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BROWSE AVAILABILITY AND RESOURCE UTILISATION BY THE EASTERN BLACK RHINOCEROS (*DICEROS BICORNIS MICHAELI*) ON TWO WILDLIFE CONSERVANCIES IN KENYA

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A dissertation submitted in partial fulfilment of the requirements for the degree of M.Res. Wildlife Conservation.

As the nominated University supervisor of this M.Res. project by Lara Jackson, I confirm that I have had the opportunity to comment on earlier drafts of the report prior to submission of the dissertation for consideration of the award of M.Res. Wildlife Conservation.

Signed: ……………………………………

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As the nominated Marwell Wildlife supervisor of this M.Res. project by Lara Jackson, I confirm that I have had the opportunity to comment on earlier drafts of the report prior to submission of the dissertation for consideration of the award of M.Res. Wildlife Conservation.

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MW Supervisor's name: Dr. Philip Riordan

Abstract

The designation of protected areas, in response to habitat encroachment and pressure from anthropogenic activities, is one of the primary global conservation strategies for the management of vulnerable species. Fenced reserves tend to be small, with finite resources imposing an artificial ecological carrying capacity (ECC). Wildlife populations in fenced areas grow rapidly and may exceed the ECC of the environment, resulting in effects like vegetation changes and declines in population growth rates. For megaherbivores, such as the black rhinoceros, population growth rates are predominantly limited by food availability. Thus, resource availability and utilisation studies are essential to determine whether there are adequate resources to support a viable population within fenced reserves and to implement appropriate management plans. This study was conducted on the Lewa-Borana Landscape (LBL), which includes two conservancies that vary due to intrinsic physical differences. Browse availability (BA) and the utilisation of resources by black rhino were investigated. Key findings indicate that BA did not differ between the two conservancies. However, BA in forest habitats was 18% higher than hills and 20% higher than plains. An assessment of current management strategies (exclusion zones) revealed that BA inside the zones was 22% higher than outside. However, higher quantities of BA were not correlated with the age of the exclusion zone, suggesting that the vegetation in some zones may have exceeded 2.0m in height and become inaccessible to black rhino. Although exclusion zones are successfully increasing BA, they are not being managed in a way that optimises food quantities for black rhino. Selectivity indices revealed that black rhino select for *Acacia drepanolobium*, an important food source that has declined on the LBL in recent years, this could have implications regarding resource availability and population viability. Finally, black rhino select for herbs and low growing succulent species during the wet season. This appears to be a behaviour that has evolved to avoid competition with other large herbivores, such as elephant, and has been documented in other black rhino populations. Overall, this study has resulted in several key findings that have implications for habitat manipulation, current management strategies and the conservation of fenced black rhino populations across Africa.

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List of Abbreviations

Abbreviation	Meaning
ANOVA	Analysis of Variance
BA	Browse Availability
BC	Borana Conservancy
DBH	Diameter at Breast Height
ECC	Ecological Carrying Capacity
GLM	Generalised Linear Model
GPS	Global Positioning System
IUCN	International Union for Conservation of Nature
LBL	Lewa-Borana Landscape
LWC	Lewa Wildlife Conservancy
PA	Protected Area

1 Introduction

1.1 Protected Areas

Human population growth and the subsequent encroachment into regions of wilderness is resulting in increasingly fragmented landscapes, confining species to small areas and threatening biodiversity (Miller et al., 2015; Barnes et al., 2016). The designation of protected areas (PA) is one of the main global conservation strategies for the management of vulnerable and declining species (Packer et al., 2013). Since 1970, the coverage of PAs in Africa has increased to ~3.1 million km^2 and fenced reserves have proved crucial in preventing the extinction of threatened species, such as the black rhinoceros (*Diceros bicornis*) (Newmark, 2008; Buk & Knight, 2010; Packer et al., 2013).

Although PA management appears to be the most viable conservation strategy given the anthropogenic pressures that are and will continue to be exerted on the environment, many consequential challenges arise (Davies-Mostert et al., 2015). For example, the extent of a PA can be limited by a lack of intact habitat, funding and the capacity to employ patrol squads or rangers; such restrictions impose an ecological carrying capacity (ECC) that reduces the ability of the environment to support wildlife populations (Newmark, 2008; Saout et al., 2013).

Furthermore, the isolation of fenced reserves has the potential to impact wildlife populations in negative feedback loops (Newmark, 2008). Small and closed populations are subject to a higher rate of loss of genetic diversity and may become inbred more quickly; subsequently, they are more vulnerable to demographic and environmental stochasticity or catastrophic events like disease outbreak (Frankham et al., 2002). Thus, it is vital to understand the ecological requirements of the fauna within protected reserves so that effective management strategies can be implemented.

1.2 Ecological Carrying Capacity

In the absence of threats (e.g. poaching), populations within fenced areas grow rapidly (Smith, 2006). Wildlife inside PAs must be carefully managed to ensure that there are adequate resources to support a growing population and therefore assessments of wildlife distribution, abundance and resource availability are vital to determine appropriate management strategies (Gros et al., 1996; Fuller & Sievert, 2001). Estimating the ECC – the number of individuals in a population that can be supported by the resources in a specified area – is a common approach for the management of endangered species (McCullough, 1992; Morgan et al., 2009). Whilst ECC estimates for carnivores are based on species-specific interactions between predators and prey, megaherbivores are assumed to be predominantly limited by food availability (Sinclair, 2003; Hetherington & Gorman, 2007; Landman et al., 2013).

Exceeding the ECC can reduce access to resources and supress population growth rates (Campbell & Reece, 2014). In fenced reserves, where the free movement of animals is restricted, megaherbivore assemblages can quickly accumulate. Due to their large body size and energetic requirements, megaherbivores can cause large-scale fluctuations in vegetation cover in savannah ecosystems (Birkett & Stevens-Wood, 2005; Landman et al., 2013). For example, varying elephant (*Loxodonta africana*) densities caused continual fluctuations between woodland and open grassland states in the Serengeti-Mara region over the past 100 years (Dublin, 1995). Elephant are ecosystem engineers and can change environmental states through the destruction of trees and breaking of branches (Guldemond & Van Aarde, 2008). Whilst this improves access to nutrient-rich resources for other browsers, habitats are altered unfavourably as elephant densities increase (Owen-Smith, 1988; Rutina et al., 2005; Makhubu et al., 2006; Kohi et al., 2011; Landman & Kerley, 2014). Elephant damage to woody vegetation in the Addo Elephant National Park, South Africa, reduced species richness, density and biomass (Kerley & Landman, 2006). Such vegetation changes reduce resource availability and subsequently the ECC, suppressing population growth rates. This was demonstrated in the declining black rhino population in Hluhluwe-Umfolozi Park (South Africa) and the moose (*Alces alces*) population in Ontario (Reid et al., 2007; Street et al., 2015).

Increasing wildlife densities can exacerbate the effects of competition. The impacts of elephant and giraffe (*Giraffa camelopardalis*) populations can combine to substantially reduce browse availability (BA) to black rhino and other herbivores (Birkett, 2002). For instance, in the Sweetwater Reserve in Laikipia (Kenya), heavy browsing by giraffe, elephant and black rhino, caused *Acacia drepanolobium* cover to decrease by 25% in 5 years (Birkett, 2002). What's more, elephant damage and the consequent changes in BA can shift black rhino foraging behaviour along a browse-grass continuum (Landman et al., 2013). Heavy browse pressure exerted by giraffe on tree canopies suppresses growth and reduces the ability of plants to regenerate, contributing to reductions in woody vegetation and overall BA (Birkett, 2002).

Lastly, large mammals that are limited by resources, have low reproductive rates, long gestation periods and long life-spans, are subject to density-dependent regulation when stocking rates are close to, or exceed the ECC (Fowler, 1981). Overstocking can affect individual performance traits that slow or reduce population growth rates: e.g. by decreasing infant and juvenile survival rates, increasing the age at first reproduction and causing longer inter-calf intervals (Adcock, 2001; Bonenfant et al., 2009). Increasing white rhino (*Ceratotherium simum*) densities in Matobo National Park (Zimbabwe) decreased population growth rates, calf recruitment and age at first reproduction (Rachlow & Berger, 1998). An overestimation of the ECC and subsequent overstocking of black rhino in a newly established reserve (Eastern Shores, South Africa), resulted in a population decline of 6.1% per year from 1984-1994 (Adcock, 2001). Furthermore, density-dependent factors like territoriality in black rhino and social interactions limit access to resources, thereby restricting population growth (Adcock, 2001). Similarities have also been documented with other large mammal species including equids, bovids and moose (Owen-Smith, 1988; Freeland & Choquenot, 1990).

The impacts of exceeding the ECC on population performance are often contradictory to the goals of management who aim to increase wildlife populations as quickly as possible (Adcock, 2001). Furthermore, many estimates of ECC do not consider the non-uniform distribution of resources in nature, the social dynamics and behavioural repertoires of species, nor the topography and features of the landscape that may make some areas inaccessible (Young, 1938; Manly et al., 2002; Morgan et al., 2009). In Africa, many endangered species, such as the black rhino, are dependent upon fenced reserves for their survival and therefore, an understanding of the factors limiting population growth is crucial for successful conservation efforts (Rachlow & Berger, 1998). For megaherbivores, who are predominantly limited by food, a comprehensive understanding of resource availability and selection within a given PA is essential (Fowler, 1981; Manly et al., 2002; Sinclair et al., 2007).

1.3 Resource Use and Selection

The availability and quality of food resources are well-documented constraints to ungulate population performance (Sinclair, 1977; Boyce, 1992; Mwangi & Western, 1998). In African savannah ecosystems, food shortages can induce higher mortalities than predation and thus, a fenced reserve must have adequate quantities of resources to ensure positive population growth (Sinclair, 1977; Manly et al., 2002). Determining resource availability and identifying utilisation rates of those resources reveals how the animal meets its requirements for survival, knowledge that is crucial for conservation (Manly et al., 2002; Ganqa et al., 2005; Kassa et al., 2007; Morgan et al., 2009). For example, investigating the utilisation rates of old forest growth revealed it to be a critical factor to the existence of the spotted owl (*Strix occidentalis*) in the US (Forsman et al., 1984; Laymon et al., 1985). McLeod (1997) stated that the ECC is determined by the short-term density of wildlife populations, as a function of resource availability. This suggests that fitness, and therefore reproductive success, is driven by resource availability, with animals selecting and utilising habitats with a higher abundance of required resources (Fretwell & Lucas, 1969; Fagen, 1988).

Natural environments are highly stochastic, and resources are not uniformly distributed across the landscape. Therefore, it is important to assess resource utilisation (the quantity used in a fixed period of time), in comparison to availability (the quantity accessible to the animal), to make inferences about selectivity (Manly et al., 2002; Morgan et al., 2009). A selected or ‘chosen’ resource is used disproportionately relative to its availability. This should not be confused with preference, which denotes the likelihood a resource will be selected if offered equally with others (Johnson, 1980; Manly et al., 2002).

The results of selectivity studies should be interpreted with caution. A species may appear to be highly selected for, but if availability is low, then utilisation rates will also be low; incongruently, a resource that appears to be selected against but is available in large quantities, may in fact be an important food source (Petrides, 1975; White & Garrot, 1990; Manly et al., 2002). Additionally, resource selection is influenced by a multitude of factors – including geographical range, home range, habitat-type, population density, competition and chemical composition of forage – and selectivity can differ at each level (Johnson, 1980; Wiens, 1981; Peek, 1986; Orians & Wittenberger, 1991; Manly et al., 2002). Therefore, an indication of selectivity for or against a resource in relation to availability can suggest areas for further in-depth study (Petrides, 1975; Manly et al., 2002).

1.4 The Black Rhinoceros

Historically, the black rhino had a wide-ranging distribution that stretched across much of sub-Saharan Africa (Moodley et al., 2017). However, their numbers plummeted from ~65,000 to ~2,400 between 1970 and 1995, due to demand for rhino horn (Harper et al., 2018). Although crisis conservation efforts and the intense protection of reserves enabled populations to recover to ~5000 in 2014, the black rhino is still classified as critically endangered on the IUCN Red List (Emslie, 2012; Moodley et al., 2017). The majority of the global black rhino populations now reside in PAs that are highly secure and are regularly patrolled (KWS, 2016). Current conservation efforts rely heavily on PAs, public and government support and scientific research to ensure positive population growth (Amin et al., 2006).

