

**DIETARY AND SPATIAL STRATEGIES OF GEMSBOK (*Oryx g. gazella*)
AND SPRINGBOK (*Antidorcas marsupialis*) IN RESPONSE TO DROUGHT IN
THE DESERT ENVIRONMENT OF THE KUNENE REGION, NAMIBIA**

Inaugural-Dissertation to obtain the academic degree
Doctor rerum naturalium (Dr. rer. nat.)

Submitted to the Department of Biology, Chemistry, Pharmacy
of the Freie Universität Berlin

by

David Lehmann
from Grenoble, France

2015



ORYX PROJECT

Leibniz Institute
for Zoo and Wildlife Research of Berlin

Logo credit: David Lehmann / Oryx Project

L'homme qui, du désert ne saccage point la légende, ne peut subir l'outrage.

Tahar Ben Jelloun

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1. Gutachter: PD Dr. Christian C. Voigt
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This dissertation is based on the following manuscripts:

1. Lehmann D^{1,8}, Mfunne J.K.E², Gewers E³, Brain C⁴, & Voigt C.C^{1,8} (2013) **Dietary Plasticity of Generalist and Specialist Ungulates in the Namibian Desert: A Stable Isotopes Approach.** *PloS one*, 8(8), e72190 [doi:10.1371/journal.pone.0072190](https://doi.org/10.1371/journal.pone.0072190)
2. Lehmann D^{1,8}, Mfunne J.K.E², Gewers E³, Brain C⁴, & Voigt C.C^{1,8} (2015) **Individual variation of isotopic niches in grazing and browsing desert ungulates.** *Oecologia*. [doi:10.1007/s00442-015-3335-1](https://doi.org/10.1007/s00442-015-3335-1)
3. Lehmann D^{1,8}, Mfunne J.K.E², Gewers E³, Cloete J⁴, Aschenborn O.H-K⁵, Mbomboro L⁶, Kasoana S⁷, Brain C⁴, & Voigt C.C^{1,8} (2015) **Spatial movements of desert dwelling gemsbok (*Oryx g. gazella*) in response to spatial and temporal variation in plant productivity** (*Unpublished*)

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ZUSAMMENFASSUNG

Wüsten bewohnende Huftiere leben in Ökosystemen, welche für Degradationsprozesse und Klimaveränderung besonders anfällig sind. Anpassungen der Morphologie, Physiologie und des Verhaltens von Huftieren an Hitze und Trockenheit sind bereits relativ gut untersucht, jedoch gibt es kaum Informationen zu ihrer Ernährungsweise und den räumlich-zeitlichen Strategien bei stark variabler Verfügbarkeit von Nahrung in ariden Ökosystemen.

Ziel dieser Arbeit war die Untersuchung der Flexibilität von zwei Huftierarten in Bezug auf Nahrung und Raumnutzung. Als Fokusart dienten Spießbock (*Oryx g. gazella*) und Springbock (*Antidorcas marsupialis*), welche sympatrisch in den Wüsten der Kunene-Region Namibias leben. Die Ernährungsweise dieser zwei Huftierarten wurde über eine Analyse der stabilen Isotopenzusammensetzung von potenziellen Nahrungspflanzen, sowie von Fell- und Gewebeproben der Tiere untersucht. Die Resultate zeigen, dass die Spießbock-Population der Kunene-Region ihre Nahrung flexibler gestalten als es bisher angenommen wurde (Kapitel II). Spießböcke änderten ihre Nahrungsstrategie in Abhängigkeit von der saisonalen Trockenheit. Während regenreicher Zeiten spezialisierten sie sich auf Gräser und während trockener Zeiten wählten sie ein Mischfutter bestehend aus Blattmaterial von Büschen und Bäumen (ungefähr 30%) und Gras aus (60%). Interessanterweise scheinen Spießböcke in der Trockenzeit ebenfalls *Euphorbia damarana* zu verzehren, welches eine endemischen Pflanze mit toxischen sekundären Pflanzeninhaltsstoffen ist. Spießböcke scheinen gegenüber den giftigen Substanzen weitestgehend tolerant zu sein, so dass die Tiere die Nährstoffe und Flüssigkeit der Pflanzen im Bedarfsfall nutzen können. Im Gegensatz zum Spießbock blieben Springböcke bei einer generalistischen Nahrungsstrategie, welche von der saisonalen Trockenheit der Umwelt unabhängig war.

Des Weiteren zeigt meine Studie, dass Individuen der zwei Untersuchungsarten in ihrer Ernährungsweise unterschiedlich auf Veränderungen der Umweltbedingung, wie zum Beispiel eine verminderte Primärproduktivität von Pflanzen, reagieren (Kapitel III). Innerhalb einer Art können Individuen verschiedene Ernährungsweisen aufzeigen. Variationen im Verhältnis von stabilen Kohlenstoff- und Stickstoff-Isotopen in aufeinanderfolgenden Segmenten von Schwanzhaaren von Spieß- und Springböcken ergaben Aufschluss über die Variabilität in der Ernährungsweise entlang einer zeitlichen Achse. Die Ernährungsweise der beiden Arten unterschied sich deutlich auf Artebene, beide wiesen jedoch eine ähnliche hohe Variabilität auf. Innerhalb einer Art überlappten die individuellen Nahrungsnischen nur teilweise, was darauf hindeutet, dass sich Individuen beider Arten in ihrer Ernährungsweise zum Teil klar voneinander abgrenzen. Kapitel III beschreibt die individuelle Differenzierung

und Variabilität von Spieß- und Springbockindividuen bezüglich ihrer Ernährungsweise. Wahrscheinlich vermindern die individuell unterschiedlichen Nahrungspräferenzen sowohl innerhalb als auch zwischen den Arten die Nahrungskonkurrenz. Diese Plastizität in der Ernährungsweise könnte die individuellen Überlebenschancen von Spießbock und Springbock in trockenen Ökosystemen erhöhen.

