Dartmouth in Namibia

Dartmouth College, Environmental Studies Program, Hanover NH USA

October-November 2017

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Assessing the carrying capacity of the Kuiseb River ecosystem for Topnaar livestock

November 10, 2017

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Abstract

Carrying capacity is important for understanding ecosystem balances and sustainable population dynamics. The purpose of this study was to estimate the carrying capacity of the Kuiseb River ecosystem for Topnaar livestock, and to better understand the relationship between spatial distributions of cattle and pod-producing tree species. Two different census methods and body condition scores were used to assess the abundance and relative health of cattle in the system, and a series of tree productivity measurements were used to extrapolate the most productive areas of the riverbed. We found that cattle abundance increased with increasing relative abundance of *Faidherbia albida* trees, but mean *F. albida* pod production decreased with relative species abundance. We conclude that carrying capacity has not yet been breached within our study area, but monitoring of the riparian vegetation and livestock numbers will be important in the face of climate change and intensification of extreme weather events.

Introduction

Competition for limited resources is widespread in both natural and human systems, and can often act as a point of conflict at the interface between the two. Resources may be limiting for wildlife populations and have widespread impacts on economic systems. Recognizing an ecosystem's limits is critical for the sustainability of socio-ecological systems on both global and local scales. When a system's capacity to support a population is exceeded, resource dynamics can be altered, sometimes permanently, via environmental degradation (Tuffa & Treydte 2017). The idea that the limits of an ecosystem can be exceeded informs our understanding of what regulates populations, and forms the basis of the concept of an environment's *carrying capacity*.

There are many factors that determine the maximum population sizes that an ecosystem can support without exceeding its capacity. The dietary and nutritional needs of animal species must be met to sustain healthy populations. Water is another critical resource not only because animals need to drink, but also because the amount of water is a critical determinant of primary productivity available to consumers, and thus indirectly to the rest of the food web. In addition to resource availability, inter-species competition resulting from spatial and dietary overlap has a profound effect on population sizes. As one population increases, the pressure it exerts on an ecosystem reduces the availability of resources for other populations.

The idea of carrying capacity and its various determining factors are especially pertinent to the study and practice of pastoralism, as livestock are integral to many cultures and socioeconomic systems. Like humans and wildlife, livestock are equally dependent on an ecosystem's natural resources. They are therefore subject to population limitations imposed by finite resources. Above all other livestock species, cattle are predominantly valued by people around the world not only as sources of food- but also as a form of investment and economic stability. Thus, it necessary to consider their needs as a component of carrying capacity. Cattle have specific nutritional requirements that intensify with extreme heat or cold, making some rangelands more suitable for them than others. They require a wide variety of vitamins and minerals, such as calcium, phosphorus, and vitamins A, D, and E (Gadberry 2010). A high quantity of protein is also essential to their diet, particularly during lactation and towards the end of gestation periods (Lalman et al. 2007) and thus have a large impact on population productivity.

The ability for cattle to fulfill their resource requirements is hindered by the challenges in resource-scarce environments. Our study focuses on livestock management along the Lower Kuiseb River, one of twelve ephemeral rivers traversing the Namib Desert in Namibia. The desert is characterized by minimal rainfall and low primary productivity. Rainfall averages at less than 10 mm per year, and many organisms depend predominantly on fog and groundwater because rainwater is not a reliable water source (Eckardt et al. 2011). These environmental factors limit the abundance of life that can survive in this harsh ecosystem. However, animals can access higher abundances of key resources sequestered in ephemeral rivers. The Kuiseb provides sources of food and water for plants, wildlife, and livestock, forming a biodiverse riparian ecosystem, or "linear oasis" (Kok & Nel 1996). Two seed pod producing trees, *Acacia erioloba* and *Faidherbia albida*, are key resources affecting carrying capacity as wildlife and livestock rely on their seed pods as their primary food source (Moser 2006). Per annum, an *A. erioloba* tree produces an average of 135 kg of pods, while a *F. albida* tree produces an average of 120 kg. These pods are high in protein and carbohydrates, and they have sufficient levels of calcium and phosphorus to fulfill the nutritional requirements of cattle (Jln et al. 2017). Due to the crucial role that these trees have in forage provisioning, part of our study assessed their relative abundance and pod productivity.

Despite the aridity of the surrounding desert environment, these pod producing trees, and the nutrients they provide, enable the pastoralist lifestyles of local communities to persist. For the Topnaar, an indigenous Namibian people who live along the Lower Kuiseb River, pastoralism is entrenched as a cultural and economic practice. The Topnaar people have lived in the Lower Kuiseb River region for nearly 800 years, raising livestock under extreme desert conditions (Desert Research Foundation of Namibia 2015). Historically, the Topnaar were nomadic, but their mobility has become increasingly limited by expanding human populations, international borders, exclusion from conservation areas, and decreased access to water (Jacobson 1995). Those who have not found work in urban centers continue to dwell along the Kuiseb river, where they keep a variety of cattle, goats, sheep, and donkeys. Although Topnaar livestock management practices have been successful in the past (Desert Research Foundation of Namibia 2015), it is unclear whether the Kuiseb can support the current number of livestock. For instance, in the past year, it was reported that livestock numbers significantly decreased in the Lower Kuiseb River (J. Kooitjie, *pers. comm.*, 27 October 2017), which might indicate that livestock have exceeded the Kuiseb's carrying capacity. Understanding the degree to which livestock can be supported by key resources in the Lower Kuiseb is critical for assessing the sustainability of this socio-ecological system and for the continuation of Topnaar pastoralism.

These livestock populations and this ecosystem provide an ideal sample for assessing carrying capacity because the variables in an arid environments that affect carrying capacity are especially clear and their effects are particularly profound. Furthermore, there are less confounding factors contributing to population pressures than in other socio-ecological systems. Understanding carrying capacity can help prepare pastoralists here and in other arid environments for adaptive livelihood strategies, given the inevitable effects of climate change. Therefore, we have taken a multiphase approach to studying population pressures and environmental conditions as they relate to livestock carrying capacity in this system. We first estimated the current livestock population size, utilizing two different methods. We then evaluated the spatial patterns of pod producing trees, as well as livestock distributions and health, and the relationships between them. In doing so, we aim to determine whether the region's carrying capacity has been exceeded and the implications for Topnaar pastoralism along the Kuiseb River.

Regarding the census, we hypothesize that there will be approximately 400 cattle in the lower Kuiseb region based on the most recent approximations. With regards to the spatial patterns of pod producing trees and livestock, we hypothesize that there will be a positive correlation between tree pod productivity and cattle density, as well as an increased density of productive trees and cattle further upstream because of greater water availability resulting from the geomorphology of the Kuiseb. Cattle health will also correlate with higher densities of productive trees. Finally, we hypothesize that cattle have reached, or are close to reaching, carrying capacity in the lower Kuiseb river region due to limited access to key resources.

Methodology

Study area description

Our study area encompassed a 55 kilometer stretch of the riverbed previously identified by Morgan (2017; see figure 1). It was extended to 65 kilometers in order to further expand the reach of our cattle census. The study area was selected in order to build upon previous research and existing data. The portion of the Lower Kuiseb River that comprises our study area contains the Topnaar settlements Kharabes, Soutriver, Natab, Oswater, and Homeb, which allows for analysis of our variables in relation to community locations.

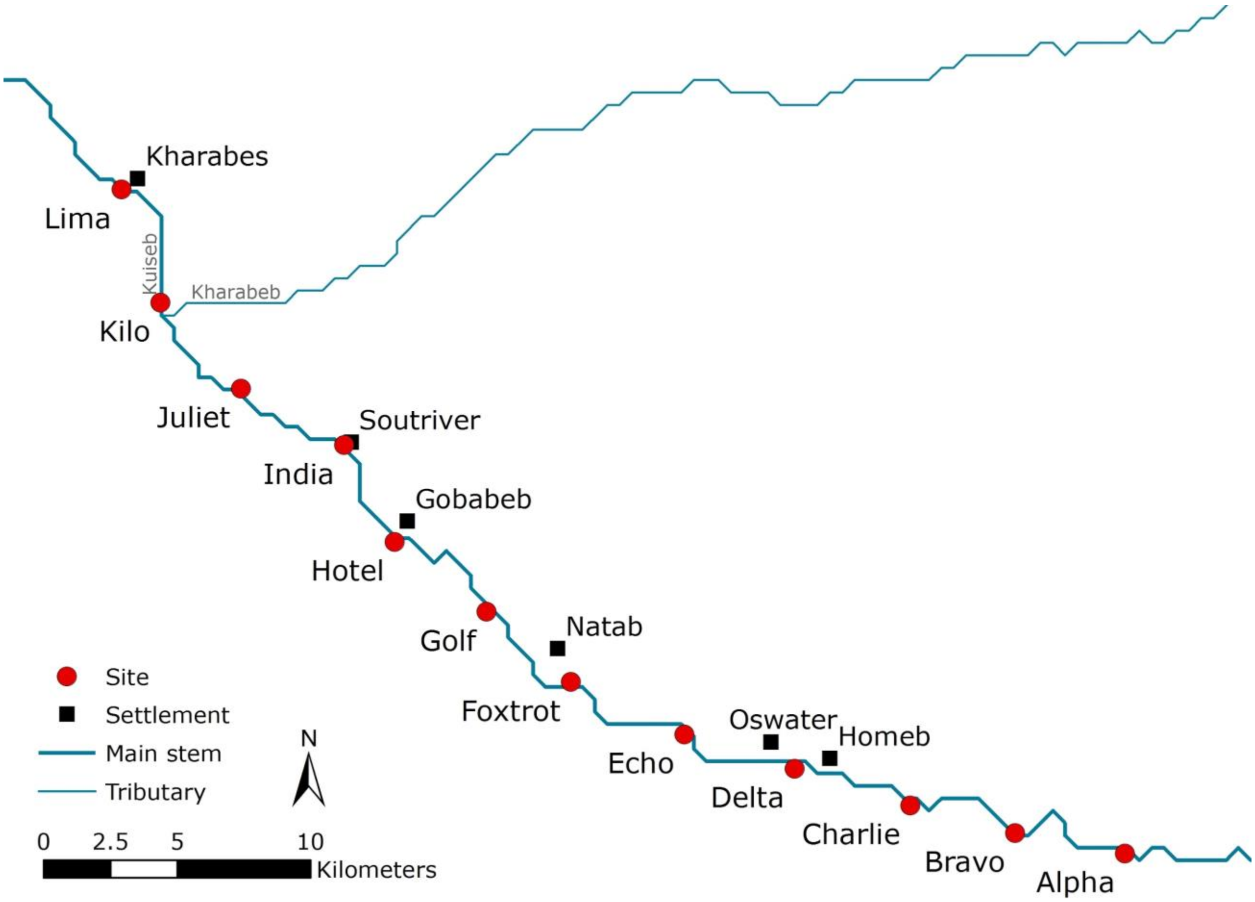

Figure 1. The 65-kilometer study area stretch showing transects and settlements (Source: Morgan 2017).

Cattle Abundance and Health

Complete Enumeration

In order to gauge the populations of wildlife and livestock species a complete enumeration of all animals was performed. Starting upstream 5 kilometers above transect Alpha, every cow, sheep, goat, donkey, and wild ungulate species observed from the track we traveled along the Kuiseb riverbed was recorded as we drove downstream, ending 5 kilometers past our final transect Lima. For this census method the study site was expanded by 10 km in order to include livestock that had wandered into the area immediately outside of the initial study area. The enumeration was done in the span of one day to prevent recounting.

Mark and recapture

In addition to complete enumeration, we used the mark and recapture method along with the Lincoln-Peterson estimator to approximate the amount of cattle in the study site. This method is suitable for this study site because the system is closed and a proportion of the cattle are marked with unique identification ear tags. By writing down identification numbers we essentially “marked” cattle, and by writing down the total number of cattle sighted, we were able to determine the specific proportion of these marked to unmarked cattle.

The formula for the Lincoln-Peterson estimator is listed below:

$$N = Kn/k$$

Where N is total population size, K is the number of animals captured on the second visit, n is the number of animals marked on the first visit, and k is the number of animals recaptured that were marked.

On day one between the hours of 16:00 and 19:00 starting at transect Alpha and ending at transect Hotel every head of cattle was recorded, along with every identification number. On day two between the hours of 16:00 and 19:00 starting at transect Hotel and ending at transect Lima every head of cattle was recorded, along with every identification number. This data was compared with the data from our complete enumeration day, in which we also recorded cattle identification number along with total cattle counts. We then applied the Lincoln-Peterson estimator (Lettink & Armstrong 2003) to approximate total number of tagged cattle and multiplied this by the proportion of untagged to tagged cattle to ascertain cattle population size.

Cattle Body Condition Scores (BCS)

We used a body condition score index template to determine the health of cattle that were identified during the 3-day livestock census (Appendix 1). Individuals were scored with values 1-5, with 5 indicating the most body fat and suggesting highest health. Cattle were scored using the same template regardless of age, sex, or position. This information was useful for evaluating the effects of tree pod productivity and settlement proximity on cattle health. Since each cow’s geographic location was recorded, the spatial distribution of body index scores may reveal existing correlations between cattle health, distance from Topnaar settlements, and proximity to areas of high pod productivity.

Abundance and Productivity of Acacia erioloba and Faidherbia albida

Kuiseb River Transects and Pod Productivity Measurements

To assess the overall pod productivity of *A. erioloba* and *F. albida* trees in the Kuiseb River study area, we first divided the river into 12 transects identical to those used by Morgan (2017), designated as Alpha, Bravo, Charlie, Delta, Echo, Foxtrot, Golf, Hotel, India, Juliet, Kilo, and Lima in an upstream to downstream order (Figure 1). We chose to utilize these transects due to the abundance of ecological data previously collected from them. In studying the pre-existing transects, we were able to build upon the wealth of knowledge developed by Morgan (2017). Within each transect, we employed four different productivity measurements on both tree species. These measurements were conducted during the morning between 8:00 and 13:00 over a four-day period. Pod density was evaluated via sample pod counts for every tree. Tree trunk circumferences were recorded at approximately breast height. Trees were subjectively rated on a productivity scale of 1-5 based on their pod density, and “herbivory plots” were cleared under one *F. albida* tree from each transect. The “herbivory plots” measured 3x3 meters and were revisited after a period of 48 hours to ascertain fallen pod counts and livestock activity. Five *A. erioloba* trees and five *F. albida* trees were randomly selected in each transect, for a total of ten trees per transect. However, tree selection was partially influenced by trunk accessibility, as many *A. erioloba* and *F. albida* trees were enveloped in brambles, making it logistically unfeasible to measure trunk circumference.

Tree Pod Counts

We recorded four sample pod counts for each sample tree to assess pod productivity by using a 10x10 cm cardboard square as an to estimate pod density. The purpose of the cardboard square was to confine the observational field of view to a uniform volume, in which we could more easily count pods to estimate pod density. To ensure consistency and eliminate additional variables, one group member was selected to conduct pod counts throughout the entire data collection period. This group member stood at four evenly spaced positions around the base of each tree, from which the square was held at arm’s length and the total number of individual pods that laid within the square’s borders was counted. Individual counts were then averaged to obtain an area specific pod count to indicate each tree’s pod density. These pod counts were intended to correlate with the subjective productivity rating we assigned to each tree.

Subjective Rating

Subjective tree pod productivity ratings were based on a ground level observation of pod density. Subjective ratings for both *A. erioloba* and *F. albida* were assigned using the uniform 1-5 rating scale, with 1 being the lowest pod density and 5 being the highest pod density. Both tree species were assessed using the same standards, instead of being assessed relative to their own species despite differing phenologies. These subjective productivity ratings were expected to positively correlate with tree pod counts.

Trunk Circumference

Tree trunk circumferences were measured and recorded using a rolling measuring tape. Circumferences measurements were collected at approximately breast height. This method was intended to help us determine whether a correlation exists between tree circumference and the other metrics of productivity that we tested, such as the average pod density, subjective rating, and canopy cover size. Subjective tree pod productivity ratings were expected to positively correlate with tree pod counts from method 1.

Canopy Cover

The canopy cover areas of the *A. erioloba* and *F. albida* trees that we sampled were determined using imagery collected from an unmanned aerial vehicle (UAV) in 2016. The coordinates we gathered using the GPS device were mapped on the UAV-derived orthophotos at each site. The area of each tree crown was then calculated by drawing a polygon to represent each crown and calculating its area in ArcMap 10.4.1. This was used to develop a relationship between canopy size and our pod density measurements, which could be applied to other trees in the study area to estimate pod productivity at a broader scale. If a correlation were to exist between canopy cover and our pod density measurements, canopy cover could potentially be used as a proxy for predicting pod productivity over larger expanses of the Kuiseb River, which would streamline similar studies in the future.

Relationships between livestock and pod-producing trees

Tree and Livestock Distributions

In addition to obtaining a complete census of livestock within our study area, we recorded every animal's geographic location at the time we encountered them on a GPS device. Plotting these coordinates on a satellite imagery map allowed us to acquire a visual representation of where cattle and other livestock were most abundant along the lower Kuiseb River. Coordinates were also recorded for the *A. erioloba* and *F. albida* trees that were measured for pod productivity. Plotting these data sets on a satellite imagery map and comparing their respective distributions to one another helps inform an understanding of the relationships between tree distribution, cattle distribution, and their respective distances from Topnaar settlements. A visual representation of cattle and tree distribution, and tree pod productivity in relation to settlement location may simultaneously answer two questions: 1). Are cattle and other livestock most abundant in areas of high pod productivity? and 2). How far are cattle inclined to travel away from settlements in order to access areas of high pod productivity?

Sampling Spatial Heterogeneity in Transects (SSHIT) Method

In order to assess livestock activity and utilization of tree pods, as well as tree pod productivity, we conducted research using the SSHIT method, which was established by Grotz et al. during the Dartmouth program in 2015. Unlike prior studies utilizing this method in 2015 and 2016, we focused solely on the enumeration of cow and donkey dung, and of *F. albida* and *A. Erioloba* pods. For this method, we examined a 20 km section of the Lower Kuiseb River by traveling 10 km upstream and 10 km downstream from the Gobabeb Research and Training Center campus. Mirroring the 2016 Dartmouth group's SSHIT method application, this river section was divided into increments of 2 kilometers (Freehafer et al. 2016). Collecting data from the same transects would allow us to compare our findings to those from previous years and make inferences about tree pod utilization and livestock movement. At each of these 10 sites, we collected data from 50x2 meter transects situated behind the first line of trees, and from parallel transects 20 meters farther from the channel (see figure 2). Thus, for each site along the river, four transects were studied.

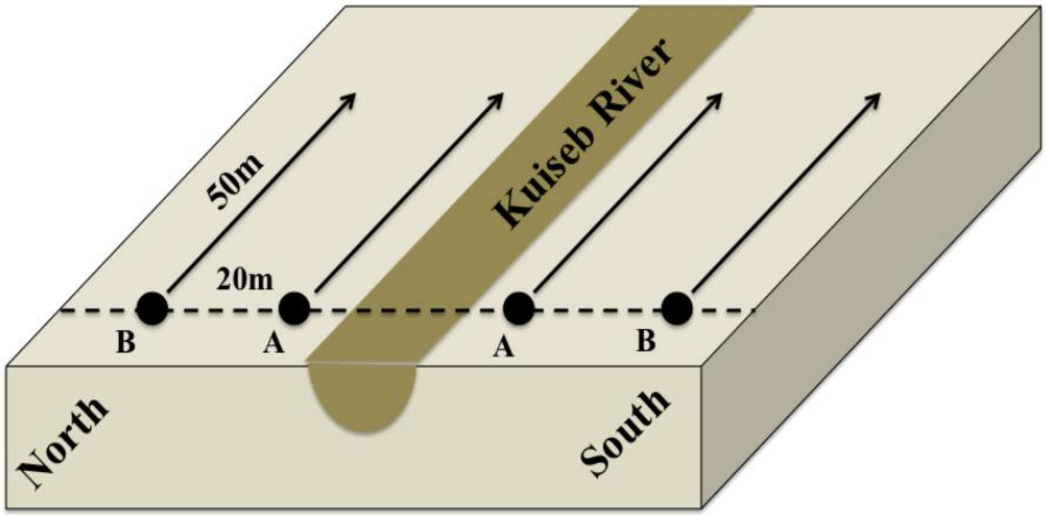

Figure 2. Diagram of the Kuiseb River transects used in each of the eleven 2 km sections during SSHIT method data collection (Source: Grotz et al. 2015).

Herbivory plot

Herbivory plots were made by clearing 3x3 meter areas underneath one *F. albida* from each transect. *F. albida* was selected because it was in the midst of its most pod productive time of year. These plots were intended to assess both livestock utilization of tree pods as a food source and tree pod production. Markers were placed in each corner of the plots in order to make them more recognizable and easier to locate upon revisitation. The total number of pods were counted prior to clearing of the plot, and preexisting dung, tree pods, and other debris were then removed. Once cleared, the plots were left and revisited after approximately 48 hours. Upon revisitation, we recounted the number of tree pods, identified and counted dung from various livestock species, and noted any livestock or wildlife tracks traversing the plot.

Methods for Determining Carrying Capacity

We employed a commonly used method for determining a rough short term estimate for livestock carrying capacity (Frost 2017). Using the data we gathered and data from the literature, annual forage production in the study area was calculated and divided by one standard animal unit year. A standard animal unit month is the amount of forage needed for one lactating 494 kg cow in one month, this number was multiplied by 12 to get a standard animal unit year (Meehan et al. 2016). In order to estimate the total number of individual *A. erioloba* and *F. albida* trees in the study area, the species densities of these pod-producing trees in each of our transect blocks (same as Morgan 2017, the source for tree numbers) were applied to approximately ten 500-meter segments spanning 2.5 kilometers in either direction along the river bed. These densities were multiplied by the width of each 500-m segment to estimate the number of trees in each segment. The sums of these segment counts were used as the estimates of the total number of *A. erioloba* and *F. albida* in the entire study area. All this information on resource availability and resource needs were inputted into the following equation to generate an estimate of study area carrying capacity in standard animal units per year:

$$C = (AN + Fn) / (U(12))$$

Where C is standard animal units per year, A is the yearly yield of pods per one *A. erioloba* tree in kilograms, N is the number of acacia trees, F is the yearly yield of pods per one *F. albida* tree in kilograms, n is the number of *F. albida* trees and U is the kilograms of dry matter consumed per month for one animal unit month.

Statistical analysis and GIS Mapping

We used JMP Pro 10.13.1 to determine if there were statistically significant relationships between different variables collected in our data. Linear regression was used to analyze the relationship between various tree productivity measurements.

We collaborated with Bryn Morgan to construct spatial maps using ArcGIS 10.4.1. Satellite imagery was used to pinpoint settlement locations, and species locations were placed on the map using GPS coordinates.

Results

Abundance and Health of Cattle

Complete Enumeration

We sighted 290 cattle and 277 goats in the riverbed during three census drives upstream and two downstream. The spatial distribution of cattle is presented in Figure 3 while the spatial distribution of goats is in Figure 4, with both showing marked heterogeneity in their space use. Because the censuses were conducted over the course of four days, many individuals are likely incorporated into these figures more than once. On the last day, however, we avoided duplicate counts by driving down the entire 65-kilometer study site, reflecting a complete enumeration of cattle (130 individuals) visible from the riverbed.

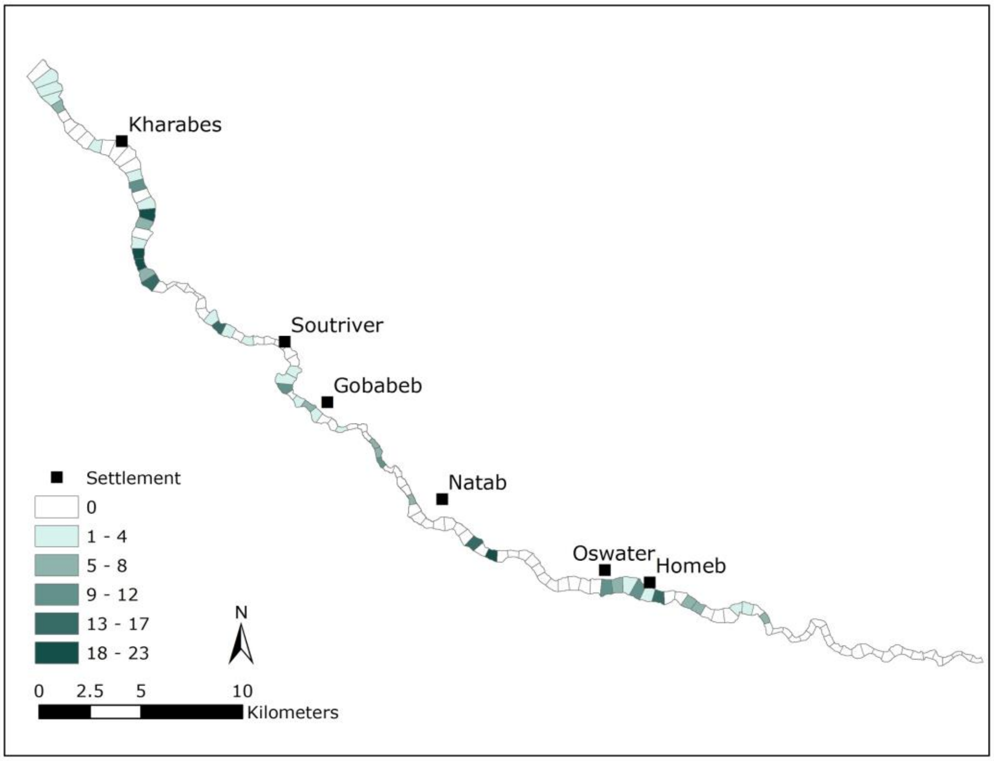

Figure 3. Heat map showing the distribution of cattle spottings (N = 290). The top left corner is the furthest downstream point of the study site, and the bottom right corner is the furthest upstream point.

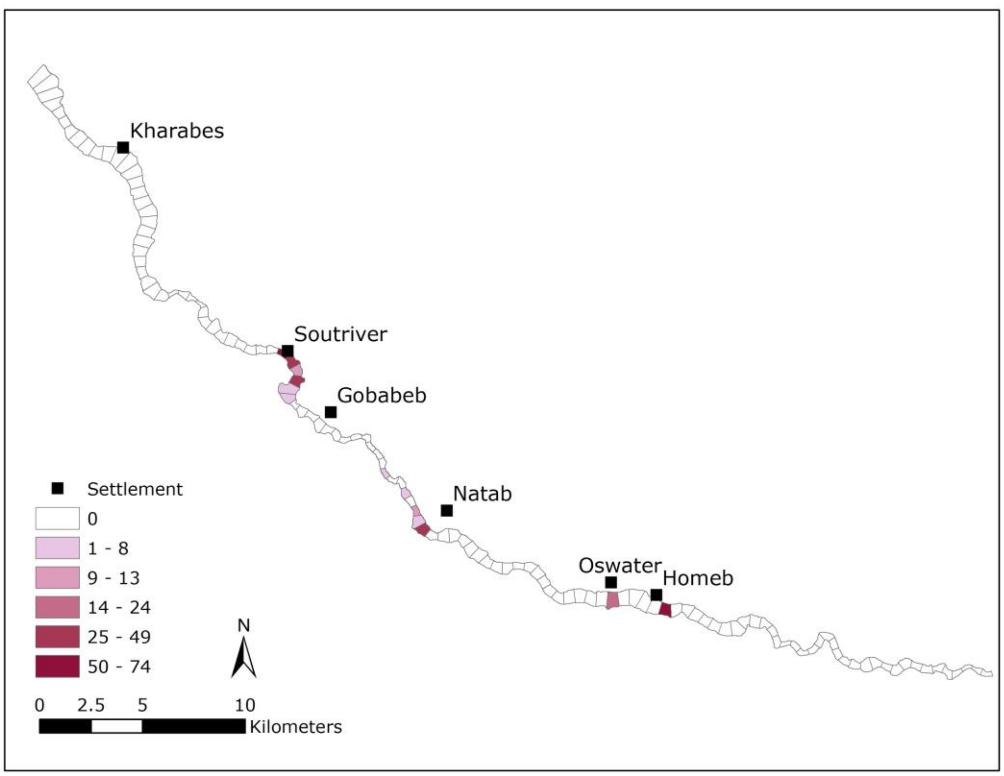

Figure 4. Heat map of goats along the study site (N = 277).

Mark and Recapture Method

We saw 41 tagged cattle on the first day and 43 tagged cattle on the second day. Out of the 43 tagged cattle observed on the second day, 18 had previously been recorded. Knowing this information allowed us to apply the Lincoln-Peterson estimator:

$$N = Kn/k$$

$$N = (43)(41) / (18)$$

$$N = 98$$

We determined the total population size of tagged cattle to be approximately 98. The proportion of total cattle to "recaptured" cattle on the second day was 3.22:1, so by multiplying this proportion by the estimated total population of tagged cattle we determined the total population of cattle in the study region to be approximately 316.

Wildlife Sightings

In addition to the cattle and goats, we recorded observations of eleven other species on the census drives (see Table 1).

Table 1. The 12 different animals encountered in the study area and their frequencies (N = 791).

Species	**Sightings**
Cattle	290
Donkey	97
Goat	277
Sheep	12
Dik dik	1
Oryx	11
Springbok	15
Ostrich	2

Jackal	3
Guinea Fowl	3
Rooster	2
Dog	1

Wildlife sightings occurred more frequently towards the ends of the study site away from the settlements and also away from the livestock groups. A herd of springbok between Gobabeb and Natab was one exception, as seen on Figure 5.

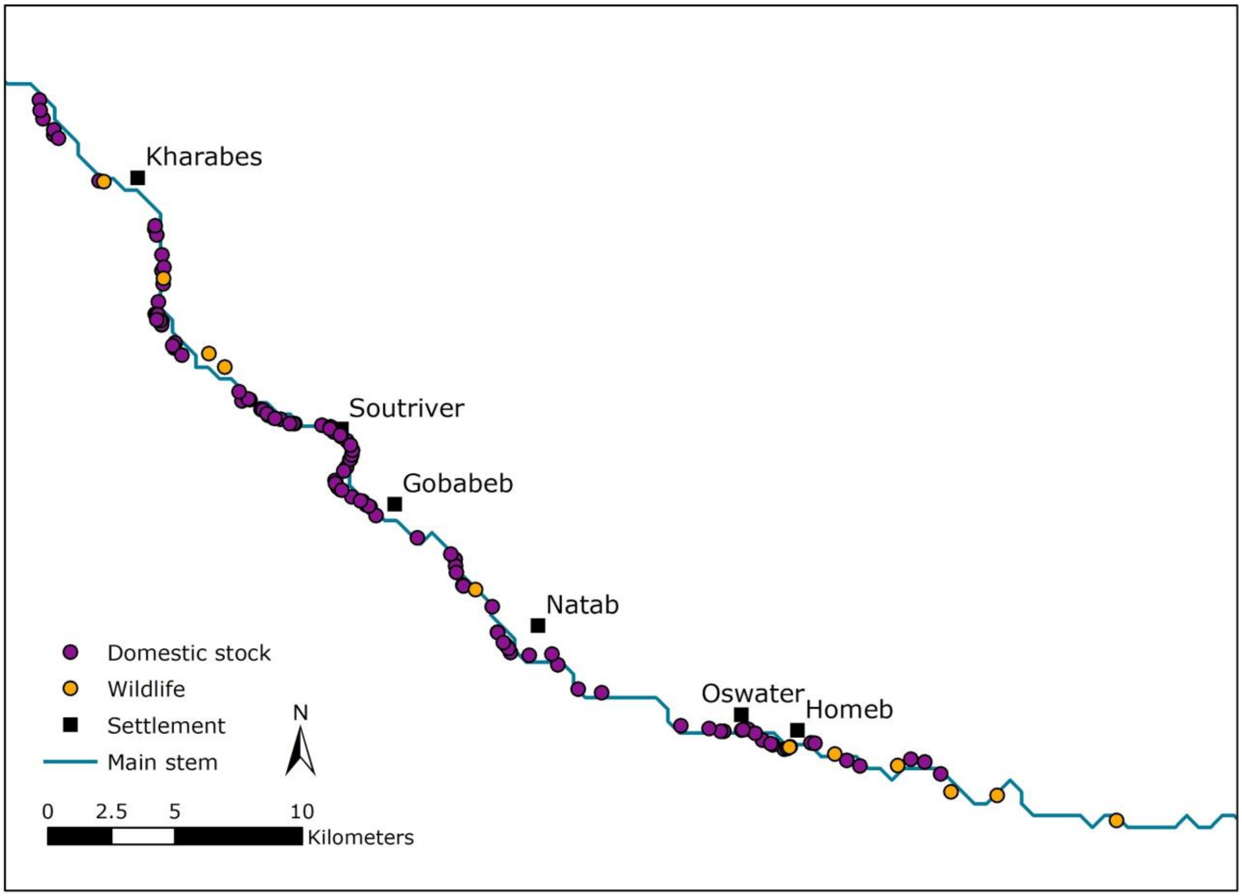

Figure 5. Map showing the spatial distribution of both wildlife and livestock (N = 788). The livestock species were cattle, goats, sheep, and donkeys.

On average, the wildlife were more than twice as far from the settlements than were livestock, a difference that was statistically significant (t-test, $N = 788$, $p < 0.0001$).