Kenya is a stronghold for the critically endangered eastern black rhino (*D. b. michaeli*) with ~80% of the global population distributed across state, private, county council and community lands (Amin et al., 2006; Emslie, 2011). Approximately 45% of the population resides in private land and protected reserves; here, population growth targets are set at 6.5-9.0% to avoid the loss of genetic diversity (Adcock, 2001; Buk & Knight, 2010; KWS, 2016). However, in some fenced reserves, population growth has been limited by vegetation changes, overstocking and competition with other herbivores (Birkett, 2002; Buk & Knight, 2010).

The black rhino is predominantly a browser, ingesting large quantities of herbs, low-growing shrubs, succulents and woody vegetation (Matipano, 2003; Schroder, 2008). Despite consuming a wide variety of species and having the ability to feed on coarser material compared to other herbivores, black rhino are highly selective for both species and size class (Emslie & Adcock, 1994). Understanding the resources available to, and used by black rhino can (i) provide estimates of the ECC to prevent overstocking and safeguard resources; (ii) indicate changes in resource availability, as highly selected species will decline in quantity and quality first; (iii) highlight areas where habitat manipulation would be most efficient to minimise competition; (iv) reveal habitat changes and declines in the functional ability of the environment to provide black rhino with adequate resources (Muya & Oguge, 2000; Adcock, 2001; De Boer & Ijdema, 2007; Luske et al., 2009). Thus, enabling management to devise strategies that maximise resources for black rhino and ensure population growth in order to meet government conservation targets (Adcock, 2001).

1.5 Lewa Wildlife Conservancy and Borana Conservancy

Lewa Wildlife Conservancy (LWC) and Borana Conservancy (BC) located in Kenya, are two established and well-managed fenced reserves. LWC was converted from a livestock ranch to the Ngare Sergoi Rhino Sanctuary in 1984, in response to global population declines (Lewa, 2018). In 1995, the remaining area was converted to a reserve, fenced off from the surrounding community lands and wildlife encouraged back onto the landscape; to this date, conserving black rhino remains the primary objective of management at LWC (Lewa, 2018).

Despite being managed as a contiguous landscape, LWC and BC differ. BC is situated in the foothills of Mount Kenya at an elevation between 500-1000m above LWC. It experiences higher levels of precipitation, has a different soil composition, less wildlife and moreover, cattle ranching still remains a prominent part of conservancy management (Giesen et al., 2017). It's more recent establishment and higher density of livestock mean that the vegetation structure may differ from LWC. Given the physical differences between LWC and BC, browse availability (BA) – a factor that is critical for the persistence of black rhino populations – may vary between the two landscapes. Elephant and giraffe have always been present on BC, but black rhino were only reintroduced in 2013; therefore, browsing pressure may have been lower than experienced on LWC (Roques et al., 2001; Lewa, 2018). In addition, there are fewer black rhino inhabiting BC (25 individuals) compared to LWC (68) (Lewa, 2018). High browsing pressure can slow the growth of shrubs and prevent the establishment of woody seedlings; therefore, levels of BA are hypothesised to be lower in LWC than BC (Pellew, 1983; Prins & Van der Jeugd, 1993).

1.5.1 Vegetation Changes

Long-term studies (1962-2016) revealed changes in habitat structure and vegetation cover on LWC, specifically from woodland to open grassland (Figure 1.1). An overall decrease in the density and cover of woody vegetation was attributed to an increase in wildlife populations (e.g. elephant and giraffe) and varying precipitation patterns (Giesen et al., 2017). Tree and shrub cover declined from 24% in 1980 to 9% in 2016, a trend that is exacerbated by heavy browsing pressure (Giesen et al., 2017). This decline is of concern to LWC management because woody vegetation constitutes more than 63% of black rhino diet (Muya & Oguge, 2000), so declining coverage could have severe implications for population viability.

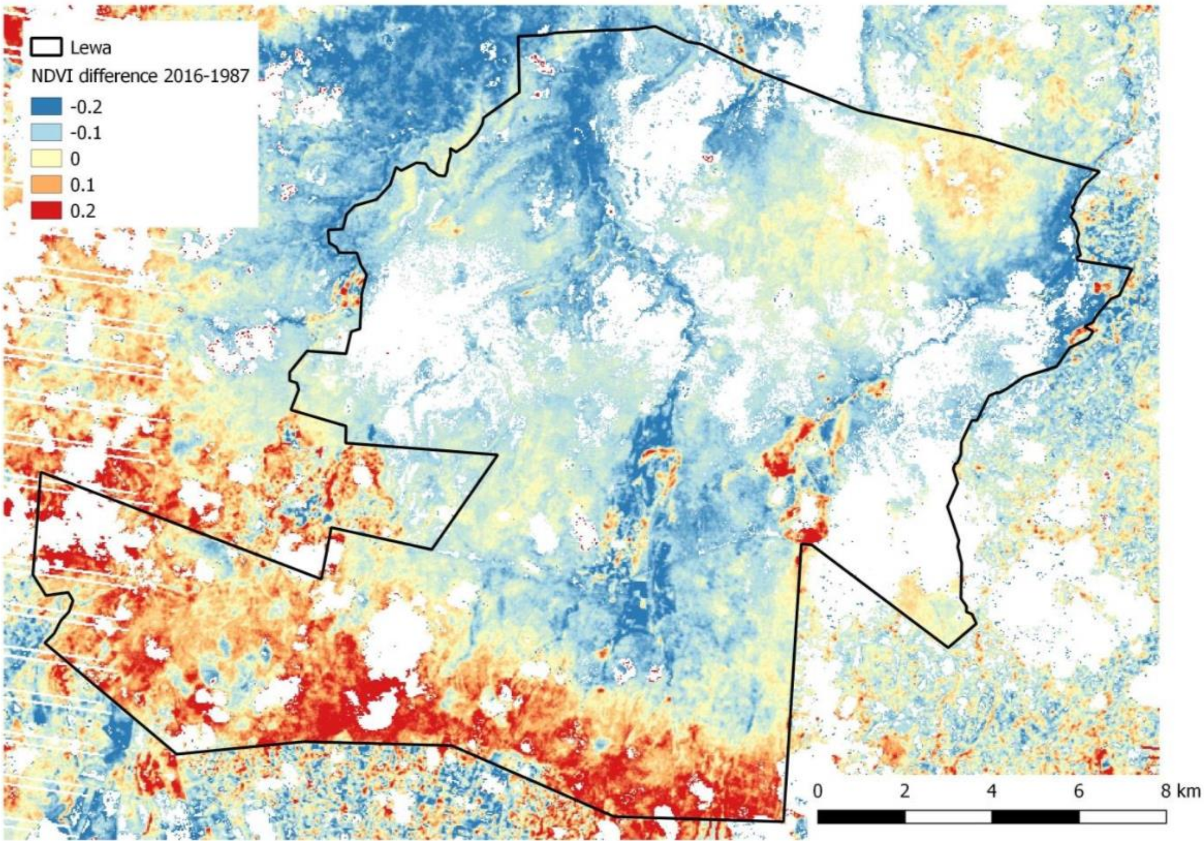

Figure 1.1 – A normalised difference vegetation index (NDVI) analysis for LWC between 1987-2016; red areas indicate a substantial increase in tree cover, blue areas illustrate declining tree cover (Giesen et al., 2017).

1.5.2 Exclusion zones

In an attempt to increase BA for black rhino and reduce competition between megaherbivores, exclusion zones were established on LWC. Partial exclusion zones are surrounded by electric fences at a height of 1.7-2.0m, enabling black rhino and other herbivores to pass underneath and access vegetation that is protected from the browsing impacts of elephant and giraffe (Dupuis-Desormeaux et al., 2016). Total exclusion zones are completely fenced, and no animal can gain access to the vegetation. Thus, it was predicted that total exclusion zones would have higher levels of BA due to the absence of any browsing pressure. The first exclusion zone was established in 1995 and the most recent in 2012, but no subsequent assessments of BA have been conducted. Therefore, it is unknown whether this method is successfully increasing BA.

Whilst some exclusion zones have experienced decreased browsing pressure, others have been heavily browsed by elephant, who by-passed the fence, or by fire that reduced the amount of woody vegetation (Giesen et al., 2017). Moreover, the black rhino population on LWC has increased from 15 in 1984 to 65 in 2018; meaning, higher browsing pressure will have been exerted on the vegetation to support the growing number of individuals. Moreover, African ecosystems can undergo secondary succession, a transition from open savannah (dominated by microphyllus trees such as *Acacia* spp.) to a closed woodland community (Smith & Goodman, 1986; Archer et al., 1988; Franco-Pizana et al., 1996). By protecting areas of vegetation, browsing pressure and damage inflicted by herbivores is alleviated; this may allow broad-leaf species to grow more quickly. In this case, *Acacia* spp. are eventually over-topped, shaded and a climax community is established (Smith & Goodman, 1987). However, allowing vegetation inside an exclusion zone to reach a climax community would not benefit black rhino as they can only access browse between 0–2.0m (Adcock, 2016). Therefore, it is important to establish the efficacy of exclusion zones in increasing BA for black rhino.

It is vital to determine how vegetation changes may impact BA as reductions in food quantities could prevent positive black rhino population growth and reduce the ECC. Given the critically endangered status of black rhino and the renewed threat of poaching, it is imperative that management continue to employ strategies that maintain adequate resources. A comprehensive assessment of resource use in comparison to resource availability, and a review on the current management strategies used to enhance black rhino feed, will guide the best course of action for stakeholders on LWC and BC.

2 Aims and Objectives

The overarching aim of this project is to assess BA for, and utilisation by, black rhino on LWC and BC with the specific objective of understanding the status and availability of food resources for this critically endangered species. This study will assess the utilisation of resources by black rhino on LWC and BC in comparison to resource availability, thus indicating plant species that are selected for. This information is crucial for the maintenance of black rhino in fenced reserves where a finite number of resources are available to sustain viable populations. This study will also assess whether current management techniques (exclusion zones) are viable strategies for enhancing BA.

The main objectives of this study were:

Objective 1: To investigate browse availability (BA) for black rhino on LWC and BC.

Hypotheses:

- BA will vary between conservancies.
- BA will vary between habitat-types.

Objective 2: To determine whether current management strategies (i.e. exclusion zones) successfully increase browse availability (BA) for black rhino.

Hypotheses:

- BA will be higher inside exclusion zones.
- BA will be higher inside total exclusion zones compared to partial zones.
- BA will be higher inside older exclusion zones compared to younger zones.

Objective 3: To determine resource selectivity by black rhino across the conservancies.

Hypothesis:

- Black rhino are utilising species disproportionately to what is available across the conservancies.

3 Methods and Materials

3.1 Study Site

LWC and BC form a contiguous habitat of 375km^2, known as the Lewa-Borana Landscape (LBL), that straddles the Laikipia-Meru districts of north-central Kenya (00 06’-00 07’ North, 370 21’-370 32’ East) (Figure 3.1). Holistic management strategies enable the free movement of animals between LWC and BC, but both conservancies are fenced externally. Strategically placed fence gaps allow migratory species like elephant to move in and out of the conservancies, but black rhino are restricted (Dupuis-Desormeaux et al., 2015). Despite covering a small geographic area, LWC and BC are home to numerous populations of threatened species, including Grevy’s zebra (*Equus grevyi*), the white rhinoceros and the eastern black rhino, that hold strategic importance for conservation (Low et al., 2009).