Basierend auf den Untersuchungen zur Ernährungsweise mit Hilfe von Isotopen stellte ich die Hypothese auf, dass sich Spießböcke und Springböcke in ihrer räumlich-zeitlichen Bewegung unterscheiden. In Kapitel IV untersuche ich, wie der als sesshaft geltende Spießbock mit flexibler Nahrungsnische auf dem Populationsniveau hinsichtlich seines Raumzeitmusters auf eine Verknappung von Futterpflanzen reagieren würde. Dazu dokumentierte ich die zeitliche Variabilität des Aktionsradius und die Habitatnutzung von Spießböcken, welche ich zuvor mit GPS-Halsbändern ausgerüstet hatte. Die Resultate zeigen, dass Springböcke der Kunene-Region tatsächlich als sesshaft einzustufen sind, da sie kein Migrationsverhalten zeigten, wenn das Futterangebot wesentlich reduziert war. Die Spießböcke wählten ihr Habitat nach der Verfügbarkeit von Ressourcen, der Topographie und des Risikos, von Raubtieren gejagt zu werden, aus. Individuen unterschieden sich hinsichtlich ihres Aktionsradius sowie der Habitatnutzung, was mit der Beobachtung einer individuellen Ernährungsweise konsistent ist. In meiner Doktorarbeit zeige ich ökologische Mechanismen auf, welche Wüsten bewohnende Huftiere nutzen, um in einer wasserarmen Umgebung überleben zu können. Spießböcke und Springböcke ernähren sich unterschiedlich und reagieren mit unterschiedlichen Strategien auf Nahrungsknappheit bei extremer Trockenheit. Individuen beider Arten waren zwar spezialisiert, was auf individuelle Strategien der Nahrungssuche deuten könnte. Diese könnten jedoch auch mit der Nutzung verschiedener Habitate, welche sich in der Primärproduktivität, der Pflanzensammensetzung, sowie der Topographie und Vegetationsdichte unterscheiden, zusammenhängen. Die Resultate meiner Arbeit sind für eine Optimierung der Managementstrategien von Wüsten bewohnenden Antilopen relevant. Die gewonnenen Erkenntnisse könnten zudem Aufschlüsse über den zu erwartenden Erfolg von Wiederansiedlungen oder Umsiedlungen von Wildtierpopulationen in Wüstengebieten geben.

SUMMARY

Desert ungulates live in adverse ecosystems that are particularly sensitive to degradation and global climate change. The morphological, physiological and behavioural adaptations of ungulates towards heat and drought stress are relatively well studied. However, only little work focused on their dietary and spatio-temporal strategies to overcome severe shortages of food resources in deserts.

The aim of this thesis was to investigate the dietary and spatial flexibility of two ungulate species that live in the xeric Kunene Region of Namibia; grazing gemsbok (*Oryx g. gazella*) and browsing springbok (*Antidorcas marsupialis*). The diet of these two ungulates was investigated using stable isotopes analyses of animal and plant tissues. The results suggested that the gemsbok population was more flexible in its diet than previously suggested in the literature (Chapter II). Individual gemsbok had a mixed diet of grass and succulent plants (60%), shrubs and trees (30%) during the broad dry periods (including 10% of uncertainty), whereas they focused primarily on fresh sprouts of grasses during periods of rainfall. Interestingly, isotopic data also indicated that gemsbok relied also on *Euphorbia damarana* during dry periods, an endemic plant that is rich in toxic secondary plant compounds. In contrast, springbok maintained a predominantly browser diet, independent of dryness.

Further investigation revealed that individual gemsbok and springbok used different dietary tactics when facing similar environmental changes; i.e. fluctuations in plant primary productivity (Chapter III). Variations in stable carbon and nitrogen isotope ratios of tail hair increments were used as proxies for individual dietary plasticity. Isotopic food niches of populations of the two species were mutually exclusive, but similar in breadth. Within species, individual dietary niches overlapped only partially, suggesting that both populations included individuals with distinct isotopic food niches, but also individuals with a similar diet. The data presented in chapter III suggest an isotopic dietary niche segregation of the two desert ungulate species. Similar, yet isotopically distinct feeding habits of individuals, occurring within both species gemsbok and springbok populations, may reduce intra species competition for food resources and, thus, may facilitate ungulates' survival in desert environments.

Based on the isotopic data of used food resources, I further hypothesised that gemsbok differed in their spatio-temporal movements in order to support such dietary flexibility. In Chapter IV, I have therefore investigated how gemsbok individuals, a sedentary ungulate species with high dietary flexibility on a population level but pronounced individual specialisation respond in habitat use to fluctuations in plant primary availability. I report

SUMMARY

temporal variation of home ranges and habitat use of gemsbok equipped with GPS collars. The results showed that gemsbok in the Kunene Region were sedentary during the study period, even during extensive drought periods. Gemsbok selected their habitat according to plant primary productivity and resource accessibility, topography and estimated risk of predation by large predators. However, individuals differed in their home ranges and habitat uses, possibly reflecting their specific dietary preferences, as illustrated in Chapter III.

In this thesis, I revealed fundamental ecological mechanisms that allow desert-dwelling ungulates to exist in arid environments, particularly when facing unpredictable and severe food shortages. Gemsbok and springbok occupied distinct isotopic niches and displayed specific dietary habits when coping with drought. However, studied individuals of both species were highly specialised, a complementary mechanism that may reduce intra-specific competition. To support such complex dietary behaviours, ungulates responded to resource fluctuations by using a combination of interlacing local habitats that differ in plant productivity, plant composition, topography and vegetation cover. The results of this thesis have implications for both local and global management of desert dwelling antelopes. As this work was conducted on two of the most abundant wildlife species in the Kunene Region, local communities have shown their interest in implementing these results in their management plans by defining protected areas and restricting the access to hunters and livestock during the periods of drought. At a larger scale, the dietary specialisation of ungulate individuals might have implications for the reintroduction or relocation of endangered animals in arid environments.

CHAPTER I: GENERAL INTRODUCTION

Ungulates are very successful mammals, inhabiting almost all ecosystems, even relatively hostile habitats such as deserts. Desert ungulates such as the Arabian oryx (*Oryx leucoryx*), gemsbok (*Oryx g. gazella*) or springbok (*Antidorcas marsupialis*) are among the largest mammals in desert and semi-desert environments. The ability of these ungulates species to survive long periods of drought mainly depends on the water content of the used food (Taylor, 1968; Schmidt-Nielsen, 1979; Jhala *et al.*, 1992). But feeding on plants imposes a large problem to ungulates in hot and arid environments because desert plants have low protein and water content. Consequently, desert ungulates have developed a number of remarkable morphological, physiological and behavioural adaptations.

Adaptations of ungulates towards desert life

Body size and heat dissipation

Ungulates living in desert environments are usually large-bodied. Therefore, they have a low surface to volume ratio. On the one hand, a large body reduces the rate at which core body temperature increases with increasing ambient temperature because of the relatively high thermal inertia (McNab, 1983). In addition, pelage thickness decreases with increasing body size, which may help dissipate heat by reducing the insulation capacity. On the other hand, a large body could make it difficult for ungulates to dissipate heat when facing hyperthermia or to find shade when vegetation cover is low (Louw & Seely, 1982). Large animals also require more energy for maintenance than smaller ones (Schmidt-Nielsen, 1979, Louw & Seely, 1982). Usually, desert-dwelling ungulates exhibit light to brownish pelage that reflects a large portion of solar radiation (Hofmeyr, 1985). In addition, some ungulates such as gemsbok antelopes possess long and highly vascularised horns, which facilitate dissipation of excess heat from their horns (Taylor, 1966).

