct solar radiation. Relative humidity is a percentage of how much humidity would be required to make the air saturated with moisture. The HOBO units record this relative humidity through the use of a hygrometer, which measures the electrical resistance, weight, volume, or transparency of various substances that react to humidity. Since the HOBO units must be placed in the absence of direct solar radiation to best measure temperature, we constructed cardboard radiation shields to place over the devices. The cardboard shields were flagged to secure them to the hummock surface. However, after 2 days of data collection, one of the HOBO solar radiation shields failed. As such, we analyzed the data from only the first two days.

Results

Full sample analyses

Effect of hummock volume on proxies for plant performance
An ANCOVA test was used to test for an effect of hummock volume on the percent volume of live !nara, photosynthetic efficiency, and the ratio of live to dead !nara, controlling for the effect of valley location. There is neither a significant relationship between hummock volume (β_3= -5.572e-6) and the percent volume of live !nara, nor between valley location (!Nara Valley versus Gobabeb Valley) (β_2= 0.0106734) and the percent volume of live !nara ($F_{2,22}$ = 0.4243, p= 0.6595). There was neither a significant relationship between hummock volume (β_3= -0.000171) and average total PI (average photosynthetic efficiency), nor between valley location (β_2= 0.4816367) and average PI (n= 13, $F_{2,10}$ = 0.9088, p= 0.4339). There was no relationship between hummock volume (β_3= -0.000184) and the ratio of live to dead !nara after controlling for the effect of valley ($F_{2,22}$ = 3.9084, p= 0.0607). However, there is a significant effect of valley location (β_2= 0.3916396) on the ratio of live to dead !nara (n= 25, t= 2.29, p= 0.0317). Figure 1 illustrates this finding.

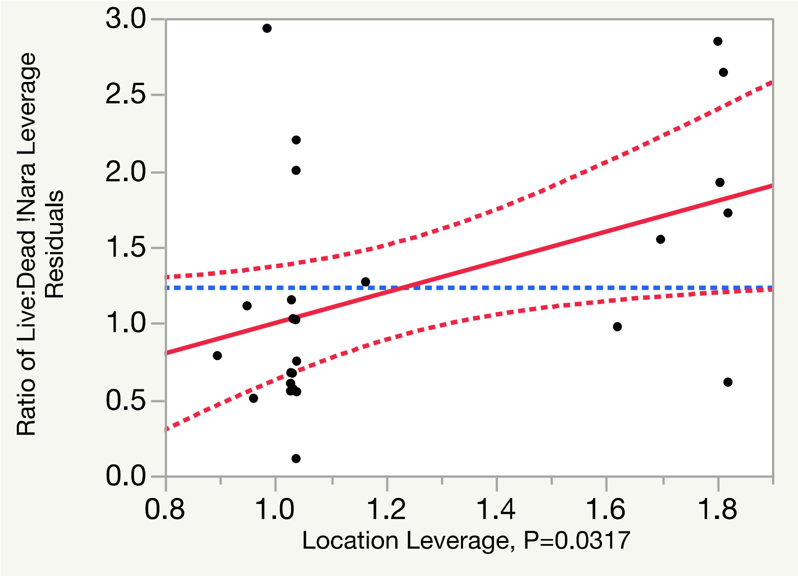

Figure 1. Leverage Plot: Effect of Valley on the Ratio of Live to Dead !Nara After Removing the Effect of Hummock Volume: An ANCOVA test was utilized to determine if there was a significant relationship between hummock volume and the ratio of live to dead !nara while controlling for the effect of valley location. It was found that the valley location had a significant effect on the ratio of live to dead !nara (n= 25, t= 2.29, p= 0.0317). This finding shows that !nara plant performance differs between local environments, such as between !Nara and Gobabeb Valley, even when accounting for hummock volume.

Effect of hummock volume on slope and proxies for herbivory

There was neither a significant relationship between hummock volume (β_3= 0.0001376) and average hummock slope, nor between valley location (β_2= 1.8812818) and average slope ($F_{2,22}$ = 1.2295, p= 0.3118). Although not statistically significant, the mean slope in !Nara Valley (least squares mean= 24.968545) was slightly higher than that of Gobabeb Valley (least squares mean= 21.205981). Furthermore, the data was analyzed, excluding one very large hummock, 0662 (total volume = 8,495.67m^3, !Nara Valley), from the study. This exclusion can be justified based on the pattern observed between slope and hummock volume in the data. Using an ANCOVA test, we tested for a significant effect of hummock volume (β_3= 0.0059989) and valley location (β_2= 1.3832658) on average hummock slope. When excluding hummock 0662, there is a significant effect of hummock volume and location on hummock slope ($F_{2,21}$ = 15.9715, p= <0.0001). Figure 2 shows the leverage plot of total hummock volume on slope (n= 24, t= 4.92, p= <0.0001).

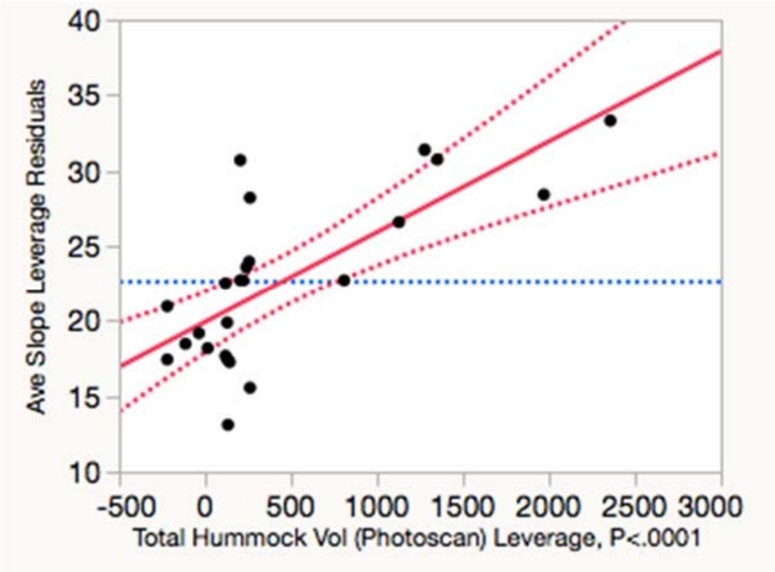

Figure 2. Leverage Plot: Effect of Hummock Volume on Slope after Removing the Effect of Valley Location: An ANCOVA test was used to determine if there was a significant relationship between hummock volume and slope while controlling for the effect of valley location. When excluding a large outlier, it was found that hummock volume has a significant effect on average slope (n= 24, t= 4.92, p= <0.0001). This supports the original hypothesis that there is a positive relationship between hummock volume and slope.

There was neither a significant relationship between hummock volume (β_3= -1.959e-5) and average percent lateral shoots browsed, nor between valley location (β_2= -0.030863) and percent lateral shoots browsed ($F_{2,22}$ = 1.8012, p= 0.1886). There was no significant relationship between hummock volume (β_3= -7.299e-6) or valley location (β_2= 0.0986003) and spike density ($F_{2,22}$ = 1.2557, p= 0.3045). Although neither relationship is significant (total hummock volume p-value= 0.8361, location p-value= 0.1380), it is worth noting that spike density was higher in !Nara Valley (least squares mean= 1.1281811) compared to Gobabeb Valley (least squares mean= 0.9409805).

We found no evidence to support our initial hypothesis that hummock volume would have a positive relationship with fruit density; however, there was a significant effect of hummock volume (β_2 = -0.000621) and valley (β_3 = 2.2634783) on fruit density (n= 25, $F_{2,22}$ = 5.3515, p= 0.0128), whereby valley was found to have a significant effect on fruit density (t= 3.24, p= 0.0038). The mean fruit density in !Nara Valley (least squares mean= 5.4903306) was significantly higher than that of Gobabeb Valley (least squares mean= 0.9633739). Figure 3 is a leverage plot that shows the effect of valley on fruit density.

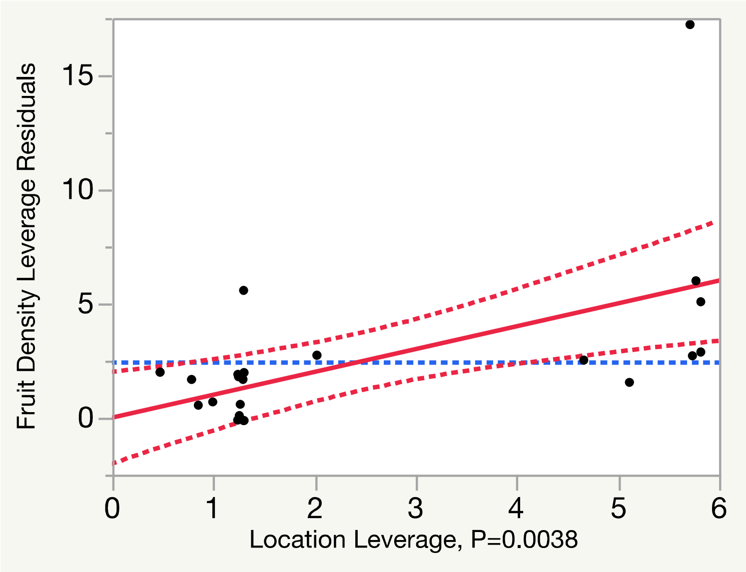

Figure 3. Leverage Plot: Effect of Valley on Fruit Density after Removing the Effect of Hummock Volume: Fruit density was calculated by dividing total fruits by the volume of live !nara biomass for each hummock. An ANCOVA test was used to determine the effect of hummock volume on fruit density while controlling for the effect of hummock location (!Nara or Gobabeb Valley). Hummock volume did not have a significant effect on fruit density, but location had a statistically significant effect on fruit density (n= 25, t= 3.24, p= 0.0038). The mean fruit density in !Nara Valley was 4.92500, compared to 0.9633739 in Gobabeb Valley. This relationship shows that female fruit production is higher in the observed sample in !Nara Valley, which indicates that local environments influence plant performance.