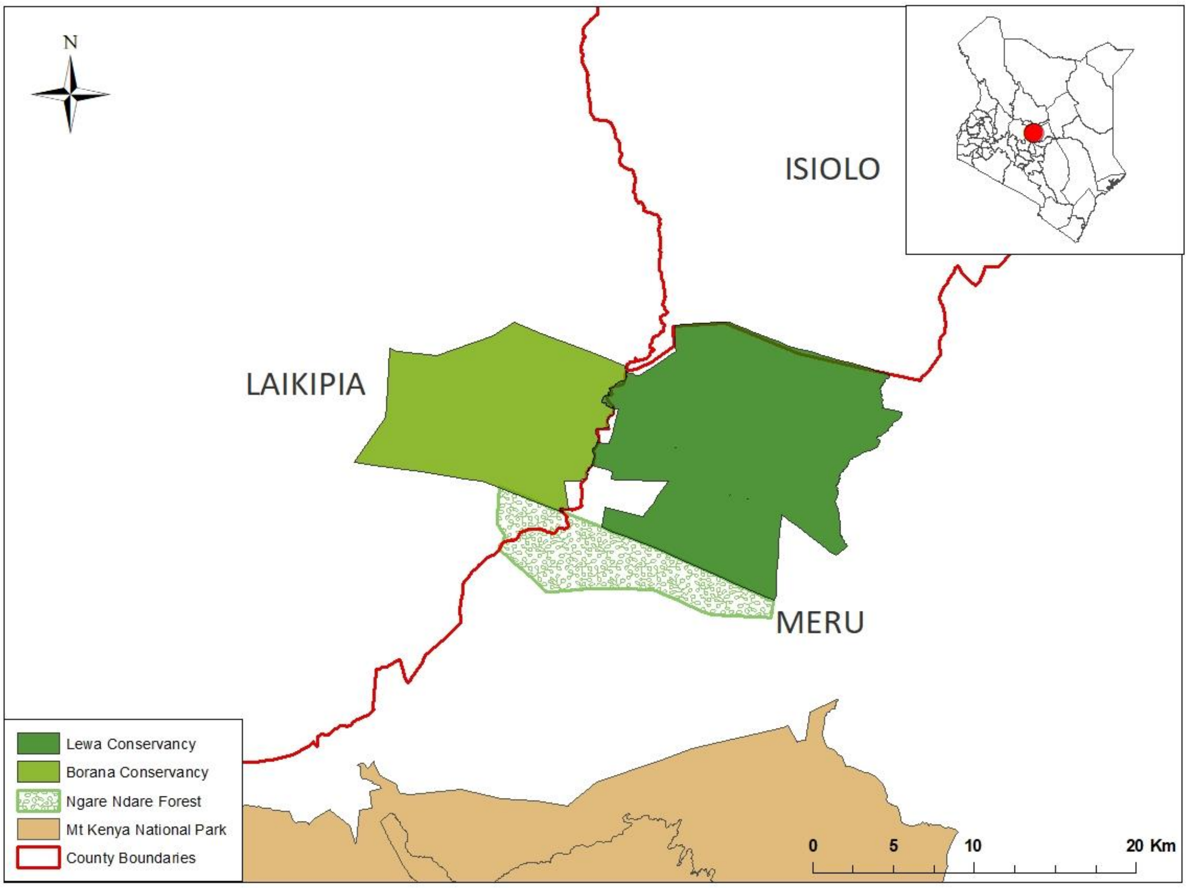

Figure 3.1 - The location of the LBL in north-central Kenya (top right), and the geographical placement of LWC, BC and the Ngare Ndare Forest in relation to the counties of Isiolo, Laikipia and Meru.

3.1.1 Climate and Habitat

The LBL is classified as a tropical savannah system, with both properties experiencing a semi-arid climate (that can be vulnerable to drought), and a bimodal rainfall distribution consisting of the long rains from March-May and short rains from October-December (Botha, 1999; Peel et al., 2007; LWC, 2014). Variations in precipitation are influenced by mountainous regions; e.g. Laikipia receives a lower amount of rainfall due to its proximity to Mount Kenya (Shorrocks & Bates, 2015). Furthermore, the microclimates of LWC and BC differ due to a variety of intrinsic physical differences in topography, elevation, soil composition, drainage and rainfall (Shorrocks & Bates, 2015; Giesen et al., 2017).

The LBL is dominated by three main habitat-types: (1) plains, (2) hills and rocky outcrops, (3) forest. The extensive plains system is dominated by *Pennisetum* grasses, perennial herbs that grow immediately after the rains, and two species of *Acacia* (*A. drepanolobium* and *A. seyal*). Vegetation found on hill and rocky outcrops vary due to the diversity of soils they grow on, including sandy substrate, clays and volcanic ash. An array of trees (predominantly *Acacia* spp.) and shrubs (*Commiphora* and *Grewia* spp.) are abundant in this habitat-type, as well as herbs (*Commelina* spp., *Justica* spp.), grasses and climbers. Lastly, the Ngare Ndare Forest is becoming increasingly dominated by climax species such as *Olea africana* and *Juniperus procera* as canopy cover becomes denser and fast-growing pioneer species give way to mature trees. Ngare Ndare is thought to be 200 years old and was incorporated into the LWC boundary in 1980. It extends along the southern border of the LBL but is only accessible from LWC. The forest habitat in BC consists of remnant forest fragments at the boundary of the reserve (Giesen et al., 2007; NRT, 2016).

3.2 Data Collection and Analysis

Data were collected over a ten-week period, from March to May 2018, during the long rains wet season. A number of study days were lost to heavy rainfall which made roads impassable on the LBL. GPS (Global Positioning System) coordinates were exported to ArcMap 10.5 (ESRI, 2014) and statistical analyses were performed in R (R Core Team, 2017). A confidence level of 95% and P value of <0.05 were considered to be significant.

3.3 Resource Availability

3.3.1 Browse Availability on the LBL

To assess the availability of food resources for black rhino across the LBL, BA was measured. This factor is highly influential in determining the number of individual black rhino a reserve can support (Adcock, 2016). Stratified random sampling was utilised, firstly to select the three habitat-types on LWC and BC – plains, hills and rocky outcrops, forest – and secondly to randomly generate seven plots within each habitat-type. In depth vegetation studies have occurred previously on LWC (Figure 3.2) and the coverage of each habitat-type is known. However, knowledge of the percentage cover of each habitat-type and accurate vegetation maps are lacking for BC. BA was assessed across 42 plots in total; 21 plots (7 plains, 7 hills, and 7 forest) in LWC and 21 plots in BC (Figure 3.3). Each plot was a minimum of 150m apart, ensuring independence, and locations were recorded using a Garmin GPS 62s.

The visual method developed by Adcock (2016), specifically to assess BA, was applied in this study. BA was assessed to a medium level of detail to enable a greater sampling effort, thereby giving a more accurate representation of BA within each habitat-type. This involved clumping several plant species together and measuring the average characteristics of the clump as opposed to each individual plant. In each cylindrical plot (16m diameter, 2m height), the following parameters were measured: average canopy height (up to 2m), average canopy depth (width), the species and number of plants within each clump, the rank of each species within a clump - with the most important given the score of 100 - and all other plants given a value relative to that.

These parameters were used to estimate the biomass of browse and the relative importance of each plant species in every plot and habitat-type (Morgan et al., 2009). This method has been proven reliable and robust, with insignificant variation between actual and estimated BA values across numerous studies (Adcock, 2004).

Plants were identified in Maasai/Maa names by an experienced ranger and local vegetation expert and were later translated using Letilet's Tales (Allen & Ole Yenko, 2013), Some Wild Flowers of the Ngong Hills (Wedekind & Sutton, 2009) and Kenya Trees, Shrubs and Lianas (Beentje, 1994).

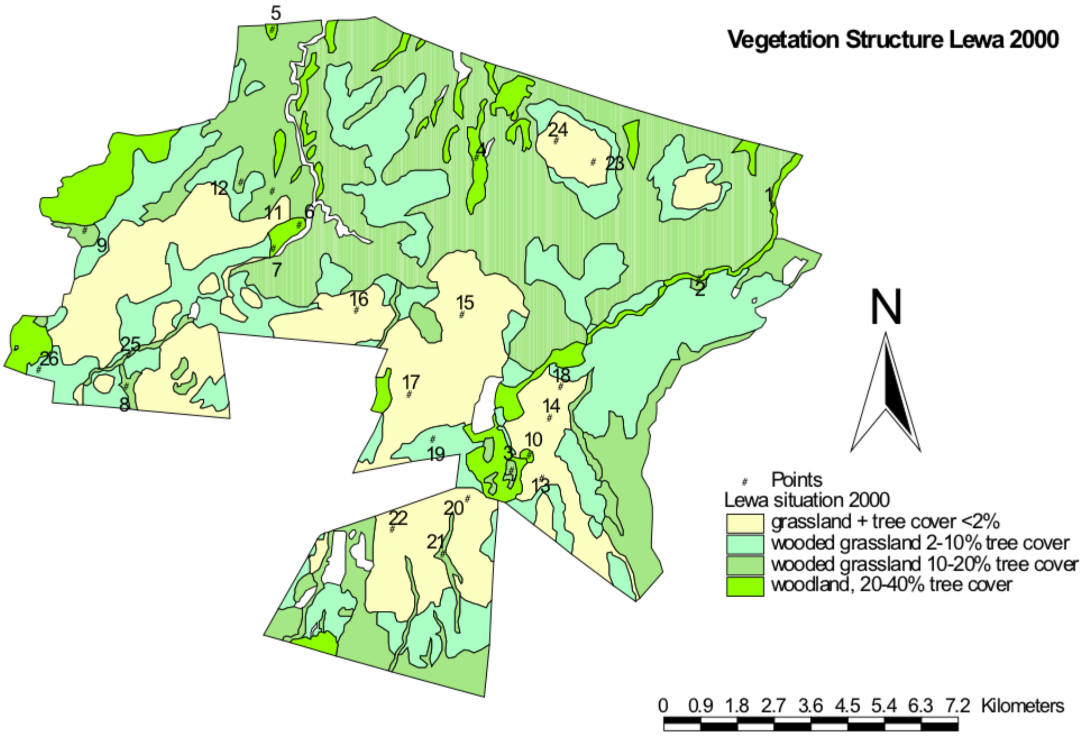

Figure 3.2 – The vegetation structure on LWC, assessed in 2000 (Giesen et al., 2007).

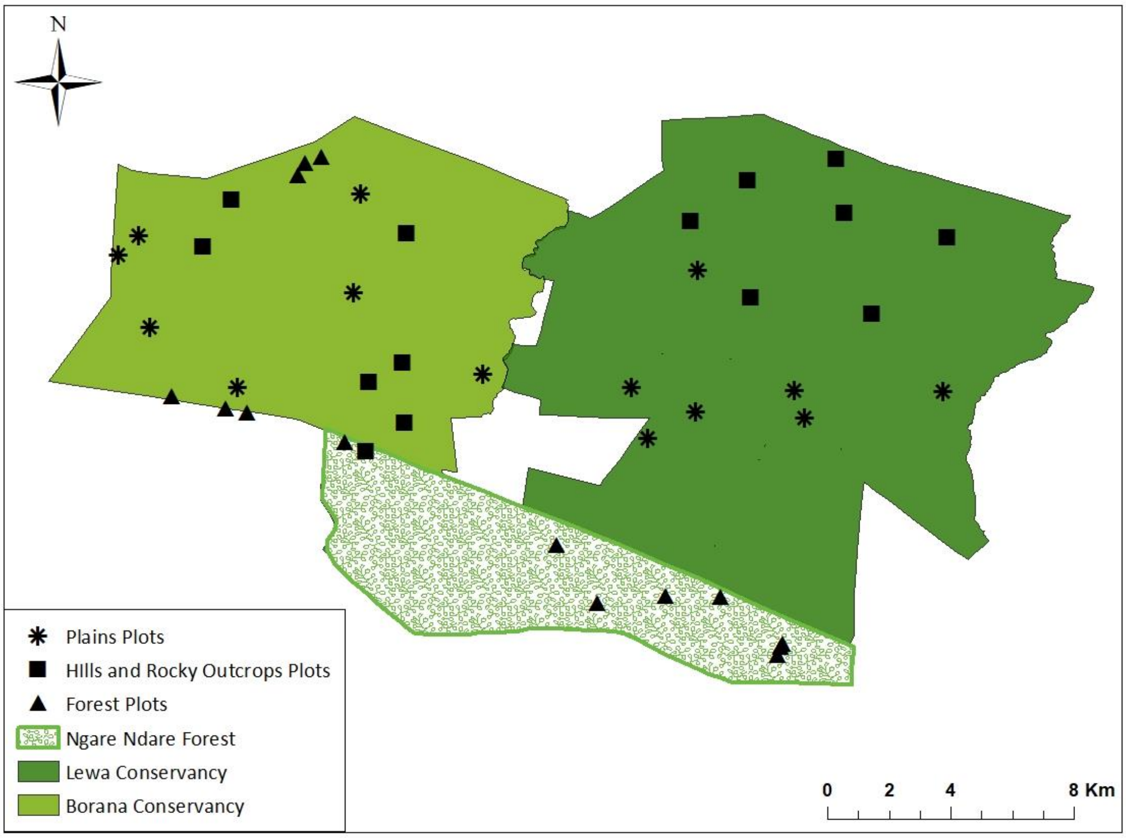

Figure 3.3 – The BA plots assessed in three habitat-types (Plains, Hills and Rocky Outcrops, Forest) on LWC and BC.