Optimisation of digestion

To cope with the low digestibility and low water content of their forages, desert ungulates slow down their rate of digestion, thus facilitating nutrient uptake in their intestinal tract (Choshniak *et al.*, 1988). For example, grazing addax antelopes (*Addax nasomaculatus*) increase the fermentation of ingested grasses by reducing the food transit time through the rumen (Hummel *et al.*, 2008). But dehydration that might occur from heat and water shortage

may render digestion and nutrient uptake more difficult as it may increase saliva osmolarity and reduce saliva flow (Brosh *et al.*, 1986; Choshniak *et al.*, 1988; Hummel *et al.*, 2008).

Water conservation

Desert-dwelling ungulates might also respond to nutritional and water stress by reducing their mass-specific metabolic rate and, thus, total evaporative water loss. Arabian oryx (*Oryx leucoryx*) has been demonstrated to exhibit the lowest mass-specific water influx of all ungulates living in hot and dry environments (Ostrowski *et al.*, 2002). As free water is rare in arid to hyper-arid environments, ungulates may specifically mobilize fat reserves to produce oxidative metabolic water. For example, oxidative water may represent approximately 15% of the total water flux in Arabian oryx (Ostrowski *et al.*, 2002). To yield a positive water balance, many desert ungulates increase the urea concentration of their urine and decrease faecal water loss (Tracy & Walsberg, 2000; Ostrowsky *et al.*, 2002; 2006). At peak ambient temperature, many desert ungulates raise their body temperature above their homoeothermic level. This enables them to save water that would have else been used for evaporative cooling. The excess heat is then dissipated at night when temperatures fall. This adaptive heterothermy is mostly driven by water limitation and not by the inability to sustain constant core body temperatures (Ostrowski *et al.*, 2003; Hetem *et al.*, 2010). To prevent neuronal damage by adaptive heterothermy, blood flow towards the brain passes through a mesh of veins and arteries, the carotid rete, where it is cooled down by heat exchange with blood that returns from the nasal membranes, where temperature is reduced via evaporative cooling (Maloney *et al.*, 2002; Ostrowski *et al.*, 2002).

Behavioural responses to heat and drought

Besides morphological and physiological adaptations, desert-dwelling ungulates may also respond to increased temperature by adjusting their behaviour. Gemsbok and springbok may cope with high ambient temperatures by moving into the shade of vegetation. In the shadow, they often create small depression in the ground in which they lay down. This behaviour facilitates the conductance of excess body heat to the ground (Bigalke, 1972; Nagy & Knight, 1994; Ostrowsky *et al.*, 2002). During hot periods, ungulates shift their activity period into the cool night. This is particularly beneficial for the water budget of desert ungulates, since the water content of desert plants increases up to 40% of total mass at night (Schmidt-Nielsen, 1990; Nagy & Knight, 1994). Ungulates also adjust their body position to minimise their

exposure to sun and wind, thereby reducing the heat input via solar radiation by up to 60% (Berry *et al.*, 1984, Hofmeyr & Louw, 1987).

Diet and habitat use

Individuals inhabiting harsh environments might display different strategies in dietary and migratory behaviours to cope with shortage of potential food resources (Berger *et al.*, 2008). It is easy to understand that the survival of desert dwelling animals closely depends on the abundance of suitable food sources (Parker & Barbosa, 2009). However, the availability of such plant sources in arid environments might greatly vary over time and often in an unpredictable manner. Thus, when facing shortages of food resources, ungulates may have at least two options: either staying and broadening their diet to include less preferred forages, or moving towards less xeric environments where their preferred food resources are still available (Holdo *et al.*, 2009). However, the ability of ungulate individuals to shift their home range and integrate alternative food sources in their diets depends largely on their intrinsic degree of dietary specialisation, which is considered to be inversely related to body size (Bell, 1971; Jarman, 1974; Demment & van Soest, 1985; Hofmann, 1989). Thus, one might expect small antelopes to be more specialised in their diet than larger bodied ungulates, and may therefore be more willing to move to other areas than large antelopes when aridity increases and the availability of food resources declines.

Specialist vs. generalist feeder

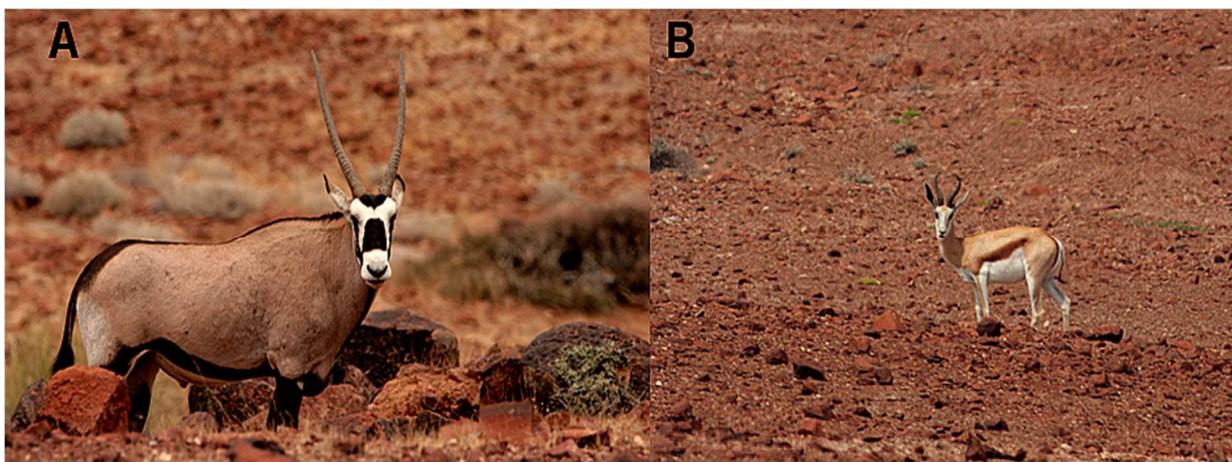
Owing to a small digestive tract with low food retention capacity and high metabolic rates small-bodied ungulates usually display relatively high dietary specialisation, since they cannot process forage of low nutrient values (e.g. dry grass) (Demment & van Soest, 1985; Hofmann, 1989; Nagy & Knight, 1994). For example, several species of small African duikers are specialised on highly nutritive and digestible items (Gagnon & Chew, 2000). However, some other small ruminant species specialise on a specific food source but broaden their diet when needed. Mixed feeders, such as springbok, include a wide variety of plants in their diet (grasses, shrubs and succulents). Their survival may not depend on the availability of a particular plant species and they may cope better with the shortage of one or more plant food sources than other specialist feeder (Van Zyl, 1965; Bigalke, 1972; Skinner & Louw 1996, Vorster, 1996; Stapelberg *et al.*, 2008).