Effect of distance from the Kuiseb River bed on plant performance

With regard to the second hypothesis, an ANCOVA test was used to determine if there was a significant effect of distance from the Kuiseb River bed (measured along the valley) on the percent volume of live !nara, the ratio of live to dead !nara, and photosynthetic efficiency, while controlling for the effect of valley location. There was no significant effect of distance from the Kuiseb River bed (β_3= -4.959e-6) or valley location (β_2= 0.005218) on the percent volume of live !nara (n= 25, $F_{2,22}$ = 0.2326, p= 0.7944), nor between distance from the Kuiseb River bed (β_3= 7.4838e-5) or valley location (β_2= 0.2947725) on the ratio of live to dead !nara (n= 25, $F_{2,22}$ = 1.3387, p= 0.2827), nor between distance from the Kuiseb River bed (β_3= 0.0007562) or valley location (β_2= 0.5250664) and average PI (photosynthetic efficiency), (n=13, $F_{2,10}$ = 2.3767, p= 0.1431). Although the location did not have a significant effect on photosynthetic efficiency (t= 1.52, p= 0.1599), the mean PI was higher in !Nara Valley (least squares mean= 4.6423792) compared to that of Gobabeb Valley (least squares mean= 3.5922464). Appendix 5 shows the regression plot of photosynthetic efficiency as a function of distance from the Kuiseb River bed, controlling for the differential effect by valley.

Effect of distance from the Kuiseb River bed on proxies for herbivory and slope

There was no significant relationship between distance from the Kuiseb River bed (β_3= -2.22e-5) or valley location (β_2= -0.051703) and the percentage of lateral shoots browsed (n= 25, $F_{2,22}$ = 1.4440, p= 0.2575), or between distance (β_3= -0.001577) or valley location (β_2= 1.4240629) and slope (n= 25, $F_{2,22}$ = 2.3286, p= 0.1210). Although the location did not have a significant effect on percent lateral shoots browsed (t= -1.67, p= 0.1097), the percent lateral shoots browsed was roughly 1.59 times larger in Gobabeb Valley (least squares mean = 0.27767320) than in !Nara Valley (least squares mean= 0.17426736). Appendix 6 shows the regression plot of percent lateral shoots browsed as a function of distance from the Kuiseb River bed, controlling for the differential effect by valley. There was a significant effect of distance from the Kuiseb River bed (β_3= -0.00013) and valley location (β_2= 0.0485241) on spike density (n=25, $F_{2,22}$ = 5.4440, p= 0.0120). Distance along the valley to the river bed had a significant effect on spike density (t= -2.75, p= 0.0116). Figure 4 shows the leverage plot of distance along the valley to the river bed against average spike density.

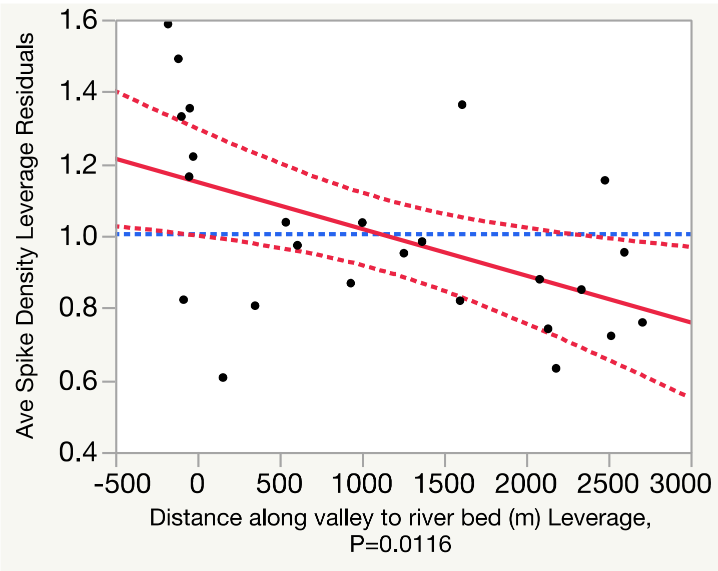

Figure 4. Leverage Plot: Effect of Distance from the Kuiseb River Bed on Spike Density After Removing the Effect of Valley Location: An ANCOVA test was used to determine the effect of hummock volume on spike density while controlling for the effect of hummock location in !Nara or Gobabeb Valleys. Location did not have a significant effect on spike density, but distance along the valley from the river bed had a statistically significant effect on spike density (n= 25, t= -2.75, p= 0.0116). These data show that with increased distance from the river bed, there is a significant decrease in spike density.

Effect of slope

Neither slope (β_3= -0.010917) nor valley (β_2= 0.3502472) had a significant effect on average PI ($F_{2,12}$ = 0.4054, p= 0.6772). There was also no significant effect on spike density (β_2= 0.0745203, β_3= 0.0097275, n= 25, $F_{2,22}$ = 1.7767, p= 0.1926). Contrary to our initial hypothesis, there was no significant effect of slope (β_2= -0.043636) or valley location (β_3= -0.000172) on percent lateral shoots browsed (n= 25, $F_{2,22}$ = 1.0751, p= 0.3585). Although there was no significant relationship between valley location and percent lateral shoots browsed (t= -1.38, p= 0.1812), the mean percent lateral shoots browsed was roughly 1.47 times higher in Gobabeb Valley (least squares mean= 0.27251032) than in !Nara Valley (least squares mean= 0.18523849). Appendix 8 shows a regression plot of percent lateral shoots browsed as a function of slope, controlling for valley.

There was, however, a significant effect of slope (β_3= -0.066462) and valley location (β_2= 1.9789471) on fruit density (n= 25, $F_{2,22}$ = 3.8082, p= 0.0380). Valley location had a significant effect on fruit density (t= 2.74, p= 0.0119). This means that the average fruit density was significantly higher in !Nara Valley (least squares mean= 5.1033680) than in Gobabeb Valley (least squares mean= 1.1454739). Figure 5 is a leverage plot showing the effect of valley on fruit density.

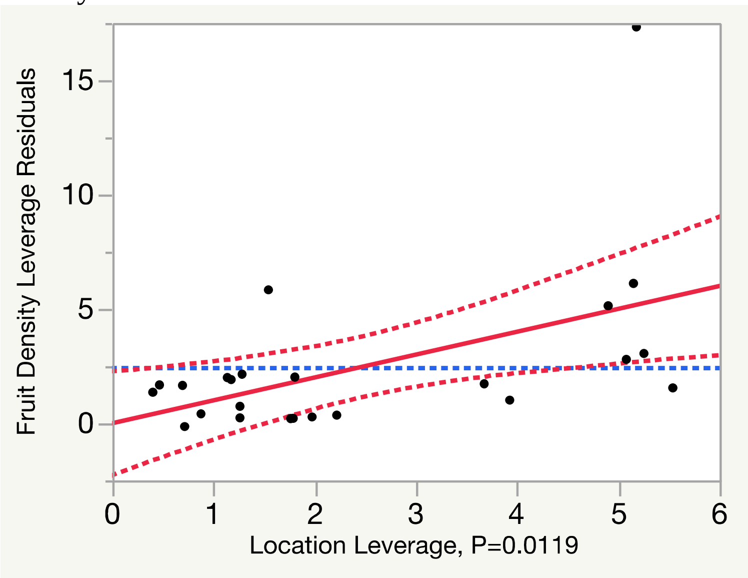

Figure 5. Leverage Plot: Effect of Valley on Fruit Density after Removing the Effect of Slope: An ANCOVA test was used to determine the effect of slope on fruit density while controlling for the effect of hummock location in !Nara or Gobabeb Valleys. Slope did not have a significant effect on fruit density ($t= -0.58$, $p= 0.5695$) after controlling for the effect of valley; however, valley location did have a significant effect on fruit density ($t= 2.74$, $p= 0.0119$). These data show that when accounting for differences in slope among hummocks, fruit density is still significantly higher in !Nara Valley, which indicates that there are other factors of !nara's niche in that local environment that may be impacting its performance.

Effect of aspect on plant performance

The effect of aspect on PI was first analyzed using a one-way ANOVA with average PI data from six aspects where PI was measured (N, NW, NE, S, SW, SE) blocked by hummock ID. Aspect did not have a significant effect on average PI ($F_{5,70} = 1.1125$, $p= 0.3617$). Although not statistically significant, the South aspect had the highest mean PI value of the six aspects across all hummocks (mean= 4.82232).

Furthermore, when the PI values of NW, N, and NE are averaged for the northern side, the PI values of SW, S, and SE are averaged for the southern side, and the variance is thereby reduced, the ANOVA test finds that there is a significant effect of aspect on PI ($n= 13$, $t= 1.860166$, $p= 0.0367$). This means that the South side (mean= 4.89933) has a significantly higher average PI than the North side (mean= 3.53178). Figure 6 represents this finding. Additionally, when blocked by hummock ID, there is still a significant relationship ($t= 1.764582$, $p= 0.497$), although weaker than the relationship whereby all PI values were aggregated across hummocks.