Table 2. average distance of animal types from their closest settlements. The livestock category includes cattle, goat, sheep, and donkeys.

Animal Type	**Mean Distance from Closest Settlement**
Livestock	3.212 kilometers
Wildlife	8.048 kilometers

We assigned each animal to its nearest transect and found that the most amount of cattle were found in Kilo and Delta, while the most goats were seen in India and Delta.

Table 3. The amount of animals found in or around each transect block (N = 793).

	TRANSECT											
ANIMAL TYPE	**Alpha**	**Bravo**	**Charlie**	**Delta**	**Echo**	**Foxtrot**	**Golf**	**Hotel**	**India**	**Juliet**	**Kilo**	**Lima**
COW	0	5	15	47	20	15	28	15	17	28	83	28
DIK DIK	0	0	1	0	0	0	0	0	0	0	0	0
DOG	0	0	0	1	0	0	0	0	1	0	0	0
DONKEY	0	0	0	22	11	6	2	11	21	28	2	10
GEMSBOK	10	1	0	0	0	0	0	0	0	0	0	0
GOAT	0	0	0	95	0	33	23	1	167	0	0	0
GUINEA FOWL	0	0	2	1	0	0	0	0	0	0	0	0
JACKAL	0	1	0	0	0	0	0	0	0	1	0	1
OSTRICH	0	0	0	0	0	0	0	0	0	2	0	0
ROOSTER	0	0	0	0	0	2	0	0	0	0	0	0
SHEEP	0	0	0	8	0	0	0	0	12	0	0	0
SPRINGBOK	0	0	0	0	0	0	5	0	0	0	10	0

The number of cattle significantly decreased with distance travelled upstream (Figure 6; R square = .29, N = 12, p = 0.0020).

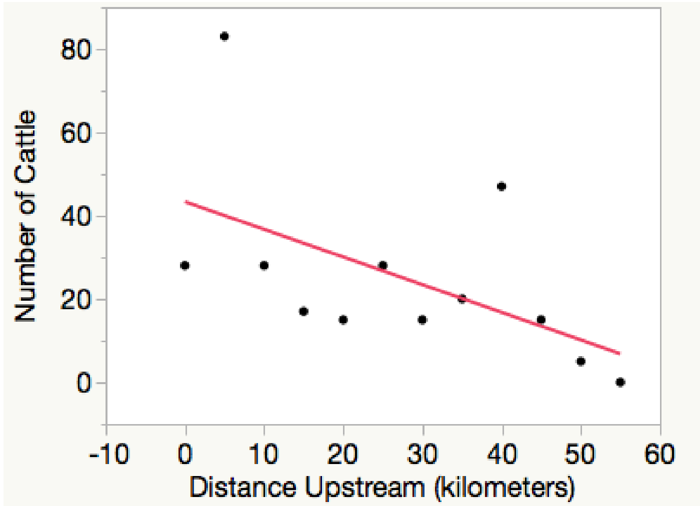

Figure 6. A moderate negative correlation between cattle abundance and kilometers upstream. Each point represents one transect (Alpha-Lima).

Cattle Body Condition Scores (BCS)

Out of our combined counts of livestock over the three-day data collection period, we assessed 102 cows for body condition. Most cows received a body score of 2 or 3, a few cows received a 1 or 4, and no cows received a score of 5. The average body score across all scored cattle was 2.7.

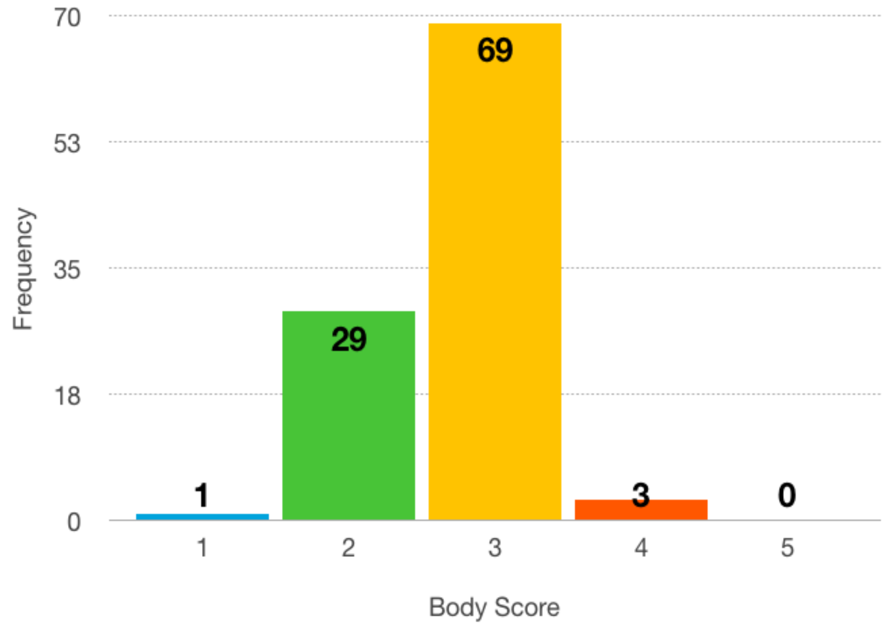

Figure 8. Frequency of individual cows' Body Condition Score recorded during census methods.

We found no significant relationship between body score and distance or angle from closest settlement. However, as shown in Figure 9, 80% of cows were spotted upstream from their closest settlement (mean angle from closest settlement less than the absolute value of 90 degrees, see Appendix 2).

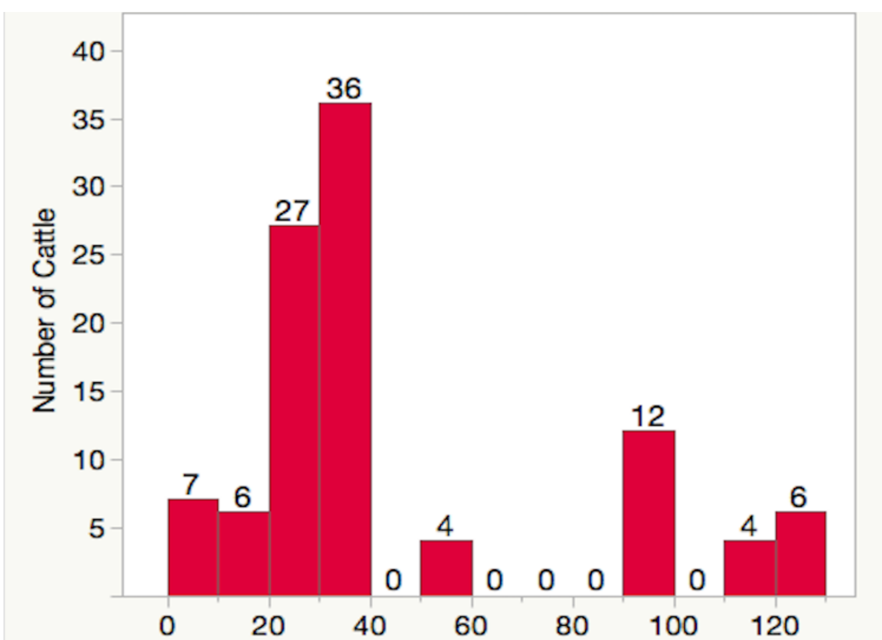

Figure 9. The absolute value of the angle cows were sighted at from the settlement they were closest to (N = 100).

Abundance and Productivity of Trees

Tree Productivity Measurements

We collected data from 60 *F. albida* trees, but only 56 *A. erioloba* trees due to the low abundance of *A. erioloba* individuals in transect Juliet. The *F. albida* trees we examined had higher average pod counts (t-test, N = 116, $p < 0.0001$) and subjective productivity scores (t-test, $p < 0.0001$) for every transect. Two additional t-tests were conducted between the species and their mean productivity scores and mean trunk circumferences. The p-values were <.0001 and .0024 respectively, indicating statistically significant differences between these productivity measurements and tree species as well.

Table 4. The average pod count, productivity score, and trunk circumference for *F. albida* and *A. erioloba* trees in each transect (N = 116).

	Faidherbia albida pods				*Acacia erioloba* pods			
Transect	Mean Pod Count	Mean Productivity Score	Mean Trunk Circumference	Mean Canopy Size	Mean Pod Count	Mean Productivity Score	Mean Trunk Circumference	Mean Canopy Size
Alpha	41.70	3.2	1.94	196.76	0.15	1.0	1.04	23.58
Bravo	27.55	2.6	1.92	432.30	0.15	1.0	1.84	65.42
Charlie	29.20	3.0	2.32	346.01	1.60	1.4	1.54	62.24
Delta	56.60	4.2	3.94	519.59	2.00	1.2	1.64	239.96
Echo	25.00	2.8	2.12	145.94	2.20	1.4	1.98	87.67
Foxtrot	27.65	3.0	3.30	340.86	0.90	1.2	2.36	141.74
Golf	32.75	3.2	3.48	295.87	3.20	1.6	3.62	183.88
Hotel	20.90	2.2	2.46	234.87	3.65	1.4	1.36	81.32

India	23.35	2.8	5.34	633.56	0.15	1.0	2.86	212.12
Juliet	0.90	1.0	1.10	27.42	0.00	1.0	1.20	32.10
Kilo	1.65	3.2	3.36	436.69	1.65	1.2	2.00	134.48
Lima	15.75	2.0	2.04	115.42	0.60	1.0	1.58	30.84

We found that averaging the four pod count angles we recorded for each tree significantly correlated with the subjective productivity scores we assigned to each tree. The mean pod scores ranged from 0 to 79.25.

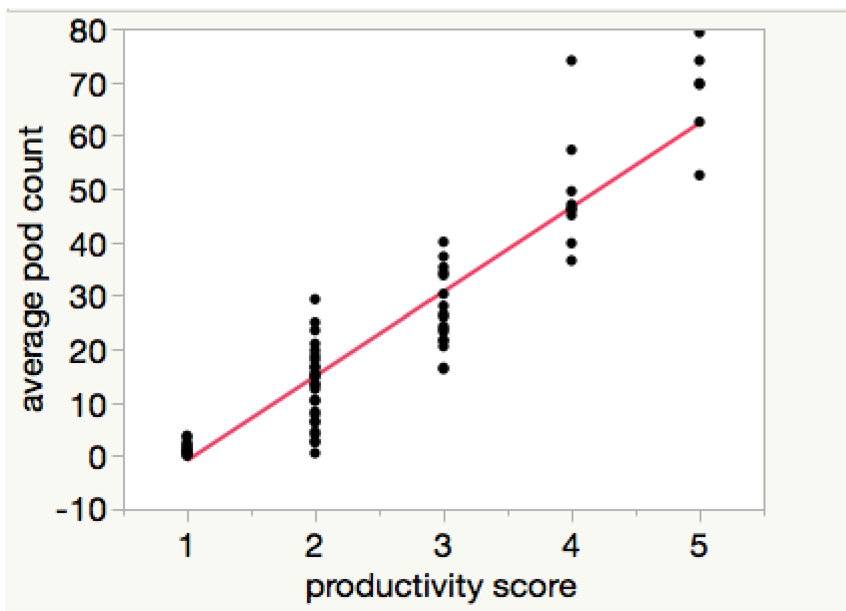

Figure 10: A strong positive relationship between productivity scores and average pod counts (R square = 0.89, N = 115, p <.0001). This relationship can be described by the equation y = 15.80165x – 16.73567.

While the positive linear relationship between productivity score and pod count was strong, the positive linear relationship between pod count and trunk circumference remained significant but explained less of observed variation in pod count (see Figure 6).

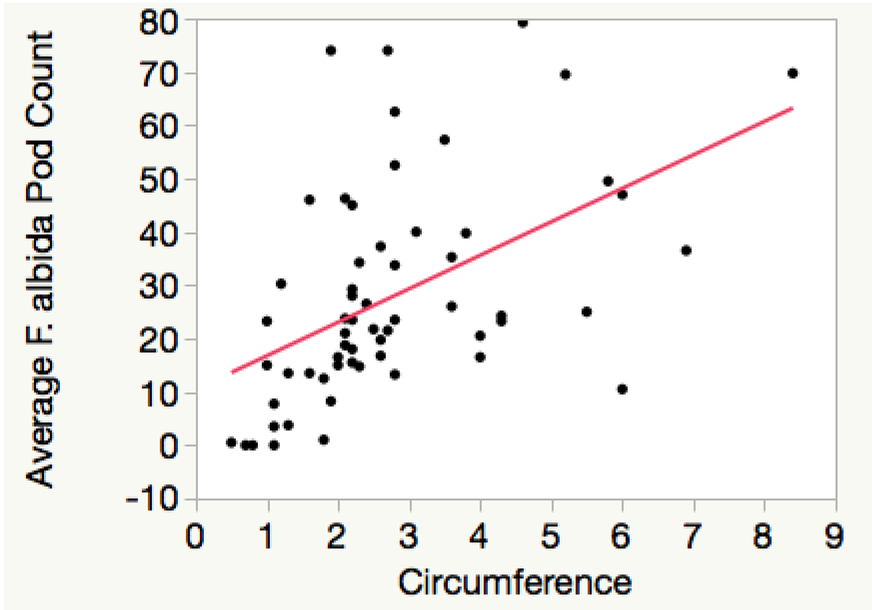

Figure 11. A weak positive relationship between pod count and trunk circumference described by the equation y = 0.03467x + 1.86223 (R square = 0.25, N = 116, p <.0001). Circumference was measured in meters.

There was a moderate positive correlation between the canopy area (m^2) and average pod count for each focal *F. albida* tree during the study period A separate analysis of *A. erioloba* trees revealed no significant relationship between canopy and pod count during this time of year which is out of season for their pod production phenology.

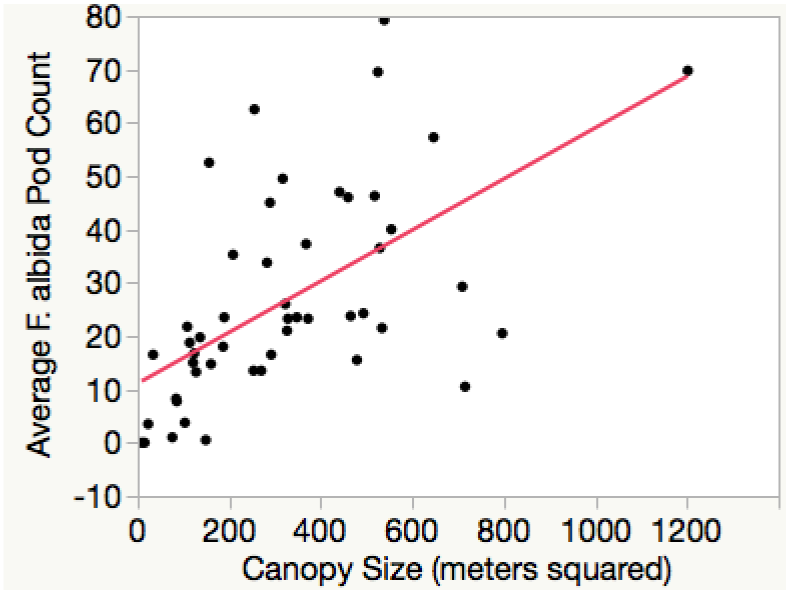

Figure 12. A moderate positive correlation between canopy area and pod count described by the equation y = .04795x + 11.10930 (R square = 0.35, N = 50, p <.0001).

Mean number of pods in F. albida trees increased with distance travelled upstream (Figure 13; R square = 0.54, N = 12, p = 0.0070).

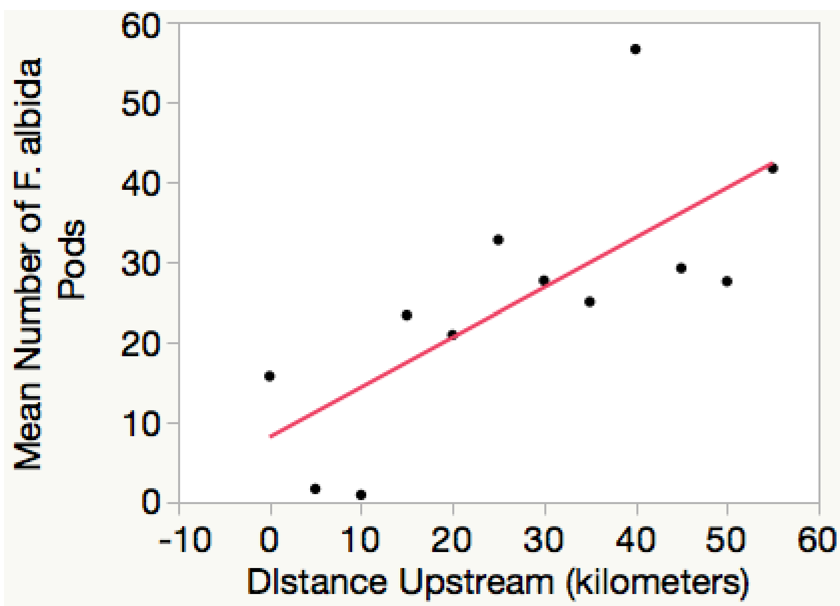

Figure 13. A moderately strong positive correlation between kilometers upstream from the start site and the average number of F. albida pods counted in the trees. Each pod represents one transect (Alpha-Lima).

Relationships Between Livestock and Pod-Producing Trees

Relative Abundance

We found a moderately strong, positive relationship between the relative abundance of the two pod producing tree species and cattle distribution (R square = .54, N = 12, p = .0064). In areas with high densities of *A. erioloba* and *F. albida*, there was a significantly higher cattle presence.

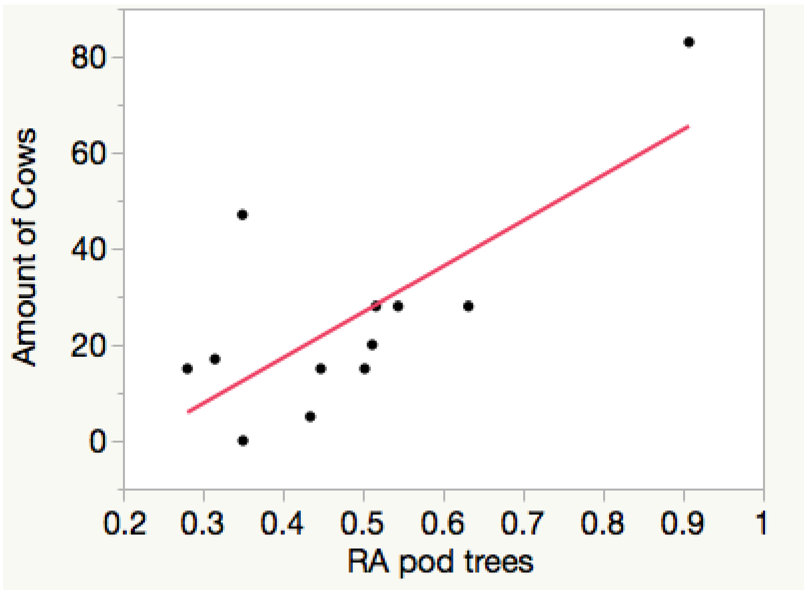

Figure 14. Relationship between relative abundance (RA) of *A. erioloba* and *F. albida* and the amount of cattle in and around each transect. Each point represent one transect (Alpha-Lima). This relationship can be described by the equation y = 95.05570x - 20.79301.

We found no significant relationships between cattle abundance and *A. erioloba* density, *F. albida* density, *A. erioloba* relative abundance, and *F. albida* relative abundance.

SSHIT Method Findings

We found no relationship between the number of dung piles and tree pods counted on the ground through linear regression. The p-value = 0.4682, meaning that we accept the null hypothesis that the two variables are not correlated.

Herbivory plots

Transects Alpha, Bravo, Charlie, Delta and Echo had the most amount of fallen pods, both initially and after 48 hours, while transects Foxtrot, Golf, Hotel, India, Kilo, and Lima had very few pods. While the herbivory plots resulted in a wide range of data, we found no statistically significant relationships between any of the variables seen in Table 5 after conducting both t-tests and linear regression. Within these plots, we found no correlation between livestock activity and the amount of pods on the ground.

Table 5. Number of pods, dung, and tracks found in 3x3 meter^2 boxes swept in the sand and checked after two days under an F. albida tree in each transect. Data from transects Hotel, India, and Juliet are incomplete due to time restraints.

Transect	Initial pod count	Second pod count	Cow dung	Donkey dung	Cow tracks	Donkey tracks
Alpha	90	52	0	0	no	no
Bravo	29	12	0	0	no	no
Charlie	177	99	3	0	yes	no
Delta	96	41	2	0	yes	no
Echo	60	82	0	0	yes	no
Foxtrot	2	3	1	0	yes	no
Golf	2	3	1	0	no	no
Hotel	2	n/a	n/a	n/a	n/a	n/a
India	2	n/a	n/a	n/a	n/a	n/a
Juliet	n/a	n/a	n/a	n/a	n/a	n/a
Kilo	4	1	2	2	no	no
Lima	5	0	2	2	yes	yes

Estimated Carrying Capacity

Morgan 2017 found the number of *A. erioloba* and *F. albida* trees in the study area to be 29,010 and 23,273 respectively. Annual pod yield for *A. erioloba* and *F. albida* was determined to be 135 kg/year and 120 kg/year maximum from previous studies (Bernard 2002) and kilograms of dry matter consumed per month for one animal unit month was determined to be 355 kilograms (Meehan et al. 2016). Using this knowledge we were able to make the following calculation for carrying capacity:

$$C = (AN + Fn) / (U(12))$$

$$C = ((135\ \text{kg})(29{,}010) + (120)(23{,}273)) / ((355\ \text{kg})(12))$$

$$C = 1{,}574.91\ \text{standard animal units/year}$$

Discussion

Abundance and health of cattle

The difference between our mark and recapture estimate of 316 cattle and our complete enumeration value of 130 could be due to several factors. First, we most likely did not see every cow in the Lower Kuiseb River during our total-transect census drive. In areas with high tree density, it was difficult to see past the banks of the river. Firsthand accounts also informed us that many cows were too weak to leave the settlements, so it was unlikely that we would ever see them. Additionally, the mark and recapture method has inherent error, as it is a tool for approximate estimation. The recapture rate was 41.9%, and according to Hilborn et al. 1975, if the recapture rate is less than 50% then the actual population size is usually 10-20% smaller than the estimate. Even without adjusting for this error, both census estimates are still significantly lower than the original hypothesis that we would find 400 cattle in the riverbed. This could be attributed to the recent drought, a lack of food, or the possibility that Joel’s estimate was inaccurate. Additionally, Joel’s estimation was conducted after research within Topnaar community settlements, rather than in the riverbed, and likely took into account cattle outside of our study area.

In order for cows to be considered healthy on the BCS scale, they must have a body index score of at least 2.5 (Bewley et al. 2008). The average body score was 2.7, suggesting that most cows are on the line between healthy and unhealthy. These findings are bolstered by the interviews conducted in communities by Bang et al. 2017. The researchers reported that they saw cattle too weak to stand, and one woman even claimed that she lost over 100 cattle in a single year. These relatively low body scores and supporting reports of unhealthy cattle in communities could be due to decreased vegetation as a result of drought in the last few years. Because we did not see the cows in the settlements, we were not able to account for the cows that were too weak to walk in the river bed. Thus, average cattle health may be even poorer than we estimated because we did not factor in these cows.

The finding that cattle numbers decrease as distance upstream increases is contrary to our initial hypothesis that we would find more cattle upstream due to increased pod density and water availability. This could be attributed to the fact that the riverbed widens and the tree density decreases downstream, which allows more space for cattle to roam, and gave us the ability to see more of them without vegetation blocking our view. There also may have been more cattle downstream and clustered around the Kharabes settlement because this was the only settlement where we did not see herds of goats. Perhaps more cows were found further downstream because they did not have to compete with other livestock for pods, or because people in Kharabes own more cattle and fewer goats than other settlements.

In addition to the cattle and goat populations, we also sighted more wildlife towards the ends of the study site away from settlements. Livestock and wildlife compete for similar resources such as tree pods and water, so our data supports the idea that wildlife is being edged out and forced away from human settlements by this inter-species competition.

Abundance and productivity of Acacia erioloba and Faidherbia albida

The higher pod density counts found with the *F. albida* trees is not surprising, given that *F. albida* trees were in their productive season when the data was collected, as they produce the most pods in September and October. In contrast, *A. erioloba* trees are the most productive between December and March (Morgan 2017). Hence, *F. albida* likely provide the most abundant food source for cattle at this time of year, but may provide fewer pods during the rest of the year.

We found that there is a strong correlation between the pod productivity scores and the average pod density counts for each tree. This supports the validity of using the cardboard square method as a means of measuring pod productivity. In future experiments, we recommend using this method to assess the viability of an *A. erioloba* or *F. albida* to produce pods.

Our hypothesis that tree pod production would increase further upstream was supported by the data. During seasonal floods, water flows from the Khomas Hochland Mountains from the East downriver to Walvis Bay on the Atlantic Ocean (Morin et al. 2009). As the water flows down the river, it soaks into the ground and is taken up by vegetation. This phenomenon is called transmission loss because water becomes increasingly more scarce downstream (Dahan et al. 2008). Perhaps the trees upstream produce more pods on average because they have had greater access to water, and this water is concentrated in a more defined channel, as seen on the cattle and goat heat maps.

Relationships between livestock and pod producing trees

Interestingly, there is a greater abundance of cattle downstream, even though there is a significantly lower density of pod producing trees downstream. This unexpected result could be due to a variety of reasons. It is possible that due to the greater density of trees upstream, a substantial number of cattle were hidden from view by tree thickets, which could have skewed our census data. However, this is unlikely because cows' mobility would then be reduced. Cows may also prefer open spaces, and correspondingly move downstream where the river is much wider and spread out. The absence of goats downstream may imply that cattle do not have to compete with goats to forage and thus more cattle can occupy these areas. Another possible explanation is that the majority of cattle are owned by Topnaar people who live in downstream settlements like Kharabes. Restricted by water sources inside their owners' home settlements, cattle may not travel long distances upstream to areas of higher pod densities even if there is more food there. However, we did find that 80% of cows we recorded were upstream from the closest settlement. Since higher densities of *F. albida* trees with higher densities of pods are upstream, it is reasonable to infer that cows move upstream to utilize food resources in these areas.

The SSHIT method findings yielded no statistically significant correlations between any of the variables that it tested for. Contrary to its employment by Freehafer et al. 2016, this method was not an accurate predictor of the total number of pods found in each transect. This discrepancy may be because of our sample size of ten transects across a 20 km stretch of the Kuiseb was too small and therefore insufficient for detecting any trends. Alternatively, the fact that cows do not strictly defecate where they eat could inhibit the effectiveness of this method. Furthermore, this method has multiple sources of error. First, the four researchers conducting pop and dung counts may different counting preferences; some may be more generous with they consider as falling within the 50x2 transect, while others may be stricter. Second, the transects in which we conducted counts were not perfectly linear due to the obstruction of impassable foliage or geologic structures. Dung counts are also easily skewed because it is often difficult to differentiate between individual piles of dung. Most importantly, the SSHIT method does not take the activity of goats into account because it is not feasible to accurately quantify their dung. However, goat activity is important to measure because they share tree pods as a food source with cattle, and may even compete for them. Hence, the SSHIT method does not account for the interaction of goats and the Kuiseb ecosystem.

The findings from herbivory plots were useful because they suggest that trees with higher pod densities drop also drop more pods, which this study assumes. These findings also support the data from pod density counts and subjective productivity scores of *F. albida*, confirming that there is indeed greater pod density upstream. The herbivory plot results may be due to the greater number of cows downstream because they collectively eat more pods at a faster rate. This would be exacerbated by the lower density of *F. albida* downstream because less forage is produced.

Livestock Carrying Capacity

Based on our census estimates and our estimation of carrying capacity in standard animal units per year, we conclude that the ecosystem's carrying capacity is not currently at risk of being breached. By converting the goats, sheep and donkey to standard animal units using conversion rates found in the literature (.15 for goats, .2 for sheep and .4 for donkey) and adding them together with cattle we reached a total demand of 398.75 standard animal units per year (Meehan et al. 2016). Even when considering all cattle along the Kuiseb river as in a 2014 census, when 540 cattle and 2,367 goats were counted standard animal units per year only reaches 895--just 57% of carrying capacity (Morgan 2017). However, our model is a rough estimate of carrying capacity and several assumptions were made and several significant variables were left out.

When we calculated carrying capacity, we assumed every single tree had the maximum yield possible for its species. Given that our average subjective rating for every transect was 2.77 out of 5 this was most likely not a realistic assumption. If we were to weigh the yields we used off of this subjective rating average, roughly 55%, carrying capacity would be much closer to being breached. In the future we suggest a more thorough study be done to determine a more accurate average pod yield per tree as well as determining seasonal variability. Placing a net under trees to collect pods over a longer period of time could potentially provide the information necessary to inform a more accurate carrying capacity.

The formula we used to calculate carrying capacity is an overly simplistic frame that does not incorporate several important variables. Some variables were omitted because our current understanding of the system did not allow us to know to what degree these variables should properly be taken into account. It is our hope that over time other groups and other studies can analyze and incorporate additional elements to create a more dynamic and precise equation. One factor that we hope future groups can assess is a harvest efficiency determinant. In other examples of carrying capacity equations, this coefficient reflected the amount of biomass that would realistically be used by cattle (Meehan et al. 2016). Through our own experiences conducting the SSHIT method and the herbivory plots, we realized that not all pods are eaten. Many pods get lost inside of bushes or buried in the soil, recycling into the system without being consumed. By conducting more thorough herbivory plots and by coming up with experiments to determine an accurate ratio of fallen to eaten pods, this factor could also be implemented into the equation to further limit carrying capacity.

During our cattle census drives, we observed cattle utilizing plants besides the *A. erioloba* and *F. albida* trees. We witnessed cows actively eating Ostrich grass and found bushes that had been heavily consumed by cattle. Further studies could explore the nutritional content of ostrich grass, or other species eaten by cattle, and the role they play in cattle diets. By incorporating as many plant species as possible into a carrying capacity formula, we can gain a better insight into the population sizes this region is able to sustain.

The formula we used calculated carrying capacity for the study region as a whole, yet due to the extreme spatial heterogeneity of the landscape and the potential reduction of mobility due to water restrictions, this may not be the most accurate way of expressing the concept. Several studies have been done exploring the relationship between carrying capacity and distances from watering sites. A 2015 study by Cowley et al. found that the majority of feeding occurred within 3 km of water even in poorly watered paddocks. They used this result to conclude that a 3 km radius from water should be used to calculate carrying capacity and stocking rates instead of a 5 km radius (Cowley & Walsh 2015). Furthermore, other sources indicate that forage located 1.6 kilometers away from water sources is only 50% utilized and resources located over 3.2 kilometers away from water are hardly utilized at all (George & Lile). Although we know this does not perfectly fit the study region, as the mean cattle distance from water was 3.4 kilometers away, we did find evidence of increased cattle activity closer to water since all herbivory plots closest to settlements had cattle tracks. Furthermore, although the majority of cattle were not found upriver where there's a larger number of pod producing trees, 80% of cattle were found upriver of their nearest water source. This could demonstrate that cattle utilize the most productive areas of land that are near to water resources. It is therefore possible that even if carrying capacity for the study area as a whole remains unbroken, localized carrying capacities around water could be breached. In the future we hope to develop carrying capacity estimates for specific watering areas, and if they are broken study the effects of this breach. If localized carrying capacities are found to be a relevant metric, we theorize that increasing the spread of watering areas throughout the study area could raise carrying capacity.

Lastly, in order to establish a more accurate carrying capacity estimate, tree productivity measurements should be conducted at different times of the year to understand how many pods *A. erioloba* trees produce during their peak season. Carrying capacity is essential for linking human socioeconomic activities and ecosystem balances, and determining animals' limiting factors and their movements is an important step towards understanding this relationship. Although our simplified estimate of carrying capacity in the region indicated livestock populations were well inside of their bounds, anecdotal evidence of recent die-offs may indicate that this is not the case. Introducing more detailed elements into our equation of carrying capacity may help provide greater insight into the population dynamics of the Kuiseb River.

Conclusion

Overall, we conclude that livestock are spatially restricted by several limiting factors in the Kuiseb river region, the most relevant being water. Water availability also affects tree pod production, density, and relative abundance. To improve water accessibility and thus cow health, more water should be made available at different parts of the river so that cows are not restricted by their one settlement. While this is a simple suggestion to make from a purely ecological framework, water accessibility in the Kuiseb River has intricate environmental and political complications. Water is extremely scarce, and while some settlements on the river have free access to boreholes, other settlements must pay for their usage (Bang et al. 2017). Balancing human and animal water needs will be an increasing challenge in the future as tension between the settlements and water companies rises, and as climate change increases extreme weather events such as droughts.

Understanding a region's carrying capacity is essential for linking human socioeconomic activities and ecosystem balances. Livestock have powerful economic significance in the Topnaar villages and in most other pastoral communities around the world. Community members invest their money in livestock, primarily due to cultural norms, but also because of their lack of other options (Olbrich et al. 2016). Banks are far away, and there are few other livelihoods for the Topnaar to pursue. Investing in livestock is unique in the sense that this capital is living and, therefore, can die. In order to sustainably grow and maintain human, livestock, and wildlife populations, carrying capacity should be considered in pastoral communities because it has important consequences for financial security and food security.