To determine whether BA varied between the two conservancies and between habitat-types (plains, hills, forest), a two-way analysis of variance (ANOVA) was conducted. Despite the data being normally distributed, the assumption of homoscedasticity was violated. Thus, a generalised linear model (GLM) with a quasipoisson distribution was performed as the dispersion parameter was not fixed, and the model was fit to count data (Beckerman & Petchey, 2012). Tukey's *post hoc* test was performed to test for difference between the three habitat-types (Dytham, 2011).

To determine whether browse species diversity differed between LWC and BC, and the three habitat-types, two diversity indices were calculated:

1 - The Shannon-Wiener index (Equation 3.1) is a robust technique that is commonly used in ecological studies as it emphasises the richness component of diversity; it also accounts for the relative abundance of different species and the number of species present (Nagendra, 2002; Spellerberg & Fedor, 2003). High values are indicative of high species diversity and uniformity/evenness in BA, whilst low values illustrate low diversity and uniformity (Shannon & Weaver, 1949).

Equation 3.1

$$H' = \sum_{i=1}^{S} (p_i)(\ln p_i)$$

S = the total number of species

pi = number of individuals of species i ÷ by the total number of plants

2 - In comparison, Simpson's Diversity Index (Equation 3.2) accentuates the evenness component of diversity and is more responsive to species that are dominant (Nagendra, 2002). The value of D ranges between 0 (no diversity) and 1 (infinite diversity).

Equation 3.2

$$D = 1 - \left(\frac{\sum n(n-1)}{N(N-1}\right)$$

n = the total number of individual plants in a particular species

N = the total number of individual plants of all species

3.3.2 Browse Availability in Exclusion Zones

Nine partial exclusion zones (black rhino and small herbivores can enter; elephant and giraffe are excluded) and all three total exclusion zones present on LWC (no animal can enter) were selected for sampling (Figure 3.4). Three plots inside each exclusion zone and three plots outside were randomly sampled - giving a grand total of 72 plots (36 inside, 36 outside). All plots were at least 150m from each other, ensuring independence. As detailed above, the method developed by Adcock (2016) was employed to quantify BA. The age of construction of the sampled exclusion zones was also recorded (Table 3.1).

Due to experimental design (3 plots within one exclusion zone), nested ANOVAs were performed to determine whether (i) BA differed between partial and total exclusion zones, (ii) there was a difference in BA inside and outside partial zones, (iii) there was difference in BA inside and outside of total exclusion zones. However, because the model violated the assumption of homoscedasticity, BA scores from the three plots sampled inside each exclusion zone were averaged, giving one BA value per zone. Subsequently, a GLM with a quasipoisson distribution was performed for part (i) and (ii). For part (iii), a GLM with a quasi-inverse distribution was conducted because there was less variability in the scale-location diagnostic plot than a quasipoisson distribution.

Lastly, to determine whether the construction age of the exclusion zones on LWC was correlated with BA, a GLM with a quasipoisson distribution was performed.

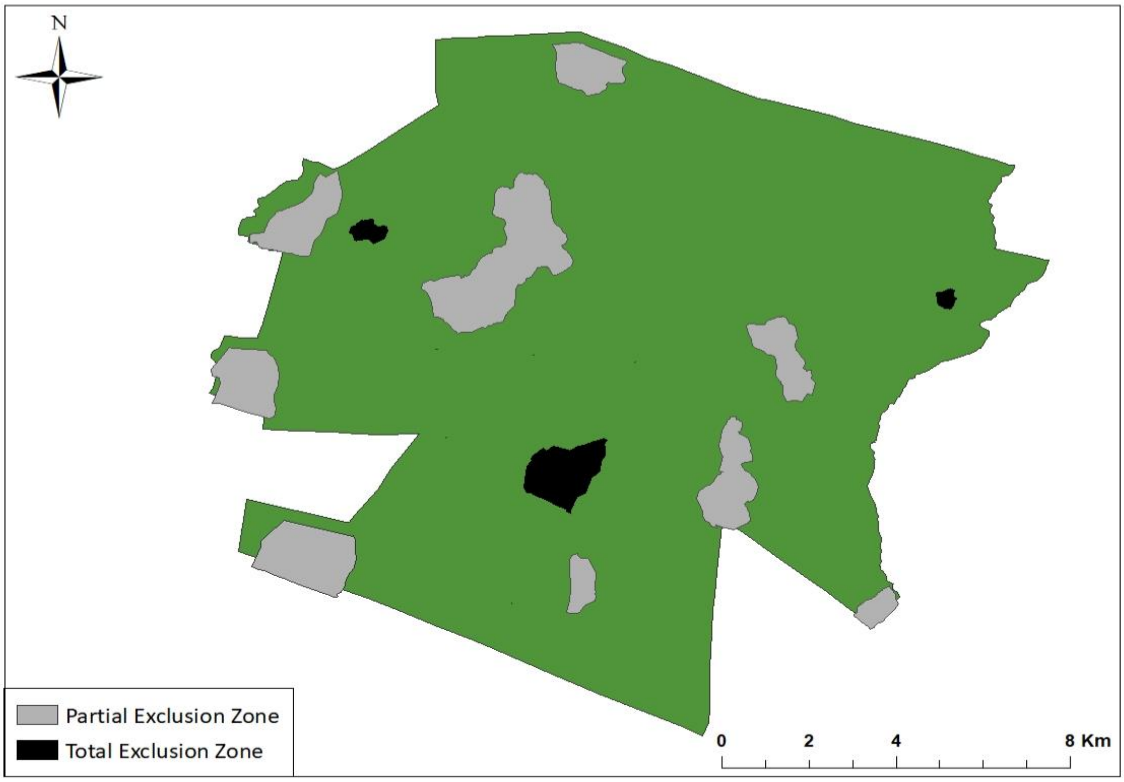

Figure 3.4 – Partial (n=9) and total (n=3) exclusion zones sampled on LWC.

Table 3.1 – The exclusion zones that were sampled and the corresponding age of construction.

Exclusion Zone	**Classification**	**Age of Construction**
Anna Mertz	Partial	1995
Wilderness	Total	1996
Digby	Partial	2001
HQ	Partial	2001
Kona Safi	Partial	2001
Safari Camp	Total	2001
Mawingo	Partial	2002
Sirikoi	Total	2003
Luai ya Charlie	Partial	2004
Mwitia	Partial	2004
Matunda	Partial	2006
Karionga	Partial	2008

3.4 Resource Selectivity

To assess resource utilisation and selection of specific browse by black rhino on LBL, an indirect observational technique called backtracking was used. Rhino tracks, fresh dung or individuals were located early in the morning and their feeding pathway was followed on foot. At all times, a distance of 1000m was maintained behind the animal so that foraging behaviour was not influenced by human presence.

The plants consumed by black rhino were identified to the species level, the number of freshly browsed stem tips (cuts) were recorded, the height class of the plant was measured (A: 0.00-0.50m, B: 0.50-1.00m, C: 1.00-1.50m, D: 1.50-2.00m) and the parts of the plant that were eaten (All, Stem, Leaves, Shoots) were noted. Feeding trails were followed opportunistically across the LBL and only vegetation that had been freshly clipped was recorded to ensure that the plants had been consumed by the focal individual. Trails were terminated if a distance of 30m was traversed without any further signs of feeding (as it was assumed that the individual had stopped browsing and started walking) or if the individual was located sleeping. Due to the ongoing intensive rhino monitoring programme on the LBL, it was possible to identify all focal animals. The individual was recognised via ear notches, horn morphology, scars, marks and through the knowledge of the rhino scientists and rangers. Hence, no rhino was sampled twice, avoiding pseudoreplication.

Plants that had been consumed by black rhino were easy to identify due to their distinctive browsing style of cleanly severing twigs at a 45^0 angle. This enabled black rhino feeding to be discerned from the marks or impressions made by other herbivores, such as eland (*Taurotragus oryx*), giraffe and elephant. This allowed other browsing species to be excluded from data collection, even if more than one herbivore had fed on the same plant. black rhino browse between 0-2.0m, thus, plants with foliage above 2.0m were excluded from data collection (Oloo et al., 1994; Adcock, 2016).

Selectivity indices indicate whether resource utilisation deviates from resource availability (Boulanger et al., 2009). To determine whether black rhino were browsing plant species disproportionately to their availability across the LBL, Jacob's Selectivity Index (Equation 3.3) was utilised (Jacobs, 1974). The calculated values ranged between -1 and +1 depending on the extent that black rhino avoided or selected plant species, with -1 being complete avoidance and +1 being complete selection. Values were calculated for individual plant species, the functional group of the plant (herbs, shrubs, trees) and plant families.

Equation 3.3

$$D = \frac{r - p}{r + p - 2rp}$$

r = the proportion of a species consumed by the black rhino,
p = the proportional availability of that particular species.

To determine the diversity of black rhino diet compared to availability across the LBL, Shannon-Wiener (Equation 3.1) and Simpson's Diversity Indices (Equation 3.2) were used. A chi-squared analysis (Equation 3.4) was performed to test for a difference in species diversity between the observed (plants consumed) and expected (plants available) values.

Equation 3.4

$$\mathcal{X}^2 = \sum \frac{(O - E)^2}{E}$$

Further chi-squared tests were also used to test for a difference in the height class of plants consumed by black rhino. Observed values corresponded to the height class of each plant consumed by black rhino during backtracking. Expected values corresponded to an equal selection across the categories, this is because the assessment of BA within plots required the height of vegetation clumps to be averaged, hence actual availability data were not obtained.

4 Results

4.1 Browse Availability on the LBL

A comparison of browse availability (BA) on LWC and BC revealed that there was no difference between the two conservancies (Z=-0.087, d.f.=41, P=0.93). However, habitat-type had an effect on BA.

BA was higher in forest habitats compared to hills (Z=-4.198, d.f.=41, P<0.001), and in forest compared to plains (Z=-4.690, d.f.=41, P<0.001), though there was no difference in BA between plains and hills (Z =-0.748, d.f.=41, P=0.732) (Figure 4.1).