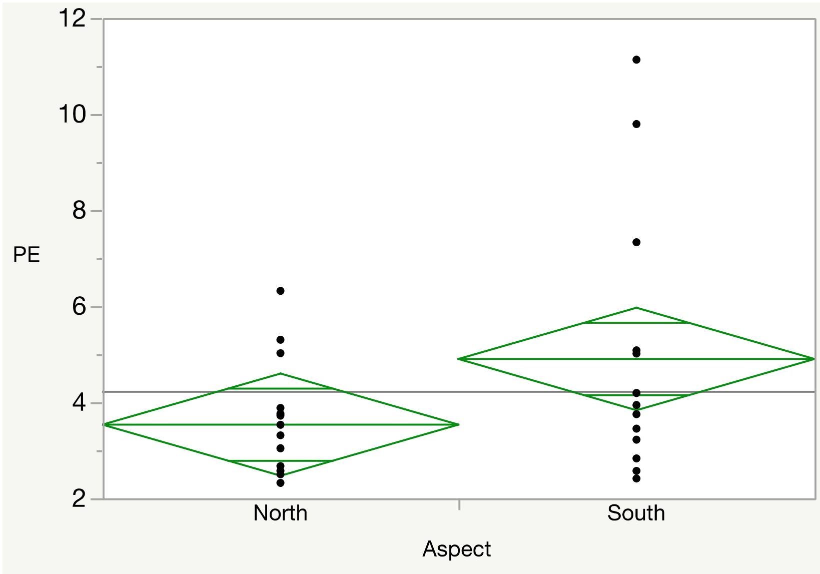

Figure 6. ANOVA: Effect of Aspect (N, S) on Photosynthetic Efficiency: An ANOVA test was used to determine if there was an effect of aspect (North vs. South, averaged from N, NW, NE and S, SW, SE, respectively) on photosynthetic efficiency. Although there was no statistically significant relationship between aspect and PI when analyzing the data across six aspects (n= 13, $F_{5,70}$ = 1.1125, p= 0.3617), there was a statistically significant effect of aspect on PI values of NW, N, and NE are averaged for the northern hemisphere and the PI values of SW, S, and SE are averaged for the southern hemisphere (n= 13, t= 1.860166, p= 0.0367). The South side had a mean total PI of 4.89933, compared to 3.53178 for the North side. These findings are relevant for understanding differential plant performance within hummocks, which can inform understanding of !nara local-scale environments.

Effect of aspect on proxies for herbivory

An ANCOVA test was used to determine if there was a significant effect of aspect on the percent of lateral shoots browsed. There was no significant effect of aspect on the percent lateral shoots browsed (n= 25, $F_{7,132}$ = 1.8866, p= 0.0766). The effect of aspect on PI was first analyzed using a one-way ANCOVA with spike density data from all eight aspects (N, NW, W, SW, S, SE, E), controlling for the effect of valley. The ANCOVA test found that there was no significant relationship between aspect and location and spike density (n= 25, $F_{8,164}$ = 1.5168, p= 0.1549). However, there was a significant relationship between location and spike density, as previously found (t= 2.92, p= 0.0039). The mean spike density in !Nara Valley (least squares mean= 1.1320313) was higher than that of Gobabeb Valley (least squares mean= 0.9596105). Figure 7 shows the leverage plot for the effect of valley on spike density.

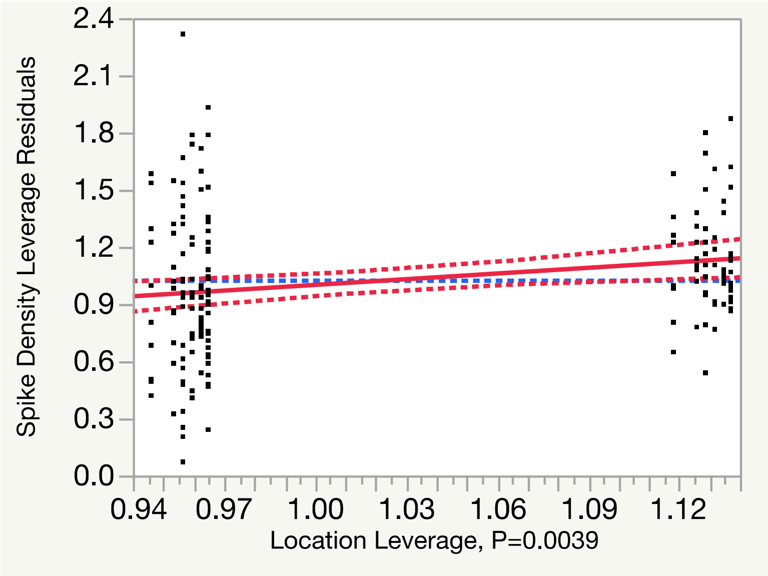

Figure 7. Leverage Plot: Effect of Valley on Spike Density after Removing the Effect of Aspect: Average spike density was calculated for hummocks by dividing the number of spikes by the length of stems, averaged across 5 stems per clump, with 8 clumps per hummock. An ANCOVA test was used to determine if there was a significant relationship between hummock aspect and spike density. The ANCOVA test found that there was no significant effect of aspect on spike density when controlling for the effect of valley (n= 25, $F_{8,164}$ = 1.5168, p= 0.1549). However, there was a significant relationship between location and spike density (t= 2.92, p= 0.0039). These patterns show that spike density is more strongly influenced by location than hummock aspect. The average spike density in !Nara Valley (least squares mean= 1.1320313) was significantly higher than that of Gobabeb Valley (least squares mean= 0.9596105).

Sub-sample microclimate analyses

Effect of volume and time of day on relative surface air humidity

A preliminary graph of the average relative surface air humidity during the afternoon (3pm-9pm), night (9pm-3am), morning (3am-9am), and midday (9am-3pm) periods was created for the sub-sample hummocks (GB1 and KE1). The graph revealed that the difference in average relative humidity between the large (KE1) and small (GB1) hummocks remained throughout the day.

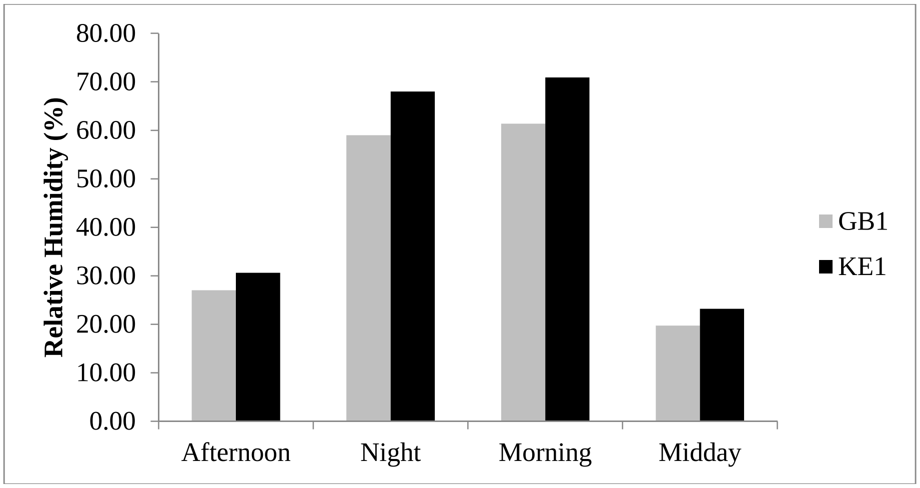

Figure 8. Preliminary Graph: Effect of Volume and Time of Day on Relative Humidity: The average relative surface air humidity during each quarter of the data collection days was compared between one larger (KE1) and one smaller (GB1) hummock in Gobabeb Valley. There is no notable change in the difference between relative humidity on each hummock between the 4 different times of day.

Effect of volume and time of day on surface air temperature

A preliminary graph of the average surface air temperature during the afternoon (3pm-9pm), night (9pm-3am), morning (3am-9am), and midday (9am-3pm) periods was created for the sub-sample hummocks. The graph revealed that the difference in average surface air temperature between the larger (KE1) and smaller (GB1) hummocks remained throughout the day.

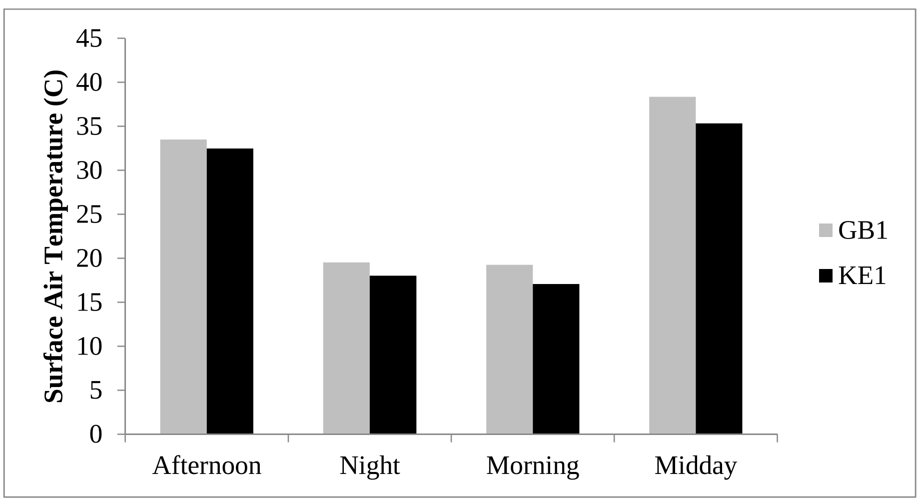

Figure 9. Preliminary Graph: Effect of Volume and Time of Day on Surface Temperature: The average surface air temperature during each quarter of the data collection days was compared between one large (KE1) and one small (GB1) hummock in Gobabeb Valley. There is no notable change in the difference between surface air temperature on each hummock between the 4 different times of day.