Acknowledgements

We would like to thank the Gobabeb Research and Training Centre, Gillian, and all of its staff for allowing us to use their equipment, facilities, and incredible knowledge base. Thank you to Joel, Morgan, and Eugene for the insightful and informative lectures. Additionally, thank you to Liz Studer and Flora Krivek-Tetley for their guidance and infectious enthusiasm for science. Our project also would not have been possible without Dartmouth College or the mentorship of our incredible professor Doug Bolger. Lastly, thank you to Jeff Kerby and Bryn Morgan for their invaluable support every step of the way. Jeff helped us see the big picture and Bryn pushed us to drive forward, no matter how many times we stalled.

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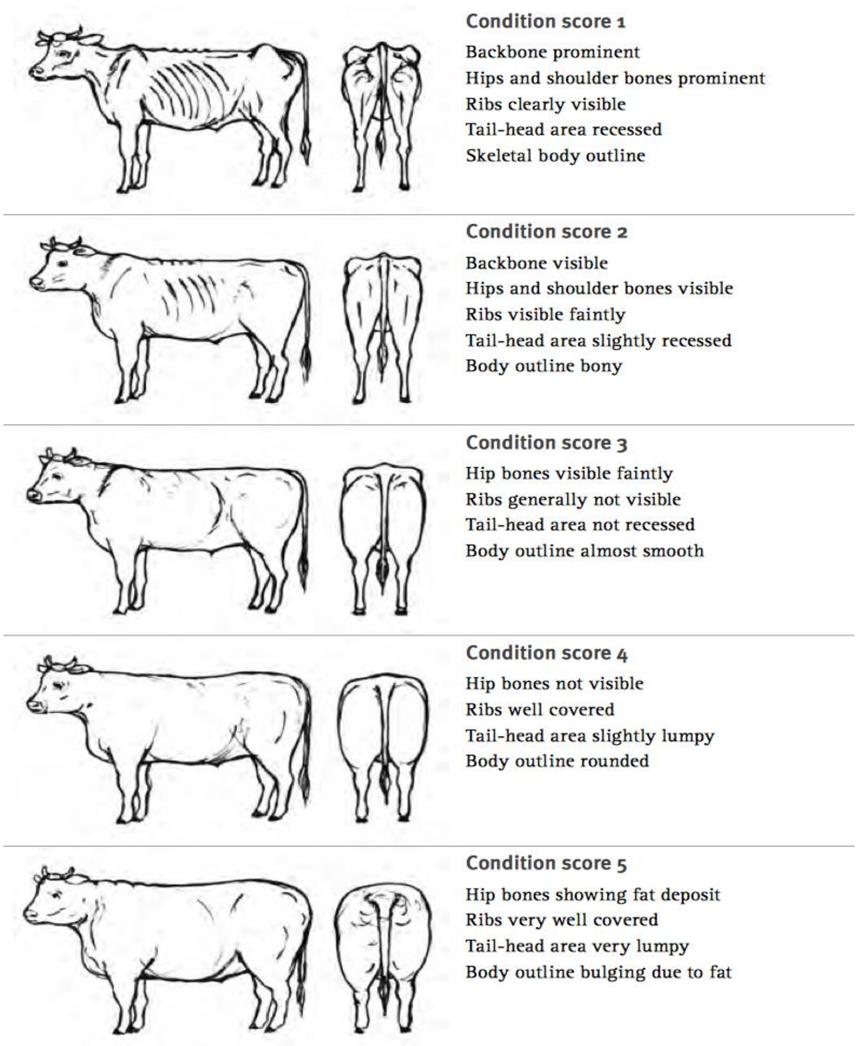
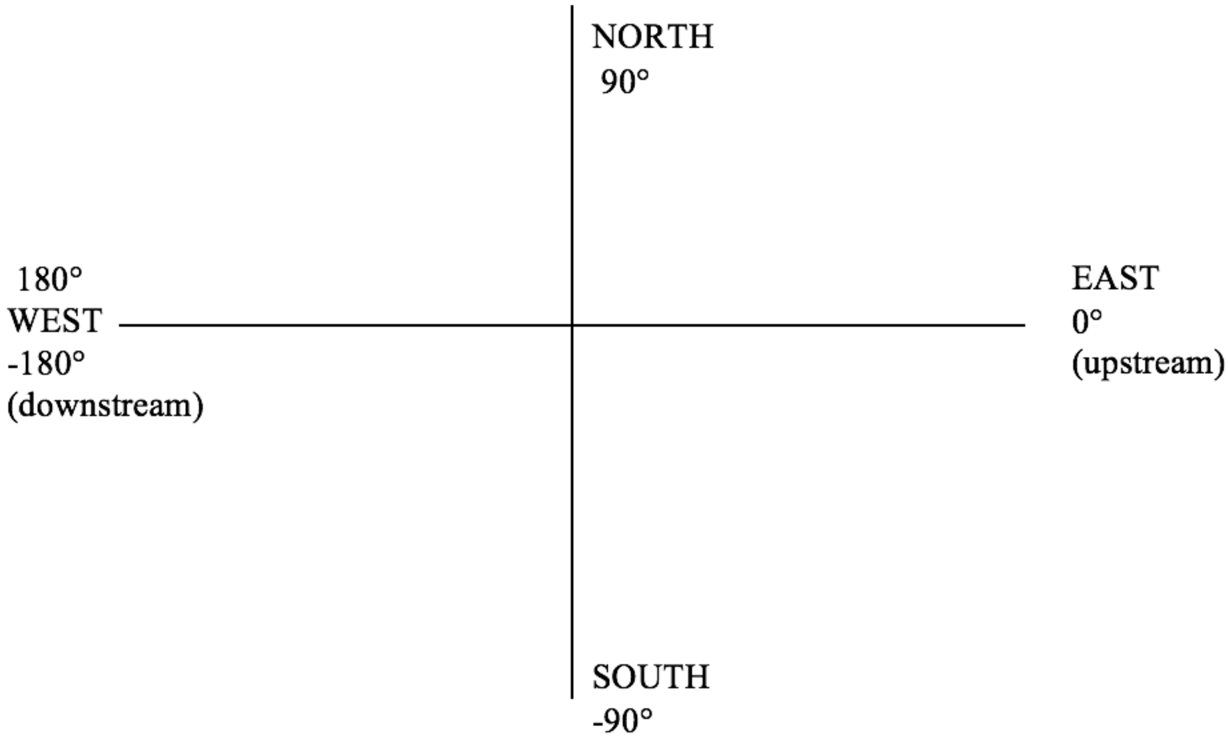
Appendices

Appendix 1: Cattle Body Condition Score Index



Legend: This scoring index was used to assess the health of cattle we sighted along the riverbed (Grotz et al. 2015).

Appendix 2: Compass rose used to assess upstream/downstream angle from village



Legend: The origin of the compass rose represents the nearest settlement to a cow. If the cow is found in the first or fourth quadrant between -90° and 90°, then it is East and therefore upstream from the settlement. If it is found between -180° and 180° then it is West and therefore downstream of the settlement. This method assumes that the river is linear.

Topnaar Livestock Management in the Lower Kuiseb: Strategies, Obstacles, and Outcomes

November 10, 2017

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Abstract

The Topnaar people living in the Kuiseb River Valley of the Namib-Naukluft National Park (NNP) have farmed livestock for hundreds of years. In the face of changing circumstances in the Topnaar socio-ecological system, we seek to (1) understand current Topnaar livestock management strategies, (2) understand the challenges faced by Topnaar livestock farmers, and (3) the effects of Topnaar management practices on livestock health and abundance. Using systems theory as a framework for our research, we drafted and administered a 22-question survey to twelve Topnaar livestock owners about animal demographics, management practices, perceived threats to livestock, and NPP polices. We also conducted individual interviews with two key informants: the Chief Warden of the NNP and the head of the Topnaar Traditional Authority. To understand the challenges faced by Topnaar livestock farmers and the outcomes of their current practices, we focused on the relationships between perceived causes of livestock deaths and management practices including vaccinations, supplementary fodder, and herding. Our data identified predation as the most significant perceived cause of small stock mortality by number of farmers impacted. In addition, we found that there was no significant relationship between vaccinations or consumption of supplementary fodder and any source of small stock mortalities. There were also no statistically significant relationships between management practices and livestock body condition scores.

Introduction

Systems theory describes a set of interrelated and interdependent parts that, when changed, exert an impact on other parts of the system and overall system function. Open systems also include inputs (or “inflows”) from and outputs (or “outflows”) to an external environment. These inflows and outflows result in outcomes—including the quantity of a “standing stock” in the system—and may cause positive or negative feedback loops. In socio-ecological systems, resource systems and governance systems set the conditions for “action situations,” in which actors transform resource unit inputs into outcomes. These socio-ecological systems are embedded in both related ecosystems and in social, economic, and political settings, all of which may impact any of the system’s primary components (see Figure 1; McGinnis and Ostrom 2014). In the Lower Kuiseb River Valley of western Namibia, the interactions between actors in the indigenous Topnaar community with the resource and governance systems of the Namib-Naukluft National Park (NNP) in the context a dynamic ecological setting comprise a complex socio-ecological system.

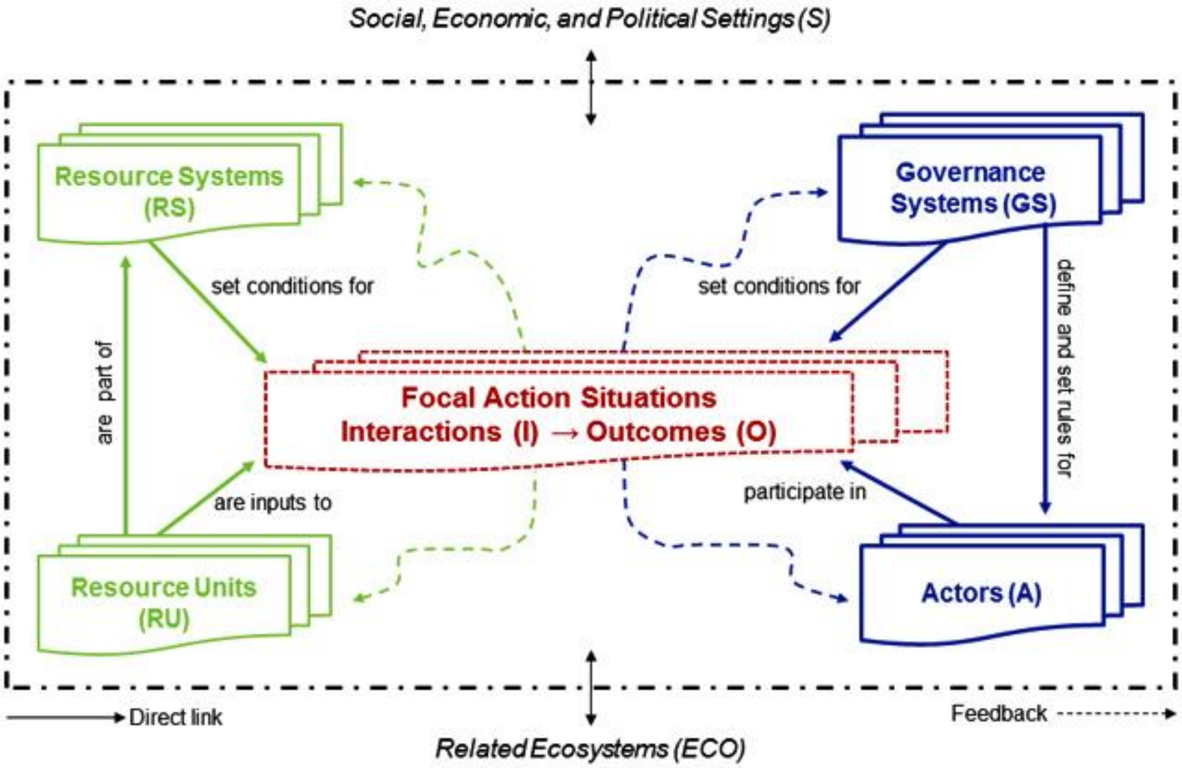

Figure 1 A Socio-Ecological System (McGinnis and Ostrom 2014)

For more than three centuries, the Nama-speaking Topnaar resided in mobile settlements scattered along the ephemeral Lower Kuiseb River. Precipitation and flooding in the upper Kuiseb catchment manifest in occasional, temporary flows of water along this ephemeral river, which recharge a subterranean aquifer. This underground water table feeds a variety of deep-rooted trees and vegetation that provide shade and nutrition to wild and domestic animals, including *Acacia erioloba* and *Faidherbia albida* (Schachtschneider and February 2010). This oasis of riverine vegetation divides barren gravel plains from the hyper-arid dunes of the Namib Sand Sea, thus creating a unique convergence of three diverse central Namib ecosystems (Schachtschneider and February, 2010).

However, the nomadic Topnaar historically ranged far beyond the Lower Kuiseb: from the relatively fertile Namibian interior to the port city of Walvis Bay. This massive land area—extending over 2000 kilometers along the Kuiseb—afforded the Topnaar a wide range of livelihood options. Traditionally, many Topnaar augmented small stock, cattle, and donkey farming in the highlands and the Kuiseb with harvesting the wild !nara (*Acanthosicyos horridus*) melons growing in the Namib Sand Sea dunes, gathering marine resources along the coast, and trading with Europeans in Walvis Bay (Budack 1983; Botelle and Kowalski 1997; Kinahan 2017). However, livestock continue to hold significant cultural and financial import for the Topnaar people. Small stock and cattle are often kept for subsistence meat and milk consumption, while donkeys provide both meat and transportation in the form of donkey carts. All livestock species are also sold to purchase necessities, and their historical significance gives them a valuable cultural role in the Topnaar tradition (Vigne 2000). Continued traditional management techniques include keeping animals in kraals (log enclosures) and herding them with human herders or dogs. Often, Topnaar livestock is managed communally but owned individually, as multiple households often share a single kraal (Widlok 2010). Historically, however, their nomadic lifestyle provided Topnaar farmers with the greatest advantage to maintaining herds in an arid, marginal landscape. Their livestock enjoyed a wide range along the Kuiseb and into interior grasslands (Kinahan 2017).

Yet, the Topnaar live in only a fraction of this historical area today. In 1884, German colonists coerced the Topnaar chief Piet !Haibib into selling a large section of the Topnaar territory (Kinahan 2017). The German colonial government of South West Africa declared a portion of this area the Namib-Naukluft National Park in 1907, and the park was expanded under the South African apartheid government in 1978. Early colonial conservationists restricted Topnaar movement within the park, subjected the slaughter of their animals to a permit system, prohibited killing problem predators, and occasionally threatened them with expulsion from the Kuiseb (Kinahan 2017). Today, the Namibian Ministry for Environment and Tourism manages the NNP (*NNP Management Plan* 2013). In theory, the policies of the Namibian government, as well as those specific to the NNP, prioritize the sustainable development of the Topnaar communities living within the confines of this park. However, this governance structure continues to limit Topnaar actors' access to livestock-enriching resource systems. First, NNP zoning laws demarcate only a small land area for livestock farming, thus eliminating the mobility that historically enabled Topnaar farmers to maintain their herds in an arid, marginal environment (Werner 2003; Magnusdottir 2013; Kinahan 2017). Moreover, human-wildlife conflict complicates the relationship between biodiversity conservation and local communities. Many Topnaar farmers contend that livestock predation has increased since the creation of the NNP **(**Botelle and Kowalski 1997). While national legislation establishes a standardized protocol for livestock predation compensation, overlapping NNP policy does not mandate any payment for livestock losses (R. Solomon, *pers. comm.*, 3 November 2017). Previous communications with Topnaar farmers also suggests complications in tangible application of these policies **(**Botelle and Kowalski 1997**)**. We attempt to understand these current practical applications through interviews with park officials and Topnaar farmers. Moreover, our study will address gaps in the existing literature by examining discrepancies between actual park legislation and Topnaar understanding of these policies.

Changes in the lower Kuiseb ecosystem also impact Topnaar livestock farmers, particularly tenuous access to the water resource system. Many extra-local actors rely on the Kuiseb aquifer; it has supplied water to Walvis Bay since 1923, and to Swakopmund and Rossing Mine since 1974 (Christelis and Struckmeier 2011). The Topnaar traditionally depended on natural springs for their water, but also began to utilize the aquifer in the late 1970s after the South African government installed bore holes to encourage settlement (Dieckmann et al. 2013). Yet, recharge is rare in the Lower Kuiseb. During the period of 1982 to 2010, groundwater is decayed a rate of nearly 14.8mm^3 per year (Benito et al. 2010). This water table degradation threatens the vegetation structure along the river that provides fodder, shade, and habitat for Topnaar livestock. Extreme climatic events such as floods and droughts are also likely to be more frequent and intense (Dieckmann et al. 2013). Like the rapidly dwindling groundwater resources, extreme floods could lead to loss of livestock, damaged infrastructure, and changing vegetation structures, as the Topnaar experienced in exceptional 2011 flood. Moreover, an analysis of flood data since 1986 indicates a possible shortening of the drought cycle from seven to ten years to three years, as surface flow did o reach the middle or lower reaches of the Kuiseb in 2007, 2010, 2013, or 2016 (Morgan 2017). Some Topnaar households have already responded to recent drought by replacing cattle with goats and sheep, which are less fodder- and water-intensive (Seo and Mendelsohn 2008; Dieckmann et al. 2013). Understanding current livestock management strategies within the context of this ecological system and the potential changes it will undergo through climate change is crucial for maintaining and improving traditional livelihoods in the Topnaar community amidst unpredictable changes in their land.

In addition, the social, political, and economic setting of rapidly changing rural demographics exerts a significant influence on the capabilities of Topnaar livestock farmers. The Topnaar have experienced a decline in their rural population since the establishment of their semi-permanent, subsistence-based desert lifestyles (Botelle and Kowalski 1997). Many young Topnaar no longer find traditional lifestyles attractive, especially after recent years characterized by drought and hardship (Titus 1998). Instead, many Topnaar seek wage employment in nearby Walvis Bay (Widlok 2000). Rural livelihoods remain dependent on livestock farming and subsistence harvesting of the !nara melon, but the lucrative pull of urbanization is rapidly changing Topnaar community structure.

These ecological, political, and social components interact in a manner that promotes unique adaptations to raising livestock in an arid environment. However, they also present challenges to maintaining large numbers of healthy livestock in the context of rapidly changing ecology and social structures. Our study analyzes the effects of these complex linkages through systems theory, focusing on the inflows and outflows that influence quantities of healthy livestock. Our three objectives are to: (1) understand current Topnaar livestock management strategies, (2) understand the challenges faced by Topnaar livestock farmers, and (3) identify the impact of Topnaar management strategies on the health and abundance of livestock.

Methods

To address our research objectives, we created a survey directed at Topnaar livestock farmers living in 12 rural settlements along the Kuiseb River Valley (see Appendix 1). Each section of the survey addressed a different aspect of livestock ownership and management, including livestock demographics, mortality rates and causes, and livestock movement. Some questions also explored perceptions of National Park regulations, and the effects of those perceptions on livestock-based livelihoods.

With the assistance of two translators, we delivered this questionnaire to a group of 12 Topnaar livestock owners and herders spread across 7 villages. One of these translators was a member of

Topnaar Traditional Authority, who scheduled our interviews and introduced us to the livestock owners.

We organized our analysis into the following sections: respondent demographics, livestock demographics, management practices, threats to livestock, and effects of management practices on livestock health and abundance. Under respondent demographics, we explored the respondents' age distribution and livestock management position (owner, herder, manager). We considered same variables for respondents' household members, and examined the main reasons respondents cited for farming livestock. These questions were geared towards understanding if and how urbanization trends influence the Topnaar socio-ecological system.

For livestock demographics, we analyzed the total number of livestock owned, the gender and age of these animals, and the average size of a herd. We also examined controlled inflows and outflows to the standing stock of Topnaar animals, including the number of livestock bought, eaten, and sold over the past year. Further, we compared the body conditions of different types of livestock we observed on Topnaar farms during our interviews using a standard livestock condition assessment metric (NSW).

Next, we sought to understand the nature and prevalence of different Topnaar livestock management strategies. The management strategies identified were: using a herder, using a dog, using supplementary feed, vaccinating livestock, and sharing a kraal with farmers outside of the immediate family. We also analyzed the length of time that livestock spent outside the kraal browsing and foraging.

To understand threats to Topnaar livestock, we assessed the most prevalent causes of livestock mortality over the past year for different types of livestock. We also identified the locations where Topnaar farmers perceived the most frequent predation incidents through a mapping exercise accompanying each survey. Using an interactive aerial map of the area around each village, we asked the Topnaar farmers to identify where predation events occur.

Finally, we analyzed how different management strategies impact Topnaar livestock loss and health (observed body conditions). We explored the relationship between human and canine herding and loss to predation using ANOVA through the statistical software JMP. Next, we explored the effect of vaccination on livestock mortalities from disease, drought, and predation. Due to a small sample size on the quantity of animal deaths from these factors, we conducted contingency analyses comparing categorical variables. These categorical variables were: whether farmers vaccinate (Y/N) and whether they lost any livestock to disease, drought, and predation (Y/N). We applied the same contingency analyses to the relationship between supplementary feed and loss to disease, drought, and predation. We also analyzed the correlations between average livestock body condition and whether farmers herd, vaccinate, or provide supplementary feed.

We also conducted semi-structured interviews with two key informants: Riaan Solomon, the Chief Warden of the Namib Naukluft National Park, and Chief Seth Kooitjie, the head of the Topnaar Traditional Authority. The goal of these semi-structured interviews was to gain more insight into the interactions between different components of the socio-ecological system that influence Topnaar livestock management. Our questions for Mr. Solomon focused on disentangling NNP policies from broader Namibian national park policies, in addition to understanding his discretionary power as a law enforcer in the park (see Appendix 5). Using the information gathered from these interviews and official NNP policy available online, we compared and contrasted how the Mr. Solomon and Topnaar farmers understand and interpret official regulations regarding predation and livestock movements.

Finally, we situated the data from our surveys and the information from these semi-structured interviews in the relevant scientific literature. We compared demographic survey responses with historical census data to reveal patterns in Topnaar livestock management practices over time. Finally, we used historical livestock census data to assess the change in total Topnaar small stock population over the past 40 years, as well as the impact of flood events on livestock populations.

Results

Respondent Demographics

Our respondents were mostly livestock owners or herders, with few having both responsibilities (Figure 2a). Respondents were mostly adults and few were senior citizens (Figure 2b)

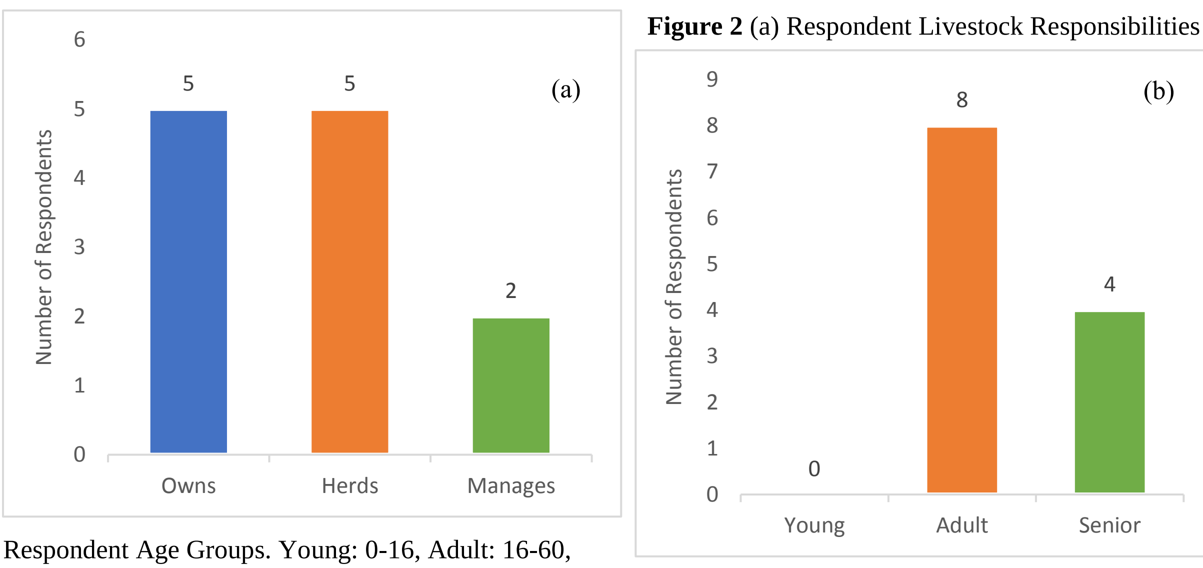

Figure 2 (a) Respondent Livestock Responsibilities (b) Respondent Age Groups. Young: 0-16, Adult: 16-60, Senior: 60+.

All of the other members respondents’ household live at home, and the majority of them are adults, with few young people and one senior (Figure 3a). More than half of the respondents’ family members manage livestock in some capacity (Figure 3b).

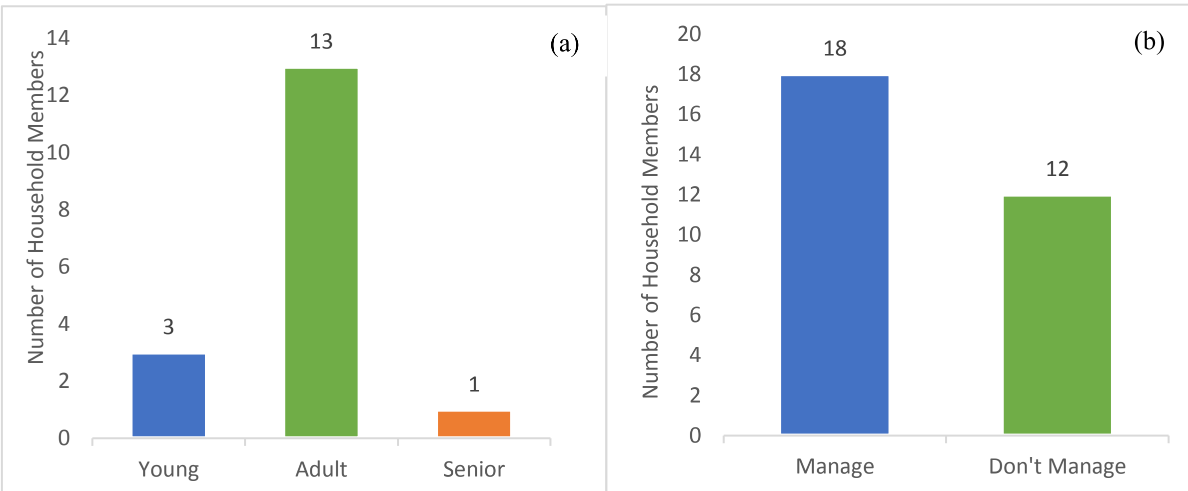

Figure 3 (a) Age Groups of Household Members (b) Number of Livestock Managing Household Members

Interviewees did not overwhelmingly cite one purpose their livestock; rather, most farmers keep livestock for multiple reasons. Most utilize their animals for consumptive purposes (i.e. milk and meat), to sell and for cultural purposes. Few see their livestock as inheritance (Figure 4).

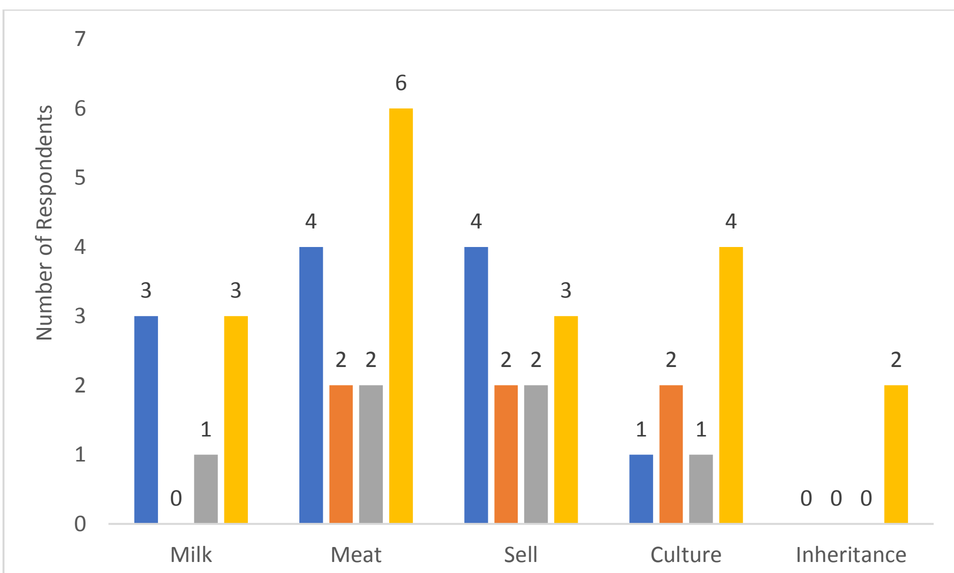

Figure 4 Reasons Cited for Keeping Livestock. Blue for Goats, Orange for Sheep, Gray for Cattle, and Yellow for Donkey

Topnaar Livestock Demographics

Table 1 summarizes our respondents' livestock demographics. All 12 respondents owned small stock, while only five owned donkey and cattle. One cattle owner had 50 cows, which skewed the total and average number of cattle owned upwards.

Table 1 Livestock Demographics Over the Past Year

	Small Stock	Cattle	Donkey
Current Stock			
Total Number	355	100	46
Average Per Owner	29.58	20	9.20
Average Per Capita	29.58	8.33	3.83
Total Female	264	100	34
Total Male	24	0	12
Inflows			
Bought	54	0	0
Total Young	67	1	10
Outflows			
Slaughtered	21	0	0
Sold	23	1	1
Predation Loss	183	1	1
Disease Loss	33	3	3
Poisonous Plants	1	0	0
Drought	33	3	0

Inflows to the standing stock of domestic animals include the 121 small stock, 1 cow, and 10 donkeys purchased or born within the last year (Table 1). 294 small stock, 8 cattle, and 5 donkeys were sold, slaughtered, or otherwise perished in the last year, and comprise outflows from the standing stock (Table 1). In total, 132 heads of livestock entered the system and 307 left the system in the past year; thus leading to a net negative flow of 175 animals (Figure 5).

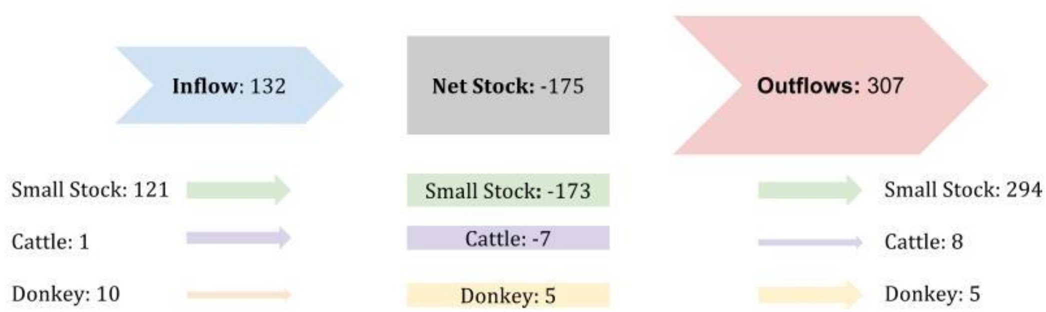

Figure 5 Total Inflow, Outflow, and Net Change of Livestock

Of 49 small stock observed in respondents' kraals, the average body condition was 2.52 on a four-point scale. Out of 11 cattle observed, average cattle condition was 2.24 on a five-point scale. Out of 2 donkeys observed, the average body condition was 2.00 on a four-point scale.

Table 2 Body Conditions of Livestock

	Small Stock (1-4 Scale)	Cattle (1-5 Scale)	Donkey (1-4 Scale)
Average Body Condition	2.52	2.24	2.00

Current Topnaar Management Practices

Our survey results showed that the majority of small stock owners use either a herder (66.67%) or a dog (50%) to control the movements of their livestock. Nearly half of cattle owners use dogs to herd their cows (42.86%), but few personally herd or employ a human herder (20%). Similarly, most small stock owners use supplementary feed for their small stock (75%) while most farmers with cattle and donkey do not use supplements for those animals (33% and 40%, respectively). 83.33% of cattle farmers vaccinate their cattle—a higher percentage than that of small stock owners who vaccinate (66.67%). Only 33% of donkey owners vaccinate their donkeys. Less than one third of interviewed farmers share their kraal with non-family members (Table 3).

Table 3 Percentage of Respondents Using Various Management Strategies

	Small Stock	Cattle	Donkey
Herd (%)	66.67	20	0
Dog (%)	50	42.86	0
Supplementary Feed (%)	75	33.33	40
Vaccination (%)	66.67	83.33	33.33
Kraal Share (%)	30		

Survey responses revealed that the time that livestock spend browsing and foraging outside the kraal differ between species of livestock. Small stock mostly return home every night, and spend an average of 6.3 hours outside their kraals every day. The results were more varied for cattle; 50% of cattle owners said that their cattle return home a few times a week, while 17% answered every night and 33% answered hardly ever. Some cattle owners clarified that sick and old cattle return home every night or a few times a week, while healthy individuals hardly ever return (Figure 6).