Such dietary plasticity has also been observed in larger ungulates. White-tailed deer (*Odocoileus virginianus*) and historic populations of bison (*Bison antiquus*) showed flexible

feeding habits when their preferred food resource declined (Borgnia *et al.*, 2010; Lagory *et al.*, 1985; Rivals & Semprebon, 2011). Hence, plant source selectivity and dietary orientation might not only be defined by body size, but also by the quantitative availability of food resources in space and time. The ability of desert dwelling ungulates to use alternative food sources in an opportunistic way might be crucial for overcoming drastic changes in plant food sources in arid environments, and thus for survival. Yet, whether or not desert ungulates show this behaviour is by and large unknown.

Gemsbok and springbok: two model species with contrasting feeding habits

Gemsbok (Pic. 1A) and springbok (Pic. 1B) live at relatively high densities in the so-called Damaraland, one of the driest areas in the Kunene region of Namibia. Both species overlap largely in their geographical distribution in Southern Africa, but differ in dietary preferences (Gordon & Illius, 1996). Whereas springbok include a variety of shrubs, herbs and grasses in their diet (Nagy & Knight, 1994; Bergström & Skarpe, 1999), gemsbok are recorded as specialist grazers (Hypergrazer: Cerling *et al.*, 2003; Grazer: Ambrose & DeNiro, 1986). Grasses and shrubs differ in their content of secondary plant compounds and their morphology, making them suitable, in terms of food resource, only to those herbivores which are adapted to digest them. Accordingly, sympatric ungulate species that are exposed to the same environmental changes such as heat and drought may respond in different ways. By looking at stable isotope ratios on the plant and consumer level, I asked how gemsbok and springbok adjust their feeding habits and spatio-temporal movements to adverse and unpredictable ambient conditions.



Picture 1: A. gemsbok (*Oryx g. gazella*), B. springbok (*Antidorcas marsupialis*). Both species are pictured free-roaming in their natural habitat; Kunene Region, Namibia. *Credit photo: David Lehmann*

Stable isotopes as indicators of animal dietary preferences

Use of stable isotopes analyse in animal ecology

Over the past decades, stable isotopes of carbon and nitrogen have been increasingly used as tracers for dietary preferences, trophic positions and spatial movements (Summarized in Fry 2006, Hobson & Wassenaar, 2008). Light isotopes (^{12}C , ^{14}N) are more abundant in the environment than heavier isotopes of the same element (^{13}C , ^{15}N) (Dawson & Siegwolf, 2007). In ecological studies, researchers usually determine the ratio of heavy to light isotopes and refer to it as δ -notation, expressed as $\delta^{13}\text{C}$ in parts per mill (‰) difference between the sample and an international standard (e.g. Vienne Pee Dee Belemnite limestone for carbon and atmospheric N_2 for nitrogen; Dawson & Siegwolf, 2007).

Stable isotope ratios of animal tissues can provide accurate information on the relative contribution of isotopically contrasting food resources to the diet of animals (Ambrose & DeNiro, 1986). The underlying assumption of the isotopic approach in the study of animal ecology can be summarized as “you are what you eat ... \pm a few per mill”. This is because isotopes are assimilated into body tissue according to their ratio in the average diet of an animal. A prerequisite for isotopic studies is that habitats or food sources are isotopically contrasting. Desert plants differ in their stable carbon isotope ratios depending on their metabolic pathway of CO_2 fixation, which is either the C_4/CAM (grasses and euphorbia) or the C_3 (trees and shrubs) photosynthetic pathway (Tieszen *et al.*, 1979). Thus, stable isotope ratios in tissues of gemsboks and springboks should vary according to whether they consume grass (C_4 plant) or herbs (C_3 plant) or a combination of both, and should document seasonal changes in dietary preferences and potentially spatial movements. In addition, nitrogen isotope ratios in plant matter are indicative of regional patterns of aridity and environmental conditions (Sealy *et al.*, 1987; Cerling *et al.*, 2006). Tissues with different isotope retention times, i.e. tissues that differ in cellular turnover time may help answering questions on diet and water ingested within different retrospective time windows (Macko *et al.*, 1999). Metabolically active tissues, such as blood, liver or muscle (Chapter II), give integrated information on diet over the last weeks or months preceding tissue sampling. In contrast, metabolically inert tissues, such as keratinous hair or horn (Chapter III), contain information about the diet integrated at the time of tissue formation (Hobson & Wassenaar, 2008). Hence, it is possible to infer the dietary histories of gemsbok and springbok and to define their isotopic niches in the Kunene Region of Namibia based on isotopic δ -space by combining the isotopic signature of tissues with contrasting turnover-rates, such as fur, muscle and liver

(Chapter II) and as well investigating chronological isotopic variations within individuals using serial tail hair increments (Chapter III).

An isotopic niche is defined by the subset values of the overall isotopic composition of an individual's tissues in the δ -space of a given environment. The axes of the δ -space are the isotopic gradients of the stable isotopes ratio investigated (e.g. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) (Newsome *et al.*, 2007; Layman *et al.*, 2007; Schmidt *et al.*, 2007; Martínez del Río *et al.*, 2009), defining the degree of specialisation in isotope and diet used at the individual and species levels for both gemsbok and springbok. Martínez del Río and colleagues (2009) define an individual as an isotopic specialist, if tissues deposited at different times (e.g. distinct isotope turnover-rates in tissues or chronological increment of inert tissues such as tail hairs) have similar isotopic composition. If these tissues or sampled serial hair increments differ in isotopic composition, the individual occupies a generalist isotopic niche. Moreover, individuals can be dietary generalists but at the same time isotopic specialists, if they feed on the same resource mixture at all times (Martínez del Río *et al.*, 2009).