Discussion

In this study, we applied a niche construction theory perspective while examining three main “axes” of !nara’s niche: biotic interactions with herbivores, landscape context, and microclimates. In doing so, we explored the effects of !nara niche characteristics including hummock volume, slope, and aspect within the context of the local environment of the Kuiseb River bed.

In the context of NCT, our data indicate that plant performance is not affected as strongly as we expected by total hummock volume. In contrast to volume, valley location more strongly affects certain proxies for performance, such as percent live !nara. These patterns may be better explained by other biotic or abiotic factors not explored in this study, such as interactions with other species. For instance, more intense herbivory in Gobabeb Valley compared to !Nara Valley may have influenced the differences in percent volume of live !nara that we found. Incorporating a broader set of factors would contribute to the understanding of !nara's niche within the local environment, and thus to the understanding of !nara performance and survival within the context of ecological NCT. Our limited sample size may obscure the relationship between hummock volume and plant performance indicators, such as percent volume of live !nara, photosynthetic efficiency, and defense against/avoidance of herbivory. If future studies incorporate a larger sample size and continue to find that the effect of valley location outweighs that of hummock volume, it could be evidence against the importance of niche construction via hummock formation among !nara plants.

Furthermore, this study only included eight hummocks from !Nara Valley within roughly 1200m of the Kuiseb River bed, and therefore, may not completely represent the differences between the two valleys with regards to distance and the impacts this may create due to herbivory or water table availability. These differences may also be attributed to location of livestock water sources in Topnaar settlements, although not directly examined in this study.

Interestingly, photosynthetic efficiency differs within individual hummocks, which indicates differential performance within hummocks, and possible insight into limiting abiotic factors. We found that the southern sides of hummocks have a higher photosynthetic efficiency than the northern sides. From an ecological perspective of NCT, the next step in this analysis would compare percent live volume of !nara as well as the ratio of live to dead !nara between the two aspects on each hummock. Due to the time constraints of this study, we were unable to analyze the data further. This type of analysis would deepen the understanding of differential success attributed to a specific abiotic factor within !nara's niche, and thus inform prospects for !nara cultivation or sustainable use in the context of a changing climate.

In the sub-sample microclimate analysis, we observed that hummock volume does not have a notable effect on relative surface air humidity or on surface air temperature. Despite the pattern that larger hummocks have significantly steeper slopes, meaning that they cast a larger shadow when the sun is not directly overhead (see Appendix 11), we cannot conclude from our results that any increase in shade affects surface air humidity or temperature. If KE1 had a higher surface air humidity and lower surface temperature than GB1 during the morning and afternoon periods, it would have been evidence that larger hummocks, with their increased amount of shade, are a more amenable environments for !nara plants to reduce transpiration water loss. However, the performance of GB1 (PI=3.67), measured by photosynthetic efficiency, was recorded to be higher than that of KE1 (PI=3.24), so volume did not affect plant performance in the expected manner.

Further Research

With regard to !nara niche construction, there are several areas that warrant further research. First, it would be useful to collect data for wind speed at the top of several !nara hummocks. Wind speed could also be measured at the top and bottom of the hummock, as well as on different aspects in order to test for differences in these locations. These data could be used to test for a relationship between wind speed and percent live cover of !nara. Ultimately, this would increase the knowledge base for understanding !nara niche construction and the effects of abiotic factors on plant performance. However, due to the frequent fluctuations in wind, these data would be best suited to a long-term study (Gerber, M., pers. comm., 11/1/2016).

Moreover, there is little in the current literature pertaining to !nara root structure and soil moisture; therefore, we suggest that future studies be done using soil corers. Mapping known paleochannels and water tables could further inform this work. In addition, hummock density, hummock volume, and photosynthetic efficiency could be studied in relation to the paleochannels for a better understanding of how water resources may impact !nara location or performance.

Additionally, although our project only studied females, future studies could include male !nara to understand the similarities or differences between the slope, photosynthetic efficiency, and other factors between the sexes. This could provide insight into differential niche construction of male and female !nara, building upon past work on sex and size distribution of !nara (Wommack et al. 2013).

Reflecting upon this project, there are a few ways in which to improve upon the research methods for studying niche construction of !nara. In particular, we recognize the value in collecting herbivory data on !nara clumps 1) near the top of the hummock and 2) near the perimeter. This distinction is similar to the photosynthetic efficiency protocol developed in this study, and the data from this design would aid in comparison of !nara herbivory and performance at the different locations on the hummocks. Additionally, the methodology could be improved by standardizing the manner in which average clump height is measured on each hummock. In this study, we measured the height of arbitrarily selected clumps along each eight transect lines corresponding to aspects. We recommend that future height measurements are taken at both the top and bottom of the hummock along each transect line and then averaged to give a more complete representation of height across the entire hummock. We believe that a measurement for top and bottom of the hummock is important in order to understand the differences within the niche created by the hummock.

Building upon our case study, we suggest that local scale environments of !nara hummocks are studied. This could include similar air humidity, air temperature, and soil temperature data samples along aspect lines. Soil temperature could also be monitored at various soil depths if available instrumentation permits.

Furthermore, we suggest that future groups record data to calculate the fruit density on all eight aspects of hummocks rather than calculating this value for the entire hummock. We believe this may provide insight on the effects of herbivory within a single hummock, and could be used to test for patterns in herbivore usage between hummocks in Gobabeb and !Nara Valleys.

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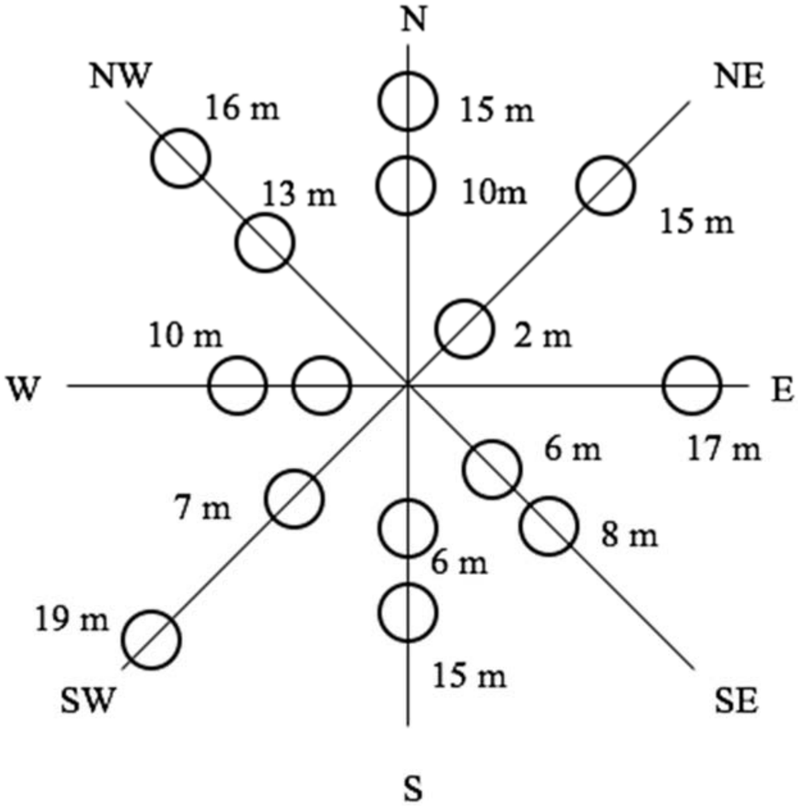
Appendices

Appendix 1. Table of !Nara Hummock IDs and Locations

Hummock ID	Location	Degrees Latitude	Degrees Longitude
GB1	Gobabeb Valley	-23.5644	15.0361
KE1	Gobabeb Valley	-23.5634	15.0366
GB4	Gobabeb Valley	-23.564515	15.034981
KE7	Gobabeb Valley	-23.5655	15.0382
PX201	Gobabeb Valley	-23.56866	15.04072
PC205	Gobabeb Valley	-23.58867	15.05181
PC05	Gobabeb Valley	-23.5901	15.05114
PC09	Gobabeb Valley	-23.59077	15.05191
PC08/GB16	Gobabeb Valley	-23.59021	15.05194
PC100	Gobabeb Valley	-23.587958	15.048973
PC102	Gobabeb Valley	-23.587848	15.047976
PC201	Gobabeb Valley	-23.58611	15.05138
PC11	Gobabeb Valley	-23.59204	15.0515
PX100/GB9	Gobabeb Valley	-23.572714	15.041466
PX101/GB8	Gobabeb Valley	-23.57096	15.041061
200DUNE	Gobabeb Valley	-23.56796	15.03991
200LOWDUNE	Gobabeb Valley	-23.56766	15.04049
0662	!Nara Valley	-23.51144	14.958742
0283	!Nara Valley	-23.51183	14.95695
LF400	!Nara Valley	-23.50832	14.95869
SF400	!Nara Valley	-23.50793	14.95663
6271	!Nara Valley	-23.503779	14.957193
5632	!Nara Valley	-23.504149	14.958857
0343/5701	!Nara Valley	-23.514317	14.95806
0502	!Nara Valley	-23.514505	14.95845

Legend: In past student reports, hummocks have sometimes been marked using new identification codes for previously marked hummocks. This table clarifies the GPS coordinates of the hummocks used in this study, as well as their known IDs.