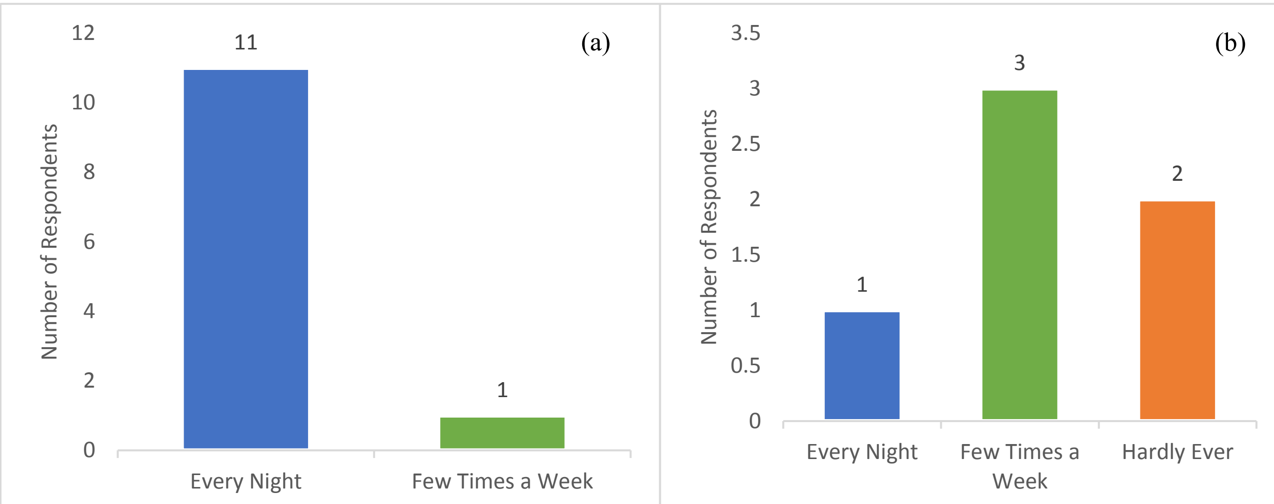

Figure 6 (a) Frequency that Small Stock Return Home (b) Frequency that Cattle Return Home

Threats to Topnaar Livestock

Survey results demonstrated that Topnaar livestock farmers lose their livestock to the following threats: predation, disease, poisonous plants, theft, and drought.

Table 4 Percentages of Farmers Citing Various Reasons for Livestock Loss

	Goat	Sheep	Cattle	Donkey
% yes to predation	83.33	66.67	16.67	16.67
% yes to disease	54.55	50	50	20
% yes to poisonous plants	8.33	33.33	20	0
% yes to theft	8.33	16.67	0	0
% yes to drought	58.33	16.67	33.33	0
% yes to other reason	18.18	16.67	16.67	0

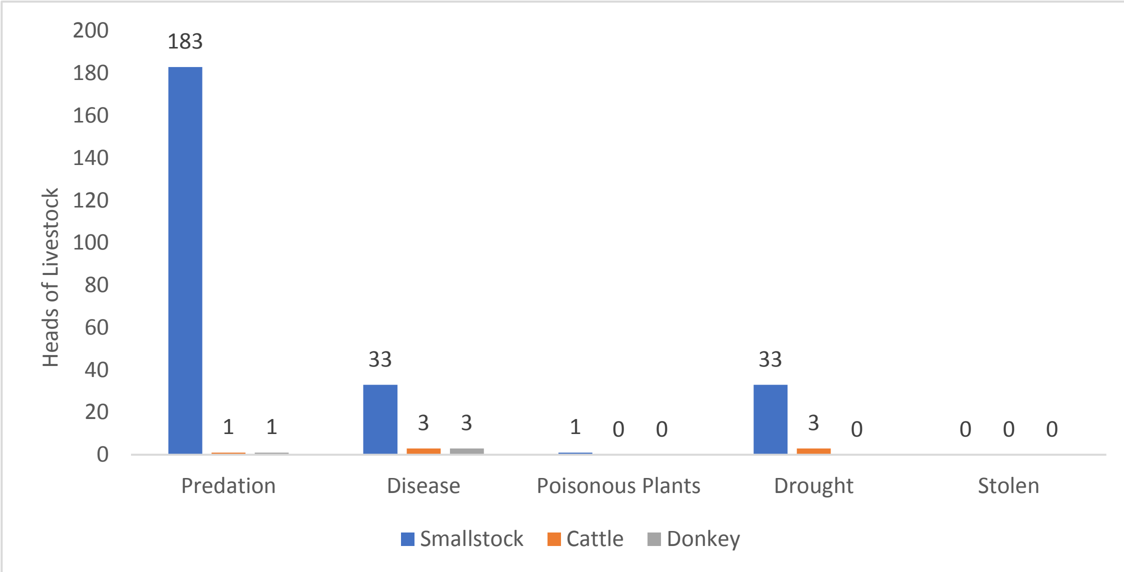

Figure 7 Number Livestock Losses due to Various Factors, By Species

Disease and predation were overwhelmingly the most frequently cited causes of small stock death. Relatively few cattle and donkey were lost to predation or disease. In general, livestock owners did not perceive poisonous plants, theft, or other causes to be serious threats to their livestock (Table 4). This was substantiated by one-way ANOVA tests on the numbers of livestock lost. Loss to predation, disease, and drought were significant while loss to poisonous plants was not (Table 5). When asked if there were any other causes for livestock losses, some farmers explained that a few of their animals occasionally mix with other herds and do not return home.

Table 5 Statistical Significance of Livestock Loss

	Predation	Disease	Poisonous Plants	Drought
Livestock Loss	185	39	1	36
Prob>|t|	0.0408	0.0475	0.0728	0.0153

We also assessed the effects of specific predators on livestock numbers. Because cattle and donkey did not experience significant losses to predation, focused our analysis on goats and sheep.

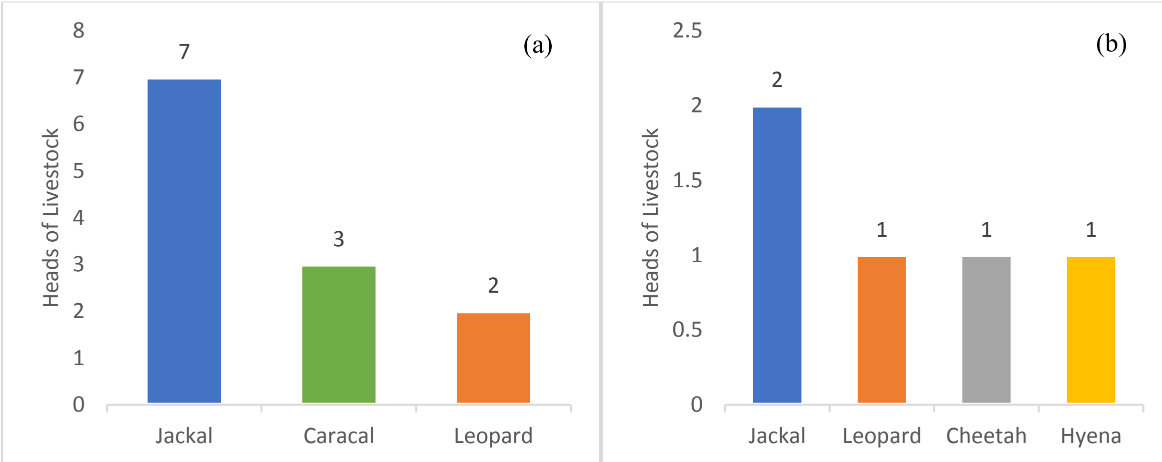

Figure 8 (a) Goat Losses to Specific Predators (b) Sheep Losses to Specific Predators

Our results show that livestock owners perceive the jackal as the main threat to goats and sheep (Figure 8). NPP Chief Warden Riaan Solomon, substantiated these findings in an interview, also naming the black-backed jackal as the main problem predator for Topnaar livestock farmers.

Figure 9 is heat map of predation sites identified by nine respondents. Topnaar farmers perceive predation mostly in the riverbed, with a few exceptions in some upstream settlements. Respondents living in Natab, Oswater, and Homeb identified predation both in the riverbed and on the gravel plains. Respondents interviewed at the same settlements often identified the same predation sites, indicated by the darker hue on several marked locations.

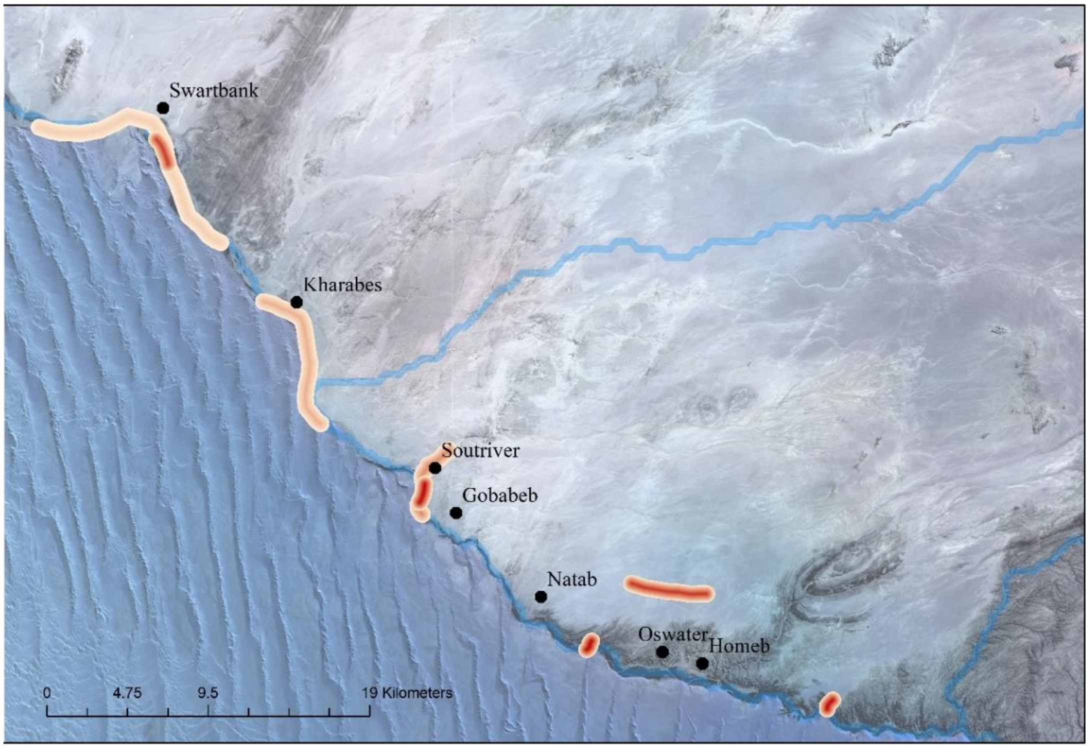

Figure 9 Predator Heat Map

Figure 10 depicts losses to disease, separated according to livestock species. We included only goats, cattle, and donkey due to a lack of data on disease in sheep. Few donkeys and sheep died from disease, but we further explored specific diseases that respondents perceived as serious threats to goats and cattle. Lung sickness is the main disease affecting both goats and cattle (Figure 11). Interviewees also demonstrated general lack of knowledge of what type of disease or illness was killing their cattle and goats.

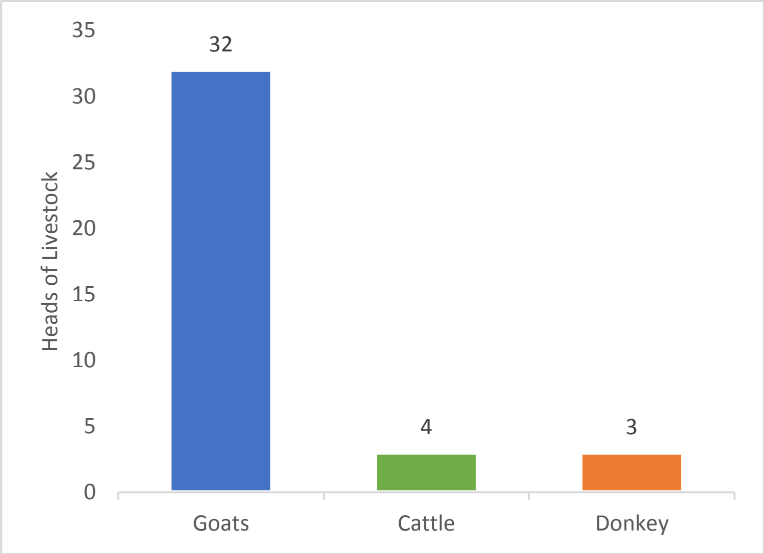

Figure 10 Livestock Deaths from Disease, By Species

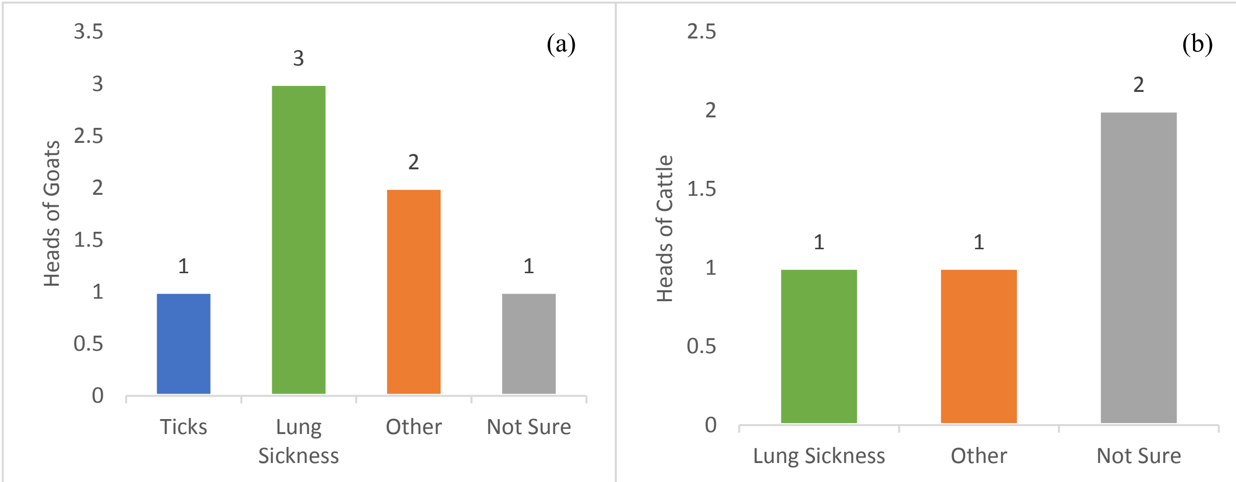

Figure 11 (a) Number of Goats Lost to Specific Diseases (b) Number of Cattle Lost to Specific Diseases

Effects of Topnaar Management Strategies on Livestock Loss and Health

Results indicate a connection between herding and livestock loss to predators. Those who herded using dogs, people, or both experienced far less predation loss than those who didn't (Figure 12). Although the sample size was too small for an ANOVA test on the different types of herding, we were able to compare more generally the difference in predation loss for those who didn't herd versus those who did (person or dog). Farmers who didn't herd lost an average of 40 heads of small stock to predators, while farmers who herded (person or dog) lost an average of only 9.4. This difference is significant at the 5% level (Figure 13). We could not perform similar statistical significance tests for cattle or donkeys due to a small sample size. We also found no significant difference between using both human and canine herders and using just one herding option.

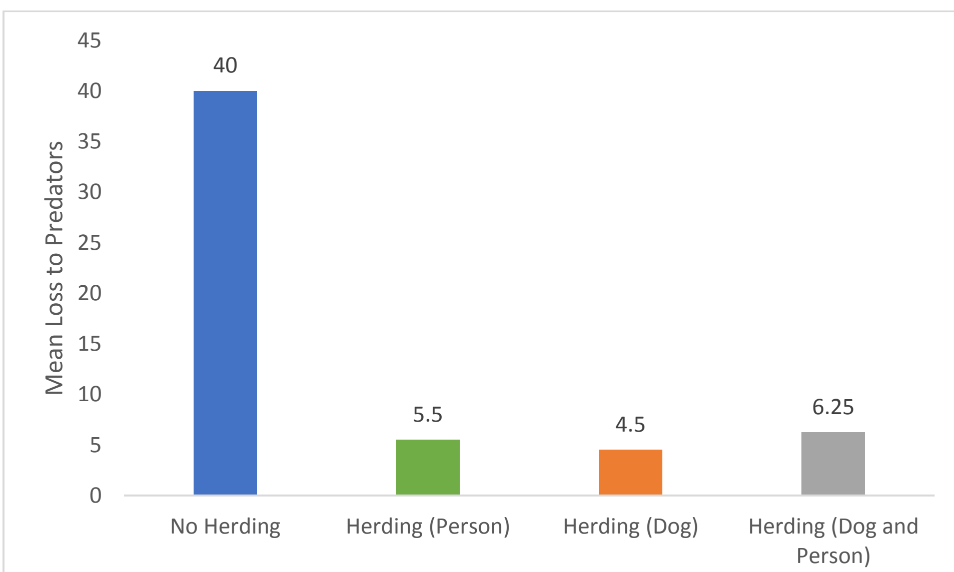

Figure 12 Comparing Mean Small Stock Loss to Predators Under Different Herding Practices

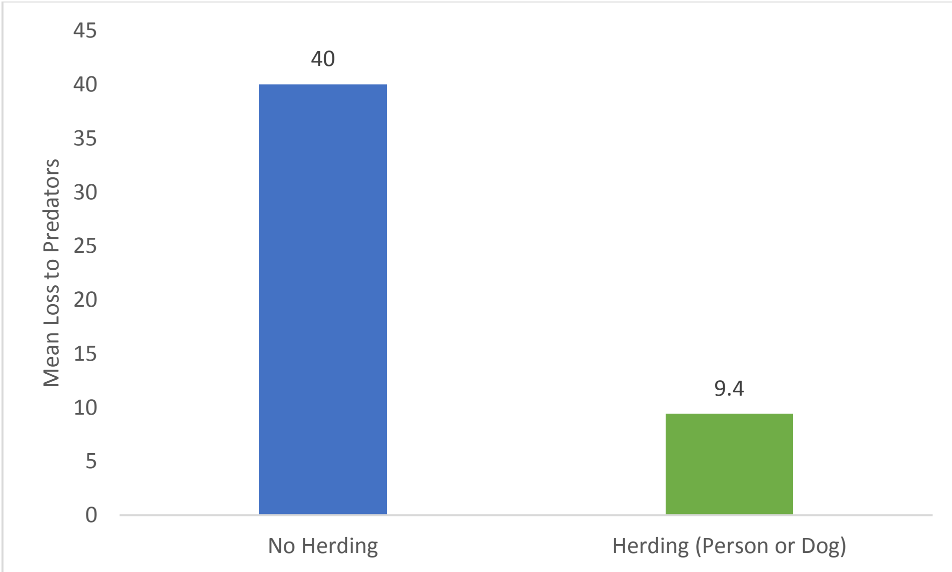

Figure 13 Mean Number of Small Stock Lost to Predators When Using Herd Dog or a Herder (N=12, F=11.2960, P>t=0.0121)

Results reveal no association between vaccination and deaths to disease, drought, or predation. We also ran a Fisher's test due to a small sample size, which also indicated no association between these variables (Table 6).

Table 6 Testing Association Between Vaccines and Livestock Loss

Test	*Prob>ChiSq*	*Fisher's 2-Tail Prob*
Vaccine vs. Disease	0.2207	0.5455
Vaccine vs. Drought	0.2733	0.5152
Vaccine vs. Predation	0.6788	1.0000

We hypothesized that the provision of supplemental feed would enhance animal health, thereby allowing animals to better defend against predators, disease, and drought. However, contingency analyses reveal no association between supplemental feed and any of those outcomes (Table 7).

Table 7 Testing Association Between Supplementary Feed and Livestock Loss

Test	*Prob>ChiSq*	*Fisher's 2-Tail Prob*
Supplement vs. Drought	0.3115	0.5227
Supplement vs. Disease	0.5018	1.0000
Supplement vs. Predation	0.2581	1.0000

Finally, an analysis of the relationship between management practices (vaccine, supplements, herding) and average body condition indicates no statistically significant relationship. However, the difference between the mean body condition of herded animals (2.63) and non-herded animals (2.17) was comparatively greater than the difference in body condition means for the wo other management practices (Figure 14).

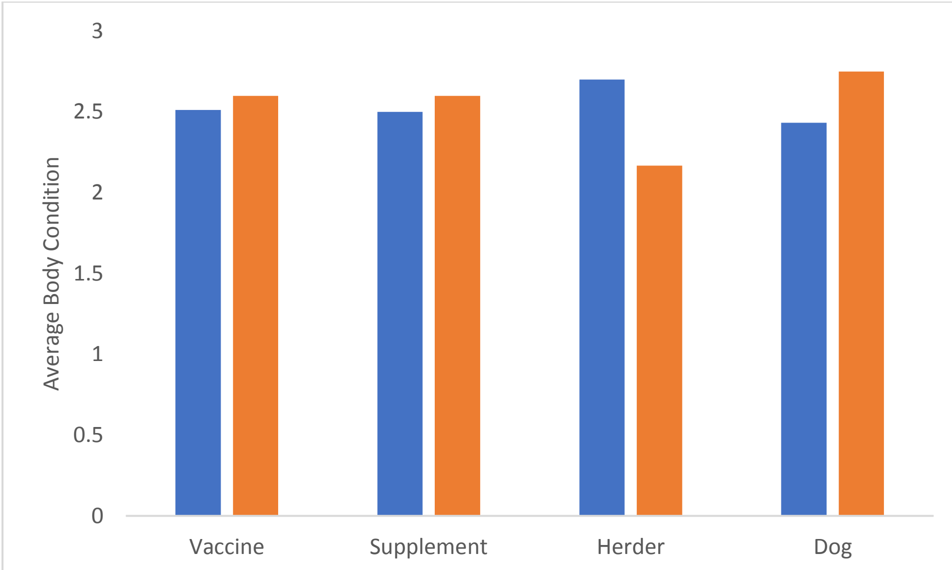

Figure 14 Mean Small Stock Body Condition When Using Vaccines, Supplements, Herder, or Dog. Blue for Yes, Orange for No (N=12, F=0.0218, P>t=0.5569; N=12, F=0.0493, P>t=0.8299; N=12, F=0.9148, P>t=0.3688; N=12, F=0.1027, P>t=0.7569).

Perceptions of Namib-Naukluft National Park Policies

Results from the surveys of Topnaar farmers and the semi-structured interview with Mr. Solomon revealed differing perceptions and interpretations of NNP policies on predation and movement of livestock (Table 8).

	NNP Legislation	Mr. Solomon Interpretation	Topnaar Community Interpretation
Livestock Movement	Movement is restricted to only a $200km^2$ multi-use area in the Lower Kuiseb River valley.	Livestock should not stray very far from Topnaar settlements.	Livestock are mostly free to move as far as they need to.
Human-Wildlife Conflict I: Predation Response	Topnaar farmers can kill predator animals only if they catch the animal in their kraal. They must report the incident to MET within 10 days. They can never use a gun (MET 2013).	Topnaar farmers shouldn't kill predator animals but if they do, he is unlikely to follow-up on the incident, unless it is very serious.	Farmers have no agency to do anything about predators.
Human-Wildlife Conflict II: Compensation	There is no compensation given for livestock losses due to predation under normal circumstances. MET will send an investigating officer to the site of HWC if a complaint is filed.	MET investigates all reported incidents of HWC. Compensation is only distributed if a community trust fund is established, which has not happened yet for the Topnaar.	Compensation is never given and MET does not respond to their reports of HWC; MET does nothing

Table 8 Differing Perceptions of Park Policies Based on Positionality

Examining Topnaar Livestock Demographics Over Time

Using historical data from Gobabeb Research and Training Center, we assessed changes in the total Topnaar cattle population over the last forty years. There are multiple gaps in the livestock census data, especially during the period from 1996 to 2002. Nevertheless, the cattle population has grown by a factor of 22: from 30 animals in 1978 to 658 by 2013.

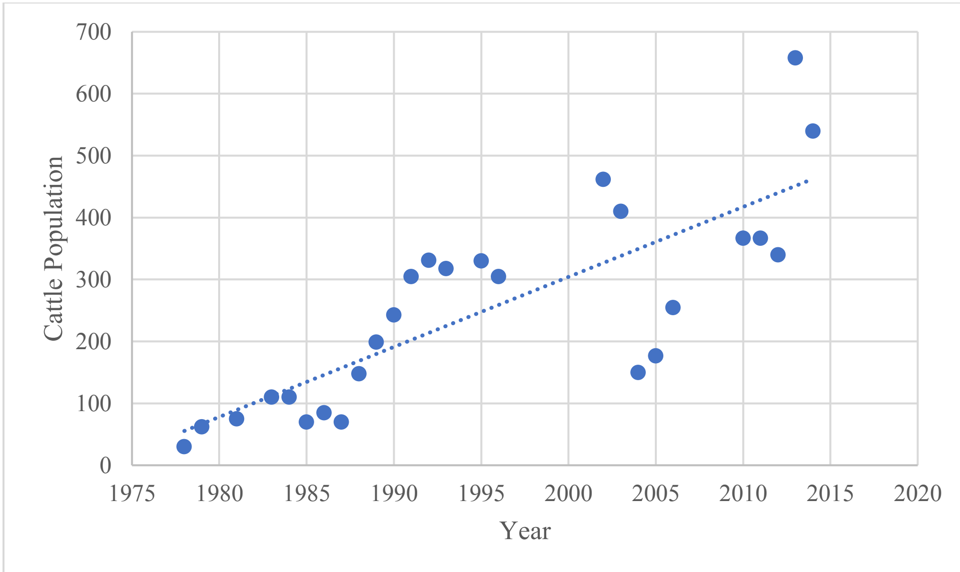

Figure 15 Change in Topnaar Cattle Population Over Time; R^2= 0.39, p-value = 0.0043

There are also multiple gaps in the historical census data for Topnaar small stock. This is especially true for the period between 1997 and 2001. Like cattle, small stock populations have increased over the past 40 years. The number of small stock grew from 1475 in 1978 to 2367 in 2014: an average growth by a factor of 1.6.

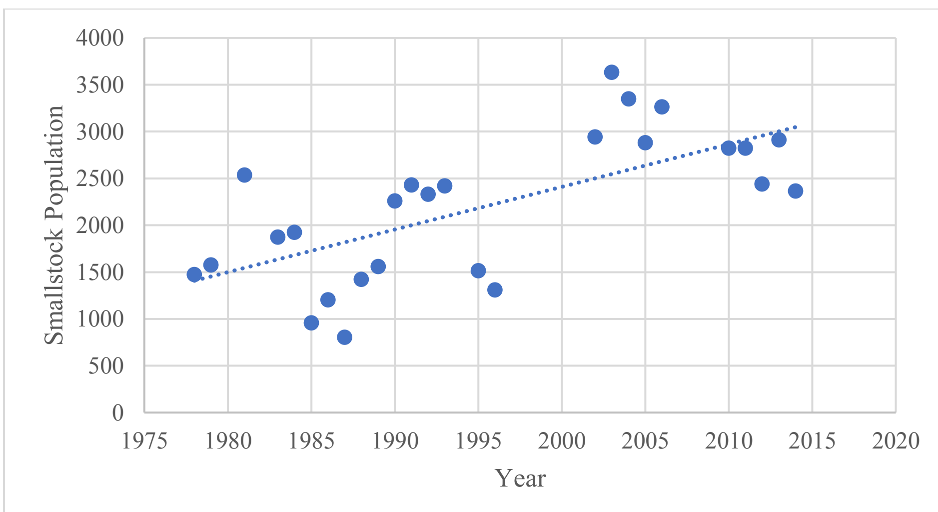

Figure 16 Change in Topnaar Small Stock Population over Time; R^2= 0.42, p-value = 0.0027

An analysis of the relationship between seasonal flood magnitude and Topnaar livestock populations, both small stock and cattle, was insignificant.

Discussion

Current Topnaar Livestock Management Practices

Our interviewees who owned cattle were not purposefully increasing the size of their herds. This is substantiated by the fact that, out of one hundred cattle in the households that we interviewed, there was only one calf, and no cattle had been purchased. One farmer cited extreme drought as a reason for not breeding his cattle. He recognized a decreased carrying capacity in the system, due to the lack of cattle fodder under drought conditions, resulting in cows that were too thin to reproduce. Past studies support this link between severe drought, reduced fodder, and decreased cattle carrying capacity in the system, identifying drought conditions in Namibia as the primary limiting factor in wild fodder production. Subsistence farmers, including our Topnaar survey respondents, are especially vulnerable to drought, as a large portion of their livestock fodder comes from foraging (Sweet and Burke 2000). Like Topnaar, livestock farmers in Namibia's Omaheke region perceive drought as a main cause of cattle mortality (Figure 7). Omaheke cattle travel 6km and 10km in search of fodder under drought conditions—much further than their usual range (Hangara et al. 2011). Similarly, one of our Topnaar interviewees explained that she had not seen her cattle in weeks because they had ventured as far as Walvis Bay—roughly 100km from her home. As drought reduces the carrying capacity of cattle's typical foraging areas, the animals must travel longer distances in search of fodder.

While drought conditions made cattle exchanges less attractive to Topnaar farmers, 54 (of 355 total) small stock were bought and 23 were sold in the past year. Perhaps these larger figures for buying and selling can be explained by the relative resilience of small stock in drought conditions. Our comparisons of small stock and cattle body condition scores showed that small stock had a 0.3 higher condition score on average, despite our use of a five-point scale for cattle and a four-point scale for livestock and a small cattle sample size (see Table 2). The difference between these body condition scores would have been still higher had we used the same metric to assess small stock and cattle body condition. A greater cattle sample size would also render our data more representative of the actual differences in livestock body condition. Previous literature and also suggests that small stock are better suited to handle extreme drought conditions than cattle. Goats and sheep have comparatively smaller body sizes and require less fodder, which allows them to survive under conditions that cattle cannot. Goat digestive physiology makes them especially well-suited to drought, as they have low metabolic requirements and an exceptionally efficient digestive system that responds quickly to change. Moreover, goats' ability to rapidly change the volume of their fore (anterior) gut in response to environmental changes allows them to maximize food intake and utilization in drought (Silanikove 2000). Topnaar key informants did not reference any physiological adaptations of goats to drought, but did comment that many farmers were switching from cattle to small stock to reduce animal mortalities (S. Kooitjie, *pers. comm.*, 3 November 2017).

While small stock may be more resilient to drought and its aftermath, both herding practices and livestock mortalities demonstrate that they face greater threats from predation than cattle and donkeys. Two thirds of survey respondents employ either a human, a dog, or both, to herd their sheep and goats (see Table 3). Cattle, in contrast, are infrequently herded, and donkeys are not herd animals. Different foraging distances could partially account for this disparity in management practice. While cattle travel long distances in search of fodder, sheep and goats remain close to their kraal, where most return every night (see Figure 6). However, greater susceptibility to predators could also drive this relatively stringent control of small stock movement (see Figure 7). 83% percent of goat farmers and two thirds of sheep farmers reported that some of their animals died from predation in the last year, while only 17% of cattle and donkey owners reported such deaths. This discrepancy aligns with findings that subsistence farmers in Namibia tend to herd sheep and goats in areas where predator and theft risks are high, but allow cattle to occupy a spot far from the village (Sweet and Burke 2000). Moreover, Topnaar farmers perceive black-back jackals, which prefer to prey on small stock, with the greatest frequency (see Figure 8). Notably, our team encountered potential sources of error regarding perceived and actual causes of livestock mortality throughout the data collection process. For example, during this study period, another Dartmouth research team (Cervenka et al. 2017) encountered a dead goat that was bloated and foaming at the mouth. The following day, the goat's lower half had also been consumed by predators (see image below). While the animal originally perished from disease, a farmer could interpret this scavenging as evidence of death by predation. These misidentifications may manifest as errors in our data.

Figure 17 Misleading Signs of Predation

Nevertheless, statistical analyses indicate herding can significantly decreases predation risk for small stock (see Figures 12 and 13). While our results indicate no difference between canine and human herders, dogs are the most cost-effective option (see Table 9). Note that the average small stock per capita and average loss to predation may be skewed due to a small sample size. Further research can verify the results suggested in this table.

	Herding (Person)	Herding (Dog)	No Herding
Herding Costs (/month)	500-800	200	0
Small Stock Price (/goat)	600	600	600
Average small stock/capita	29.58	29.58	29.58
Worth of Average Stock (N$)	17,748	17,748	17,748
Stock Worth After Herding Costs (N $)	9,948	15,348	17,748
Average Loss to Predation (#)	5.5	4.5	40
Average Loss to Predation ($)	3,300	2,700	24,000
Net Stock Worth	6,648	12,548	-6,252
# of Stock Needed to Sell to Offset Losses	5.5	4.5	40
# of Stock Needed to Sell to Make Profit	18.5	8.66	40

Table 9 A Hypothetical Cost-Benefit Analysis of Herding.