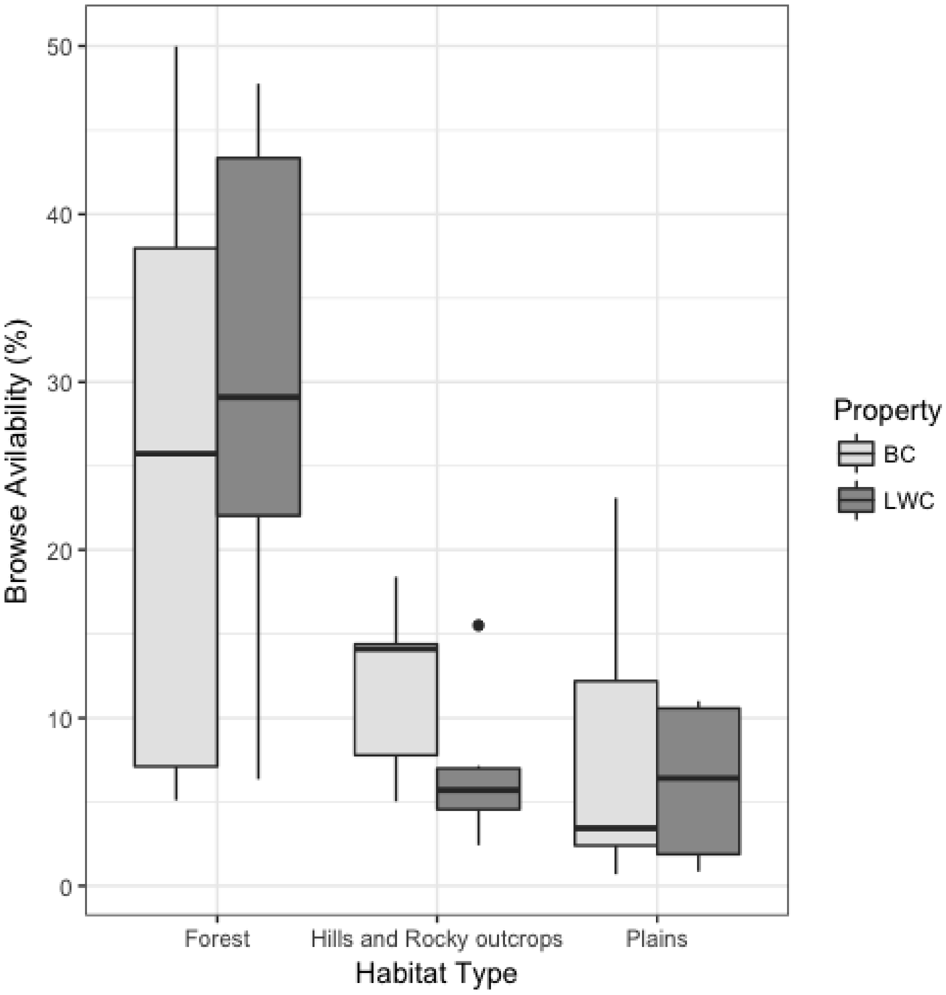

Figure 4.1 – Percentage of available browse in each of the three dominant habitat types on LWC and BC with the median, upper and lower quartiles displayed.

In the 42 vegetation plots sampled, a total of 7896 individual plants were recorded, 3397 of which were found on LWC, and 4499 were found on BC. Of the 72 palatable plant species recorded, 59 were found on LWC and 50 on BC. BC (Shannon index, H=3.314; Simpson index, D=0.935) had higher plant diversity than LWC (H=2.950; D=0.914).

Across both conservancies, 54 of the palatable plant species were found in forest habitats, 57 in hills and rocky outcrops and 33 in plains. Plant diversity was highest in forests (H=3.255; D=0.944), followed by hills (H=3.199; D=0.936) and plains (H=2.312; D=0.812) (Table 4.1).

Table 4.1 – The diversity of Browse Availability (no. of palatable species) recorded in three dominant habitat-types (forest, hills and plains) on the LBL, based on Shannon-Wiener Index and Simpson's Diversity Index

Habitat-type	**No. of Plants** (n = 7896)	**No. of palatable species** (n = 72)	**Shannon Wiener Index**	**Simpsons Index**
Forest	2543	54	3.255	0.944
Hills & Rocky Outcrops	2574	57	3.199	0.936
Plains	2779	33	2.312	0.812

4.2 Browse Availability in Exclusion Zones

BA was higher inside partial exclusions zones compared to areas outside the zones (Z=-4.305, d.f.=17, P<0.001). Similarly, BA was higher inside total exclusion zones compared to outside (Z = 4.695, d.f. = 5, P<0.001). For both partial and total exclusion zones, BA values appeared to vary more inside the zones, compared to outside (Figure 4.2). However, BA did not differ between partial and total exclusion zones (Z=0.315, d.f.=13, P=0.759). Furthermore, there was no correlation between BA and the construction age of exclusion zones (Z=0.531, d.f.=11, P=0.607).

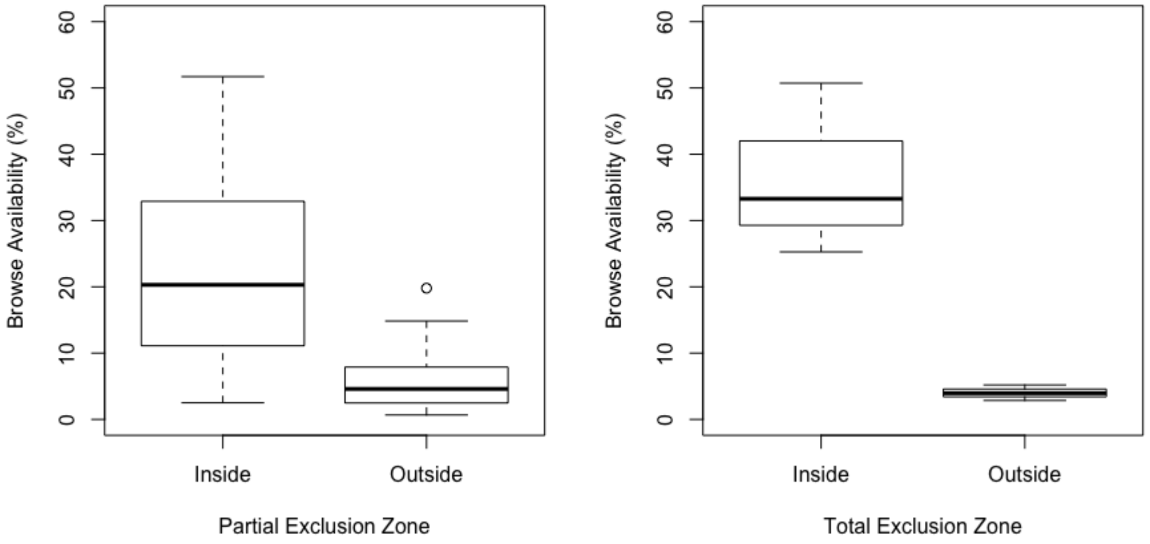

Figure 4.2 – Percentage of available browse inside partial and total exclusion zones, compared to outside exclusion zones.

4.3 Resource Use

In total, 20 individual black rhino were followed. Sixteen backtracks were conducted on LWC and four on BC. Plants from 26 families were recorded and at least 72 species were consumed; Latin names were determined for 71 of these. A total of 1485 individual plants with 8643 cuts were recorded to have had some, or all plant parts consumed (Appendix A). The families that were represented by at least four species include: *Malvaceae* (8), *Fabaceae* (7), *Lamiaceae* (4), *Solanaceae* (4). The most dominant species in the dietary composition of the black rhino were: *Amaranthas dubius* (177 plants, 1020 cuts), *A. drepanolobium* (168 plants, 887 cuts), *Commelina benghalensis* (150 plants, 993 cuts), *Pavonia patens* (132 plants 1035 cuts) and *Pennisetum stramineum* (124 clumps of grass, 124 cuts).

Black rhino diet composition was less diverse (H=0.409; D=0.922) than the food plants available across the LBL (H=3.323; D=0.933). During BA plots and backtracking, a total of 84 plant species were recorded. Of those, only 73 species were found in BA plots, meaning that an additional 11 species were consumed by black rhino. Although 72 plant species were consumed during black rhino backtracking, only 52 of those species were also recorded in the BA plots (Table 4.2). A chi-squared test revealed that the diversity of food plants available to black rhino was higher than the diet diversity ($\mathcal{X}^2$=6.04, d.f.=1, P<0.05).

Table 4.2 – Diversity indices for Black Rhino Diet v Plant Availability. Species that had been consumed by black rhino but were not found in BA plots were excluded.

	No. of Plants	**No. of Species** (n = 84)	**Shannon-Wiener Index**	**Simpsons Index**
Plant Availability	7892	73	3.323	0.933
Plant Use	1361	52	0.409	0.922

Jacobs' selectivity index was calculated on a total of 72 plant species (Appendix B). Plant species that were consumed by black rhino but not recorded in vegetation plots (n=11) were excluded. Species that were available on the LBL (n=30) but not recorded to be eaten by black rhino during backtracking received a Jacobs' index value of -1. Of the 52 species that were recorded in both BA plots and backtracking, the five species most selected for and against are displayed in Table 4.3 (most selected for: *Cyphostemma serpens*; most selected against: *Rhus vulgaris*). Jacobs' index also revealed that black rhino selected for herbs (D=0.16), over shrubs (D= -0.30) and trees (D=0.06) (Table 4.4). Of the families representing herbs, *Vitaceae* spp., *Fabaceae* spp. and *Amaranthaceae* spp. were most selected for; *Convolvulaceae* spp., *Euphorbiaceae* spp. and *Pedaliaceae* spp. were most selected against (Table 4.5). Of the families representing shrubs, *Acanthaceae* spp., *Solanaceae* spp. and *Celastraceae* spp. were most selected for; *Araliaceae* spp., *Asteraceae* spp., *Euphorbiaceae* spp., *Lamiaceae* spp., *Meliaceae* spp., *Oleaceae* spp., *Primulaceae* spp. and *Rutaceae* spp. were most selected against (Table 4.6). Of the trees, *Fabaceae* spp. was the only family selected for – this encompasses *Acacia* spp.; *Euphorbiaceae* spp., *Oleaceae* spp., *Rosaceae* spp. and *Rubiaceae* spp. were most selected against (Table 4.7). There was a difference between the height class of the plants eaten by black rhino, with individuals selecting plants in height class A (0.0-0.5m) ($\mathcal{X}^2$=4013.84, d.f.=3, P<0.001) (Figure 4.3)

Table 4.3 – Jacobs index values for the main species that were available to, and consumed by black rhino on the LBL

Species	**Plants Available** (n = 7880)	**Plants Consumed** (n = 1162)	**Jacobs Index**
Cyphostemma serpens	1	4	+ 0.93
Acacia drepanolobium	172	168	+ 0.77
Indigofera bogdanii	2	2	+ 0.74
Pavonia patens	186	132	+ 0.68
Unidentified 1 (Oloidelata)	35	27	+ 0.68
Rhus vulgaris	174	1	- 0.93
Lippia kituiensis	226	2	- 0.89
Hibiscus aponeurus	330	4	- 0.85
Emilia discifolia	339	7	- 0.76
Asparagus africanus	140	3	- 0.75

Table 4.4 – Jacobs index values for the functional groups that were available to, and consumed by black rhino on the LBL

Functional Group	**Plants Available** (n = 7880)	**Plants Consumed** (n = 1162)	**Jacobs Index**
Herbs	4670	778	+ 0.16
Shrubs	1879	169	- 0.30
Trees	1331	215	+ 0.06

Table 4.5 - Jacobs index values for the families representing herbaceous species that were available to, and consumed by black rhino on the LBL

Herb: Family	**Plants Available** (n = 4670)	**Plants Consumed** (n = 778)	**Jacobs Index**
Vitaceae spp.	1	4	+ 0.92
Fabaceae spp.	35	27	+ 0.65
Amaranthaceae spp.	38	17	+ 0.46
Solanaceae spp.	144	61	+ 0.46
Malvaceae spp.	1285	301	+ 0.25
Rhamnaceae spp.	41	8	+ 0.08
Polygonaceae spp.	511	95	+ 0.06
Convolvulaceae spp.	1	0	- 1.00
Euphorbiaceae spp.	34	0	- 1.00
Pedaliaceae spp.	15	0	- 1.00
Rubiaceae spp.	2	0	- 1.00
Acanthanceae spp.	28	1	- 0.65
Lamiaceae spp.	258	10	- 0.64
Commelinaceae spp.	1591	150	- 0.37
Asteraceae spp.	686	104	- 0.05

Table 4.6 – Jacobs index values for the families representing shrub species that were available to and consumed by black rhino on the LBL

Shrub: Family	**Plants Available** (n = 1879)	**Plants Consumed** (n = 169)	**Jacobs Index**
Acanthaceae spp.	11	6	+ 0.72
Solanaceae spp.	19	8	+ 0.66
Celastraceae spp.	632	118	+ 0.64
Rhamnceae spp.	57	18	+ 0.58
Malvaceae spp.	76	9	+ 0.14
Plumbaginaceae spp.	19	2	+ 0.08
Rosaceae spp.	30	3	+ 0.05
Araliaceae spp.	3	0	- 1.00
Asteraceae spp.	73	0	- 1.00
Euphorbiaceae spp.	6	0	- 1.00
Lamiaceae spp.	390	0	- 1.00
Meliaceae spp.	13	0	- 1.00
Oleaceae spp.	50	0	- 1.00
Primulaceae spp.	70	0	- 1.00
Rutaceae spp.	12	0	- 1.00
Verbenaceae spp.	278	2	- 0.87
Asparagaceae spp.	140	1034	- 0.63