Characterizing isotopic niche width of communities and individuals

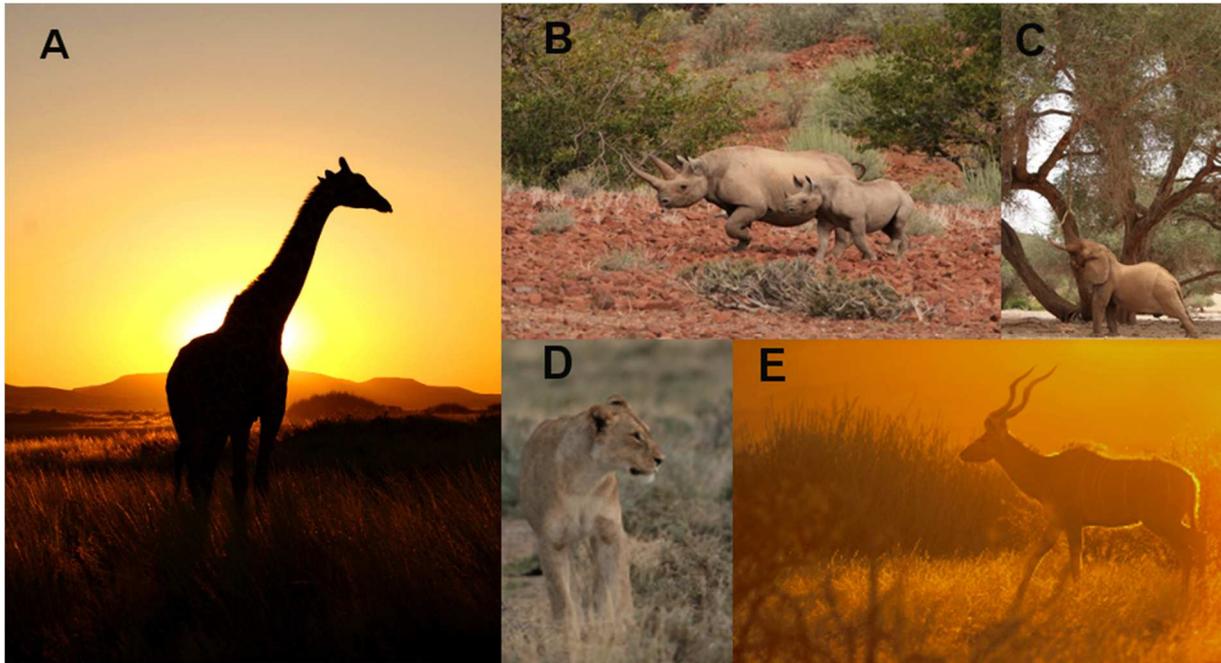
Although the use of stable isotope ratios to infer animal diet has become common, the development of appropriate statistical methods to accurately derivate community structure and isotopic niche width from these data is important. For example, Bayesian computation allows calculating metrics of isotopic ellipsoid niche at both species and individual levels (Layman *et al.*, 2007; Jackson *et al.*, 2011). These metrics describe the isotopic area (in $\%o^2$) and positions occupied by population species or individual in a given environmental isotopic space, and thus allow the statistical comparison of isotopic niche variations between and within species. Isotopic niche differences in width and position might occur between two sympatric animal species, such as springbok and gemsbok, subject to similar variations in plant food resources. Bayesian computation also allows quantifying variations in isotopic niche width between individuals of the same species, which is relevant since individual consumers may have different dietary preferences. Hence, using Bayesian standard ellipse to quantify the isotopic niche width and their overlaps of both population and individuals might help inferring different degree of isotopic specialization (Layman *et al.*, 2007; Jackson *et al.*, 2011). Further, this method accounts for uncertainty in the sampled data and corrects biases of low sample size, allowing robust comparison between data sets differing in sample sizes (Jackson *et al.*, 2011). In Chapter III, I directly compare the isotopic niche width between and within both gemsbok and springbok population and quantify their degrees of overlapping.

Aims of the study

In this thesis, I aimed to provide a better understanding of how ungulates survive in desert environments in particular when challenged by extreme and unpredictable fluctuations in the availability of their food resources and by prolonged periods of heat and drought. I have chosen two focal species that differ in size and feeding habit: gemsbok antelopes (*Oryx g. gazella*) are larger than springbok (*Antidorcas marsupialis*) and thought to feed more on grass. The study site in the Kunene Region of Namibia, formally called Damaraland area, is adjacent to one of the driest deserts on earth, the Namib. I first investigated variation in the consumption of plant food sources in space and time by using stable isotope analysis of both metabolically active and inert animal tissues, at the population (Chapter II) and individual level (Chapter III) of both species. I then investigated the movement patterns of gemsbok in relationship with plant primary productivity, habitat characteristics (i.e. plant types and assemblages) and topography, and estimated risk of predation by large predators as well as the variation of these characteristics in time, using both empirical assessment and satellite imageries and tracking animal movement using GPS collars (Chapter IV). Besides serving as an example of how ungulates are behaviourally adapted to desert environment, I also attempted to provide local human communities with fundamental knowledge on the ecology of two of their main socio-economic wildlife resources, which, if implemented in their sustainable management plan, would allow them to better manage their wildlife and reduce food sources competition with their livestock. Finally, understanding how both ungulate species adjust their feeding and spatial patterns to adverse and xeric environmental conditions may help, on a more general level, to predict the response of other ungulate species to desertification and global climate change.

Study site

Fieldwork took place in the Kunene Region in the north-western Namibia (Maps 1 & 2). In this arid environment, I selected two main field sites: the Torra Conservancy and the Palmwag Concession (Map 2). The Torra Conservancy is being managed by the local community that ensures development and sustainable use of natural resources. This conservancy is a pioneer in community-based wildlife resources management in Africa. It was registered as the first conservancy by the Ministry of Environment and Tourism of Namibia in 1998 and aims towards the sustainable use of its natural resources (NASCO). The Torra Conservancy consists of a territory of about 3,522 km², where 1,200 people live besides free roaming wildlife such as elephant (*Loxodonta Africana*), black rhinoceros (*Diceros bicornis bicornis*), lion



Picture 2: Some other charismatic inhabitants of the Kunene Region. A. giraffe (*Giraffa camelopardalis*), B. black rhinoceros (*Diceros bicornis bicornis*), C. elephant (*Loxodonta Africana*), D. lion (*Panthera leo*) and E. greater kudu (*Tragelaphus strepsiceros*). Credit photo: David Lehmann

(*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), brown and spotted hyena (*Hyaena brunnea*, *Crocuta crocuta*), giraffe (*Giraffa camelopardalis*), endemic Hartmann's mountain zebra (*Equus zebra hartmannae*), springbok, gemsbok and greater kudu (*Tragelaphus strepsiceros*) as well as small duikers such as steenbock (*Raphicerus campestris*) and klipspringer (*Oreotragus oreotragus*) (Pic. 2).

The human-wildlife conflict is high in this area; desertification has reduced the surface of fertile ground and livestock density steadily increases as a result of developing human communities, therefore increasing the competition for food sources between wild ungulates and livestock. The incomes of the conservancy arise from trophy hunting, tourism and hunting for meat. In 2011, the conservancy was assigned 800 springbok and 150 gemsbok for this specific year as consumptive quotas but actually only used 80 gemsbok and 260 springbok individuals for their own use (Direct communication from Torra Conservancy; NACSO 2011), out of populations estimated of around 5970 springbok and 1920 gemsbok (NASCO, 2011; Environmental Information Service Namibia, www.the-eis.com). During the course of my thesis I managed to join two communal hunts in 2011 and 2012 where I collected fresh tissues samples from both gemsbok and springbok.