Interestingly, within villages, small stock farmers often identified the same predation sites (see Figure 9). However, the small number of farmers that we interviewed in each settlement provided little opportunity for contrasting data. We also employed a gradient buffer in our final map that both reflects the varying nature of predator movement and increases the margin for error. Similar studies have also used geographic information systems (GIS) software to map the movements of wildlife, but contextualized participant responses with field observations and historical data, including aerial photographs (Steklis, Madry, et al. 2005; *GIS For Wildlife Conservation* 2006). These multi-layered approaches mitigated the bias inherent in using only one type of data, while maximizing the capability of GIS technology to show many layers of spatial data in a single frame. Though historical predator mapping of areas surrounding Topnaar communities does not exist, it would be useful to ground our participants' responses in current field observations or aerial imaging.

Urbanization trends present another complexity in the Topnaar livestock management system. According to survey results, all of our respondents' household members live at home in rural settlements. However, this finding is likely misleading; demographic survey questions asked for other people currently living in the respondent's household, thus excluding relatives living and working in urban centers. Anecdotal evidence from survey respondents indicates that many young Topnaar have left rural settlements to work or attend school in the nearby port city of Walvis Bay. This follows the broader trend of rural to urban migration in southern Africa's local and indigenous communities, partially motivated by climate change conditions that render rural livelihoods less attractive (Serdeczny et al. 2017). Some elderly people are limited in their ability to care for livestock; conversations with survey respondents revealed a pattern of elderly household members who declined to participate in labor-intensive management practices like herding. Those with financial flexibility often hire young herders from other regions. For example, we interviewed one hired herder from the Ovambo region of Namibia, and two from Angola. Herders from other areas may employ different management practices than traditional Topnaar farmers. For example, subsistence livestock management practices in Angola are more water intensive, as the presence of rivers and lakes eliminates water scarcity (*Angola Country Commercial Guide* 2017). This study suggests that urbanization may exert an influence on management practices, but the dynamics of this relationship require additional research,

Challenges Faced and Outcomes Generated by Topnaar Livestock Farmers

Survey results indicate that goats are more susceptible to drought than sheep (see Table 4). However, this finding is likely inaccurate, as our data is skewed due the far greater popularity of goats relative to sheep. According to one Topnaar farmer, this phenomenon is a result of better responses to drought in goats than sheep. While previous research suggests that small stock are more likely to survive drought than cattle, authors do not differentiate between goats and sheep (Jonsson 2010). This, too, is an area for future study.

Disease—especially lung sickness (*bovine pleuropneumonia*) —is the most significant perceived cause of mortality for Topnaar cattle and donkey (see Table 4). However, there is no significant relationship between vaccinating cattle and death from disease (see Table 6). High cattle vaccination rates can be partially explained by their high value relative to smallstock. However, they are also susceptible to disease; lung sickness is one of the largest threats to cattle in southern Africa (Table 2, Amanfu 2009). Conversely, few farmers vaccinate donkeys (see Table 2). In fact, surveyed Topnaar farmers were incredulous when asked if they vaccinated their donkeys. This reaction reflects the idea that most donkeys are resilient to adverse conditions and are not perceived as highly susceptible to illness (Smith and Pearson 2005). One Topnaar interviewee compared his donkeys to wild animals, as they move freely, do not return home at night, and experience comparatively few losses to predation, disease, and drought (see Figure 7). These behaviors are common across southern Africa reflect the donkey's physiological adaptations; as selective foragers, donkeys spend less energy finding food and obtain a higher quality diet than cattle (Smith and Pearson 2005).

We also examined the relationship between vaccinating small stock and losses to disease, drought and predation. While a small sample size prevented statistical analyses from indicating significance between any of these factors, anecdotal evidence suggests that many Topnaar farmers are suspicious of vaccinations (see Table 6). One respondent informed us that he avoided vaccines because they make animals sick. Many farmers also face financial and spatial barriers to purchasing vaccines at the Agra Store in Walvis Bay. Likewise, a small sample size resulted in an insignificant relationship between the use of supplementary fodder and small stock losses (see table xx). However, we realized that "supplementary fodder," takes on a variety of meanings to our Topnaar respondents. Some farmers provide *Faidherbia albida* seed pods collected from the nearby ephemeral riverbed to young sheep and goats who are too small to leave the kraal. Other farmers with greater financial resources provide purchased, nutrient-enriched feed to all of their livestock. Field observations indicate that the latter group of livestock enjoy greater body condition.

Qualitative Assessment of the Socio-Ecological System

The Namib-Naukluft National Park (NNP) governance structure also impacts the Topnaar socio-ecological system. However, Topnaar perceptions of relevant NNP policies are characterized by a lack of knowledge. These misperceptions are complicated by non-standardized application and enforcement of these policies, which subject to individual interpretation by park wardens and other MET employees (R. Solomon, *pers. comm.*, 3 November 2017). NNP policies have restricted the land area occupied by Topnaar people to only a tenth of their range through the creation of a multi-use zone in the park. This multi-use zone is the only legal space for livestock farming (MET 2013). While we expected Topnaar farmers to criticize this land reduction, most farmers did not believe that the NNP restricts the movement of their livestock (see Table 8).

In contrast, we predicted relative satisfaction with NNP predator policies. While civilians are not permitted to carry firearms within Namibian National Parks, flexible enforcement allows Topnaar farmers to kill predators if the animal is found consuming livestock within the kraal, so long as they report the incident to MET within ten days (Met 2013, R. Solomon, *pers. comm.*, 3 November 2017). However, most Topnaar farmers do not perceive that they have any agency in dealing with predators, and feel frustrated by the NNP's lack of a compensation policy for livestock lost to wildlife (see Table 8). The NNP does not compensate Topnaar farmers for livestock losses under most circumstances, though they will send MET officers to deal with problem predators (R. Solomon, *pers. comm.*, 3 November 2017). Perhaps Topnaar have gradually come to terms to their reduced land area, but are unable to accept regulations on predator management, since predation continues to be a major cause of small stock mortality (see Figure 7). It is imperative to standardize the application of NNP human-wildlife conflict policies, and to ensure that Topnaar farmers fully understand their rights within the constraints of these policies.

Another confounding component of the Topnaar socio-ecological system is water allocation. In the early 1970s, the Topnaar traditional leader provided water for his 300 livestock from a shallow hole in the riverbed near his residence in Homeb. However, a dropping water table pushed him into a series of government negotiations to acquire hand-pumped, then diesel-generated, boreholes for the region upstream of the Swartbank mountain range. The chief's livestock herd substantially declined following the pattern of the water table due drought-inflicted decreases in fodder vegetation. Chief Kooitjie also commented that differences in water table levels result in more productive trees in the upstream area where he lives, and less vegetation around the downstream settlements. These water table differences are both geographic and political in nature; mountains form a "bowl" in the water table around the chief's upstream settlement, and the parastatal NAMWATER tends to overdraw water from its downstream boreholes. As a result, recent drought conditions have proven more deleterious for downstream livestock than for their upstream counterparts. (S. Kooitjie, *pers. comm.*, 3 November 2017).

Conclusion

All aspects of Topnaar livestock management are components of the dynamic socio-ecological system composed of Topnaar people, the ephemeral Kuiseb River basin, and the Namib-Naukluft National Park (NNP). Our interactions with this system and our subsequent analyses produced findings that can inform future livestock management.

First, we found that small stock are more popular than cattle among Topnaar farmers. One explanation is the comparative resilience of sheep and goats to current drought, as evidenced by their physiology. These animals also experience greater controlled inflows and outflows to their standing stock, as they are bought, sold, and slaughtered more frequently than cattle. Predation, another small stock outflow, is one of the most serious challenges for Topnaar livestock farmers. Compounded by inconsistent NNP policy applications, Topnaar residents perceive that they have little agency in dealing with predators. Going forward, it is essential to standardize the application of NNP policies and to educate farmers accordingly. Herding small stock was the only practice shown to significantly mitigate livestock mortality from predation. Topnaar farmers do not typically herd cattle. Our theoretical cost-benefit analysis suggests that herding with a dog is maximizes profits and small stock health.

Disease is another threat to Topnaar livestock, especially cattle. The most common disease is *bovine pleuropneumonia,* colloquially known as lung sickness. Two-thirds of Topnaar farmers vaccinate their livestock, but those who do not face significant spatial and financial barriers. Donkeys, in contrast, are the most resilient species of Topnaar livestock. Farmers compare them to wild animals, and they are notorious across Namibia for their resilience to drought and perceived immunity to illness.

Other components of the socio-ecological system also impact management practices. As climate change makes it unattractive to pursue traditional rural livelihoods, some young Topnaar migrate to Walvis Bay for employment. Their absence may impact management practices. Politicized distribution of water scarcity also impact the system, as Topnaar settlements enjoy uneven access to government boreholes and parastatal NAMWATER pumps. This disparity in water allocation systems raises major issues for livestock farmers.

At present, Topnaar livestock management systems are responding to the current, severe drought, while working to mitigate the impacts of disease and predation. Going forward, optimal livestock management will devolve agency to farmers while maximizing profitability of droughtadapted livestock. Future research is needed to determine which management practices are optimal for unpredictable and imminent climatic changes.

Suggestions

For future Dartmouth groups:

1. When conducting interviews, avoid broad, open-ended questions, as they produce a variety of responses that are difficult to analyze. Moreover, these questions can be overwhelming to respondents. Stick to concise, specific questions, preferably with answer choices, as these frame your participants' answers.
2. Before conducting surveys on the ground, in local communities, it is invaluable to receive feedback from a member of that specific community. We received feedback from two Topnaar staff members employed at Gobabeb. Without their input, the survey we initially drafted would have been far less appropriate for the Topnaar community.
3. Clarify your research focus before drafting survey questions. Every question that you ask should be directly pertinent to the goals of your project, as you want to respect individuals' time and create a survey that is concise and informative. In a few circumstances, we interviewed individuals with limited time, resulting in incomplete survey responses. While it is better to have a partially-completed survey than no survey at all, a concise document should prevent this from occurring.
4. Time limits the scope of your project, as you only have a week to collect data. It is helpful to amass as many interviews as possible. Carefully planning and scheduling your interviews with your community liaison will allow you to do this. However, you must remain flexible, as your interviewees have limited time and their schedules are subject to change.
5. We found it valuable to present survey respondents with tangible compensation for their time. We gave every household that we surveyed a bag filled with basic household necessities, including tea, coffee, sugar, flour, and cooking oil. While we do not want to reinforce the negative association between western tourists and handouts, it is important to show appreciation for your interviewees' generosity with their time and knowledge.
6. If working in a group composed of four or more students, it is best to split the group in a 2-2 or 3-2 arrangement for conducting interviews. While two or three students remain at the research base, two can go with the community liaison or translator to interview households. This technique reduces the risk of overwhelming interviewees, while increasing the efficiency of the data entry process. Group members remaining at the research base should be compiling data from previous interviews and working on other aspects of the project.

To inform Topnaar livestock management:

1. There is a marginally significant negative correlation between herding and livestock losses due to predation. This means that herding livestock probably decreases deaths from predation. More data and future studies can substantiate this relationship. It follows

that, if a Topnaar farmer can afford to hire a herder, or can herd livestock individually, he or she would benefit from doing so.

2. There is some discrepancy between written NNP legislation, Chief Warden Solomon's interpretation of these policies, and Topnaar community perceptions of how these regulations impact their livestock management. It would be beneficial to clarify and standardize some of this legislation for all parties involved, especially policies concerning compensation for the loss of Topnaar livestock due to predation. Topnaar farmers should understand their legal rights when dealing with predators, and they should be familiar with the reporting protocol for human-wildlife conflict. We hope that these clarifications might reduce animosity between Topnaar community members and employees of the National Park.
3. Surveying the Topnaar community revealed a possible relationship between the type of livestock and sustainability of management under drought conditions. For example, some farmers identified smallstock as better acclimated to the post 2011-flood environment in the Kuiseb River Valley, whereas cattle required higher amounts of food and water that are no longer sustainable for this community.

For continued research:

1. Investigate the suitability of different livestock species to the current drought conditions in the Lower Kuiseb River Valley. This would involve a comprehensive analysis of how sheep, goats, donkeys, and cattle respond to different challenges presented by the drought (ie lack of fodder for grazing and browsing and susceptibility to predation and disease).
2. Identify the most common disease for each species of livestock managed by the Topnaar, and establish if Topnaar farmers are vaccinating against this disease. Our research attempted to address this topic, but failed to obtain comprehensive results. We did not survey enough farmers, leading to a lack of significant data.
3. Analyze how other Namibian National Parks have worked with their resident and neighboring local communities to govern multi-use areas. Discuss opportunities for increased understanding of current NNP policies, and the possibilities for development within the constraints of multi-use areas.
4. Identify which demographic of Topnaar herders (either young, adult, or elderly) experiences the most success with livestock management, quantified by number of losses due to disease, predation, and poisonous plants. Investigate possible reasons for the success of this demographic.
5. Investigate the politics of extraction from the Kuiseb River water table. Especially focus on the differing interests and positionalities of actors such as the nearby cities of Walvis Bay and Swakopmund, the commercial farms, mines, and industries, and local communities such as the Topnaar.

Acknowledgements

We would like to thank all of the people who made this project possible. First, we extend our gratitude to the Gobabeb Research and Training Center. We thank Eugene and Gillian for the academic mentorship, and we thank Richard and Jeffrey for the community expertise. We also thank Lori for her tireless support, input, and patience in every stage of this project.

We would also like to express our appreciation for Riaan Solomon, the Chief Warden of the NNP, for dedicating his time and energy to our project. Chief Seth Kooitjie also spent many hours offering his wisdom, and we are thankful. Dennis, another member of the Topnaar Traditional Authority, served as our translator and community liaison, and we appreciate his efforts.

We would also like to thank our Dartmouth peers and leaders for their tireless contributions to this project. We are so grateful for the work of Liz Studer, Flora Krivak-Tetley, Jeff Kerbey, Bryn Morgan, and Professor Doug Bolger. They provided a wealth of guidance, moral support, and academic expertise throughout this process

Finally, we are so thankful to the Topnaar community for welcoming us, for patiently and thoughtfully answering our survey questions, and for sharing their perspectives. We sincerely hope that our research will be useful for informing future livestock management within the community. We are also always grateful to the wonderful Wild Dogs team for keeping us well-fed and happy throughout our time in Namibia. We will miss you all when we head back to New Hampshire!

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Appendices
Appendix I

COMMUNITY LIVESTOCK SURVEY 2017

We are university students from Dartmouth College in the United States. When Dartmouth students visited Topnaar communities last year, we learned that they were most interested in learning more about livestock management. We are working with Gobabeb this week to collect information about livestock in your community. We hope that what we learn from you all can help you and other community members with livestock management. We will also give this information to Joel Kooitjie and Chief Kooitjie to address your concerns about your livestock.

All the answers you give us are completely confidential. We'll write up a summary of what we learned as part of a report that we'll give to Gobabeb, Chief Kooitjie, and Joel Kooitjie. However, we will not include your name in the final results or share your specific information with anyone.

<u>Household demographics</u>

1. Interviewee

Name	Age[1]	Gender	Position[2]

2. Household[3] composition

#	Age	Gender	Live at home?	Manages livestock?
2		M F		
3		M F		
4		M F		
5		M F		
6		M F		
7		M F		
8		M F		
9		M F		
10		M F		

[1] Young (0-15), Adult (16-60), Senior (60+)
[2] Owner, herder, etc.
[3] Household: Any person who sometimes lives in this house

3. Settlement: ____

Livestock demographics

4. Do you share your kraal with other people not in your household? Y N

   If yes: How many other people? ______________________

5. How many animals do you manage?

	Goats	Sheep	Cattle	Donkeys
Adult females (#)				
Adult males (#)				
Young (#)				

6. In the last year, how many of livestock in this kraal were bought, sold, or eaten?

	Goats	Sheep	Cattle	Donkeys
Eaten				
Bought				
Sold				
If sold: Why?				
If sold: Where?				
If sold: How did you get your livestock there?				

7. Why do you have your goats/sheep/cattle/donkeys?

	Goats	Sheep	Cattle	Donkeys
Milk				
Meat				
To sell				
Cultural purposes				
Inheritance				
Other				

If other: What reason?				

8a. In the past year, were any of your goats killed by predators? Y N

If yes:

How many? ____

Which predators? (Pictures)

[Cheetah] [Leopard] [Jackal] [Hyena] [Caracal] [Not sure] [Other]

If other: Specify: ____

Where this year? (Map)

8b. In the past year, were any of your sheep killed by predators? Y N

If yes: How many? ____

Which predators? (Pictures)

[Cheetah] [Leopard] [Jackal] [Hyena] [Caracal] [Not sure] [Other]

If other: Specify: ____

Where this year? (Map)

8c. In the past year, were any of your cattle killed by predators? Y N

If yes: How many? ____

Which predators? (Pictures)

[Cheetah] [Leopard] [Jackal] [Hyena] [Caracal] [Not sure] [Other]

If other: Specify: ____

Where this year? (Map)

8d. In the past year, were any of your donkeys killed by predators? Y N

If yes: How many? ____

Which predators? (Pictures)

[Cheetah] [Leopard] [Jackal] [Hyena] [Caracal] [Not sure] [Other]

If other: Specify: ____

Where this year? (Map)

9a. In the past year, were any of your goats killed by disease?   Y   N

If yes: How many? ____

Which diseases?

[Ticks]   [Lame sickness]   [Lung sickness]   [Rabies]   [Other]   [Not sure]

If other: Specify: ____

If not sure: What symptoms? ______________________________

9b. In the past year, were any of your sheep killed by disease?   Y   N

If yes:

How many? ____

Which diseases?

[Ticks]   [Lame sickness]   [Lung sickness]   [Rabies]   [Other]
[Not sure]

If other: Specify: ____

If not sure: What symptoms? ______________________________

9c. In the past year, were any of your cattle killed by disease?   Y   N

If yes: How many? ____

Which diseases?

[Ticks]   [Lame sickness]   [Lung sickness]   [Rabies]   [Other]   [Not sure]

If other: Specify: ____

If not sure: What symptoms? ______________________________

9d. In the past year, were any of your donkeys killed by disease?   Y   N

If yes: How many? ____

Which diseases?

[Ticks]   [Lame sickness]   [Lung sickness]   [Rabies]   [Other]   [Not sure]

If other: Specify: ____

If not sure: What symptoms? ______________________________

10a. In the past year, were any of your goats killed by poisonous plants?   Y   N

If yes:

How many? ____

Which plants? ____

Where do you find them? [Dunes] [Gravel plains] [Riparian zone]

10b. In the past year, were any of your sheep killed by poisonous plants? Y N

If yes:

How many? ____

Which plants? ____

Where do you find them? [Dunes] [Gravel plains] [Riparian zone]

10c. In the past year, were any of your cattle killed by poisonous plants? Y N

If yes:

How many? ____

Which plants? ____

Where do you find them? [Dunes] [Gravel plains] [Riparian zone]

10d. In the past year, were any of your donkeys killed by poisonous plants? Y N

If yes:

How many? ____

Which plants? ____

Where do you find them? [Dunes] [Gravel plains] [Riparian zone]

11a. In the past year, were any of your goats stolen? Y N

If yes: How many? ____

11b. In the past year, were any of your sheep stolen? Y N

If yes: How many? ____

11c. In the past year, were any of your cattle stolen? Y N

If yes: How many? ____

11d. In the past year, were any of your donkeys stolen? Y N

If yes: How many? ____

12a. In the past year, were any of your goats killed by drought? Y N

If yes: How many? ____

If yes: What effect(s) of the drought kill your goats?

[Fewer pods on trees] [Trees flower at the wrong time] [Less vegetation] [Lack of water] [Other]

12b. In the past year, were any of your sheep killed by drought? Y N

If yes: How many? ____

If yes: What effect(s) of the drought kill your sheep?

[Fewer pods on trees] [Trees flower at the wrong time] [Less vegetation] [Lack of water] [Other]

12c. In the past year, were any of your cattle killed by drought? Y N

If yes: How many? ____

If yes: What effect(s) of the drought kill your cattle?

[Fewer pods on trees] [Trees flower at the wrong time] [Less vegetation] [Lack of water] [Other]

12d. In the past year, were any of your donkeys killed by drought? Y N

If yes: How many? ____

If yes: What effect(s) of the drought kill your sheep?

[Fewer pods on trees] [Trees flower at the wrong time] [Less vegetation] [Lack of water] [Other]

13a. In the past year, were any of your goats lost for some other reason? Y N

If yes:

What reason? ____

How many? ____

13b. In the past year, were any of your sheep lost for some other reason? Y N

If yes:

What reason? ____

How many? ____

13c. In the past year, were any of your cattle lost for some other reason? Y N

If yes:

What reason? ____

How many? ____

13d. In the past year, were any of your donkeys lost for some other reason? Y N

If yes:

What reason? ____

How many? ____

Livestock management

14a. Does someone herd your smallstock? Y N

If yes: Who? ____

If no: Why not? ____

14b. Does someone herd your cattle? Y N

If yes: Who? ____

If no: Why not? ____

15a. Does a dog go out with smallstock? Y N

15b. Does a dog go out with cattle? Y N

16a. Do you vaccinate your smallstock? Y N

If yes:

Against which diseases?

[Ticks] [Lame sickness] [Lung sickness] [Rabies] [Other] [Not sure]

How often? ____

Where do you get the vaccines? ______________________________

Who pays for the vaccines? _________________________________

If no: Why not? ____

16b. Do you vaccinate your cattle? Y N

If yes:

Against which diseases?

[Ticks] [Lame sickness] [Lung sickness] [Rabies] [Other] [Not sure]

How often? ____

Where do you get the vaccines? ___________________________

Who pays for the vaccines? ______________________________

If no: Why not? ____

16c. Do you vaccinate your donkeys? Y N

If yes:

Against which diseases?

[Ticks] [Lame sickness] [Lung sickness] [Rabies] [Other] [Not sure]

How often? ____

Where do you get the vaccines? ___________________________

Who pays for the vaccines? ______________________________

If no: Why not? ____

17a. Do you know where your smallstock eat and drink? Y N

If yes: Where? (Map)

17b. Do you know where your cattle eat and drink? Y N

If yes: Where? (Map)

17c. Do you know where your donkeys eat and drink? Y N

If yes: Where? (Map)

18a. Do you use supplementary feed for your smallstock? Y N

18b. Do you use supplementary feed for your cattle? Y N

18c. Do you use supplementary feed for your donkeys? Y N

19a. How often do your smallstock come home?

[Every night] [Few times a week] [Few times a month] [Hardly ever]

a. *If every night:* What time do your smallstock leave in the morning, and what time do they come home at night? ____

19b. How often do your cattle come home?

[Every night] [Few times a week] [Few times a month] [Hardly ever]

b. *If every night:* What time do your smallstock leave in the morning, and what time do they come home at night? ____

19c. How often do your donkeys come home?

[Every night] [Few times a week] [Few times a month] [Hardly ever]

c. *If every night:* What time do your small stock leave in the morning, and what time do they come home at night? ____

20a. What picture looks most like your goats? ____

20b. What picture looks most like your sheep? ____

20c. What picture looks most like your cattle? ____

20d. What picture looks most like your donkeys? ____

<u>Park policies</u>

21. Can your livestock move freely within the park?

____

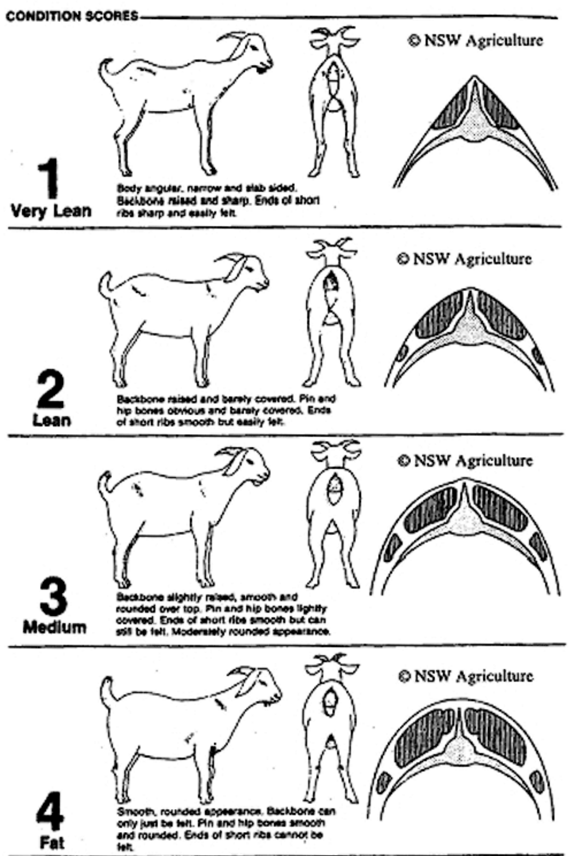
22. How does living in a national park impact the way you handle predators, if at all?

____

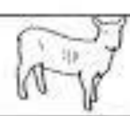
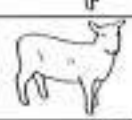
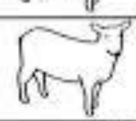
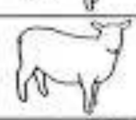
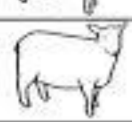
Appendix II

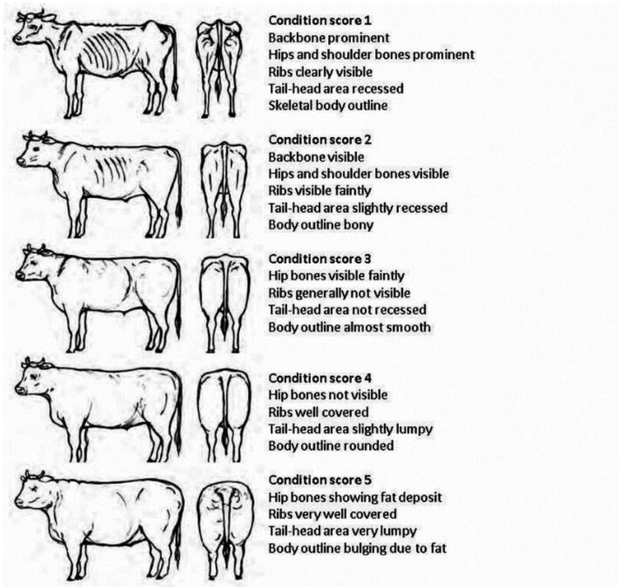
Livestock Body Condition Tables

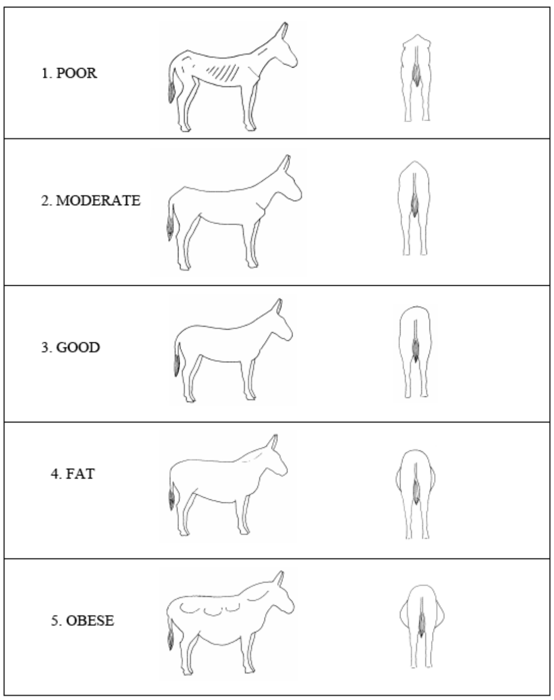
APPENDIX 1



Further reading: Condition Scoring of Goats, The New South Wales Department of Agriculture, Agfact A7.2.3

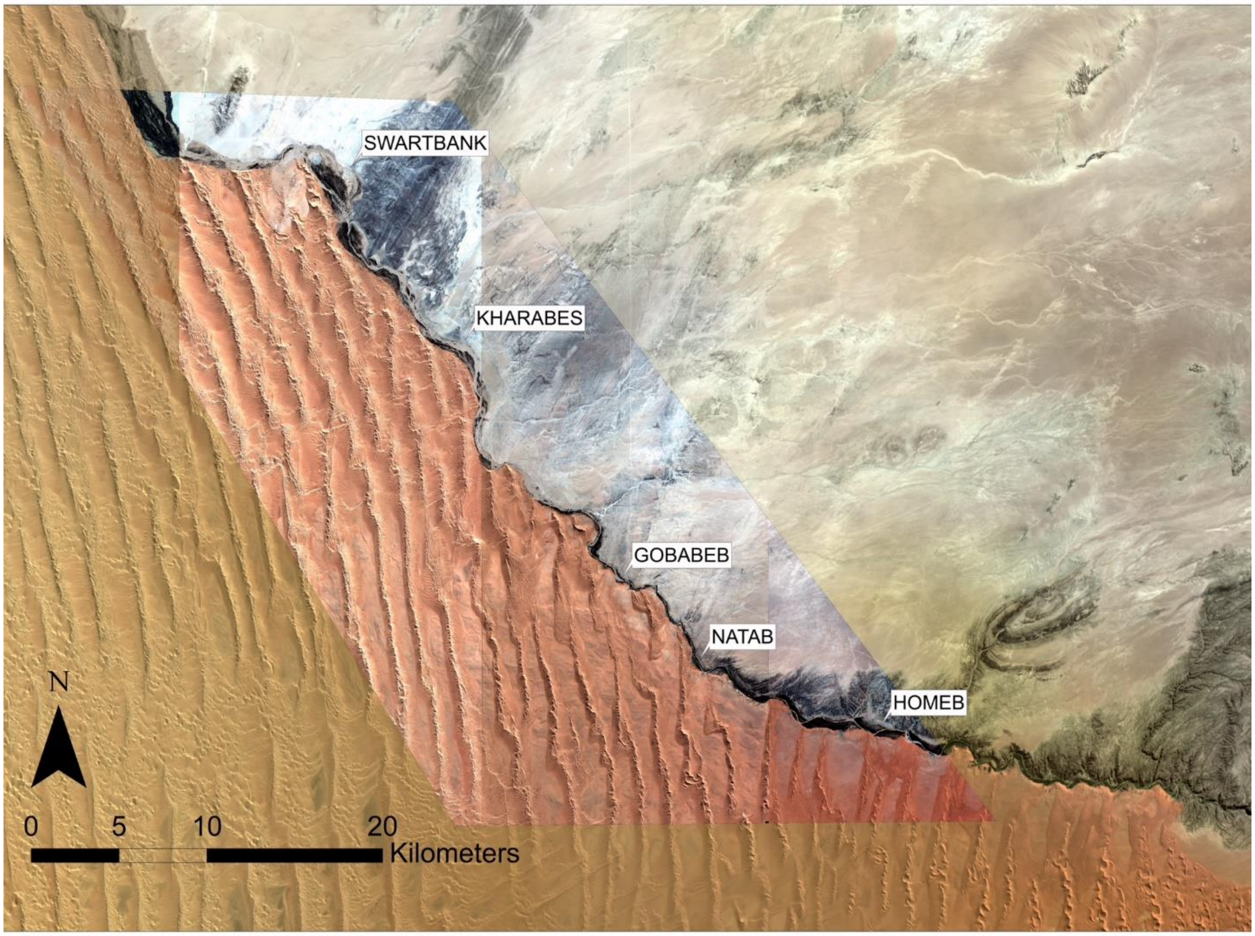
Score		Description	
1		Spine sharp, back muscle shallow,	Lean
2		Spine sharp, back muscle full, no fat	
3		Spine can be felt, back muscle full, some fat cover	Good Condition
4		Spine barley felt, muscle very full, thick fat cover	Fat
5		Spine impossible to feel, very thick fat cover, fat deposits over tail and rump	


Condition score 1
Backbone prominent
Hips and shoulder bones prominent
Ribs clearly visible
Tail-head area recessed
Skeletal body outline
Condition score 2
Backbone visible
Hips and shoulder bones visible
Ribs visible faintly
Tail-head area slightly recessed
Body outline bony
Condition score 3
Hip bones visible faintly
Ribs generally not visible
Tail-head area not recessed
Body outline almost smooth
Condition score 4
Hip bones not visible
Ribs well covered
Tail-head area slightly lumpy
Body outline rounded
Condition score 5
Hip bones showing fat deposit
Ribs very well covered
Tail-head area very lumpy
Body outline bulging due to fat


1. POOR
2. MODERATE
3. GOOD
4. FAT
5. OBESE

Appendix III

Spatial Mapping Exercise



Map 1: High definition map used to pinpoint where predators prey on livestock.

Appendix IV

Interview questions for Chief Seth Kooitjie

1. Have Topnaar livestock demographics and management practices changed during your tenure as chief?
2. How has the ecology and climate of the Lower Kuiseb changed in your lifetime?
    a. What political factors impact water availability here?
3. Is it easier to raise livestock in some Topnaar settlements than others?
4. Do you perceive any conflict between the national park and the Topnaar interests?
5. Do Topnaar livestock owners face more difficulties during certain times of the year?

Appendix V

Interview questions for Chief Warden Riaan Solomon

1. According to the Namibian Human Wildlife Conflict Policy, there is no compensation for livestock loss due to wildlife, in national parks, unless the park is zoned into multi-use areas. I believe the NNP is zoned, and that the lower Kuiseb River Valley, where the Topnaar live, is in zone four. Is this correct? If so, how does this change the way that Topnaar are compensated for lost livestock? Specifically, when a Topnaar farmer loses a cow, donkey, sheep, or goat to wildlife, what happens?
2. What changes have you observed in livestock management in the Topnaar?
3. What, in your opinion, is the biggest problem animal? Why is this the case?
4. What would be the consequences of poaching predator?
5. Are communities allowed to own guns in the national park?
6. Can the Topnaar shoot/kill problem animals within official MET/park regulations?
7. Do you think that the community is aware of these park policies on predation?
8. Have noticed any changes in perceptions of the park occurred over time?
9. Have you seen any changes in the ecosystem during your time working for the Park service?