Table 4.7 – Jacobs index values for the families representing tree species that were available to, and consumed by black rhino on the LBL

Tree: Family	**Plants Available** (n = 1331)	**Plants Consumed** (n = 215)	**Jacobs Index**
Fabaceae spp.	238	173	+ 0.90
Euphorbiaceae spp.	1	0	- 1.00
Oleaceae spp.	69	0	- 1.00
Rosaceae spp.	26	0	- 1.00
Rubiaceae spp.	55	0	- 1.00
Anacardinaceae spp.	174	1	- 0.94
Celastraceae spp.	83	3	- 0.65
Sapindaceae spp.	80	3	- 0.64
Apocynaceae spp.	113	5	- 0.59
Ebenaceae spp.	292	16	- 0.56
Boraginaceae spp.	200	14	- 0.43

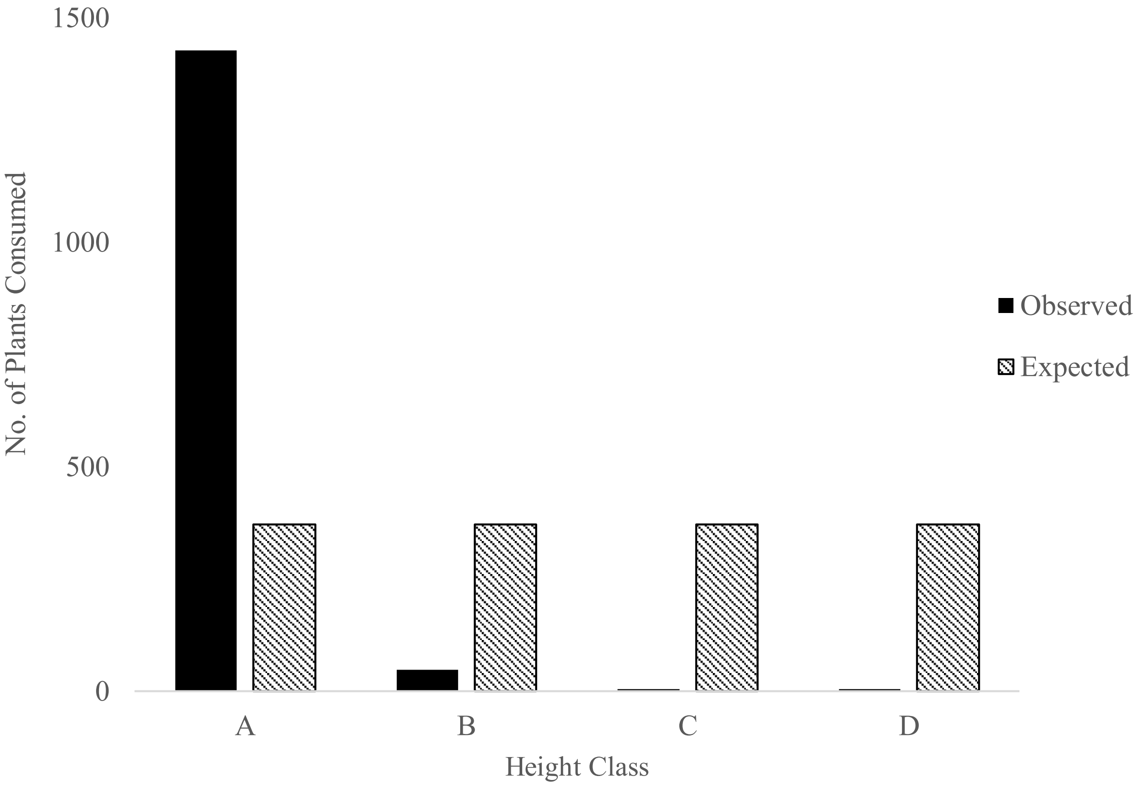

Figure 4.3 – The observed (no. of plants consumed) and expected (equal distribution across height class) values of plants consumed by black rhino during back tracking and their corresponding height class.

5 Discussion

This study investigated browse availability (BA) for black rhino and their use of resources on the LBL. Key findings indicate that BA and plant diversity are highest in forest habitats and current management strategies increase BA by 22%, though age of exclusion zone construction has no effect. During the wet season, black rhino select herbs and low growing succulent species, likely as a mechanism to avoid competition with larger herbivores (Landman et al., 2013). The coverage of *A. drepanolobium*, the key food plant selected for by black rhino, has declined in the reserve over the past few decades suggesting that black rhino may have contributed to this reduction by using this tree disproportionately to its availability.

5.1 Browse Availability as a Limiting Factor on the LBL

In the plots sampled, BA did not differ between the two conservancies (LWC and BC), despite predictions that BC would have higher quantities of browse. Predictions were based on the intrinsic physical differences between the reserves, coupled with the fact that black rhino were absent from BC until 2013 and thus, a lower browsing pressure may have been exerted on the vegetation. Whilst these results indicate that both conservancies are able to support a black rhino population of similar numbers, the conservancies are vastly different in size (LWC: 250km^2; BC: 125km^2) and BA values cannot be directly compared. Furthermore, the topographical differences between LWC and BC, notably the higher altitude of BC and its steep slopes, mean that not all the vegetation is accessible to black rhino. Regions of varying topographies can introduce uncertainty to estimates of ECC due to the inaccessibility of some areas (Young, 1938; Giesen et al., 2017). This is especially relevant to black rhino who have been found to avoid areas that are steep and lacking pathways to access browse; thus, influencing which regions of the conservancies are utilised (Kotze & Zacharias, 1993; Ganqa et al., 2005). Estimates that failed to consider topography and resource inaccessibility resulted in black rhino population growth rate declines of 6.1% per year in Eastern Shores (South Africa) and severe vegetation degradation between 1962-1977 in the Addo Elephant National Park (South Africa) (Hall-Martin & Pentzhorn, 1977; Hall-Martin et al., 1982; Adcock, 2001). Therefore, management must consider all the variables that may affect the ECC, including topography, competition, social interactions, fluctuations in precipitation and stochastic events like drought (Illius & O'Connor, 1999; Adcock, 2001).

Shannon-Wiener and Simpsons diversity indices revealed that BC had higher diversity of species palatable to black rhino than LWC. This suggests that plant species richness was higher in BC, perhaps due to the variation in topography, geology and soil composition (Giesen et al., 2017). It should be noted that in the time period of the study (10 weeks) and the number of plots sampled, it is unlikely that all species palatable to black rhino were recorded; thus, this result should be interpreted with caution.

The sampled plots revealed that forest habitats have higher quantities of BA than plains or hills habitats in LWC and BC. BA can be extrapolated for LWC because meticulous vegetation studies have determined the coverage of each habitat-type on the reserve (Table 5.1). This study calculated a BA value similar to that of Adcock (2016) of 11-12% and is therefore a valid estimate of overall BA. However, inferences cannot be made for total BA on BC, as the area of each habitat-type have not been calculated and thus, overall BA cannot be compared between LWC and BC.

Table 5.1 – Average BA score for each habitat-type sampled on LWC, multiplied by the percentage coverage of that habitat-type and summed to give an approximate value of BA on LWC.

Habitat Type	**LWC**			
	BA score (%)	*Area of Reserve (%)*	*BA score x Area (%)*	*BA units per km^2*
Forest	36	30	10.8	26.7
Hills & Rocky Outcrops	7	38	2.7	6.6
Plains	6	29	1.8	4.4
Riverine (not sampled)	-	3	-	-
	Total BA on LWC		15.2	37.6

Results demonstrated that forest areas had higher BA, but not all of these resources will be accessible to black rhino. Firstly, although the Ngare Ndare Forest was incorporated into the LBL, it is only accessible to black rhino through LWC, not BC. Secondly, the impenetrable understorey in the Forest meant that many of the plots had to be sampled just off the track; black rhino cannot readily access resources unless there are passable routes into the vegetation (Kotze & Zacharias, 1993; Landman & Kerley, 2014). Moreover, tree density in

Ngare Ndare increased from 35% in 1980 to 80% in 2000 and more mature species (*Olea africana* and *Juniperus procera*) are dominating the forest, shifting it towards a climax community (Giesen et al., 2007). As tree density and canopy cover continue to increase, a stable climax community will be reached, and the forest will be dominated by tree species that are inaccessible to black rhino (over 2.0m) (Giesen et al., 2007; Adcock, 2016; Giesen et al., 2017). Lastly, black rhino are territorial, residing in home ranges that vary in size depending on habitat quality (Reid et al., 2007; Patton & Jones, 2008; Morgan et al., 2009). For example, in Hluhluwe-Umfolozi Park (South Africa) black rhino maintained larger home ranges when the reserve experienced changes in vegetation structure and composition, enabling them to meet their nutritional requirements (Reid et al., 2007). Therefore, territoriality may result in agnostic social interactions that prevent some individuals from accessing food resources (Adcock, 2001; Campbell & Reece, 2014).

Shannon-Wiener and Simpson's Index revealed highest plant diversity in forest habitats, followed by hills, then plains. Both forest and hills had a higher plant diversity than plains, suggesting that plains habitats were dominated by fewer species. Despite this, black rhino selected more for species found on plains and hills habitats, such as *A. drepanolobium* and *P. patens*, and against forest species like *R. vulgaris* and *O. africana*. However, no backtracks occurred in forest habitats as there were no visible signs of black rhino presence (e.g. tracks, latrines, foraging), and the inhabitants were either shy and elusive or the dense vegetation made locating them impossible. Thus, the feeding habits of forest dwelling black rhino were not represented, and their use of resources remains unknown.

The randomly generated coordinates that determined the location for BA plots were, in some cases, inaccessible due to impassable roads, steep slopes and dense vegetation. Plots were still randomly selected, but often they were near a road. This may have resulted in the overrepresentation of vegetation, such as *Acacia* spp., that thrive in disturbed habitats (Rico-Gray & Oliveira, 2007).

5.2 Exclusion Zones as a Strategy for Enhancing Browse Availability

The primary goal of exclusion zones on LWC is to enhance food resources for black rhino. Based on observations, there is a stark contrast between the abundant vegetation inside exclusion zones and the land surrounding it. However, BA has never been quantified and it was unknown to what extent exclusion zones increased food availability. This study revealed that, on average, BA was 22% higher inside exclusion zones than outside of them. Thus, exclusion zones as a management strategy successfully increase the amount of browse available to black rhino.

However, BA did not differ between partial and total zones, nor did the construction age of the exclusion zone significantly increase BA. These findings contradicted the predictions. Firstly, it was expected that BA would be higher in total zones because all large herbivores are excluded and thus, minimal browsing pressure is exerted on the vegetation. However, sample size of total exclusion zones was limited to three (the number present on LWC) and thus, statistical analysis had low power to detect any differences. There did appear to be a trend: on average, BA in partial zones was 18.5% higher than outside the zones and in total zones, it was 32.4% higher. This indicates that differences may be detected through future expansion of sample size.

Secondly, it was predicted that BA would be higher in older, more established zones that have had longer to recover from browsing damage by elephant and giraffe. The oldest zone sampled was constructed in 1995, and the youngest in 2008. Despite the 13-year difference, BA was not significantly different, suggesting that 10 years is sufficient for vegetation to rebound and BA to increase. Heavy browsing (e.g. by giraffe) causes the rapid growth of new shoots in order to compensate for the removal of plant matter and in some species, like *Acacia*, the compensatory growth can exceed that of a plant that has not been browsed (Bergström, 1992). Furthermore, chemical changes occur in the browsed plant, including a reduction in the concentration of tannins; these are important defensive chemicals for forbs shrubs and trees – they reduce the protein availability of the leaves and make the plant less palatable to herbivores (Robbins et al., 1987; Bergström, 1992). Both these responses can combine in a feedback loop that enhances the negative effects of future browsing (Du Toit et al., 1990; Bergström, 1992). Exclusion zones successfully alleviate browsing pressure as plants do not have to redirect energy into compensatory growth or change its chemical composition. The lack of correlation between the age of exclusion zone and BA suggests that excluding large herbivores, reduces browsing pressure sufficiently enough that plants grow quickly and exceed heights of 2.0m (Smith & Goodman, 1987). Thus, the food resources become inaccessible to black rhino who browse vegetation almost exclusively between 0.5-1.2m, and up to 2.0m (Adcock, 2016). Therefore, whilst exclusion zones do increase the browse available to black rhino when compared to unprotected vegetation, they are not maximising the quantity of food resources because vegetation is allowed to grow beyond a height that is accessible to black rhino; this pattern was also identified in a survey by Giesen et al., (2007).