Topographically, the Torra Conservancy rises from gravel plains close to sea level in the west to an escarpment of basalts in the east where altitudes can reach up to 1,600 metres. These

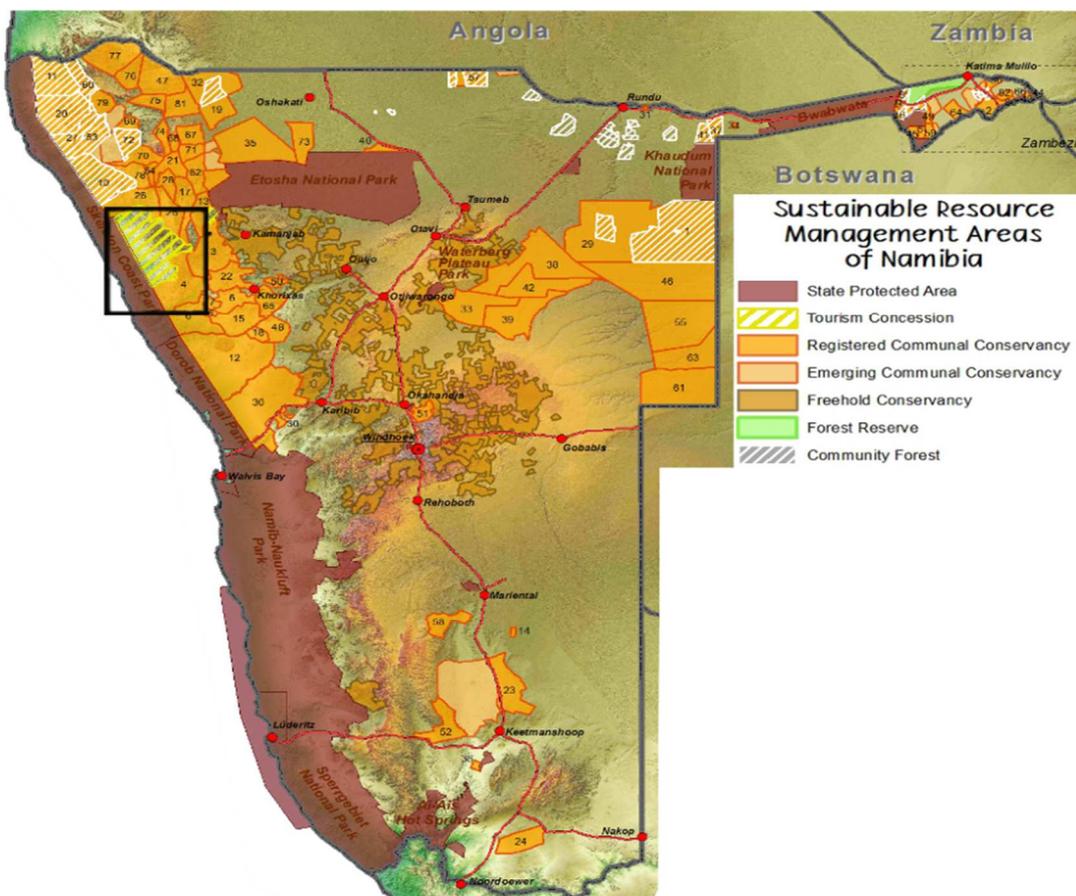
basalts underlie much of the conservancy, and were deposited during a series of volcanic eruptions which took place about 125 to 132 million years ago at the time South America and Africa split apart (Du Toit *et al.*, 1927; de Wit *et al.*, 2008). The red rocks distributed all over the landscape, giving its name to the Torra Conservancy (Torra meaning ‘red rock’ in Damara), named after the hard basalt layers of the Etendeka Mountains. The area is extremely dry, with annual average rainfall ranging from 150 mm along the hills in the east to just 50 millimetres along the Skeleton Coast (Digital Atlas of Namibia, 2002). Most rain usually falls during occasional thunderstorms in the late summer, between January and March (Digital Atlas of Namibia, 2002; Namibia Nature Foundation, 2009). However, rainfall can be extremely variable and unpredictable. The area thus experiences drastic variations in primary plant productivity within and across years, and often suffer prolonged period of drought (up to several years according to local knowledge, Namibia Nature Foundation, 2009; personal observations). The sparse vegetation cover and low height of most plants are largely a consequence of aridity, but plant growth is also limited by the scarcity of adequate substrate in most parts of the conservancy.

The plains are dominated by grass species such as *Stipagrostis sp.* and *Eriagrostis sp.* and by dense assemblage of endemic and poisonous *Euphorbia damarana* bushes. Important browse food sources such as *Petadilium spiniferum* or *Boescia foetida* are also found on plains (Digital Atlas of Namibia, 2002). Several paper-bark tree species characteristically grow on hill slopes and mountain plateaus (Digital Atlas of Namibia, 2002). Shallow drainage lines that feed into the ephemeral Springbok wasser and Huab rivers provide refuge for evergreen bushes such as *Cyperus marginatus* and the endemic *Welwitschia mirabilis*, (Digital Atlas of Namibia, 2002; NASCO, 2009). Relatively tall trees such as *Acacia sp.* and *Proboscis sp.* are rooted in deep sandy beds that hold moisture after flash floods (Namibia Nature Foundation, 2009).

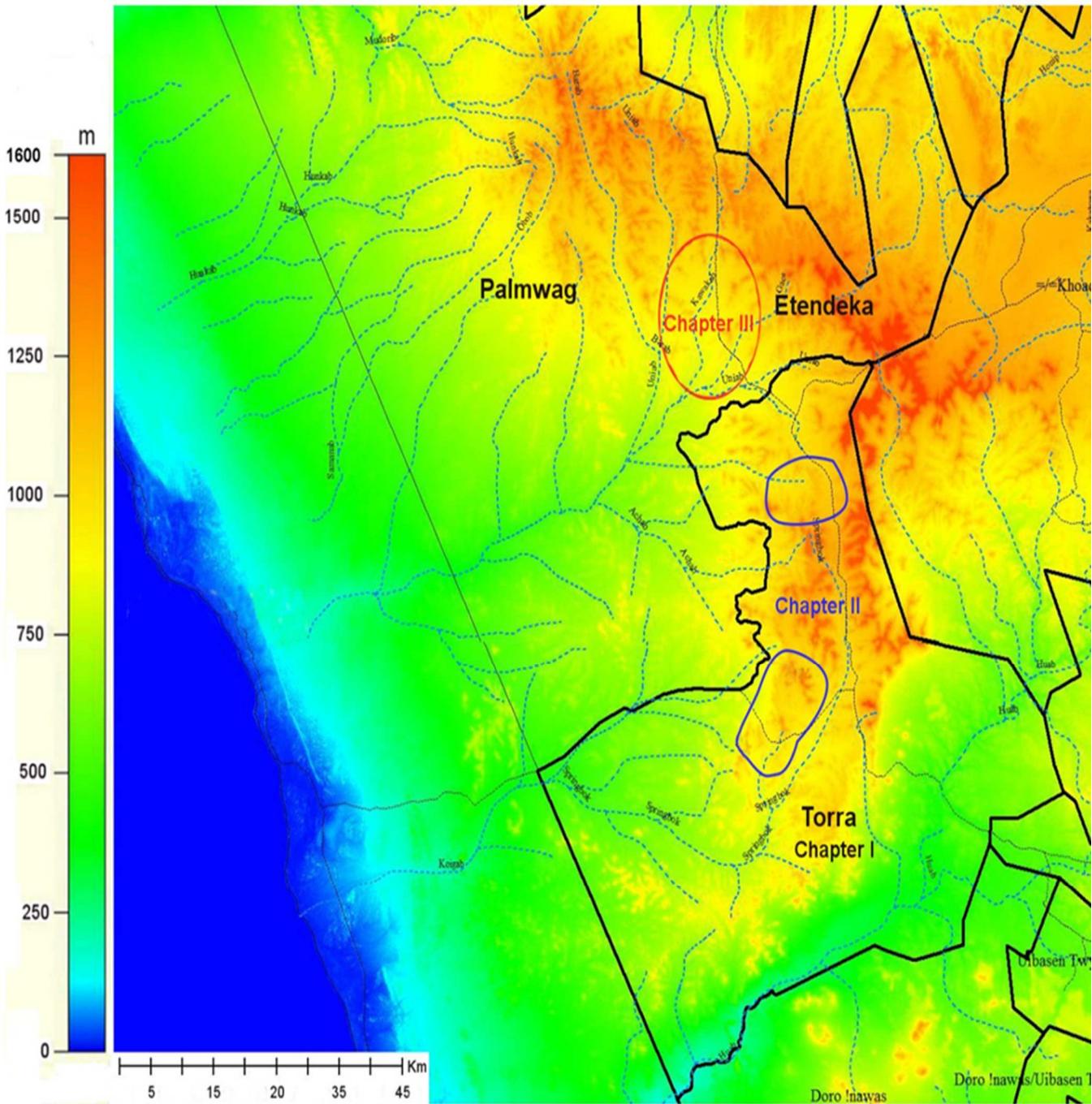
During extensive periods of fieldwork, I sampled all potential plant food sources of gemsbok and springbok for stable isotope analyses, across three different years with varying environmental conditions, such as rainfall and plant primary productivity, and across all major habitat types of the Torra Conservancy.