!Nara Herbivory: Implications for Plant Growth, Productivity, and Associated Animal Communities

November 10, 2017

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Introduction

!Nara (*Acanthosicyos horridus*) is an endemic, leafless dioecious plant of the Cucurbitaceae family located in the western Namib Desert. The largest !nara population inhabits the Kuiseb Delta, which separates the gravel plains of the northwest from the large dunes of the Namib Sand Sea to the southwest. Although the Kuiseb Riverbed possesses nutrient rich soil, which supplements plant development for a variety of species within close proximity to the river, few large plants are capable of establishing themselves farther from the river aside from !nara (Moser, 2001). Previous studies found that the !nara has several features that aid in its survival in the arid environment. !Nara possess extraordinarily long taproots between 30 to 100 meters in length with one of the world's largest xylem channels, allowing them to uptake water from underground water sources in the absence of rainfall and fog events (Henschel and Moser 2004; Klopatek and Stock 1994). Alongside their root systems, recent studies suggest that !nara can utilize moisture directly from the air by intercepting fog blowing inward from the Atlantic coast, by absorbing it through their stems and thorns (Gerber et al. 2017). In addition, !nara plants possess protective thorns as opposed to leaves, thereby reducing the flat surface area exposed to the hot desert sun and increasing moisture retention (Hebeler 2000).

Along with its remarkable physiological adaptations, the !nara plant possesses an impressive ability to efficiently collect sand grains amongst its roots and thorny vegetation; thereby forming large stable mounds of sand that build up over time. Previous studies have noted that hummock formation and the growth of a protective shield of branches assists in the survival of many Namib Desert species along the Kuiseb River (Hebeler 2000). !Nara plants provide shelter, protection, a nutritional food source, and thermoregulation for an assortment of desert-adapted species. For instance, blister beetles drink nectar from the plant's flowers, and gerbils and scorpions receive shelter in the hummock's shade or the stable sand bed to construct their burrows (Rosenzweig 1973). !Nara plants form "islands" of raised sand and produce a substantial amount of vegetative material, which provides structural complexity/stability and concentrated pockets of primary productivity and nutritious detritus in the surrounding desert landscape (Henschel and Moser 2004, Latorre et al. 2011). Considering the aridity of the Namib Desert (i.e. the area around the Kuiseb receives an annual average of merely 25mm of rain), lack of shade among the dunes, and the frequent movement of the soils due to high winds, the hummock-formation, shade-provision, and concentrated nutrient resources likely play a vital role in supporting greater biodiversity in the region, which has resulted in great interest among ecologists in developing a better understanding of the plant's life strategies.

Besides providing important habitats and functioning as an important nutritional resource for wildlife, the !nara plant also arouses interest because of its longstanding cultural relationship with the local desert-dwelling people known as the Topnaar. !Nara utilization by the Topnaar community has persisted for thousands of years. Archeologists discovered stashes of dried !nara seeds stored in caves alongside human tools out on the surrounding gravel plains dated to 8,000 years old (Dentliger 1977). Among the Nama people in Namibia, such as the Topnaar community, the !nara plant retains sociocultural and economic significance through the annual !nara melon harvest. A large proportion of rural community members continue to rely upon wild !nara harvesting and processing for income generation, nutritional supplementation and other uses (Henschel et al. 2004). Since a single !nara plant produces between 50-500 melons, which are utilized for their pulp and seeds, Topnaar !nara harvesters obtain more than a quarter of their annual income from !nara sales, in addition to obtaining a large supplement to their dietary needs (Henschel et al. 2004).

Given the perceived sociocultural, socioeconomic, and ecological importance of !nara, the current paucity in scientific understanding of the biological and ecological interactions influencing their survival and productivity is of great concern. In the Kuiseb system, one of the largest perceived threats to !nara is herbivory by Topnaar livestock, which roam and forage freely along the Kuiseb River, often consuming !nara to obtain water. Historians believe that the Topnaar began concentrated herding of large livestock as early as the 1800s in the regions surrounding the Kuiseb, and livestock remain an important part of Topnaar livelihood to the present day (Van Damme & Den Eynden 1992, Herrick et al. 2016). Although !nara plants are browsed by wild herbivores, such as springbok, the relatively recent introduction of large livestock herds centered around the Kuiseb River creates increased herbivory pressure which may affect the growth and productivity of !nara plants in the region.

Since 2013, students from Dartmouth College have collaborated with the Gobabeb Research and Training Centre to conduct monitoring experiments on !nara hummocks along the Kuiseb River and along the dunes of the Namib Desert. Data collection with each subsequent year has provided a foundation for baseline information and informed the creation of long-term data collection methods to assess the impacts of herbivory in 2016. Using previous aggregate data and methodology, the purpose of this project is to understand how !nara responds to herbivory by livestock, as well as attaining some quantifiable measurements of biodiversity and soil temperature changes associated with !nara hummocks. Given the aforementioned socioecological importance of !nara, this provides some baseline information regarding how the plant might function a keystone species in the Namib Desert environment.

We identified two central research questions: 1) What are the effects of livestock herbivory on !nara plant growth and productivity? and 2) How may !nara hummocks function to sustain and maintain biodiversity? These two areas of interest interact because of the indirect effects of herbivory pressure, including vegetation and landscape trampling, on !nara vitality. We seek to quantify and to determine if any apparent relationships can be observed in the previous year's data collected from fenced and unfenced !nara hummocks, in relation to herbivory and !nara plant vitality. We sought to couple this analysis of previously-collected data with current data collection to examine associated hummock biodiversity, along with !nara's ability to function as an ecosystem engineer in changing soil properties (i.e. soil temperatures).

Herbivory

Herbivory is a biotic interaction that affects the distribution and reproductive success of plant species (Milchunas & Lauenroth 1993). In ecological theory, herbivory by vertebrate grazing is considered as a type of disturbance. Often, herbivory limits regrowth capability because substantial plant consumption reduces available nutrient resources for regrowth, which indirectly affects resource allocation patterns for growth. For instance, a study of two Great Basin shrub species determined that *Artemisia tridenatata* cannot maintain high vigor under heavy, experimentally simulated browsing by large mammals, which makes the plant more susceptible to other environmental pressures (Bilbrough 2003). The article cites several studies that show that flower production decreased after twig removal and prevented utilization of available nutrient resources, such as nitrogen and carbohydrate, for regrowth (Bilbrough 2003). So, allocation to flowering, or other forms of regrowth, in successive growing seasons may be affected by browsing, which ultimately affects the fitness of the plant.

Additionally, herbivory may adverse effects to !nara productivity and vitality, particularly for its fruit production capacity. An early study on !nara herbivory discovered that !nara fruit production increased 5 to 10 times without donkey herbivory versus that of herbivore impacted !nara (Henschel et al., 2004). Disturbances like herbivory may increase plant diversity in communities by reducing competitive dominance among species and allowing rarer species to grow together (Rambo & Faeth 1999). Some herbivores may also shape their surrounding environment through vegetation utilization (i.e. breaking topsoil and tree), which increases structural habitat complexity and favors other organisms (Pringle 2008). For example, a long-term study in the Kenyan savanna demonstrated that Acacia-browsing elephants increased the spatial complexity and formed crevices in damaged trees, which were preferred by arboreal geckos (Pringle 2008). Furthermore, in response to herbivory, many plant species have developed adaptations to restrict their consumption by both vertebrates and invertebrates. Some species have evolved to deter herbivores with large structures, such as thorns and spines, which reduces the rate of consumption (Hanley et al. 2007). In some instances, by creating structural complexity via disturbance (i.e. browsing) but also placing intense stress on plants in other environments, total herbivore impacts on vegetation cannot be generalized across different ecosystems accurately. Thus, herbivory dynamics may be linked concurrently with !nara productivity and vitality.

Herbivory Research Objectives

We used data collected over the past year to assess patterns in !Nara plant productivity and herbivory, aiming to complete initial data analysis and improve the current long-term monitoring methodology used by the Gobabeb staff. Our hypotheses were organized around a series of research questions as follows:

!Nara Herbivory and Plant Vitality:

1) *How does !Nara plant growth and reproduction differ between fenced (exclosure) vs. unfenced (control) !Nara hummocks and with increasing distance from the Kuiseb River?*

    A. *How do exclusion of livestock herbivores and distance from the Kuiseb River impact average main !nara stem length, stem diameter, number of side branches, and plant height?*

    Hypothesis 1**:** Herbivore exclusion promotes !Nara growth, and thus fenced !nara hummocks will exhibit greater mean stem length, stem diameter, number of side branches, and plant height than unfenced !Nara hummocks.

Hypothesis 2: Due to the concentration of livestock associated with forage and livestock drinking stations near the Kuiseb River, non-fenced !nara hummocks will exhibit greater mean stem length, stem diameter, number of side branches, and stem height farther from the Kuiseb River than unfenced !nara hummocks nearer to the Kuiseb.

B. *How do herbivore exclusion and distance from the Kuiseb River impact the production of !nara flowers and fruits?*

***Hypothesis* 3**: Due to a concentration of livestock near the Kuiseb river, and because herbivore exclusion promotes the ability of !nara to invest in reproductive growth, fenced !Nara hummocks further from the river will exhibit greater numbers of fruits and flowers than unfenced hummocks near the river.

C. *How does average proportion of live biomass differ with herbivore exclusion and distance from the Kuiseb River??*

***Hypothesis* 4**: Herbivore exclusion reduces browsing and trampling pressure at !nara hummocks and thus promotes !Nara plant growth, which will result in fenced !nara hummocks and !nara hummocks farther from the Kuiseb River exhibiting greater mean proportion of live biomass than unfenced !nara hummocks and !nara hummocks closer to the Kuiseb River.

2) *Are the fences used in the !nara herbivory study effectively excluding livestock?*

Hypothesis 5: Significantly less dung will be seen within fenced !nara hummocks compared to unfenced hummocks.

3) *How does livestock activity differ at unfenced hummocks located at different distances from the Kuiseb River?*

Hypothesis 6: Hummock distance from the Kuiseb River will be negatively correlated with livestock dung density (a proxy for livestock activity).

4) *Is dung density an effective proxy for herbivore pressure and how does it relate to measures of plant growth?*

Hypothesis 7: Herbivore exclusion promotes !nara plant productivity, and thus livestock dung density will be negatively correlated with mean plant height and the proportion of live biomass.

Biodiversity

In the Namib Sand Sea ecosystem, !nara adaptations benefit a variety of organisms. Because of its importance in the desert food web, as well as in shaping the landscape by forming hummocks, the !nara plant has been proposed as a keystone species in some literature (Klopatek & Stock 1994). Keystone species are defined as "relatively low biomass species with a structuring role in their food webs", which strongly influences the abundances and organization of other species and the intraspecific dynamics within an ecosystem (Libralato et al. 2006; Piraino et al., 2002). These species are crucial to maintain a diversity of ecological communities. Identifying keystone species aids the maintenance of ecosystem integrity and biological diversity in the face of exploitation and other disturbances and stress (Libralato et al. 2006; Naeem and Li, 1997; Tilman, 2000).

There are a variety of many reasons why !nara may be viewed as a keystone species in the literature. First, !nara hummocks are crucial habitat and nutritional sources for various Namib Desert species. !Nara hummocks directly provide habitats for burrowing organisms by stabilizing sands in a hummock. The spine-covered stems provide aboveground protection for other small animals including gerbils. The plant also provides a vital source of moisture, protein, and carbohydrates to a wide range of species, including *Oryx gazelle* (Oryx), *Canis mesomelas* (Black-Backed jackal), *Camponotus detritus* (Namib Desert dune ant), and *Meroles anchietae* (Shovel-Snouted lizard) (Henschel and Moser 2004).

Another defining characteristic of keystone species is that they are exceptional relative to other species in the community in terms of their impacts (Mills et al. 1993). If a plant is a keystone species, herbivory negatively affects its plant livelihood relative to the many species that come into contact with it. Particularly, 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). While it provides a significant source of nutrition and moisture to many different organisms, and it forms microhabitats by trapping sand, !nara cannot be accurately labelled a keystone species (Klopatek & Stock 1994). This claim remains persistently unsubstantiated.

Additionally, some keystone species are disproportionately important in ecosystems due to their roles as ecosystem engineers. Ecosystem engineers are organisms that create, modify, and maintain habitats, which directly or indirectly control resource availability to other organisms (Jones et al. 1997). There exists a paucity of understanding ecosystem equilibrium variations creating habitats because of the interactions among a multitude of species, the food-web linkages across trophic levels, and the landscape modulations induced by biotic and abiotic interactions (Gilad et al. 2004). In other ecosystems, plants have been shown to create structure and habitat complexity in environments that lack spatial complexity such as the ocean (Teagle et al. 2017). Similar to !nara, kelp species create "three-dimensional habitat structure" which supports a variety of species (Teagle et al. 2017). More specifically, kelp increase the volume, heterogeneity, and complexity of habitat and provide direct food and shelter to many species (Teagle et al. 2017).

Even more so, ecosystem engineering varies resource availability which affects species distribution and abundance (Wright and Jones 2004). Different areas, especially the surrounding habitat that remains unmodified by the engineer, are influenced by the presence and absence of ecosystem engineers that influence system productivity. Ecosystem engineers increase landscape-scale species richness by creating new habitats and allowing species that would otherwise be excluded to persist (Wright and Jones 2004). For instance, at low productivity, species richness is limited by either stress or disturbance, while at high productivity, patches tend to be dominated by one or a few competitively superior species (Grime 1979). Yet, when an ecosystem engineer increases productivity in a low-productivity system, stressful conditions are ameliorated and positively affect species richness, regardless of differences in taxonomic or trophic position of the engineers (Wright and Jones 2004). !Nara hummocks demonstrate this theory of primary productivity because they provide foundational support for interconnected species amidst the low productivity of the Namib Desert ecosystem.

Additionally, since ecosystem engineers disproportionately influence the availability of resources for other species through the creation, modification or maintenance of habitats, physical structures provide a refuge that acts as thermal buffers when ambient conditions are unfavorable (Pike et al. 2013). For instance, !nara hummocks provide accessible microhabitats, such as subterranean burrows, that provide "moderate and stable thermal environments to protect against often variable and extreme environmental conditions" (Pike et al. 2013). In this report, we analyze the diversity of organisms around !nara hummocks as well as the structure and abiotic changes created by hummock formation to assess !nara as a keystone species and ecosystem engineer.

Biodiversity Research Objectives

We monitored !nara with the intent of clarifying the perception of it as a keystone species and its importance within the Namib Desert environment. !Nara plant productivity and herbivory, its hummock biodiversity, and niche construction were three categorical inquiries we sought to understand. We sought to monitor the aforementioned categories, which entailed assessing and improving the current long-term monitoring methodology used by the Gobabeb staff. Our objectives and rationale for our research questions and hypothesizes are as followed:

!Nara Hummock Biodiversity:

1) *Does livestock herbivory, hummock distance from the Kuiseb River, and !nara hummock volume influence the abundance and richness of animal species associated with !Nara hummocks?*

   Hypothesis 8: Due to greater !nara plant vitality associated with reduced herbivory, fenced !Nara hummocks and those closer to the river will support higher species abundance and richness

   Hypothesis 9: Because herbivore pressure decreases with increasing distance from the Kuiseb, there will be less variance in total species abundance and Shannon-Weiner Index values between fenced and unfenced hummocks farther from the river compared to fenced and unfenced hummocks closer to the river. The Jaccard Index values will decrease with increasing distance from the Kuiseb River.

Hypothesis 10: Due to greater habitat heterogeneity near the Kuiseb River, !Nara hummocks close to the Kuiseb will exhibit significantly greater species richness than hummocks positioned farther away.

Hypothesis 11: Due to a larger capacity to provide microhabitats and food sources, !Nara hummocks with greater volume and surface area will support higher species total abundance and richness.

2) *Do !nara hummocks support greater total abundances and richness of animal species compared to other mound-forming desert structures (i.e. rock outcroppings, acacia hummocks, and dune grass hummocks)?*

Hypothesis 12: Because of increased structural complexity and their ability to form large mounds, !Nara hummocks will exhibit greater species richness and abundance on average compared to rock outcroppings, acacia hummocks, and dune grass hummocks.

3) How may !nara function as an ecosystem engineer, changing its surrounding environment and affecting soil properties?

Hypothesis 13: Due to shading and greater belowground organic biomass, mean soil temperatures will be significantly lower in !Nara hummocks compared to surrounding bare soils.

Methods

Previous Data and Research

By the end of 2016, the Gobabeb Research and Training Centre staff installed metal wire fences at 10 female !nara plant hummocks, located at various distances from the Kuiseb River, to exclude donkeys, cattle, goats, and sheep from browsing at the hummocks. All 10 fenced !nara hummocks were paired with an unfenced hummock, which permitted herbivore access and functioned as a control for comparative analysis. In November 2016, members of the Dartmouth FSP selected these 10 hummocks to conduct an herbivory and productivity monitoring experiment.

Since March 2017, to assess potential changes on the 10 unfenced and 10 fenced !nara hummocks, the Gobabeb staff collected data on a monthly and bi-monthly basis to assess plant vitality associated with herbivory levels. For the monthly data assessment, dung collection, count, and removal occurred atop and surrounding both fenced and unfenced hummocks, as well as fruit and flower counts. In addition to the monthly data collection, bimonthly assessments for growth and herbivory occurred at 10, aluminum-tagged stems from 10 thicket bushes. For example, measurements included stem diameter at 10cm from branch tip, number of pairs of thorns, and number of side stems within 30cm from the branch tip, as well as counts for burrow sizes (i.e. small, medium and large).

Data collection for this exclosure experiment began in March 2017. For our analysis of this past year's data, we examined plant productivity (i.e. fruit and flower counts) and plant growth (i.e. stem length and diameter) as proxies for herbivory impact. Also, we counted large herbivore dung as a proxy to examine herbivore pressure, as well as observed trends in herbivory levels corresponding to hummocks' distance from the Kuiseb River. These analyses allowed us to assess trends in variables that could influence our hypotheses (i.e. herbivore distribution in proximity to the Kuiseb River) and to assess trends in !nara plant vitality after a year of livestock exclusion, which extends the work of Kittelberger et al. 2016.

Study Site Selection

We conducted our experiment to assess plant productivity and hummock biodiversity at the ten previously selected pairs of !nara hummocks (10 fenced and 10 unfenced) selected by the 2016 Dartmouth FSP members. All hummocks were female in gender and paired with another hummock of similar size and distance from the Kuiseb River.

We randomly sampled the 10 pairs of sites to create 2 stratified groups, which each had five hummock pairs at varying distances from the Kuiseb River. We assessed the first sample, consisting of 5 hummock pairs during our first 2 days of data collection (November 1st, 2017 and November 2nd, 2017), and the second sample during our last 2 days of data collection (November 3rd, 2017 and November 4th, 2017). Thus, we collected data for all twenty !nara hummocks over the course of four days.

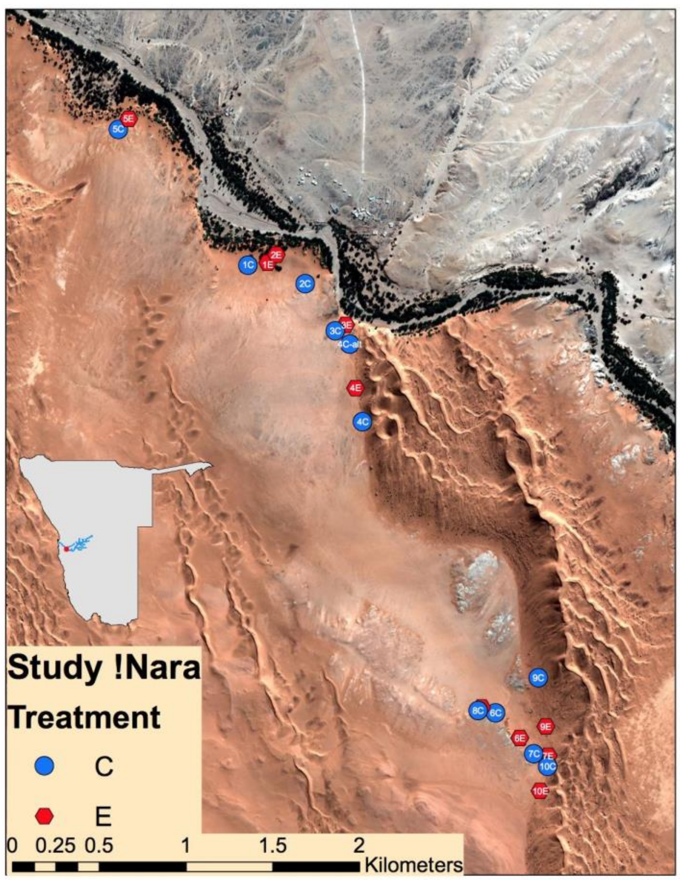

Fig. 1. – GIS map of the 20 !nara hummocks included in long-term herbivory monitoring as well as our biodiversity and temperature data collection at Gobabeb Research and Training Centre. “C” denotes a “control”, or unfenced hummock, while “E” denotes an “exclosure”, or a fenced hummock.

Bi-monthly Protocol Trials

Before conducting our data collection, we assisted a Gobabeb staff member, who currently conducts the monthly and bimonthly herbivory data collection protocols, to collect data from !nara hummocks 2E (fenced/fenced) and 2C (unfenced/unfenced) by using existing protocols for assessing !nara hummock herbivory and productivity, which Gobabeb staff has surveyed since March 2017.

After experiencing protocol methodology firsthand, we assessed the current problems with the protocols and brainstormed improvements for data collection methods. Following our field session, we considered revisions that may improve data collection efficiency, its spreadsheet coherence, and its accuracy of results.

Experimental Pilot Phase

Once we devised our initial research questions and proposed experiments for biodiversity assessment, we conducted pilot experiments to ensure that our methods would provide useful and meaningful results.

In our first trial, on the afternoon of October 29th, we deployed Sherman live animal traps, drift fences, and pitfall traps on hummocks 2E (fenced hummock) and 2C (control hummock). We conducted the following pilot experiment on each hummock as follows: we deployed fifteen Sherman traps containing a small ball of bait, composed of bread crumbs, peanut butter, and fish paste, to attract small omnivorous and carnivorous rodents. On one side of the hummock, which we chose arbitrarily, we deployed a drift fence parallel to the hummock's slope, with one pitfall at the bottom of the fence, 2 pitfalls on either side of the fence's midpoint, and one pitfall at the top of the fence. Using a small trowel, we dug a hole large enough to place the pitfall within the hummock's soil and to make it level with the soil surface, such that could catch ground-dwelling insects and other small terrestrial animals. We deployed the same arrangement of a drift fence and pitfalls on the opposite side of the hummock, yet aligned them perpendicular to the hummock's slope, to examine the possible effect of the drift fence angle on catch success. We also deployed 3 Sherman live traps at an acacia hummock positioned in between plots 2E and 2C, to see if any activity could be recorded in this alternate habitat structure. On the morning of October 30th, after collecting and assessing the pitfall and live trap data from this pilot experiment, we modified our pilot experiment to exclude live traps after receiving a low catch rate. For example, despite deploying a total of 33 traps, a single hairy-footed gerbil was captured.

On the afternoon of October 30th, we conducted a second pilot experiment to assess and to finalize our methods for data collection. We conducted the following pilot experiment on both hummocks 2E and 2C as follows: given the abundance of tracks we observed the morning following our initial pilot study, and, given that the live traps or pitfall traps did not capture much nighttime activity, we decided and used a broom to sweep standardized-sized transect to observe hummock animal communities. The following morning, we identified these animal tracks which the transects "captured".

On one side of hummock 2E and 2C, we swept a smooth surface parallel to the right and left of the drift fence with widths of 33 centimeters (cm) and lengths of 3 meters (m), totaling an area of 1-square meter each. We swept an additional transect of equal width and length perpendicular to the drift fence. On the opposite embankment of both 2E and 2C, we deployed 3 sweep transects in the same alignment (parallel to the right and left sides of the barrier fence and perpendicular at the hummock's base) as 66cm long and 3m wide, for a total area of 2-square meter. With the different measurement metrics, this second deployment allowed us to assess the extent to which sweep transect width affects the number and diversity of animals whose tracks are "captured". The drift fence and pitfall pairings remained in their previous alignments.

The following morning, we observed easily identifiable tracks within the sweep transects, as well as determined that the species number and diversity captured was not significantly different between the 1-square meter and 2-square meter transects. However, because the greater width of the 2-square meter transects made tracks more easily identifiable, we decided to sweep all future transects to 2-square meters. Additionally, after analyzing pitfall traps from our 2-day pilot data, we decided to orient all subsequent barriers parallel to the hummock slope because they yielded significantly greater capture rates compared to barrier fences placed perpendicularly to the slope.

Stem Length, Stem Diameter, and Number of Side Branches

To distinguish what, if any, effects livestock herbivory has on !nara growth rate, we calculated mean values of stem length, stem diameter, and number of side branches, utilizing data collected bimonthly from 10 !nara stems at each fenced and unfenced hummock within the long term herbivory study. Stem length had been collected from 10 branch tips, either on ten different marked !nara bushes at a hummock or on the same bush, depending on the size of the hummock. After marking ten stems 10 cm from their tips at the beginning of the study, a bimonthly measurement was recorded from the previous mark to the stem tip, and then remarked at 10 cm from the new stem tip. Stem diameter had been collected in a similar manner at the ten stem data recording locations, measured monthly using a caliper at the mark placed at 10cm two months prior. The number of side branches had been collected from these same ten stems, by counting the branch points from the top 30 cm of stem length.

Mean Plant Height

After analyzing 2017's !nara plant vitality data and completing trial runs of the current herbivory monitoring protocols, we decided that the current methods of assessing stem growth (i.e. measuring the length of the stem tip from the previous month's 10cm mark) did not provide a clear picture as to how plant growth rate differs between fenced and unfenced !nara hummocks. To test an alternative method of assessing the overall growth of !nara at a given hummock, we utilized a height measurement protocol developed by Dartmouth in 2016 for a student project focusing upon herbivory pressure. To calculate mean plant height, we measured heights among 6 to 10 previously-marked !nara plants (depending on the size of the hummock) from the base of the live plant to the top of the bush, determined as the level at which a clipboard placed on top of the bush would compress the stems.

Proportion of Live versus Dead Biomass

To supplement our assessment of herbivory impacts on !nara vitality, we also utilized a DJI Phantom 4 Advanced drone, equipped with a 20 megapixel Sony Sensor, to map the proportion of live and dead !nara at both fenced and unfenced hummocks. For each hummock, dozens to hundreds of nadir and oblique geotagged photographs were analyzed using a SfM-MVS workflow in Agisoft Photoscan Pro (Carrivick et al. 2016). A georeferenced orthomosaic was then imported into ArcMap (v 10.4.1) where a Maximum Likelihood Classification was run using a user generated signature file to generate a ‘dead !nara’, ‘live !nara’, and ‘sand (or other)’ landcover map for each hummock. Finally, to calculate proportions of live and dead biomass, we divided the surface area of live and dead !nara respectively by the sum of live and dead !nara surface area coverage on the hummock (Appendix A).

!Nara Live Volume, Fruit and Flower Counts

To parameterize the fruit and flower production by hummock size, we calculated the volume of live !nara biomass utilizing the mean plant heights for each hummock, which we then multiplied by the live biomass surface area, as calculated from the UAV images utilizing ArcMap software. Also, we analyzed the total number of small fruits with flowers and open flowers from 2017’s bimonthly data collection to assess the impact of livestock herbivory on reproduction. In our analyses, we counted the cumulative number of fruits with flowers and open flowers for the year at each hummock, and then divided this number by the live !nara volume, which was calculated by the method cited above (Appendix A).

Pitfall Trap and Drift Fence Set-Up

On the afternoon of October 31st, we randomly selected our first stratified random sample and deployed drift fences and pitfalls at hummock pairs 3, 4, 6, 8, and 9. After modifying our experiments following our second pilot phase, we conducted the following procedure at each of the 10 hummocks: we deployed a drift fence on both the eastern and western embankments that was parallel to the hummock’s slope. We installed fences on the eastern and western slopes because the sun’s arc affects daytime length and exposure on the hummocks and diurnal, desert-dwelling species. Fence length was recorded using a fifty-meter tape measure. We established this measurement to act as a proxy for our catch effort, which the meters of fencing expressed. Next, we deployed 5.5cm diameter pitfalls located at the top, bottom, and both midpoints of each drift fence.

On the morning of November 2nd, we collected the drift fences and pitfalls installed at the 10 hummocks of our first stratified random sample. On the afternoon of November 2nd, we repeated this procedure for our second stratified random sample on hummock pairs 1, 2, 5, 7, and 10. On the morning of November 4th, we collected the drift fences and pitfalls that we installed at the 10 hummocks of our second stratified random sample.

Track Count Transects

On the afternoon of October 31st, we swept 2-square meter transects at the five hummock pairs of our first stratified random sample using the following procedure: on both the eastern and western embankments of the hummock, we used a broom to sweep transects 66cm wide and 3m long, for a total of 2-square meters each. We swept transects parallel to either side of the drift fence, as well as swept a transect perpendicular to the drift fence that was located at the base of the hummock. On the afternoon of November 2nd, we repeated this procedure at the five hummock pairs of our second stratified random sample.

On the afternoon of November 3rd, we swept a single transect with a 66cm width and 3m length at microhabitats within fifty-meters of each of the 10 hummocks selected for our second stratified random sample. We selected the aforementioned microhabitats for their similar mound-forming capabilities and their close proximity to the !nara hummocks. These microhabitats included rock outcroppings, Acacia hummocks, and dune grass hummocks. At each of these transects, we used a Garmin Oregon 700 GPS to tag their waypoint coordinates and recorded their location.

I-buttons and Hobo Temperature Data Loggers

On the afternoon of October 31st, we deployed twenty pairs of I-button and Hobo temperature data loggers at all twenty hummocks in our aggregate sample. We conducted the following procedure at each hummock: we attached a uniquely-numbered I-button or Hobo logger to a half-meter length stick, and we labeled the stick to match the loggers' numerical identification. Additionally, we marked the stick 5cm above the taped data logger to identify the depth of its placement it within the hummocks' soil. We placed one data logger 5-cm deep within the soil atop and on the flattest point of the hummock, so it received sunlight exposure throughout the day. The logger was placed next to a live plant, but not directly adjacent to a stem or any dead plant material. We placed another data logger at an equal depth within the soil, 20m away from the base of the hummock, which as located on the flattest, least shaded ground. On the morning of November 4th, we collected the forty data loggers that we had deployed at the twenty hummocks of our aggregate sample.

Biodiversity Data Collection

On the morning and afternoon of November 1st and the morning of November 2nd, we visited the five hummock pairs of our first stratified random sample to assess hummock biodiversity on our transect sweeps and pitfall traps. Subsequently, on the morning and afternoon of November 3rd and the morning of November 4th, we visited the five hummock pairs from our second stratified random sample. On the morning of November 4th, we visited the 10 alternative microhabitats (i.e. rock outcropping, dune grass, and Acacia hummock) located near each of the randomly selected hummock pairs within our second stratified random sample. At approximately 8:00 AM each morning, we collected "night activity" data and "daytime activity" data at approximately 4:00 PM each afternoon.

To assess pitfall traps, we used a large spoon and/or a trowel to scoop invertebrates (i.e. insects, scorpions, spiders, etc.) or lizards out of the pitfalls, carefully sifting through sand in case species burrowed inside the pitfalls. To assess sweep transects, we counted the number of species' track crossings (i.e. a distinct entry and exit) within each transect. With existing track identification knowledge provided from guidebooks and a Gobabeb researcher, Eugene Marais, we categorized observed tracks into: lizard, gerbil, caterpillar, beetle, spider/scorpion, bird, second bird, cape fox, jackal, !nara cricket, mound, sidewinding snake, skink, and unknown. While visiting all twenty !nara hummocks of our aggregate sample, we walked the length of the hummock and recorded each observed animal species. Also, after each visit to a hummock, we re-swept all transects and cleared the contents of all pitfalls.

Biodiversity Indices

Abundance: To calculate an overall species abundance at each hummock, we summed the total number of individuals caught in pitfall traps at the hummock to the total number of animal crossings at the six track sweeps. Note: This calculation was made from compiling individual organism counts (from pitfalls) and a proxy for animal abundance, the number of distinct crossings (defined as an animal entering and exiting) at a given track sweep.

Richness: To calculate overall species richness, we counted the number of different taxa found within the pitfall traps and those crossing the track sweeps at each hummock. This calculation was made from a number of different categories represented in the data, as organisms in the pitfall traps could be identified to the species level, whereas tracks could only be identified to species groups (i.e. gerbils, lizards, etc.).