Within the 36 plots that were sampled inside exclusion zones, there was no evidence of black rhino browsing or presence (i.e. dung/tracks). This study was conducted in the wet season when succulent forbs and herbs were abundantly present on the LBL. Black rhino may use exclusion zones as a dry-season resource when forbs are scarce, plant quality is low, and they are more reliant on woody vegetation (Rutina et al., 2005; Kassa et al., 2007). Nonetheless, it raises questions as to how often black rhino utilise exclusion zones. A habitat-use survey and a dry-season study would reveal usage rates of the exclusion zones, indicating the value that black rhino place on the protected resources within.

5.3 Browse Selectivity as a Mechanism to Avoid Competition

This study was conducted during the wet season, when food plants (forbs, shrubs, trees) were abundant and diverse, offering a better representation of black rhino selectivity in comparison to resource availability on the LBL. black rhino dietary composition was less diverse than the available food plants. However, this was expected as it was unlikely that every palatable species consumed by black rhino would be recorded during sampling efforts. In total, 72 species were consumed by black rhino across the LBL, which is comparable to previous studies that recorded 59 species in Majete Wildlife Reserve, Malawi (Gyöngyi & Elmeros, 2017); 92 species in the Addo Elephant National Park, South Africa (Landman et al., 2013); 51, 53, and 41 species in three wildlife reserves in South Africa (Buk & Knight, 2010); 80 species in the Great Fish River Reserve, South Africa (Van Lieverloo et al., 2009); 103 species in Laikipia, Kenya (Oloo et al., 1994); and 70 species in the Masai Mara, Kenya (Mukinya, 1977). Backtracking only occurred in hills and plains habitats because forest black rhino could not be located; thus, palatable species that were noted during BA assessments, were not recorded as consumed by black rhino in this study. Furthermore, a large portion of black rhino browsing occurs overnight, so it is possible that some evidence of foraging was missed (Kiwia, 1986). Nonetheless, the consumption of 72 species indicates high diversity in black rhino diet, corroborating findings from other studies (Goddard, 1968; Mukinya, 1973; Hall-Martin et al., 1982).

At the species level, Jacobs Index revealed that *C. serpens*, *A. drepanolobium*, *I. bogdanii* and *P. patens* were highly selected for. However, for *C. serpens* and *I. bogdanii*, utilisation rates may not be entirely accurate because few plants were recorded in the BA plots and availability was low (Petrides, 1975; Manly et al., 2002). Therefore, *A. drepanolobium* and *P. patens* were the most palatable species to black rhino and were selected disproportionately to their availability. The species most selected against were *R. vulgaris*, *L. kituiensis*, *H. aponeurus* and *E. discifolia*. Whilst these species were well represented in the BA plots, *R. vulgaris* and *L. kituiensis* were largely found in forest plots where black rhino were not backtracked, suggesting that results for selection against these plants should be interpreted with caution. *H. aponeurus* and *E. discifolia* were found predominantly in plains and hills habitats, but also in forest areas, and therefore black rhino likely select against these plants based on their proportional availability. Studies report an array of different species that black rhino select for and against, suggesting that dietary selection is specific to site and season (Goddard, 1968; Mukinya, 1977; Oloo et al., 1994; Muya & Oguge, 2000; Ganqa et al., 2005; Landman et al., 2013).

This study also revealed that black rhino selected for herbs and trees, but against shrubs. During observations, it was noted that black rhino were feeding low to the ground, corroborated by results that there was a significant difference in the consumption of plants below the height of 0.5m, in comparison to all other height classes. Contrary to these results, Adcock (2016) found that black rhino feed almost exclusively between 0.5-1.2m; Breebart (2000) reported that ~47% of black rhino foraging occurred between 0.5-1.0m, (<0.5m= ~38%, 1.0-2.0m= ~15%); Rossouw (1998) noted that ~55% of feeding occurred between 0.5-1.0m (<0.5m= ~36%, 1.0-2.0m= ~9%); Joubert & Eloff (1971) stated that the optimum feeding height for black rhino was between 0.6-1.2m. Selecting low-growing, succulent herbs appears to be a wet season adaptation for several herbivores, including black rhino, impala (*Aepyceros melampus*) and waterbuck (*Kobus ellipsiprymnus*). This is because plant variety, abundance of food plants and nutrient quality is higher, and the animals do not have to depend on woody vegetation as much (Rutina et al., 2005; Kassa et al., 2007; Landman et al., 2013).

Furthermore, selecting herbs may have evolved as a mechanism to avoid competition with other megaherbivores such as elephant. In the Addo Elephant National Park, elephant and Black rhino showed significant diet separation during the wet season, with black rhino consuming more forbs, and elephant diversifying to grass. However, the utilisation of these vegetation-types for both species declined during the dry season, when seasonally available plant forms declined, and both elephant and black rhino shifted their dietary intake to woody vegetation and shrubs (Landman et al., 2013). Concerns have been raised regarding the adverse impacts that elephant have on black rhino through the depletion of BA (e.g. decline in *A. drepanolobium* habitats on LWC), destruction of vegetation and direct competition for resources (Birkett & Stevens-Wood, 2005; Rutina et al., 2005; Landman & Kerley, 2014). However, the selection for forbs by black rhino on the LBL, suggests that this behaviour not only allows black rhino to take advantage of the seasonal food resources, but also enables them to avoid competition with elephant (Landman et al., 2013). Previous studies (including one on LWC) found that black rhino and elephant utilise vegetation in a complimentary way. For instance, elephant utilise plants between 2.0-3.0m in height, with a diameter at breast height (DBH) of >10cm, whereas, black rhino browsing damage is limited to below 2.0m (Jachmann & Croes, 1991; Cabral, 2015).

5.4 The Impacts of Browsers on Vegetation

Long-term studies have revealed that LWC has undergone large-scale vegetation changes, including (but not limited to) the 15% decline in shrub and tree cover, specifically of *A. drepanolobium* dominated habitats. These changes were largely attributed to the combined effects of elephant and giraffe browsing, and variation in precipitation levels (Giesen et al., 2007; Giesen et al., 2017). Numerous other studies have also noted the negative impact of elephant on BA for black rhino (Birkett, 2002; Birkett & Stevens-Wood, 2005; Mills et al., 2006; Landman et al., 2013; Landman & Kerley, 2014).

Since the construction of the first exclusion zones, elephant and giraffe populations on LWC have continued to increase (Giesen et al., 2017). By partitioning off areas of vegetation, browsing pressure may have shifted to other areas of the reserve and intensified; this may explain the decrease in *A. drepanolobium* coverage from 1980 to 2000 (Giesen et al., 2007; Giesen et al., 2017). This study corroborated findings that A. *drepanolobium* is a vital food resource for black rhino (Edwards, 1998; Lush et al., 2015), as Jacobs selectivity analysis revealed that in relation to availability, this species is highly selected for by black rhino on the LBL. Thus, a combination of browsing by black rhino, elephant and giraffe (who may have been forced to shift their foraging activities), and changes in precipitation patterns may have contributed to the decline in woody vegetation seen on LWC (Giesen et al., 2007; Giesen et al., 2017). Additionally, 99.4% of the *A. drepanolobium* consumed during backtracking were below 0.5m in height. Therefore, it is possible that due to palatability and the fact that black rhino are selecting for this species, *A. drepanolobium* seedlings are not being given the opportunity to establish and grow to sufficient heights, further repressing the regeneration of woody vegetation and contributing to declines on LWC (Roques et al., 2001; Levick et al., 2009). This has been documented in Ol Pejeta Conservancy (Kenya) where 63% of *A. drepanolobium* seedling mortality was caused by browse damage and drought (Wahungu et al., 2011). This further identifies the need for reserves to protect *A. drepanolobium* to increase seedling survival and recruitment of this key food resource for black rhino (Edwards, 1998; Wahungu et al., 2011; Lush et al., 2015).

Of interest and a concept worth considering is the mutualistic relationship that exists between *A. drepanolobium* (a myrmecophyte) and the *Crematogaster* genus of ants that inhabit the tree and defend it from herbivory. A study in Laikipia, Kenya, found that severe elephant damage was inflicted on *A. drepanolobium* trees that had had their ants removed, but elephant exhibited strong avoidance of trees that were protected by colonies. This indicates that the mutualism plays a crucial role in stabilising tree coverage and driving growth in savannah ecosystems (Goheen & Palmer, 2010). The decline in *A. drepanolonium* cover on LWC may indicate an issue with this symbiotic relationship. *Acacia* spp. are particularly vulnerable to exploitation by ‘cheaters’ because they are a horizontally transmitted species, and a time lag occurs between the growth of the plant and the establishment of an ant colony (Raine et al., 2004). Cases of *Acacia* spp. being exploited by cheat ant species (who obtain the benefits of the mutualism without offering a form of defence) have been recorded globally (Raine et al., 2004; Heil et al., 2009). Furthermore, the fact that black rhino are consuming *A. drepanolobium* below 0.5m, suggests that the plants are experiencing browsing damage before an ant colony has established itself. Thus, it would be advisable to investigate the efficacy of the mutualism between *A. drepanolobium* and its ant inhabitants on LWC.

5.5 Ecological Carrying Capacity

Traditional conservation strategies have focused on increasing wildlife populations as quickly as possible, especially for species like black rhino that are vulnerable to extinction.

However, overstocking can result in a suite of negative impacts including overexploitation of resources (as seen in LWC) and density-dependent population declines as a result of decreasing quality and quantity of food resources. In female black rhino, overstocking can manifest in behavioural signs of stress, including reduced breeding performance (Adcock, 2001; Birkett & Stevens-Wood, 2005; Bonenfant et al., 2009; Patton et al., 2010). The Lewa Research Department has collected long-term demographic data on the black rhino population, revealing that growth rates have slowed from 17.8% in 2006 (a figure that greatly exceeds the national targets set by Kenya Wildlife Service), to 3.3% in 2017, and ~1% in 2018 (unpublished data). This might suggest that the black rhino population on the LBL is approaching, or has already exceeded, its ECC and that LWC and BC may be overstocked. It would be advisable for the LBL to act as a source population for other conservancies, as they have previously done with BC and the newly founded Sera Community Conservancy (Lewa, 2018).

This study provided estimates that there were 37.6 browse units/km^2 available to the 65 black rhino on LWC. However, this does not consider inaccessible areas or the competitive effects of other browsers, such as elephant, giraffe, waterbuck, impala and eland (Adcock, 2001). Herbivory results in fluctuations of BA which can negatively impact black rhino populations. One approach for ECC estimates, is to consider the combined effects of all herbivores, and not just that of the individual species (Prins & Douglas-Hamilton, 1990). Given the tendency for wildlife densities to increase rapidly in fenced reserves, incorporating these parameters during ECC calculations for black rhino may provide more realistic estimates that would ensure positive population growth, and avoid adverse effects such as those witnessed in Eastern Shores and the Addo Elephant National Park (Hall-Martin & Pentzhorn, 1977; Hall-Martin et al., 1982; Prins & Douglas-Hamilton, 1990; Adcock, 2001; Birkett & Stevens-Wood, 2005).

LWC and BC are not the only fenced reserves to experience declines in black rhino growth rates (Emslie, 2001; Hall-Martin & Castley, 2003). This issue has now been identified in several African countries, and new conservation action plans specify the need to establish new black rhino populations and manage them as a metapopulation (Emslie, 2001; Metzger et al., 2007; Morgan et al., 2009). By translocating and reintroducing individuals to new reserves, breeding populations can be established that will ultimately contribute to the conservation of this critically endangered species (Akçakaya et al., 2007; Morgan et al., 2009). However, potential negative trade-offs, including variation in growth rates, biased sex ratios, environmental changes, restricted dispersal, disease and genetic issues such as outbreeding depression, founder effects and genetic drift must be carefully assessed (Caughley, 1994; Rachlow and Berger, 1998; Schroder et al., 2005; Jolles et al., 2006; Akçakaya et al., 2007; Berkley & Linklater, 2010; Greaver et al., 2014).