Appendix 2. Example Data Record for !Nara Clump Locations



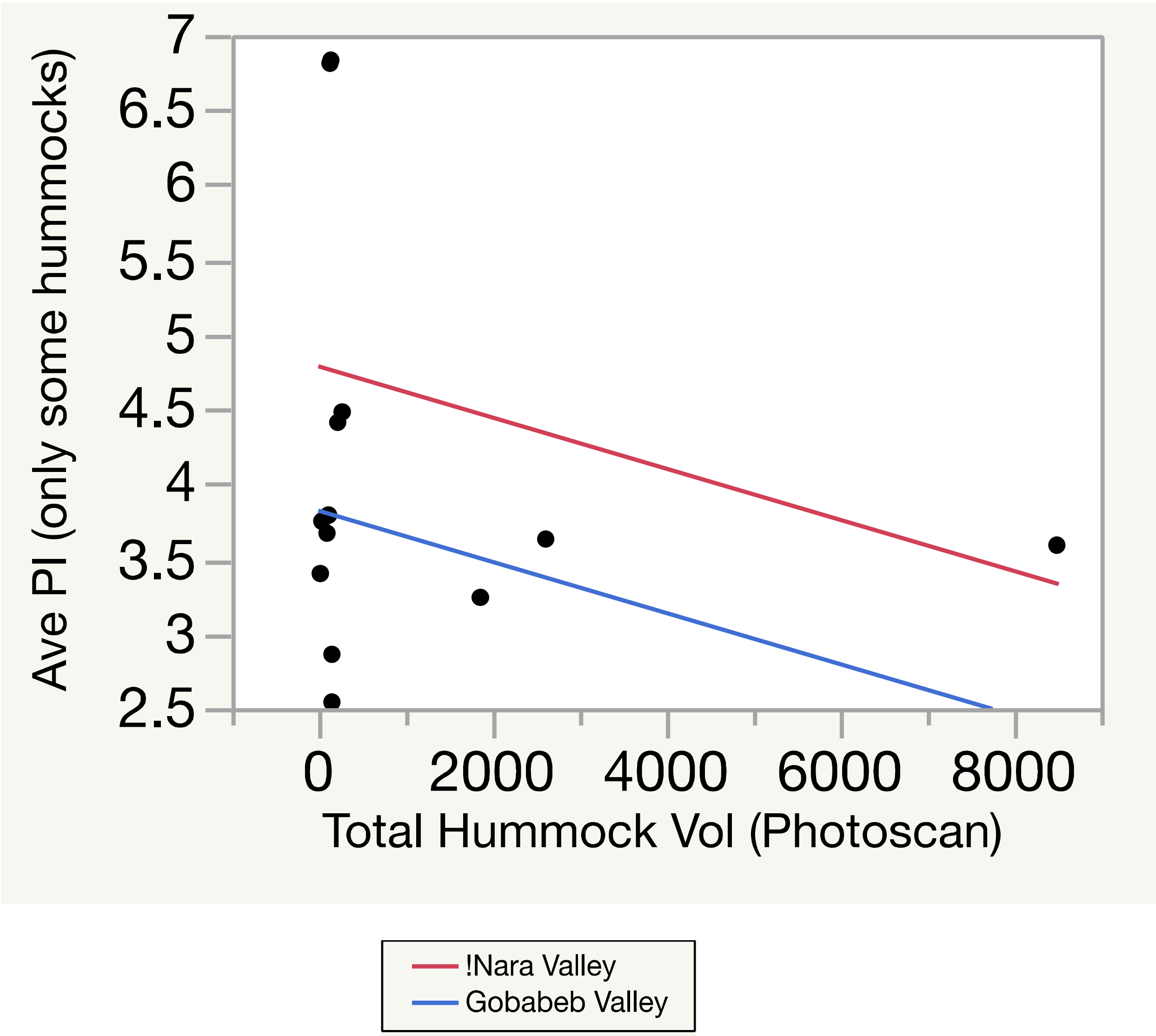
Legend: This figure shows an example of graphic record-keeping in herbivory assessment. Eight transect lines are drawn to represent the transect lines marked on physical hummocks. Using the measuring tape, clumps that intersect the transect line were drawn and labeled with their distance from the approximate center of the hummock. Along each transect line, one clump was arbitrarily selected for herbivory assessment. Note: Figure not to scale.

Appendix 3. General Workflow for UAV Image Processing

1. Load photos into PhotoScan
2. Inspect loaded images, remove unnecessary or blurred images
3. Align the photos
4. Build dense point cloud
5. Build mesh (3D polygon model)
6. Generate texture
7. Build tiled model
8. Build digital elevation model
9. Build orthomosaics
10. Export

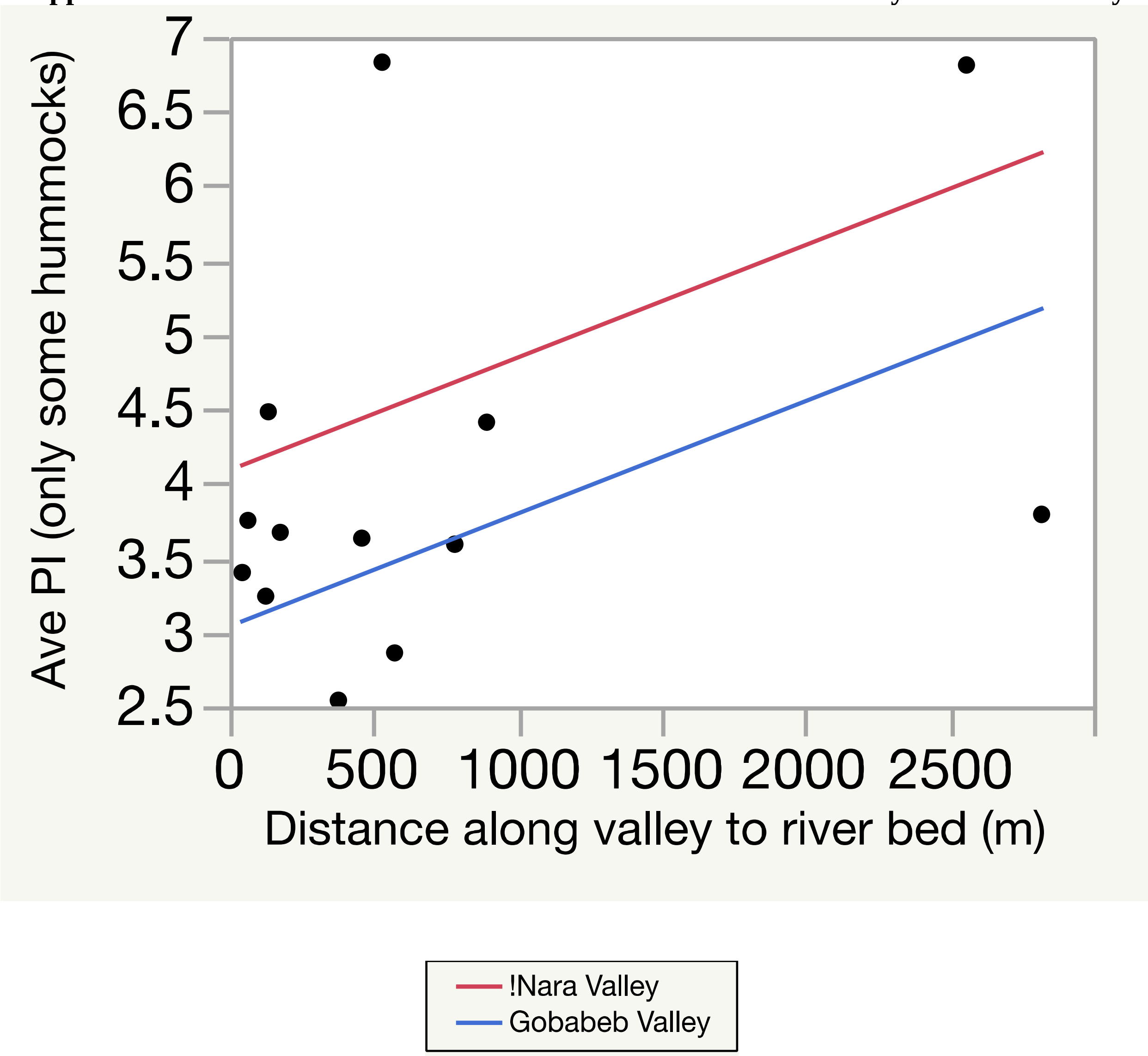
Legend: This numbered list represents the general workflow for UAV image processing in PhotoScan Pro. Through this process, drone imagery can be used to construct a textured 3D model, digital elevation model (DEM), and orthomosaic, or imagery stitched together from several different images (Agisoft PhotoScan 2016; Kerby, J., pers. comm., 11/10/2016). This process creates images that can be used in ArcGIS to calculate the ratios or percentages of live, dead, and sand pixels.