The Palmwag Concession is located north of the Torra Conservancy (19°52’54”S13°56’46”E) and includes 5,500 km² of territories where wildlife is not hunted, off road driving and grazing livestock not permitted. This reserve is owned by the surrounding conservancies but managed and operated by Wilderness Safaris Namibia. The ecosystem is very similar to the Torra Conservancy and consists of the Etendeka Mountains, rocky and gravel plains,

ephemeral riverbeds and deltas formed by the Uniab River. The annual rainfall ranges between 80 and 150 mm and the ambient temperature may reach up to 55°C during the hot dry season (Digital Atlas of Namibia, 2002). Vegetation ranges from open grassland to sparse savannahs and the primary plant productivity is highly variable across time and environmental conditions, but also often inexistent. In the Palmwag Concession, I equipped gemsbok individuals with GPS collars. I choose to perform this study in this protected are to decrease the probability of the collared gemsbok to be shot, since hunting is forbidden in the Palmwag concession. I also spent several months in the concession between 2010 and 2013, performing empirical assessment of plant communities, substrates, topography and estimating predation risk of gemsbok by large predators in each habitat types. For this study, I have developed tight and successful collaborations with the local community-based conservancies, the University of Namibia in Windhoek, the Wilderness Safaris Namibia that operates the Palmwag Concession and with the neighbouring Etendeka Concession.



Map1: Map of Namibia, including protected areas, conservancies and tourism concessions. The black rectangle delimits the study areas of my doctoral work in the Kunene Region of Namibia. The Palmwag concession (Yellow) and the Torra Conservancy (Orange). Modified from NACSO 2011; <http://www.nacso.org.na/>



Map 2: Detailed map of the study areas. Chapter I regarded the gemsbok and springbok populations of the entire Torra Conservancy (in black). Chapter II focused on individual gemsbok and springbok of the two delimited (in blue) areas of the Torra Conservancy. Chapter III only included individual gemsbok of the protected Palmwag concession (in red). Map built from topographic satellite imagery (ASTER GDEM https://lpdaac.usgs.gov/data_access)



Picture 3: Look out upon the Huab Valley in the Torra Conservancy. The three major habitat types (riverbed, open-field, and hillside) are well represented in this picture. *Credit photo: David Lehmann*



Picture 4: Coffee break at basecamp, near Aub River in the wilderness of the Palmwag concession. This picture was taken after a week spent in the bush performing vegetation survey and habitats characterization, in complete autonomy. *Credit photo: David Lehmann*

Outline of the study

The overall aim of this thesis was to gain information on the dietary plasticity of gemsbok and springbok at both population and individual levels, and to provide insights in spatio-temporal movement patterns during drought using gemsbok as a model species. The results of this study are presented in 3 manuscripts that comprise the following chapters:

Chapter II: Dietary plasticity of generalist and specialist ungulates in the Namibian desert: A stable isotopes approach

Desert ungulates live in adverse ecosystems where the abundance of potential food sources is largely variable and unpredictable through time. Nevertheless, ungulate density in such environment might be high, and the underlying dietary strategies allowing animals to survive and thrive in desert is still poorly known. In this study, I investigated how two ungulate species with contrasting feeding habits, grazing gemsbok and browsing springbok, respond to an increase in food availability during a pronounced rain period in the arid Kunene Region of Namibia as compared to drought periods. I used a stable isotope approach to delineate the feeding habits of these two ungulates across nineteen months. During the study period, I investigated two periods of drought with limited and scarce food availability for ungulates and an intermediate period with extreme rainfalls resulting in exceptional plant growth. I collected plant samples in the field and animal tissues at local communal hunts. In the isotopic space of my study area, I have documented thirteen isotopically distinct food sources and compared them to the isotopic range found in gemsbok and springbok. The results of the Bayesian stable isotopes mixing models inferred relatively high dietary plasticity in gemsbok, which fed on a mixture of plants, including more than 30% of C3 plants during drought periods, but almost exclusively on C4 and CAM plant types when food was plentiful. During drought periods, gemsbok diets may have also consisted of up to 25% of *Euphorbia damarana*; an endemic CAM plant that is rich in toxic secondary plant compounds. In contrast, results of the mixing model suggested that springbok were generalists, feeding on a higher proportion of C3 than C4/CAM plants, irrespective of environmental conditions. In this chapter, I was therefore able to illustrate two distinct dietary strategies in gemsbok and springbok which enable them to survive and coexist in the hostile Kunene arid ecosystem.