Shannon-Wiener Index: In an attempt to combine the above parameters (species richness and abundance) we calculated a Shannon-Wiener biodiversity index value (Magurran 2004) at each hummock, for pitfall catches and track data separately, utilizing the following equation:

$$H' = -\sum_{i=1}^{R} p_i \ln p_i$$

To have an overall representation of biodiversity, we combined the indices calculated from the data collected via the two sampling methods (pitfalls and track sweeps) and standardized them by using the following equation to generate a combined Shannon-Wiener index:

$$\frac{H'pitfall_i}{H'pitfall_{\bar{x}}} + \frac{H'tracks_i}{H'tracks_{\bar{x}}} = H'_{TOTAL\ FOR\ EACH\ HUMMOCK}$$

Note: *i = 1-20* hummocks

Jaccard Evenness Value: We were also able to examine how similar the two hummocks within a pair were across the entire experiment, utilizing the following formula:

$$J = \frac{S_c}{S_a + S_b + S_c}$$

where S_a = number of species unique to sample a (fenced hummock), S_b= number of species unique to sample b (unfenced hummock), and S_c= number of species shared between the two samples (fenced and unfenced hummocks).

Pollinator Collection Bowls

To gather additional biodiversity data beyond those collected from the pitfall traps (i.e. ground-dwelling insect species) and the track-sweep transects (i.e. terrestrial hummock species), we conducted a pilot survey of !nara pollinator species. The collection bowls are also known as bee bowls.

We placed 5cm-diameter, white bee bowls atop of each fenced and control hummock at 11:30 AM in an unobstructed area and collected them after five hours. A solution of 5% propylene glycol and a drop of dish soap in water filled each bowl. Next, we placed the bowls on the eastern slope, which was away from the prevailing westward wind. Where possible, we identified each pollinator down to its species, or to its lowest taxonomic designation known from the taxonomy of the region.

Data Analysis

To analyze our hypotheses, we conducted various statistical tests using JMP Pro 13 (JMP Pro 2017). We used ANOVA to examine the effects of treatment (fenced versus unfenced) and block (near vs. far) on Shannon-Wiener indices, species abundance and richness, livestock dung density, mean number of branches, stem diameter, stem length, open flowers, small fruits with flowers, and mean plant height (Table 1).

We used linear regression analysis to test for relationships between livestock dung density vs. % live biomass mean plant height. We also utilized t-tests to look for statistically significant differences in soil temperatures at 5cm depth between the top of !nara hummocks and the surrounding flat ground 20 meters from the hummock base, as well as to compare Jaccard Index values between hummocks.

Table 1. Hummock location and treatment variables. See Appendix B for other variables used in data analysis.

TAG	Latitude	Longitude	Treatment	Block
1E	-23.5644	15.0361	Fenced	Near
1C	-23.564515	15.034981	Unfenced	Near
2E	-23.5634	15.0366	Fenced	Near
2C	-23.5655	15.0382	Unfenced	Near
3E	-23.56766	15.04049	Fenced	Near
3C	-23.56796	15.03991	Unfenced	Near
4E	-23.57096	15.041061	Fenced	Near
4C	-23.572714	15.041466	Unfenced	Near
5E	-23.55741	15.02765	Fenced	Near
5C	-23.55685	15.02824	Unfenced	Near
6E	-23.58928	15.05035	Fenced	Far
6C	-23.587958	15.048973	Unfenced	Far
7E	-23.59021	15.05194	Fenced	Far
7C	-23.5901	15.05114	Unfenced	Far
8E	-23.587668	15.048183	Fenced	Far
8C	-23.587848	15.047976	Unfenced	Far
9E	-23.58867	15.05181	Fenced	Far
9C	-23.58611	15.05138	Unfenced	Far
10E	-23.59204	15.0515	Fenced	Far
10C	-23.59077	15.05191	Unfenced	Far
4C-alt	-23.56866	15.04072	Unfenced	Near

Results

Herbivory Results

To assess the impact of herbivory pressure on plant growth in relation to treatment type and distance from the Kuiseb River, we compared the variables of !Nara mean stem length, stem diameter, number of side branches, and plant height, used as proxies for plant growth, between fenced and unfenced !Nara hummocks, and between hummocks near and from the river.

In comparing mean stem length and diameter, we excluded one data point from hummock 1C that was an obvious outlier due to data entry error. We observed a significant relationship between mean stem length and distance from the river (n= 20, F= 6.1031, df= 1, p = 0.0251) (Fig. 2), but mean stem length did not vary by treatment type (n= 20, F= 2.1082, df = 1, p = 0.1658).

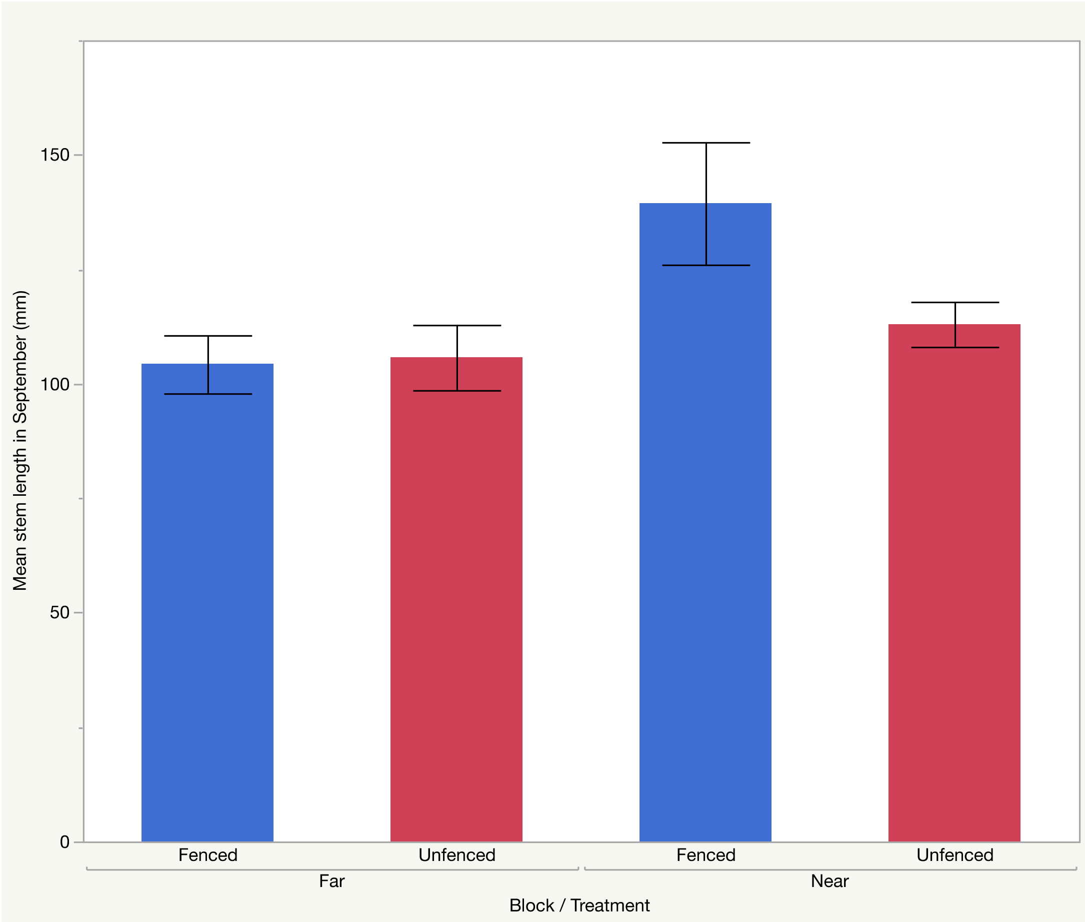

Figure 2. !Nara mean stem length varied between hummocks positioned near ($\bar{x}$ = 126.18 ±6.07 mm) and far ($\bar{x}$ = 104.98 ± 6.07 mm) from the river. Fenced !Nara hummocks near the river exhibited the greatest mean stem length ($\bar{x}$ = 139.38 ± 13.38 mm).

Mean stem diameter decreased with distance from the river (n= 21, F= 6.08, df= 1, p = 0.0246), but did not vary by treatment type (n= 21, F= 0.0171, df = 1, p = 0.8976) (**Fig. 3**). The mean number of side branches did not vary by treatment type (n= 21, F= 0.2658, df= 1, p = 0.6128) or with distance from the river (n = 21, F= 0.2064, df= 1, p = 0.6553).

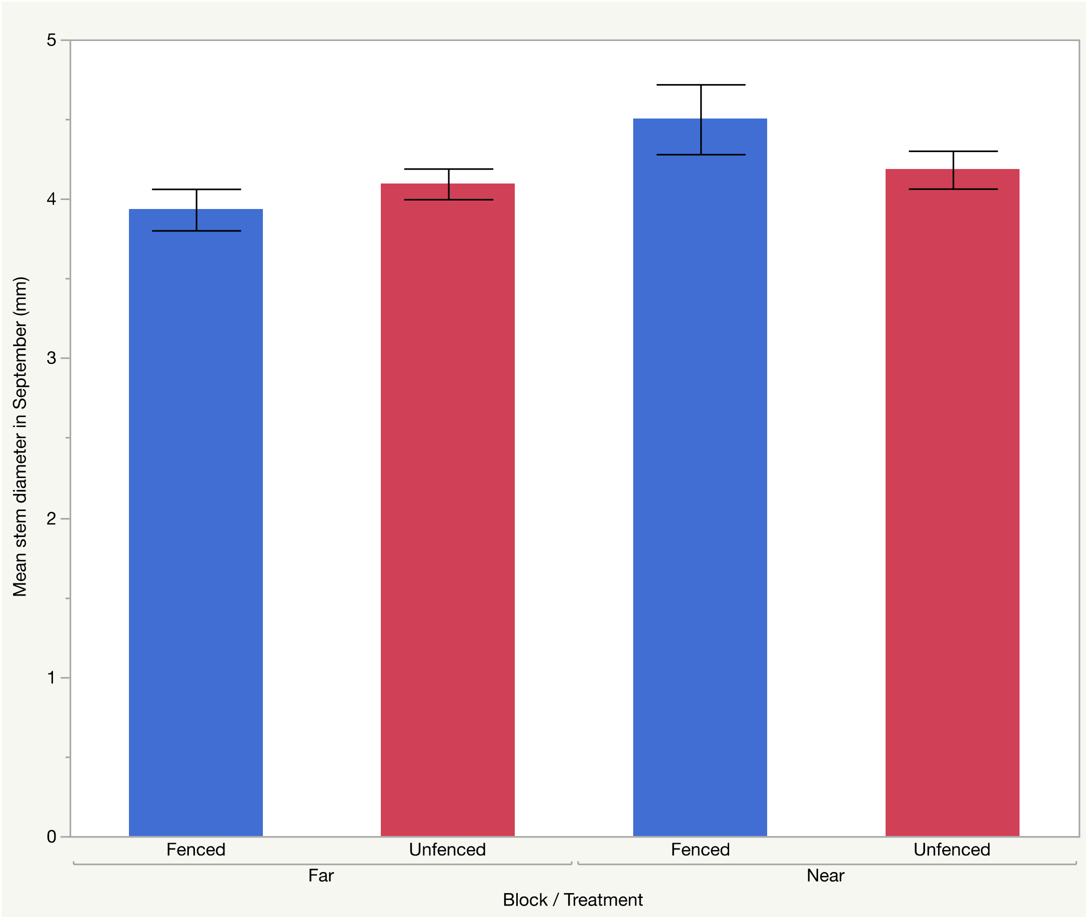

Figure 3. Mean !Nara stem diameter (mm) varied between hummocks positioned near ($\bar{x}$ = 4.39 ±0.11 mm) and far ($\bar{x}$ = 4.01 ± 0.11 mm) from the river. Fenced !Nara hummocks near the river exhibited the greatest mean stem diameter ($\bar{x}$ = 4.5 ± 0.22 mm).

Mean plant height is significantly greater in fenced hummocks (n= 21, F= 4.5776, df= 1, p = 0.0472) (Fig. 4), but does not vary with distance from the river (n= 21, F= 0.00, df= 1, p = 0.99).

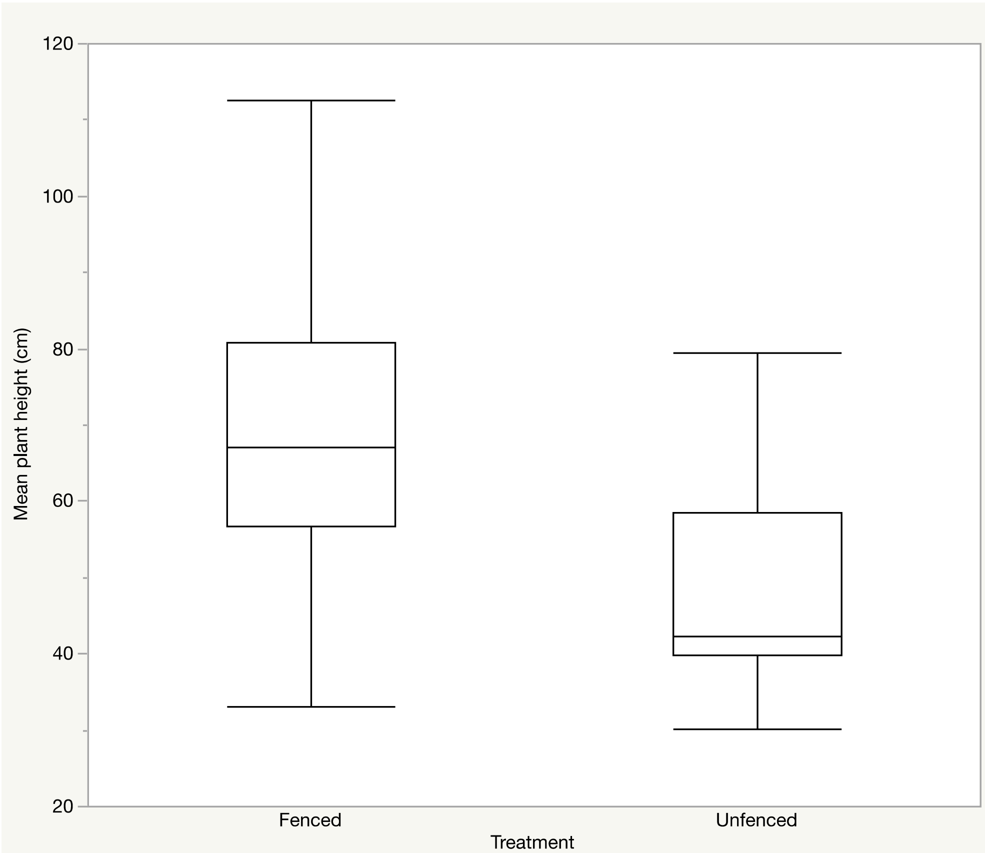

Figure 4. Fenced !Nara hummocks exhibited significantly greater mean plant height ($\bar{x}$ = 69.01 $\pm$ 6.78 cm) than unfenced ($\bar{x}$ = 50.54 $\pm$ 4.70cm) hummocks.

There was a significant relationship between the production of !Nara flowers and hummock distance from the river (n= 20, F= 4.5718, df= 1, p = 0.0483*) (Fig 5), yet the production of !Nara flowers did not vary with treatment type (n = 20, F = 0.5006, df = 1, p = 0.4894). The production of small !Nara fruits with flowers did not vary with treatment type (n = 20, F = 1.2915, df = 1, p = 0.2725) or distance from the river (n = 20, F = 0.0152, df = 1, p = 0.9034).

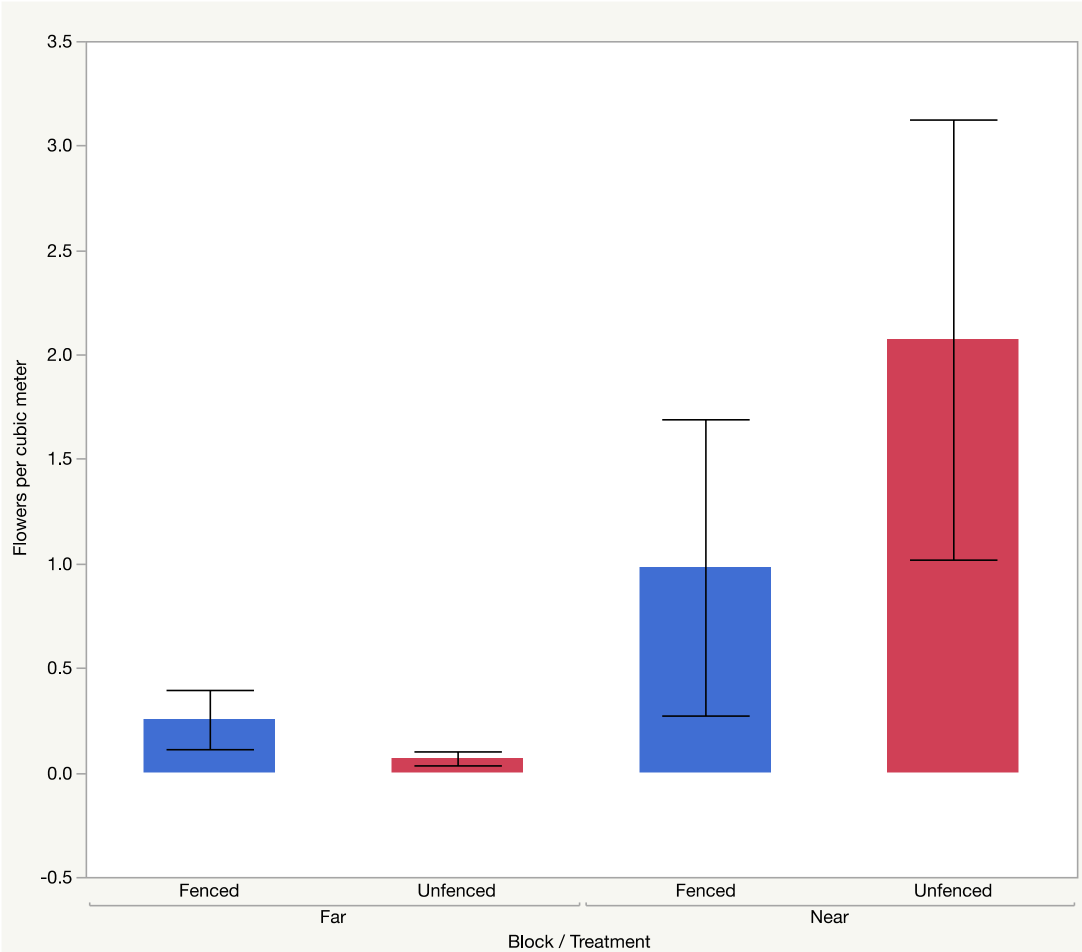

Figure 5. Cumulative !Nara flower production per cubic meter varied between hummocks positioned near ($\bar{x}$ = 1.53$\pm$ 0.45) and far ($\bar{x}$ = 0.16$\pm$ 0.45) from the river. Unfenced !Nara hummocks near the river exhibited the greatest cumulative flower production ($\bar{x}$ = 2.072 $\pm$ 2.35).

Proportion of live biomass did not vary with treatment (n = 20, F = 1.4866, df = 1 , p = 0.2404) or distance from the river (n = 20, F = 1.0758, df = 1, p = 0.3151). Additionally, the proportion of dead biomass did not vary with treatment (n = 20, F = 1.4866, df = 1 , p = 0.2404) or distance from the river (n = 20, F = 1.0758, df = 1, p = 0.3151).

In comparing the cumulative number of livestock dung, we excluded an obvious outlying observation in hummock 1C. Gobabeb staff members collected no livestock dung from fenced !Nara hummocks in the month of September 2017, which indicates and represents the effectiveness of the livestock fences in excluding herbivore activity (e.g. dung). Dung density did not vary with distance from the river (n = 10, F = 0.2458, df = 1, 0.6268). Additionally, there was no significance in the relationship between dung density and either mean plant height (n = 10, F = 1.7357, df = 8, p = 0.2242) or the proportion of live biomass (n= 9, F = 0.0349, df = 7, p = 0.8570).

Biodiversity

We evaluated the biodiversity in the fenced and unfenced hummocks, in relation to those near to and far from the river. We used pitfall traps to catch small animals and sweep transects to count tracks. We assessed abundance, richness, relative biodiversity (Shannon-Wiener index) and Evenness (Jaccard index). We predicted that hummocks closer to the river would have higher diversity due to the presence of riparian species. We also predicted that fenced hummocks would have higher diversity due to lower herbivore impact on animal habitat in the hummock.

There was no significant difference between track, pitfall, and combined abundance between near and far hummocks or fenced and unfenced hummocks (Table 1). There was a marginally, significant positive effect on distance to the river to the number of taxa observed in tracks but not on the number of taxa observed in the pitfalls. More taxa were observed in the hummocks near the river. There was also marginally, significant positive effect of distance to the river and treatment on the Shannon-Wiener index for tracks but the overall ANOVA was not significant. There was no significant effect of treatment or distance to the river on the Shannon-Wiener index for pitfalls and the combined Shannon-Wiener index (Table 1). We initially assumed that the fenced hummocks would have higher biodiversity in terms of richness and abundance, but the richness, Shannon-Weiner indices, and abundance results do not support that hypothesis. The Jaccard index for tracks, which measures similarities between pairs, was higher for pairs of hummocks near to the river ($t=1.885981$, df 8, $p=0.048$). There was no difference between pairs of Jaccard index for pitfalls.

Table 1. Results from ANOVA tests of abundance, # of taxa (richness), and Shannon indices with treatment and distance from the Kuiseb River (near vs. far block). There was no significant difference in abundance, # of taxa, and Shannon indices in near and far hummocks or fenced and unfenced hummocks. However, there was a marginally significant difference in # of track taxa between near and far hummocks. The near hummocks had higher mean track taxa (7.2 ± 0.38) than the far hummocks (5.8 ± 0.38) There was also a marginally significant difference in the Shannon indices for tracks between near and far hummocks as well as fenced vs. unfenced hummocks. However, the fenced and near hummocks had only slightly higher mean Shannon indices for tracks (1.3603 ± 0.077; 1.357 ± 0.077) than the unfenced and far hummocks (1.133 ± 0.077; 1.135 ± 0.077).

Variable	N	df	F	P	Treatment P	Block P
Track abundance	20	3,19	0.5696	0.6430		
Pitfall abundance	20	3,19	1.0003	0.4181		
Combined abundance	20	3,19	1.8181	0.1845		
# of taxa (tracks)	20	3,19	2.271	0.0795*		0.0194
# of taxa (pitfalls)	20	3,19	1.4667	0.2611		
Shannon index (tracks)	20	3,19	2.7685	0.0756	0.0563*	0.0613*
Shannon index (pitfalls)	20	3,19	0.2694	0.8465		
Shannon index combined	20	3,19	2.2822	0.1182		

We found a significant relationship between the combined (pitfalls and tracks) Shannon-Wiener indices and log transformed live volume (N=20, R^2 =0.2163 p= 0.0388) but not between the track and pitfalls Shannon indices and live volume (Table 2). The combined Shannon index was positively correlated with live volume (Fig. 5). There was also a significant relationship between the tracks and combined abundance and the log transformed live volume (Table 2). For both combined and tracks abundance, there was a positive correlation with log transformed live volume (Fig. 6, Fig. 7). However, there was not a significant relationship between the number of taxa observed from the pitfalls and tracks and the log transformed live volume (Table 2). Our results showed that most measures of biodiversity (Shannon-Wiener indices and abundance) were higher in larger hummocks which supported our initial assumptions (Hypothesis 11).The only exception was the number of track and pitfall taxa observed.

Table 2. Results from regressions of abundance, # of taxa (richness), and Shannon indices in relation to log transformed live !nara volume (m^3) indicate that there was a significant relation between combined Shannon indices, pitfall abundance, and combined abundance with increased log transformed volume. Larger hummocks in terms of volume had higher combined Shannon index values, track abundance, and combined abundance.

Variable	N	df	R^2	P
Shannon index (combined) vs. ln (Live volume)	20	19	0.2163	0.0388*
Shannon index (tracks) vs. ln (Live volume)	20	19	0.0712	0.2553
Shannon index (pitfall) vs. ln(Live volume)	20	19	0.0868	0.2072
# of taxa (tracks) vs. ln (Live volume)	20	19	0.1604	0.0801
# of taxa (pitfalls) vs ln(Live volume)	20	19	0.2072	0.0437
Abundance (tracks) vs. ln(Live volume)	20	19	0.2399	0.0284*

Abundance (pitfalls) vs. ln(Live volume)	20	19	0.0553	0.318
Combined abundance vs. ln(Live volume)	20	19	0.2907	0.0142*

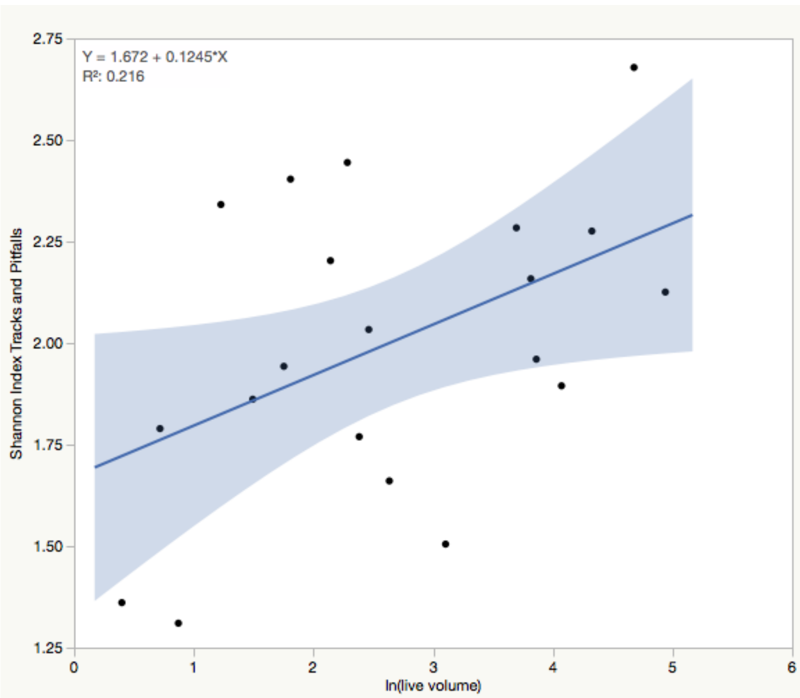

Fig. 6. Linear regression of log transformed live volume (m^3) in relation to the combined Shannon-Weiner index for all !nara hummocks showed that hummocks with higher log transformed volume had higher combined Shannon indices.

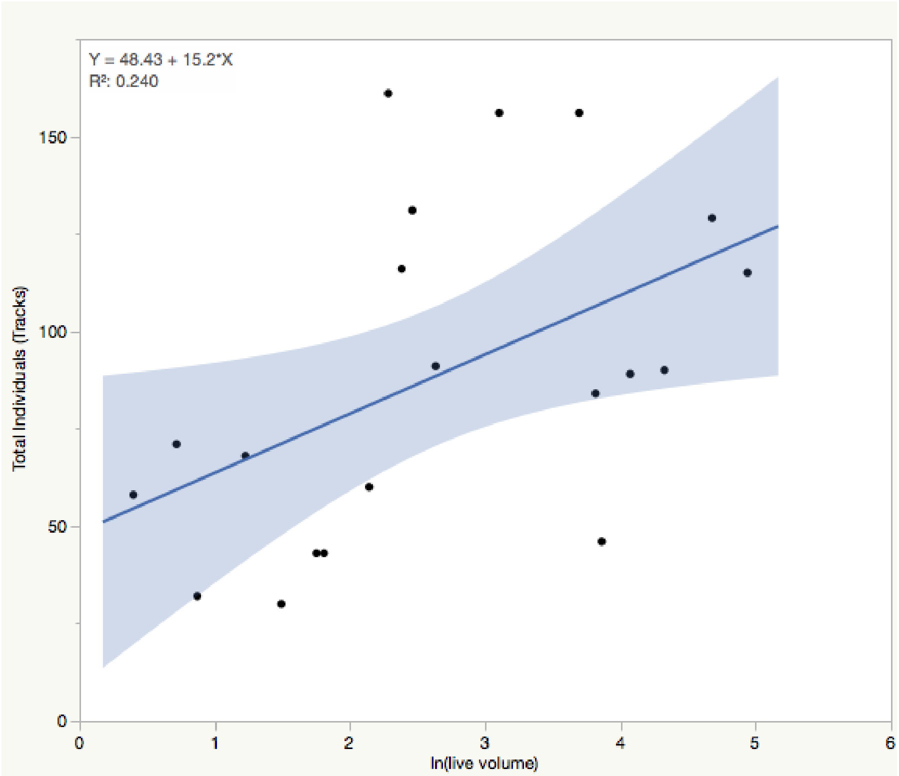

Fig. 7. Linear regression of log transformed live volume in relation to the animal abundance observed from track sweep data for all !nara hummocks indicated that hummocks with higher log transformed volume had higher track abundance.

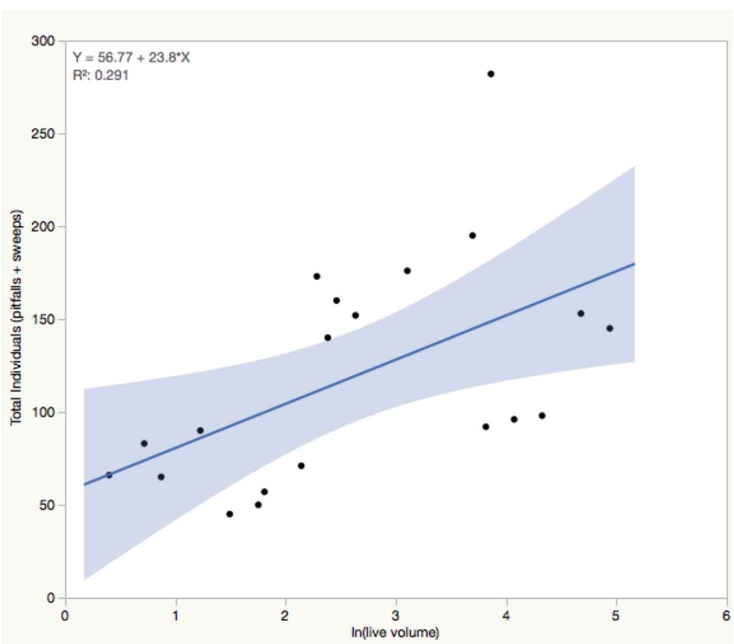

Fig. 8. Linear regression of log transformed live volume in relation to the combine abundance (pitfalls and tracks) for all !nara hummocks indicated that larger hummocks have higher combined abundance

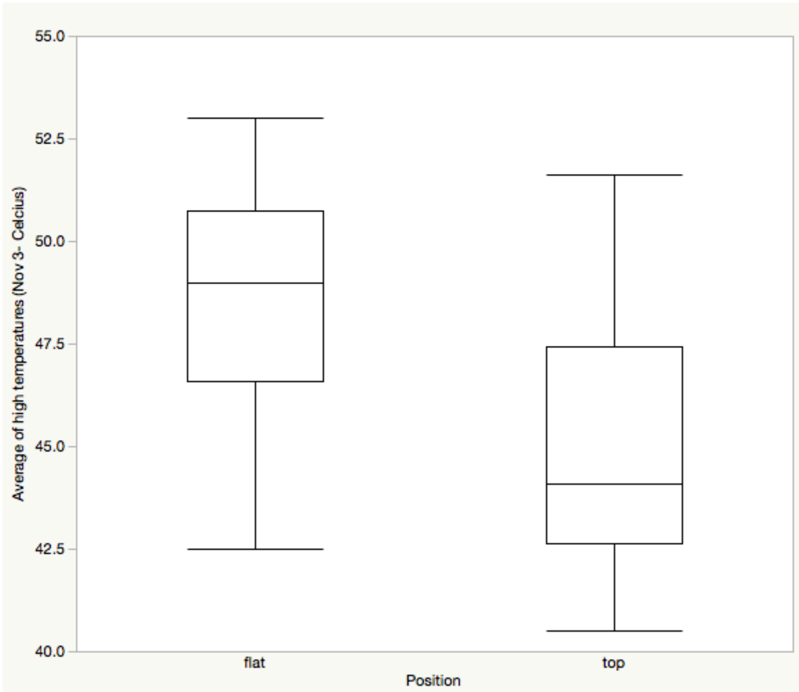

Fig. 9. T-test results analyzing temperature at 5 cm depth between the top of !nara hummock and bare soil 20 m away from hummock base show that mean temperatures at 5cm depth for the hottest 30 minutes of the day are significantly lower on top of !nara hummocks compared to surrounding soils.

Discussion

!Nara Plant Vitality and Herbivory Discussion

To establish the effects of herbivory on !nara plant vitality, we first examined whether proxies of plant growth (i.e. mean stem length, stem diameter and the number of side branches) differed between fenced and unfenced hummocks. Our results indicate that for the first three proxies of plant growth assessed in the monthly and bimonthly data collection (mean stem length, stem diameter, and the number of side branches), no significant difference exists between fenced and unfenced !nara hummocks. Although these findings contradict our first hypothesis, which anticipated greater plant growth measurements in fenced hummocks, the results from our measurements taken on average plant height indicate that fenced !nara plants exhibit significantly greater heights than !nara exposed to livestock herbivore pressures. These findings indicate that the current herbivory monitoring protocol may not be providing the most accurate metric to assess herbivory impacts, or that a sufficient amount of time has not passed since fence installation for significant effects on current metrics of plant growth to be observed. On the other hand, because we did not observe significantly greater mean stem length, diameter, and number of side branches in unfenced hummocks, our data also does not suggest the existence of an alternative relationship, whereby herbivory may stimulate plant growth, as ecologists have observed under intermediate levels of herbivory in other plant species (Bilbrough 2003).