Appendix 4. Regression Plot: Effect of Hummock Volume on Photosynthetic Efficiency



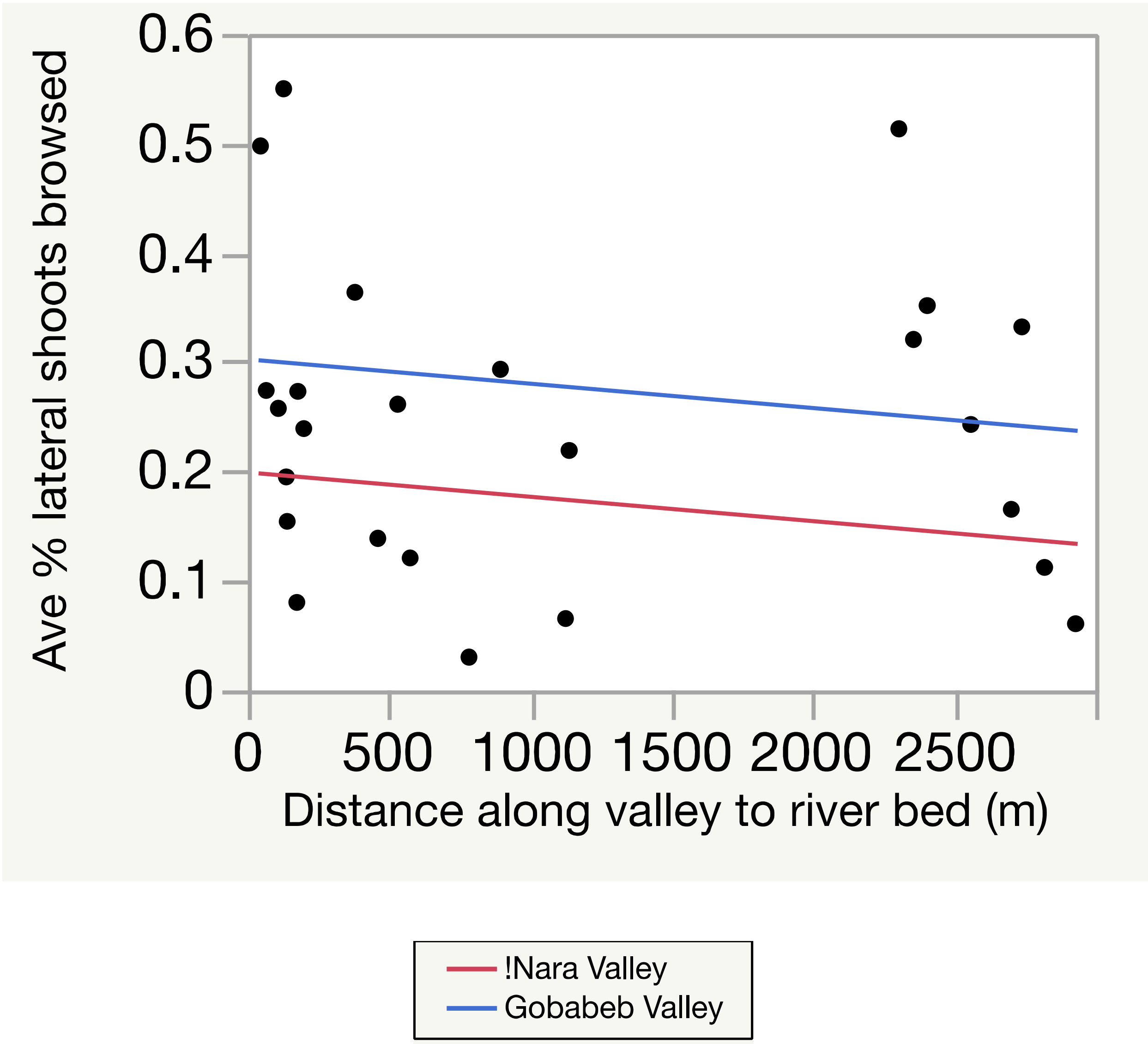
Legend: An ANCOVA test was utilized to determine if there was a significant relationship between hummock volume and photosynthetic efficiency (average PI) while controlling for the effect of valley location. There was neither a significant relationship between hummock volume and average total PI (average photosynthetic efficiency), nor between valley location and average PI (n= 13, $F_{2,10}$ = 0.9088, p= 0.4339). Although neither relationship is significant (total hummock volume p-value= 0.3510, location p-value= 0.2532), it is worth noting that PI values were higher on average in !Nara Valley (least squares mean= 4.5956087) compared to Gobabeb Valley (least squares mean= 3.6323354). This regression plots shows that there is a slight negative relationship between hummock volume and average PI, which means that larger hummocks have decreased photosynthetic efficiency. In terms of niche construction, these data suggest that smaller hummocks may be more advantageous for !nara PI. Aside from this speculation though, further data would be needed to understand the effects of hummock volume on average PI in both !Nara and Gobabeb Valleys.

Appendix 5. Effect of Distance from the Kuiseb River Bed on Photosynthetic Efficiency



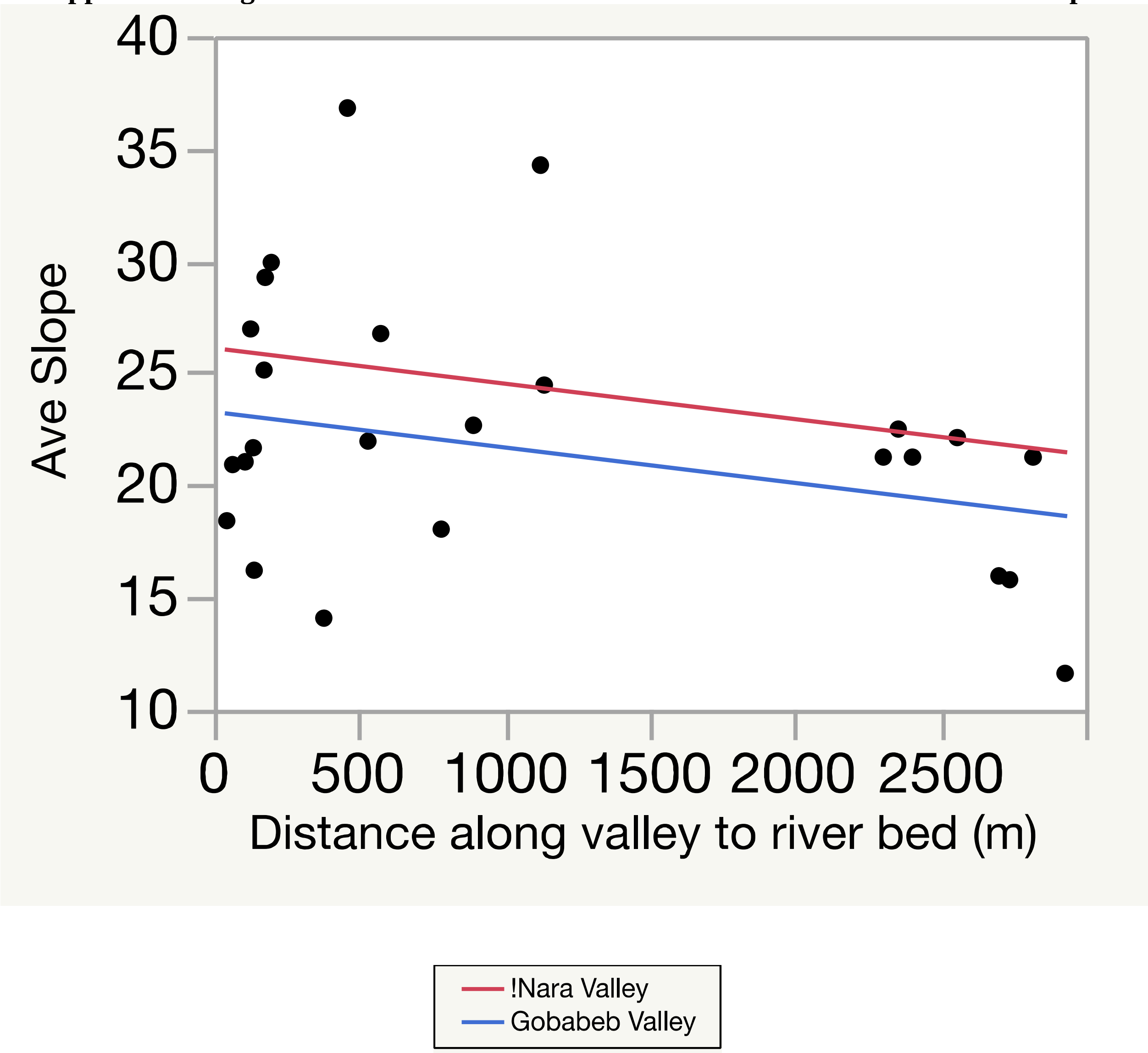
Legend: An ANCOVA test was used to determine if there was a significant effect of distance from the Kuiseb River bed (measured along the valley) on photosynthetic efficiency, while controlling for the effect of valley. There was no significant relationship between distance from the Kuiseb River bed (β_3= 0.0007562) or valley location (β_2= 0.5250664) and average PI (photosynthetic efficiency), (n=13, $F_{2,10}$ = 2.3767, p= 0.1431). Although the location did not have a significant effect on photosynthetic efficiency (t= 1.52, p= 0.1599), the mean PI was higher in !Nara Valley (least squares mean= 4.6423792) compared to that of Gobabeb Valley (least squares mean= 3.5922464). These findings suggest that hummocks farther away from the river bed have higher photosynthetic efficiency, which warrants further research into abiotic factors affecting plant performance, such as water availability. Together, these data may provide insight into differential success of !nara in stratified locations from the river bed.