5.6 Conclusions and Recommendations

Resource use and availability studies are vital given that megaherbivore populations, especially those in PAs, are predominantly regulated by food limitation (Sinclair et al., 2007). If populations within fenced areas approach or exceed the ECC, a variety of effects can occur including declines in food quantities and density-dependence regulation (Mills et al., 2006). In light of the vegetation changes that have occurred on LWC, it was important to establish how black rhino, a critically endangered species, utilise the available resources.

This study revealed that BA and plant diversity was higher in forest habitats, compared to plains and hills. However, not all the resources may be accessible to black rhino and as the Ngare Ndare forest approaches a climax community, more plants will exceed 2.0m (Giesen et al., 2007). Current techniques employed by management to enhance black rhino food resources are successful; however, they are not increasing BA to optimal quantities. In some cases, it appears that the vegetation inside exclusion zones have exceeded heights of 2.0m and are therefore inaccessible to black rhino (Giesen et al., 2007; Cabral, 2015). The youngest exclusion zone sampled had BA similar to that of the oldest zone, suggesting that 10 years is sufficient for the vegetation to rebound from browsing damage exerted by herbivores. A lack of evidence of black rhino presence and foraging in exclusion zones raises questions as to how this resource is used. Perhaps black rhino are more reliant upon exclusion zones during the dry season when plant quality declines and there are fewer palatable species available (Rutina et al., 2005).

This study was conducted in the wet season, giving a greater representation of the palatable species available for consumption. black rhino are selecting forbs and low growing plants. This is indicative of a behaviour that has evolved to avoid competition for food resources with elephant (Landman et al., 2013). black rhino strongly select *A. drepanolobium,* an important food plant whose coverage on the LBL has declined in recent years (Edwards, 1998; Giesen et al., 2007). The use of this species in quantities greater than its proportional availability suggests that black rhino may have also contributed to this decline (Giesen at al., 2017). Furthermore, the consumption of *A. drepanolobium* trees below 0.5m, suggests that the seedlings are not given an opportunity to establish themselves.

Overall, this study has resulted in several key findings that should facilitate changes in the way that black rhino are managed on fenced reserves, like the LBL. Conservation efforts should focus on increasing the cover of *A. drepanolobium*, as it appears to be an important food resource for black rhino. The use of exclusion zones for habitat manipulation can successfully increase BA. However, to optimise the browse that is accessible to black rhino, the zones should be managed on a rotational basis. By constructing a partial zone for 10 years, BA will increase significantly in comparison to unfenced areas. After this time period, the fences should be removed, enabling elephant to access the vegetation. The ability of elephant to convert woodland to shrubland will increase accessibility to browse for other herbivores and create passable routes into thickets, assisting black rhino foraging (Landman & Kerley, 2014; Ripple et al., 2015). The LBL remains one of the only reserves to use exclusion zones to enhance food quantities for black rhino. The success of this technique, combined with the suggested management of zones on a rotational basis, has implications for the management of global black rhino populations in all fenced reserves across Africa, especially as the majority of black rhino populations now reside within PAs.

Based on the conclusions of this study, the recommendations for future research on the LBL include (i) a vegetation survey on BC to determine the coverage of each habitat-type, enabling BA values to be directly compared between BC and LWC; (ii) a habitat-use study investigating the utilisation of exclusion zones by black rhino to provide information regarding the importance of the food resources inside; (iii) a resource utilisation study focusing on black rhino that inhabit forested areas on the LBL, as little is known about their feeding ecology; (iv) a comparative dry-season study to determine how BA changes seasonally, and whether differences in food availability and quality causes the dietary composition of black rhino to shift; (v) the efficacy of the mutualistic relationship between *A. drepanolobium* and *Crematogaster* ants should be investigated on LWC. Elsewhere, ants have been shown to effectively reduce browsing by elephant; therefore, ant-acacia mutualisms play a crucial role in the stability and survival of trees in savannah ecosystems

(Goheen & Palmer, 2010). Given that elephant have significantly contributed to declines in *A. drepanolobium* cover on LWC, any issues with the symbiosis should be identified.

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Appendices

Appendix A

Table A.1 - Plants consumed by black rhino during the long rains season on LWC and BC, Kenya. **A** = all plant parts eaten; **L** = leaves; **S** = stem; **Sh** = shoots.

Plant family and species	**Functional Group**	**No. of Plants** (n = 1485)	**No. of Cuts** (n = 8643)	**Parts Eaten**
ACANTHACEAE				
Barleria spinisepala	Shrub	6	47	S, L
Justicia diclipteroides	Herb	1	1	S, L
AMARANTHACEAE				
Achyranthes aspera	Herb	17	131	S, L
Amaranthas dubius	Herb	177	1020	S, L
ANACARDIACEAE				
Rhus vulgaris	Tree	1	10	S, L
APOCYNACEAE				
Carissa edulis	Tree	5	27	S, L
ASPARAGACEAE				
Asparagus africanus	Shrub	3	27	S, L
ASTERACEAE				
Acmella oleracaea	Herb	39	208	S, L
	Herb	7	62	S, L

Emilia discifolia	Herb	58	424	S, L
Helichrysum glumaceum				
BORAGINACEAE				
Cordia monoica	Tree	14	99	S, L
CELASTRACEAE				
Elaeodendron buchananii	Shrub	118	817	S, L, Sh
Maytenus senegalensis	Tree	3	11	S, L
COMBRETACEAE				
Combretum mole	Tree	4	34	S, L
COMMELINACEAE				
Commelina benghalensis	Herb	150	993	A
CUCURBITACEAE				
Coccinia trilobata	Herb	4	40	S, L

Plant family and species	**Functional Group**	**No. of Plants** (n = 1485)	**No. of Cuts** (n = 8643)	**Parts Eaten**
EBENACEAE				
Euclea divinorum	Tree	16	102	S, L
EUPHORBIACEAE				
Acalypha fruiticosa	Tree	2	5	S, L
Ricinus communis	Shrub	1	3	S, L
FABACEAE				
Acacia brevistica	Tree	1	4	S, L
Acacia drepanolobium	Tree	168	887	S, L
Acacia hokii	Tree	2	6	S, L
Acacia mellifora	Tree	1	8	S, L
Acacia nilotica	Tree	2	6	S, L
Ormocarpum trichocarpum	Tree	1	4	S, L
Unidentified 1 (Oloidelata)	Herb	27	167	S, L
LAMIACEAE				
Ajuga remota	Herb	2	9	S, L
Leonotis nepetifolia	Herb	2	7	S, L
Leucas grandis	Herb	7	31	S, L
Plectranthus kamerunensis	Herb	1	4	S, L
LYTHRACEAE				
Lythrum rotundifolium	Herb	3	17	S, L

Plant family and species	**Functional Group**	**No. of Plants** (n = 1485)	**No. of Cuts** (n = 8643)	**Parts Eaten**
MALVACEAE				
Abitulon grandiflorum	Herb	61	578	S, L
Grewia similis	Shrub	3	9	S, L
Grewia tembensis	Shrub	9	44	S, L
Hibiscus aponeurus	Herb	4	49	S, L
Hibiscus flavifolius	Herb	93	439	A
Indigofera bogdanii	Herb	2	6	S, L
Indigofera volkensii	Herb	9	35	S, L
Pavonia patens	Herb	132	1035	S, L
PLUMBAGINACEAE				
Plumbago zeylanica	Shrub	2	5	S, L
POACEAE				
Pennisetum stramineum	Grass	124	124	A
POLYGONACEAE				
Rumex usambarensis	Herb	95	421	A
ROSACEAE				
Rubus volkensii	Shrub	3	16	S, L
SAPINDACEAE				
Pappea capensis	Tree	3	10	S, L
SOLANACEAE				
Lycium europeum	Shrub	3	64	S, L
Lycium shawii	Shrub	5	30	S, L, Sh
Solanum incanum	Herb	61	343	A
Withania somnifera	Shrub	1	1	S, L
VERBENACEAE				
Lippia kituiensis	Shrub	2	48	S, L
VITACEAE				
Cyphostemma serpens	Herb	4	48	S, L

Appendix B

Table B.1 - The calculated values from Jacobs' selectivity index for the 72 plant species that were consumed by black rhino on the LBL during this study.

Species	**Plants Available** (n = 7880)	**Plants Consumed** (n = 1162)	**Jacobs Index**
Abitulon grandiflorum	160	61	+ 0.46
Acacia brevispica	14	1	- 0.35
Acacia commiphora	12	0	- 1.00
Acacia drepanolobium	172	168	+ 0.77
Acacia mellifora	13	1	- 0.31
Acacia nilotica	7	2	+ 0.32
Acacia seyal	10	0	- 1.00
Achyranthes aspera	38	17	+ 0.51
Acmella oleracaea	90	39	+ 0.50
Asparagus africanus	140	3	- 0.75
Aspilia mossambicensis	8	0	- 1.00
Barleria spinisepala	11	6	+ 0.58
Carissa edulis	113	5	- 0.54
Commelina benghalensis	1591	150	- 0.26
Cordia monoica	200	14	- 0.36
Cyphostemma serpens	1	4	+ 0.93
Dodonaea viscosa	62	0	- 1.00
Elaeodendron buchananii	632	118	+ 0.13
Emilia discifolia	339	7	- 0.76
Euclea divinorum	292	16	- 0.47

Euphorbia candelabrum	1	0	- 1.00
Euphorbia hetracoroma	34	0	- 1.00
Euphorbia tirucalli	6	0	- 1.00
Grewia tembensis	63	9	- 0.02
Helichrysum glumaceum	257	58	+ 0.22
Helinus mystacinus	41	8	+ 0. 14
Hibiscus aponeurus	330	4	- 0.85
Hibiscus calyphyllus	11	0	- 1.00
Hibiscus flavifolius	215	93	+ 0.51
Hoslundia opposita	325	0	- 1.00
Indigofera bogdanii	2	2	+ 0.74
Indigofera volkensii	326	9	- 0.69
Ipomoea cicatrices	1	0	- 1.00
Justicia diclipteroides	28	1	- 0.61

Species	**Plants Available** (n = 7880)	**Plants Consumed** (n = 1162)	**Jacobs Index**
Leonotis nepetifolia	76	2	- 0.70
Leucas grandis	157	7	- 0.54
Lippia javanica	26	0	- 1.00
Lippia kituiensis	226	2	- 0.89
Lippia ukambensis	26	0	- 1.00
Lycium europium	12	3	+ 0.26
Lycium shawii	7	5	+ 0.66
Malvastrum coromandelianum	55	0	- 1.00
Maytenus senegalensis	56	3	- 0.47
Maytenus undata	5	0	- 1.00
Myrsine africana	70	0	- 1.00
Mystroxylon aethiopicum	22	0	- 1.00
Olea africana	5	0	- 1.00
Olea europaea	64	0	- 1.00
Ormocarpum trichocarpum	10	1	- 0.19
Osteospermum vaillantii	65	0	- 1.00
Pappaea capensis	18	3	+ 0.06
Pavetta subcana	55	0	- 1.00
Pavonia patens	186	132	+ 0.68
Plectranthus kamerunensis	25	1	- 0.57
Plumbago zeylanica	19	2	- 0.17
Pyrostria phyllanthoidea	2	0	- 1.00
Rhamnus staddo	34	1	- 0.67
Rhus vulgaris	174	1	- 0.93
Rotheca myricoides	65	0	- 1.00
Rubus volkensii	30	3	- 0.19

Rumex usambarensis	511	95	+ 0.12
Schefflera volkensii	3	0	- 1.00
Schrebera alata	50	0	- 1.00
Scutia myrtina	23	17	+ 0.67
Sesanum angolenda	15	0	- 1.00
Solanum incanum	144	61	+ 0.50
Sterculia africana	13	0	- 1.00
Teclea nobilis	1	0	- 1.00
Trema orientalis	26	0	- 1.00
Turraea abyssinica	13	0	- 1.00
Zanthoxylum usambarense	11	0	- 1.00
Unidentified 1 (Oloidelata)	35	27	+ 0.68