Interestingly, although no significant difference was observed between fenced and unfenced hummocks in mean stem diameter and stem length, our ANOVA results showed that these metrics of plant growth varied significantly when considering hummock proximity (near vs. far) to the Kuiseb River. Both mean stem diameter and stem length were significantly greater at !nara hummocks near the Kuiseb River, which may be indicative of increased availability of groundwater from an elevated water table near the Kuiseb. This finding contradicts our second hypothesis, which predicted that hummocks nearer to the Kuiseb would exhibit lower mean stem diameter and stem length due to higher concentration of livestock around the river.

To establish the effect of livestock herbivory on the ability of !nara plants to invest in reproduction, we analyzed the difference in total fruit and flower production between fenced versus unfenced hummocks. We assessed the number of fruits with flowers still attached to their tips, given that this is the most ephemeral stage of fruit development, and thus the least likely to be recounted between monthly herbivory data collection. Our ANOVA analysis of fruits with flower and flower production did not support our third hypothesis, which predicted that a significantly greater number of total fruits with flowers and flowers would be observed in fenced versus unfenced hummocks. Although fruit production did not differ significantly in hummocks positioned near to versus far from the Kuiseb River, the number of flowers was observed to be significantly greater on plants closer to the Kuiseb. One possible explanation for this observation may be that !nara plants are able to produce more flowers in closer proximity to the Kuiseb due to greater access to belowground water resources. Yet, because herbivory pressure may be greater closer to the river, more of these flowers eventually become browsed prior to reaching the small fruit stage, thus reducing the difference in small fruit production near to versus far from the Kuiseb.

After observing that a large proportion of dead !nara biomass appeared to have been trampled by large herbivores, we decided to examine the impact of livestock trampling in addition to browsing on proportion of live !nara biomass. Our ANOVA results did not support the treatment component of our fourth hypothesis, which predicted that fenced hummocks would display a greater proportion of live biomass than unfenced. In addition, our examination of proportion of dead biomass revealed no significant difference between fenced and unfenced hummocks. Aside from treatment, both proportions of live and dead biomass did not differ between hummocks positioned near versus far from the Kuiseb River.

Given the wealth of data from the previous year's monthly and bimonthly data collection, we determined that the fences used in the long term herbivory study are effectively excluding livestock (Hypothesis 5) , especially evident given the fact that no cattle, donkey, and/or goat dung was counted within fenced hummocks for the most recent sampling month of September. Considering the central tenets of optimal foraging theory, which includes the idea that animals will optimize nutrient intake with the least amount of energy expenditure, we had hypothesized that livestock herbivore activity (assessed utilizing cattle and donkey dung density) would be lower at hummocks positioned further out into the Namib sand sea, given the significantly lower density of plant resource farther from the Kuiseb and the energy-intensive process of walking across sand dunes to reach these !nara hummocks (Hypothesis 6). We also predicted that signs of herbivore presence would be lower further among the dunes, given previous Topnaar livestock satellite tracking data, which indicated that cattle and donkeys only trek far into the dunes infrequently, preferring to move among the shade and concentrated forage of the Kuiseb. Results from our linear regression of September's dung density counts and hummock distance from the Kuiseb indicated that a statistically significant relationship did not exist between these two variables. A plausible reason for why no relationship was observed between hummock distance from the Kuiseb River and livestock activity may be due to the fact that the hummocks assessed in our experiment are not positioned along a wide gradient of distances from the Kuiseb. Instead, the near and far hummocks tend to occupy two clustered points, around a distance of approximately 0-500 meters and 2300-2800 meters from the Kuiseb. To distinguish a trend with a linear regression analysis, it may have been better to assess hummocks at more intermediate distances, as well as further into the Namib Sand Sea.

Considering that livestock dung density is a reliable indicator of herbivore presence/activity levels at a given hummock (based upon the lack of dung inside fenced hummocks), we also examined the relationship between cattle/ donkey dung density and mean plant height (which we concluded to provide a good metric for measuring plant vitality, based on the significant difference observed between fenced and unfenced hummocks in mean plant height), as well as proportion of live !nara biomass (which showed no variance between treatment types). Although we hypothesized (Hypothesis 7) that herbivore exclusion promotes !nara growth, we found that dung density was not significantly correlated with mean plant height. This finding does not necessarily discount our hypothesis, rather it indicates that examining the linear relation between dung density and mean plant height cannot accurately reflect significant changes in plant growth caused by herbivory pressure. The regression of dung density on proportion of biomass also showed no significance. Since we concluded that the proportion of live biomass was not a good metric for measuring plant vitality, we would no longer expect there to be a linear relationship between dung density and the proportion of live biomass.

!Nara Hummock Biodiversity Discussion

We had several main questions we addressed in our study. The first was how livestock herbivory, hummock distance from the Kuiseb River, and hummock volume affected the biodiversity (richness and abundance) of !nara hummocks. We initially assumed that hummocks with higher volume would have higher biodiversity because they contain more habitat. (Hypothesis 11).We found that larger hummocks differed significantly in terms of Shannon diversity index (combined), track abundance, and combined abundance from smaller hummocks. This is likely because hummocks provide more three-dimensional space for burrowing animals to forage and seek thermal refuge. The capacity of !nara hummocks to provide a thermal refuge for desert organisms is shown by the drastic difference in temperature between the center of the hummocks and the bare soil surrounding them ($t=-3.209$, $df= 37$, $p= 0.0014$). The mean temperature was lower by several degrees Celsius at the top of the hummock at 5 cm depth than on bare soil 20 meters away from the top (Fig. 9). This would support the hypothesis that !nara plays a critical role as an ecosystem engineer by changing the abiotic conditions inside of the hummock (Hypothesis 13)

In terms of livestock herbivory, we assumed that fenced !nara hummocks would have higher animal abundance and richness because the vitality of unbrowsed plants would be higher (Hypothesis 8). With higher vitality, the fenced !nara plants may provide more food resources as well as spatial complexity for the animals that utilize the hummocks. However, our results demonstrated that abundance, number of taxa, and the richness calculated with the Shannon-Weiner index were not significantly different between the different treatments and distances to the river. The Shannon-Weiner indices were likely not significantly different between near and far hummocks or fenced and unfenced hummocks because the index values are based on how many unique species are present and not on the total number of only a few species present, as with the combined abundance (total individuals). In this respect, dune ants were considerably more abundant than other species and were found in significantly higher numbers close to the river, which results in a significant difference in the combined abundance between near and far hummocks or fenced and unfenced hummocks (Appendix F). Interestingly, ant abundances were also significantly greater in enclosed hummocks, indicating that ants may choose to associate more frequently in areas that are less trampled by livestock, or that have greater biomass to forage around (which may be evident in the significantly greater mean !nara plant heights at enclosed hummocks) (Appendix F).

In terms of the proximity to the Kuiseb River, we assumed that species richness would be higher in the hummocks closer to the river because habitat heterogeneity is greater near the Kuiseb River (Hypothesis 10). In addition to higher habitat heterogeneity, we assumed that diversity would be higher in the hummocks close to the river because there would be a combination of desert-adapted species and savanna species at the margins of the river, where the river/savanna ecosystem transitions to the Namib sand sea. We found that the number of taxa (richness) and total number of individuals (abundance) were not significantly different in the hummocks near to and far from the river. However, there was a marginally significant difference between the number of track taxa with different distance from the river. Even though the overall ANOVA for the track taxa and the distance to the river was only marginally significant, the effect of distance to the river on track taxa was significant ($p = 0.0124$). This result may suggest that the sample size for the track taxa data may be too small to show the effect of river proximity on diversity. The Shannon index values were likely not significantly higher close to the river because the species are less evenly distributed in the near hummocks. Perhaps there are riparian species that occur in the transition zone between the sand sea and the Kuiseb River that outcompete desert-adapted species at the near hummocks and therefore diversity is lower. There may also be no significant effect of proximity to the river or herbivore exclusion on the biodiversity of !nara hummocks because the species inhabiting them are highly specialized for the environment the plant creates. For instance, some species may depend on the lower temperatures inside of the hummock to avoid the high temperature fluctuations that naturally occur in the desert (Fig. 7) Therefore, proximity to the river or herbivore pressure would not have a large effect on the total biodiversity of the hummocks.

We also compared species richness and abundance of !nara hummocks with other hummock-forming landscape features including dune grass (*Stipagrostis sabulicola*), rock outcrops, and acacia trees (*Acacia erlioba*). We made this comparison to assess the keystone status of !nara by seeing if !nara hummocks support more diversity than the surrounding desert matrix. We initially assumed that !nara hummocks would have higher species richness and abundance than the other hummock-forming features because !nara has greater structural complexity. Our few samples indicated that more total species and more individuals of different species were found on !nara relative to other features like rock outcrops of dune grass hummocks (Appendix E). However, there is an extremely small sample size associated with these findings and the collection protocol was not always consistent between samples. Therefore, it is difficult to draw significant conclusions from this information. Future groups may be able to better evaluate the keystone status of !nara by improving upon these methods of comparison with other plants and habitats.

One final interesting finding from our biodiversity assessment was that gerbil abundances, as estimated from the total number of gerbils crossing sweep transects at each hummock, were significantly greater within fenced hummocks than unfenced hummocks (Appendix G). This finding is of particular interest, given that gerbils are cited as one of the two primary !nara seed dispersers, alongside black-backed jackals (Henschel et al. 2004). As Henschel et al. note, gerbils often bury the seeds of serve as primary short-distance seed dispersers for the !nara plant through their habits of burying caches of seeds underground, where many are forgotten and are thus well-positioned for germination. Given that significantly greater abundances of gerbils are found when livestock herbivores are excluded from hummocks, these results suggest that livestock herbivore exclusion may offer a multi-faceted benefit to !nara plant reproductive success, given that: 1) more energy could theoretically be invested in reproductive structures due to a reduction in browsing and trampling of !nara stems, and 2) dispersal and germination of !nara seeds may be significantly greater when livestock herbivores are excluded from hummocks due to the fact that gerbil abundances are significantly greater in fenced hummocks. One possible explanation for why significantly more gerbils are found within the fenced hummocks may be that gerbils are more likely to construct burrows in areas of more stable soils, as demonstrated in previous scientific literature (Brown 1989). Given that donkeys and cattle often trample heavily around the base of !nara plants within unfenced hummocks where gerbils primarily construct their burrows, gerbils may be less likely to associate with herbivore-accessible hummocks.

Recommendations for Future Studies

We suggest several changes to the bi-monthly !nara monitoring protocol that would improve the accuracy and efficiency of the data collection. Firstly, we propose separating each hummock into quadrats using a pole in the center of each hummock that has several pieces of string attached. Each piece of the string would be tied off to a section of the fence to divide the hummock into 4 sections. This would help to reduce double counting of flowers, fruit, and other plant parts that are monitored in the bi-monthly protocol. This change could increase the speed of data collection while also improving the collection accuracy. We also suggest the addition of other measurements to the long-term protocol. Based on the current data in our study, we found that although the flower and fruit data did not show a significant difference with the different treatments (fenced versus unfenced), the mean plant height for the plant was significantly different between the treatment and control. Therefore, we suggest adding the mean plant height measurement to the long-term data collection protocol.

We also suggest several changes to the biodiversity study protocol to improve the study accuracy. First, we suggest standardizing the period of time spent observing hummocks for biodiversity data (pitfall, track, and observation) to make the results more comparable. For instance, we suggest adding a section to the methods/protocol where we explain a standard way of surveying the hummock for live species observations. Second, given that pollinators are a significant component of hummock biodiversity, we suggest that further study of biodiversity include a more thorough survey pollinator species using bee bowls. To improve the bee bowl method, we suggest assessing the weather ahead of time as we encountered difficulties with a pilot study on an extremely windy day. Finally, we suggest deploying more bee bowls with attached stands so they are not blown away or filled with sand while deployed on the hummocks.

Conclusion

Given the plethora of scientific literature alluding to the possibility that !nara functions as an important keystone species within the greater Namib-Kuiseb ecosystem, along with the great cultural and economic importance of the plant to local Topnaar communities, we set about in our scientific investigation to answer the following two research questions utilizing a combination of fieldwork and analysis of existing herbivory data: 1) How might livestock herbivory impact !nara plant productivity and growth? and 2) How might !nara function as an ecosystem engineer, creating a favorable environment for many desert-dwelling species and thus acting as a keystone species in the greater Namib ecosystem? From analysis of the existing herbivory study data, we determined that herbivore exclusion may promote !nara plant growth (as observed with the significantly greater mean plant heights in fenced as compared to unfenced hummocks), however enough time may not have elapsed since the beginning of the enclosure study to observe a significant difference between treatment types in other proxies for plant vitality (i.e.- mean number of fruits with flowers, open flowers, stem diameter, and stem length).

From our analysis of associated animal communities at the various hummocks, we observed that fenced hummocks do not exhibit significantly greater abundances of animals, nor greater species richness, than unfenced hummocks, indicating that livestock herbivory pressure may not be directly impacting the capacity of !nara hummocks to maintain biodiversity, or that a sufficient amount of time has not elapsed between the commencement of the experiment and our sampling for an observed effect on community structuring to be observed.

Species abundance observed from track data, combined track and pitfall species abundance, and combined Shannon-Wiener indices all appeared to be positively correlated with hummock size, indicating that herbivory may inhibit the ability of !nara plants to support biodiversity in the long term if the trampling activity of livestock inhibits the ability of !nara hummocks to enlarge. Interestingly, we found that gerbil abundances are significantly greater at fenced hummocks, indicating that herbivore exclusion may have indirect benefits on !nara reproductive success, given that these rodents are key seed dispersers of !nara. Although we only conducted a preliminary study assessing the animal communities associated with !nara hummocks compared to other hummock-forming desert landscape features, we tentatively add that the species diversity and abundance may be greater at !nara hummocks (Appendix E). In the future, we propose an expansion of this aspect of the study, which would allow researchers to substantiate their claims that !nara functions as a keystone species.

From our temperature logging data, which indicated significantly lower mean high daytime temperatures at the top of !nara hummocks as opposed to the ground alongside them, it appears as though !nara may be functioning as ecosystem engineers, modifying their surrounding landscape in such a way that makes it more favorable to other animals. Although the exact reasons of this observed trend remain unknown, we propose that future research should extend this investigation to examine how !nara are precisely altering soil conditions.

Acknowledgements

We would like to thank the incredibly committed team of Dartmouth faculty and staff, in addition to our new friends of the Gobabeb Research and Training Centre for their support and guidance in the completion of this project. Thank you to Flora Krivak-Tetley for all of her help with the logistical planning, impressive dune-driving skills, and her patience in dealing with our insatiable appetite to collect more and more field data. Thank you to Saima Shikesho, Gobabeb employee extraordinaire, for her unparalleled ability to both identify animal tracks and train a group of non-desert dwellers in the art of tracking in the Namib Desert, as well as her sage advice in constructing our final paper. We would also like to thank Liz Struder, insect connoisseur, for her ability to get all of us excited about the insect world, and for her diligent work in collecting bee bowls and supporting our final editing process. In addition, thank you to Jeff Kirby for his aerial photography skills, for all the help with analyzing our drone data, and for sharing his amazing National Geographic stories with us! We also wish to extend many thanks for Eugene Marais, known amongst the group as the master gerbil wrangler, for sharing his bountiful knowledge spanning the disciplines of desert ecology to track identification to research methods. Finally, thank you to Professor Bolger for his continued enthusiasm for ecology and belief in our project. Even when we opened our spreadsheet with over 37,000 temperature data points and questioned our ability to synthesize a final project, Professor Bolger assured us that the interesting ecological questions lay just around the corner.

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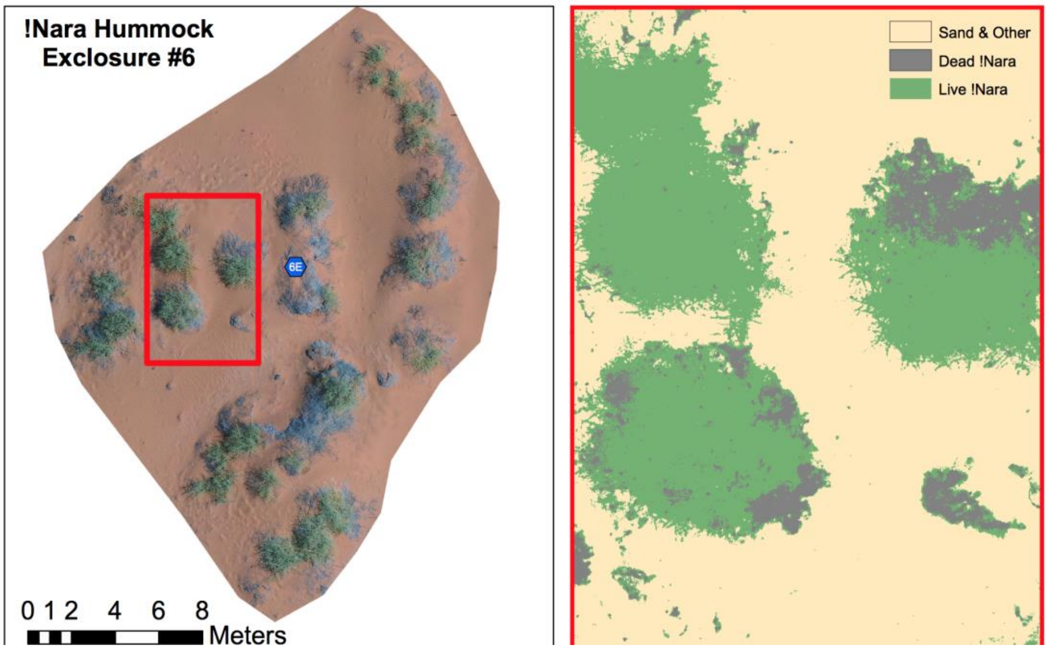
Appendices:

Appendix A: Classification of % Live and Dead !Nara Biomass for Hummock E6 from UAV Orthomosaic



Appendix B: Variables used for data analysis

TAG	Total donkey and cattle dung	Mean plant height	Mean stem length	Mean stem diameter	Mean # side branches	Small fruits with flowers	Flowers	% Live Biomass	% Dead Biomass	Live Surface Area (m^2)	Live Volume (m^3)
1E	0	112.5	177.4	4.63	3.8	0.08	0.5	0.435513624	0.095458243	42.3	47.58
1C	347	79.5	282.8	4.87	6.7	0.71	0.57	0.201541184	0.159751547	175.9	139.84
2E	0	68.889	144.1	3.85	2.4	0.35	0.64	0.217609726	0.030584683	156.22	107.62
2C	11	58.5	100.3	3.78	4.4	2.54	5.17	0.172717572	0.018354918	129.37	75.68
3E	0	65.2	131.1	5.182	9.9	4.28	3.77	0.300578339	0.093690661	15.05	9.81
3C	0	40.9	124.8	4.511	7.6	2.01	4.03	0.174439236	0.123761714	3.64	1.49
4E	0	75.7	95.2	4.572	9.1	0.18	0	0.459278547	0.108453303	14.31	10.83
4C	0	39.9	103.7	4.272	5.9	2.7	0.59	0.098604997	0.055297474	21.36	8.52
5E	0	33	149.1	4.268	5	0	0	0.025977891	0.08609181	10.34	3.41
5C	16	30.1	122.8	4.226	8.1	0	0	0.078767601	0.045344648	20.25	6.1
6E	0	80.4	103.7	4.085	6.9	0.31	0.09	0.233909426	0.086317982	73.03	58.72
6C	0	53.4	97.3	3.84	3.8	0.04	0.18	0.170105989	0.076441795	85.11	45.45
7E	0	60.1	97.9	4.165	4.2	0.17	0	0.2034284	0.044356131	19.52	11.73
7C	0	54.857143	98.7	4.131	9.2	11.29	0	0.155933279	0.260372695	4.36	2.39
8E	0	65.2	94.4	3.513	4.2	0.87	0.69	0.091541111	0.204044734	8.85	5.77
8C	31	75.2	101.2	4.299	5.9	0.09	0.09	0.143045042	0.156459133	29.64	22.29
9E	0	82.2	96.3	3.747	5.3	0	0	0.267038092	0.068452276	48.99	40.27
9C	0	41.9	134.1	4.299	7.6	0.86	0.07	0.217535111	0.11365897	33.25	13.93
10E	0	46.9	128.9	4.157	7.9	0.49	0.49	0.034319083	0.011573251	4.37	2.05
10C	0	39.375	97.3	3.906	4	0.22	0	0.039508072	0.104352923	11.31	4.45
4C-alt	23	42.3	113.3	4.129	7.2						

TAG	Total Individuals (Tracks)	Total Individuals (Pitfalls)	Total Individuals (Aggregate)	Track # of Taxa	Pitfall # of Taxa	Total # of taxa (aggregate)	Shannon Index Tracks	Shannon Index Pitfalls	ln(live volume)
1E	46	236	282	8	8	13	1.773843829	0.6394317	3.862412505
1C	115	30	145	7	7	12	0.984403039	1.58935049	4.940498912
2E	129	24	153	8	7	14	1.606942885	1.65330368	4.678606504
2C	90	8	98	8	5	13	1.202806985	1.559581156	4.326513925
3E	161	12	173	7	7	13	1.140336715	1.820075975	2.283402274
3C	58	8	66	7	2	9	1.301949981	0.376770161	0.39877612
4E	116	24	140	8	5	13	1.563237551	0.613481894	2.382320061
4C	60	11	71	6	4	10	1.422189942	1.263654432	2.142416341
5E	68	22	90	6	6	12	1.314082915	1.531153319	1.226712291
5C	43	14	57	7	6	12	1.26867945	1.648847072	1.808288771
6E	89	7	96	4	4	8	1.153228888	1.153741943	4.072780384
6C	84	8	92	7	5	12	1.125051869	1.494175138	3.816612821
7E	131	29	160	6	6	11	1.101015573	1.368340794	2.462149663
7C	32	33	65	4	5	9	0.672215865	0.91728616	0.871293366
8E	43	7	50	7	3	10	1.420496107	0.955699891	1.752672081
8C	156	20	176	7	2	9	1.287064973	0.562335145	3.104138147
9E	156	39	195	8	8	15	1.359216805	1.419921253	3.695606775
9C	91	61	152	5	5	9	1.44405194	0.597665869	2.634044788
10E	71	12	83	6	3	9	1.170944116	1.011404265	0.717839793
10C	30	15	45	4	6	9	0.626381237	1.617053153	1.492904096

Appendix C: !Nara Hummock Confirmed Species List

Grouping	**Species**
Ants	Black ant (*Oxymyrmex barbiger*) Dune ant (*Camponotus detritus*)
Beetles	Ridged dune beetle (*Onymacris laeviceps*) Black beetle (*Onymacris unguicularis*) Flat beetle (*Stip stali*) Shiny Black Beetle (*Zophosis moralesi*) Blister beetle (*Mylabris zigzaga*) Ladybird beetle (*Coccinellidae sp.*)
Birds	Dune lark (*Calendulauda erythrochlamys*)
Caterpillars	Io moth (*Automeris sp.*)
Flies	!Nara fly (*Uliidae sp.)* Pollinator fly (*sp. unknown, Dartmouth 2015*) Blow fly (*Calliphoridae sp.)*
Gerbils	Hairy-footed gerbil (*Gerbillurus paeba*)
Lizards	Shovel-snouted lizard (*Meroles anchietae*) Namaqua desert lizard (*Pedioplanis namaquensis*) Wedge-snouted lizard (*Meroles cuneirostris*) FitzSimons' burrowing skink (*Typhlacontias brevipes*)
Other insects	Silverfish/ fishmoths (*Ctenolepisma sp.)* Harvester termite (*Hodotermes mossambicus*)

	!Nara cricket (*Acanthoproctus diadematus*) Solifuge / Sun spider (*Daesiidae sp.)* Dune bee (*Anthrophora aune*) Black parasitoid wasp (*Hylaeus sp.)*
Other mammals	Cape fox (*Vulpes chama*) Cape hare (*Lepus capensis*) Steenbok (*Rhaphicerus silvestrus*)
Scorpions	Burrowing scorpion (*Opistopthalmus flavescens*)
Snakes	Sidewinding adder (*Bitis peringueyi*) Namib sand snake (*Psammophis namibensis*)
Spiders	Dancing white lady spider (*Leucochestris arenicola*)

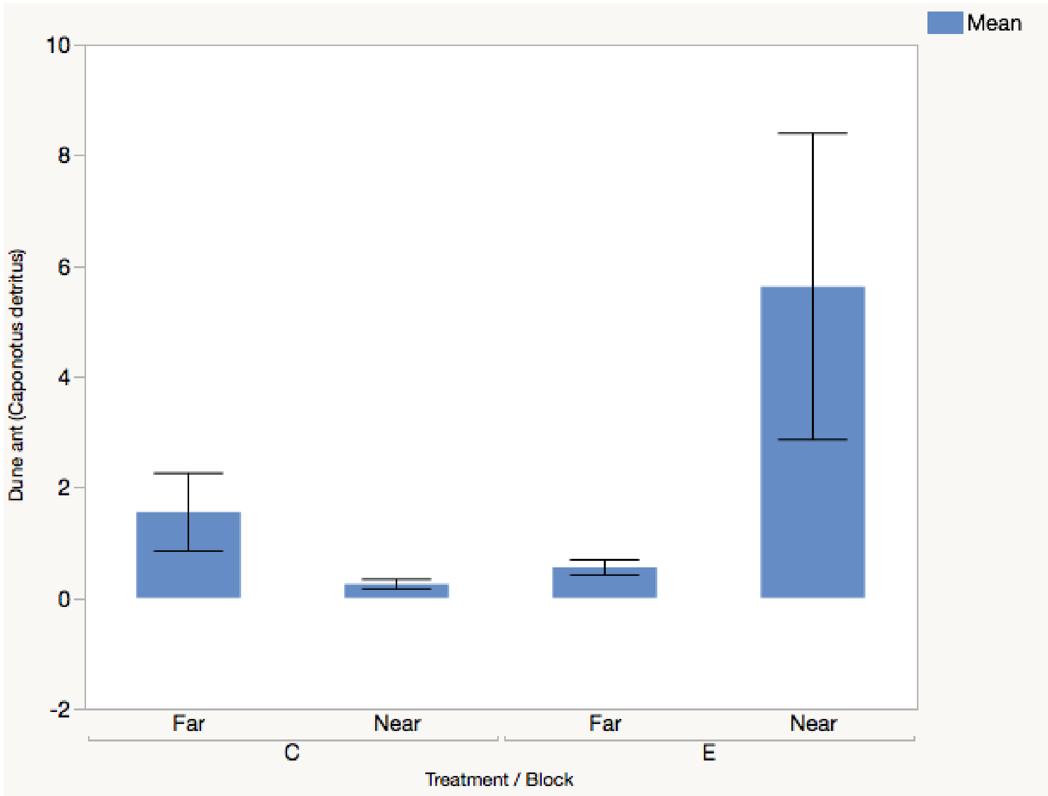
Appendix D: Alternate Hummock Sweep Transect Positions

Waypoint #	Coordinates	!Nara hummock pairing	Hummock Type	Location relative to !Nara pairing
101	S 23.56448, E 015.03638	10E	Dune Grass	northwest
102	S 23.59052, E 015.05148	10C	Rock Outcropping	northwest, across road
103	S 23.59025, E 015.05241	7E	Dune Grass	northeast, up dune
104	S 23.56461, E 015.03665	2E/2C	Acacia	between 2E and 2C, eastern side
105	S 23.56448, E 015.03638	1E	Short grass tuft	between Acacia hummock and 1E
606	S 23.59053, E 015.05091	7C	Rock outcropping	about 50m southwest
607	S 23.55659, E 015.02854	5E	Acacia	30m north
608	S 23.55715, E 015.02773	5C	Short grass tuft	20m east
609	S 23.55722, E 015.02805	5C	Rock outcropping	20m south

Appendix E: Table for Hypothesis 12 - Sweep Transect Biodiversity For Paired Alternative Hummock Habitats

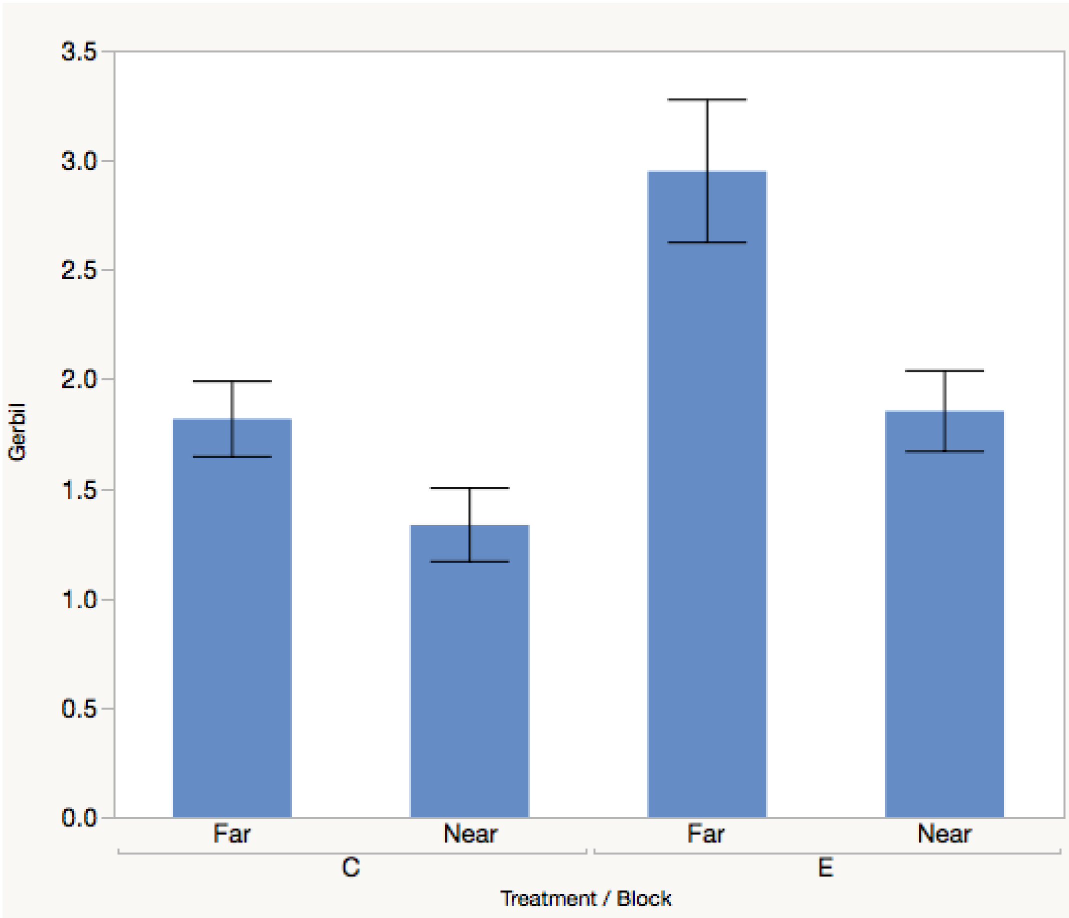
ID Number	Hummock type	Track Sweep Counts- Night of Nov. 4 (2 sq. meters)
101	Dune grass	2 Gerbil, 1 Spider/Scorpion
10E	!Nara	2 Beetle,
102	Rock outcropping	1 Beetle
10C	!Nara	2 Beetle
103	Dune grass	1 Gerbil, 1 !Nara Cricket, 1 Bird
7E	!Nara	3 Gerbil, 5 Beetle
104	Acacia	3 Beetle
2E	!Nara	1 Lizard, 2 Gerbil, 1 Beetle, 1 Spider/Scorpion, 2 Cape Fox
105	Dune grass	1 Lizard
1E	!Nara	3 Beetle, 1 Spider, 1 Cape fox/Jackal
605	Rock outcropping	1 Unknown
7C	!Nara	Nothing
607	Acacia	1 Gerbil
5E	!Nara	1 Gerbil, 2 Fitzsimon's Skink
608	Dune grass	Nothing
5C	!Nara	3 Lizard
609	Rock outcropping	Nothing

Appendix F: Distribution of Ant Abundance Between Pitfall Traps at Fenced vs. Unfenced Hummocks



App. F- ANOVA results for total ant abundances within pitfall traps show a significant interaction between treatment (fenced vs. unfenced) and block (near vs. far to the Kuiseb River), indicating that more ants are found in fenced hummocks near to the Kuiseb than all other block and treatment combinations (F=3.0163, df=3,159, p=.0317).

Appendix G: Distribution of Gerbil Abundance, as Assessed from Track Sweeps, at Fenced vs. Unfenced Hummocks



App. G - ANOVA results for total gerbil abundances (as estimated from track data) show a significant effect of treatment (fenced vs. unfenced) and block (near vs. far), indicated that: 1) more gerbils are found inside fenced hummocks than unfenced hummocks and 2) more gerbils are observed at hummocks positioned far from the Kuiseb River (n= 20, F=4.9318, df=3,142, p=0.0028).