Appendix 6. Regression Plot: Effect of Distance from the Kuiseb River Bed on Percent Lateral Shoots Browsed



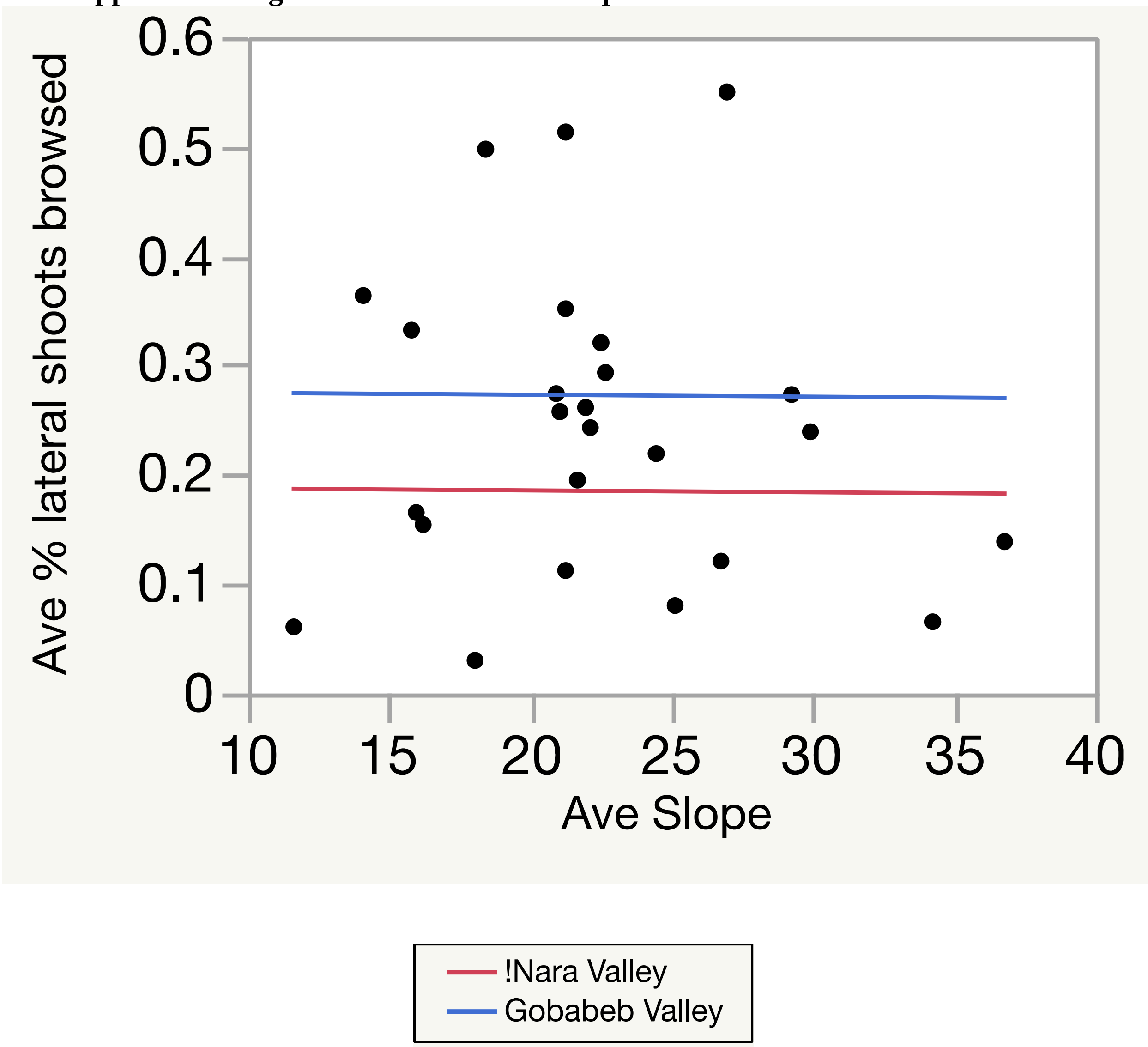
Legend: An ANCOVA test was used to determine if there was a significant effect of distance from the Kuiseb River bed (measured along the valley) on the percentage of lateral shoots browsed, while controlling for the effect of valley location. There was no significant relationship between distance from the Kuiseb River bed or valley location and the percent lateral shoots browsed (n= 25, $F_{2,22}$ = 1.4440, p= 0.2575). Although the location did not have a significant effect (t= -1.67, p= 0.1097), the percent lateral shoots browsed was roughly 1.59 times larger in Gobabeb Valley (least squares mean = 0.27767320) than in !Nara Valley (least squares mean= 0.17426736). Although not significant, these data indicate that there is greater herbivory in Gobabeb Valley than in !Nara Valley, and that hummocks farther from the river bed have a smaller percentage of lateral shoots browsed. Other data related to herbivory or livestock movements could be utilized to further inform the ways in which biotic factors and species interaction affect !nara performance and damage.

Appendix 7. Regression Plot: Effect of Distance from the Kuiseb River Bed on Slope



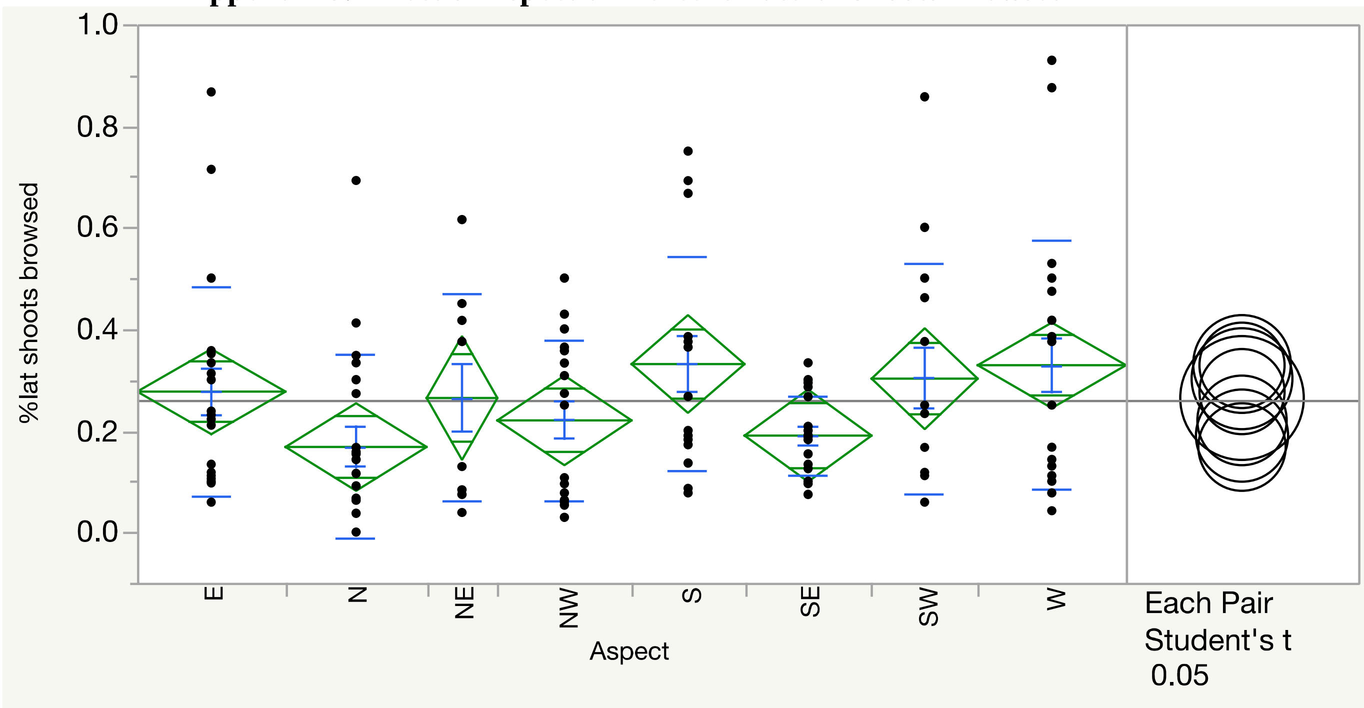
Legend: An ANCOVA test was used to determine the effect of distance from the Kuiseb River bed on slope while controlling for the effect of hummock location in !Nara or Gobabeb Valleys. There was no significant effect of distance from the Kuiseb River bed (β_3= -0.001577) or valley location (β_2= 1.4240629) on the percent volume of live !nara ($F_{2,22}$ = 2.3286, p= 0.1210). Although not statistically significant (t= -1.42, p= 0.1698), there was a slight negative relationship between distance from the Kuiseb River bed and average slope. This means that hummocks farther away from the river bed have shallower slopes. This finding has implications for !nara niche construction, and in particular, for understanding how physical alterations such as hummock slope may impact other factors such as herbivory levels.

Appendix 8. Regression Plot: Effect of Slope on Percent Lateral Shoots Browsed



Legend:
There was no significant effect of slope (β_2= -0.043636) or valley location (β_3= -0.000172) on percent lateral shoots browsed (n= 25, $F_{2,22}$ = 1.0751, p= 0.3585). Although there was no significant relationship between valley location and percent lateral shoots browsed (t= -1.38, p= 0.1812), the mean percent lateral shoots browsed was roughly 1.47 times higher in Gobabeb Valley (least squares mean= 0.27251032) than in !Nara Valley (least squares mean= 0.18523849). Contrary to the original hypothesis that steeper slopes would have smaller percentages of lateral shoots browsed, these data show that there is essentially no relationship. Moving forward, it is advisable that more herbivory assessments are done on individual hummocks, and within the !nara populations in !Nara and Gobabeb Valleys.

Appendix 9. Effect of Aspect on Percent Lateral Shoots Browsed

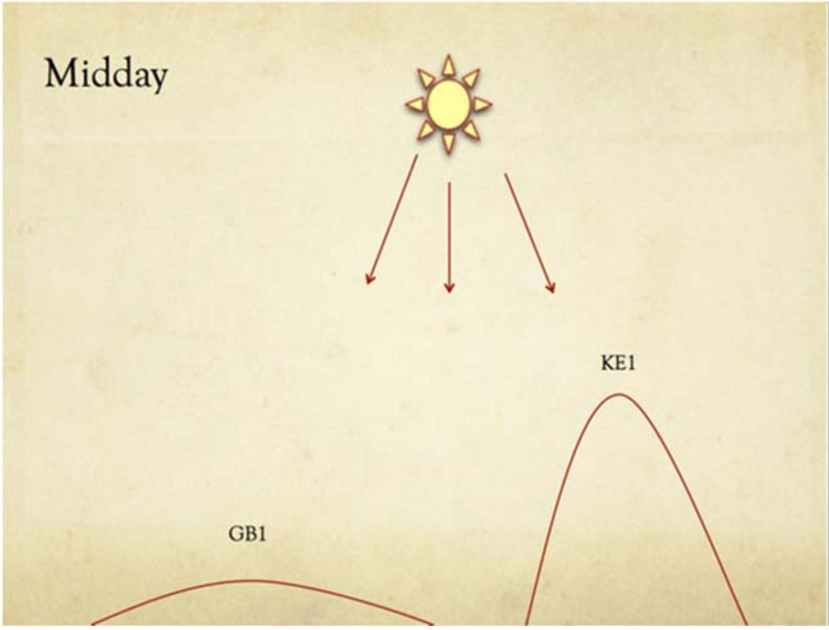


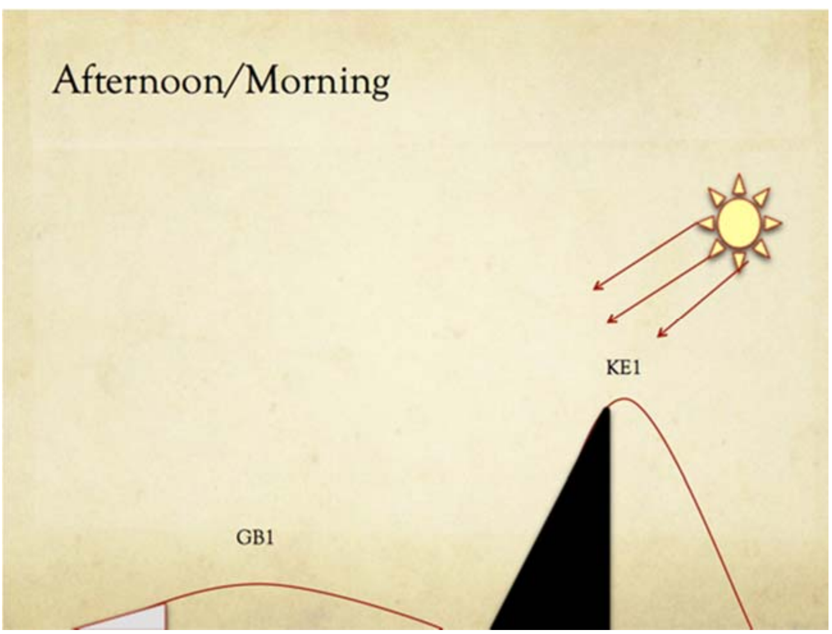
Legend: An ANOVA test was used to determine if there was a significant effect of aspect on the percent of lateral shoots browsed. There was no significant effect of aspect on the percent lateral shoots browsed (n= 25, $F_{7,132}$ = 1.8866, p= 0.0766). Although not statistically significant, these data show that the South (33.08%), Southwest (30.21%), and West (32.84%) sides had the highest percentage of lateral shoots browsed of the eight aspects. This cannot be immediately explained with the available data collected, but it is known that the North side has the highest intensity of solar radiation (Gerber, M., pers. comm., 11/1/2016). Therefore, it could be considered that the southern side is more attractive for herbivores to spend time on. This represents a preliminary suggestion, which could be further substantiated by data collection such as herbivory observations in person or via video footage.

Appendix 10. Photosynthetic Efficiency: Handy PEA device

The Handy PEA measures the chlorophyll a fluorescence of a plant sample during the fast phase of photosynthesis, which can we used as a proxy for photosynthetic efficiency. The slow phase of photosynthesis is known as PMST (P- peak, M- a single maximum, S- semi-steady state, T- terminal steady state); however, the fast phase, or OJIP rise is more easily interpreted, as the M state is often missing or misinterpreted in fluorescence measurements (Stirbet and Govindjee 2011: 2). The entire OJIP rise occurs in about 2 milliseconds, and within this sequence, each phase is characterized by a particular photosynthetic process. The O phase occurs at about 20 microseconds and is the origin of chlorophyll a fluorescence measurement (Stirbet and Govindjee 2011). At this point, infrared light exposure from the Handy PEA leads to the initial absorption of energy. After 2 milliseconds, the J phase is an intermediate level in which energy is trapped, and after 30 milliseconds, the second intermediate level, or I phase, represents the dissipation of heat energy. At 300 milliseconds, the P phase represents peak fluorescence, or the time at which electron transport and the reduction of NADPH have occurred (Gerber, M., pers. comm., 10/31/2016; Strasser et al. 2007). As chlorophyll a fluorescence is just one proxy for interpreting photosynthetic efficiency, utilizing data from fluorescence induction is most appropriate for relative comparisons, not absolute values. For the purposes of this study, photosynthetic efficiency was analyzed as a continuous variable.

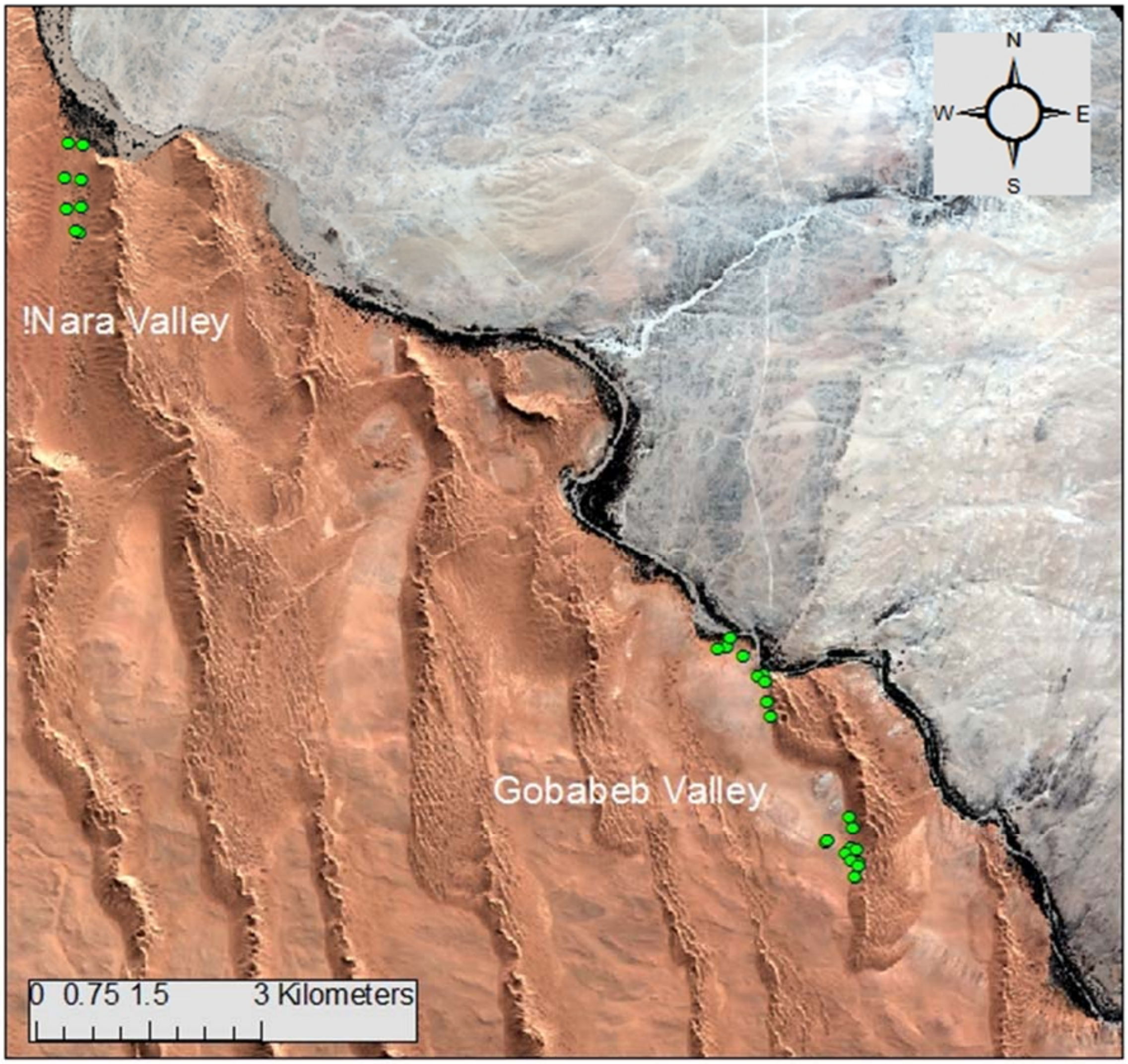
Appendix 11: Visualizing Effects of Volume, Slope, Time of Day, and Shade on !Nara Performance





Legend: In the sub-sample of our niche construction research, we sought to understand whether hummock volume and slope could influence plant performance. If larger hummocks are steeper and produce more shade when the sun is not directly overhead, then the relative air humidity and surface temperatures in the shadow side could be more amenable for plant performance.

Appendix 12. Map of !Nara Study Areas and Hummocks



Legend: This map illustrates the study region for this project. Seventeen female hummocks in Gobabeb Valley and 8 female hummocks in !Nara Valley were selected.