Chapter III: Individual variation of isotopic niches in grazing and browsing desert ungulates

Whereas in Chapter II, I described the dietary habits of the population of gemsbok and springbok roaming freely in the arid environment of the Torra Conservancy, in Chapter III, I investigated whether all individuals of each population have similar feeding preferences. It is not yet fully understood when and to what extent individuals changes their diet and, if they do so, if all individuals of a population occupy distinct or similar dietary niches. Thus, I studied the temporal variation in individual isotopic niche space in grazing gemsbok and predominantly browsing springbok. I used variation in stable carbon and nitrogen isotope ratios of tail hair increments as proxies for individual dietary plasticity. The results of the Bayesian standard isotopic ellipses computed from variations in stable isotopic compositions of individual tail hair increments suggested, and for the first time, that individual isotopic dietary niche segregated within these two desert ungulates species contrasting in their feeding habits. In this Chapter, I argue that isotopically distinct feeding preferences of individuals may reduce intra-species competition for food resources and, thus, may facilitate ungulates' survival in in such challenging arid ecosystems.

Chapter IV: Movements of desert dwelling gemsbok (*Oryx g. gazella*) in response to spatio-temporal variations in plant productivity

In Chapter II and III, I have investigated how ungulate populations and individuals cope with unpredictable variations in food sources availability. In this Chapter, I mainly focused on understanding how non-migratory desert ungulates spatially exploit their environment at a local scale in response to shortages in plant availability. In this study, I investigated the spatio-temporal variation of home ranges and habitat use of 8 gemsbok equipped with GPS collars. During the 2.5-years of this study, gemsbok did not migrate, but selected their habitat according to plant primary productivity and resource accessibility, topography and estimated risk of predation, ranked here by order of importance. I observed inter-individual variation in both home-range and habitat uses and argued that these differences reflect the individual

dietary preferences. The ability of gemsbok to exploit three interlacing and contrasting habitats at the local scale allow the efficient gathering of various food sources and thus avoid fitness cost associated with large spatial movements. This study also provided community-based wildlife management with important knowledge on gemsbok habitat preferences and may help create refuge habitats for gemsbok and other ungulates where hunting and grazing livestock are inadvisable.

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CHAPTER II

Dietary plasticity of generalist and specialist ungulates in the Namibian desert: A stable isotopes approach

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Abstract. Desert ungulates live in adverse ecosystems that are particularly sensitive to degradation and global climate change. Here, we asked how two ungulate species with contrasting feeding habits, grazing gemsbok (*Oryx g. gazella*) and browsing springbok (*Antidorcas marsupialis*); respond to an increase in food availability during a pronounced rain period. We used a stable isotope approach to delineate the feeding habits of these two ungulates in the arid Kunene Region of Namibia. Our nineteen months field investigation included two time periods of drought when food availability for ungulates was lowest and an intermediate period with extreme, unusual rainfalls. We documented thirteen isotopically distinct food sources in the isotopic space of the study area. Our results indicated a relatively high dietary plasticity of gemsbok, which fed on a mixture of plants, including more than 30% of C3 plants during drought periods, but almost exclusively on C4 and CAM plant types when food was plentiful. During drought periods, the inferred gemsbok diets also consisted of up to 25% of *Euphorbia damarana*; an endemic CAM plant that is rich in toxic secondary plant compounds. In contrast, springbok were generalists, feeding on a higher proportion of C3 than C4/CAM plants, irrespective of environmental conditions. Our results illustrate two dietary strategies in gemsbok and springbok which enable them to survive and coexist in the hostile Kunene arid ecosystem.

INTRODUCTION

Ungulate species have colonized a wide range of habitats worldwide with different and variable food resources. They even manage to inhabit areas of extreme environmental conditions such as dry savannahs and deserts [1, 2]. The survival of ungulates in these specific environments depends on the abundance of adequate food plants that offer sufficient nutrients for survival [3]. The availability of these resources often varies with time, and ungulates therefore may face challenges when undergoing a resource bottleneck. Largely, ungulates may rely on one of two strategies when facing reduced resource availability: either they stay and broaden their diet or they leave in search of their specialized, but temporarily restricted diet [4]. The use of these strategies depends, at least partly, on the intrinsic degree of dietary specialization, which is thought to be inversely related to body size [5, 6, 7, 8]. Following these predictions, small antelopes display pronounced dietary specificity with low tolerance to changes in selected food availability, whereas larger ungulates are more plastic in their feeding habits and thus dietary generalist.

Small-sized antelopes with high metabolic rates and a relatively short digestive tract with low food retention capacity tend to specialize on highly nutritive and digestible food items, since they are not well suited to internally process food sources of poor quality (e.g. dry forage) [7, 8, 9]. A high dietary specificity of small body-sized ungulates has been suggested for a variety of smaller ungulates. For example the African duikers *Cephalophus monticola* and *Cephalophus maxwelli* are specialized exclusively on a diet of fruits and stems which have low fibre content and high digestibility [10]. However, new studies have shown that some small ruminant species are able to significantly broaden their diet when needed. For example, the Cape grysbok (*Raphicerus melanotis*) is usually a highly selective browser feeding mostly on *Acacia* leaves [11]. Nevertheless this species may broaden its feeding behaviour temporarily to include grass and previously rejected plant species when Acacias were removed from the environment [12]. Other small ruminant species such as springbok (*Antidorcas marsupialis*) are mixed feeders and include grass, succulent plants and leaves of shrubs in their diet [13, 14, 15]. Additionally, they may adjust their diet in response to the availability of food sources with variable quality, preferring for example grass sprouts during the wet season [16, 17], and browsing predominantly on leaves of bushes when grass quality decreases [18].

This pattern of variable food selection has also been reported in a wide range of larger ungulates, which should not be constrained in their dietary choice by body size but by their quantitative requirements. Indeed, vicuña (*Vicugna vicugna*), white-tailed deer (*Odocoileus*

virginianus) and historic populations of bison (*Bison antiquus*) show dietary plasticity and generalization when their preferential food plants are scarce [19, 20, 21]). Gemsbok (*Oryx gazella gazella*) of the African savannah have been categorized as grazers or hyper-grazers, which implies that despite their large body size they specialize on grasses (up to 85% to 100% of their diet [22, 23]. Nonetheless, studies on gemsbok populations of the Kalahari show that they browse as well on succulent plants and also eat underground tubers (such as the so-called gemsbok cucumber *Acanthosicyos naudinianus*) during the dry season [24]. The ability to optionally use these alternative food sources may be crucial in arid environments although the high content of secondary plant compounds of these plants may hamper the digestive efficiency [8, 25, 26].

Here, we investigated the link between temporal environmental changes and feeding habits in two desert ungulate species. A knowledge about the plasticity of ungulate dietary strategies is especially important since climate change is expected to promote desertification [27], to cause loss in primary productivity and consequently to facilitate species extinction [28]. We therefore asked how antelope species respond to changes in food availability in semi-desert ecosystems.

Here, we quantitatively estimated the plasticity of feeding habits in gemsbok and springbok, which are the most abundant ungulates in the southern part of the arid Kunene region of Namibia. This environment is characterized by strong and unpredictable variation in resource availability [29]. We hypothesised that springbok and gemsbok rely on different food sources and display different patterns of resource use over time. As previous studies suggested that gemsbok are specialist grazers and springbok generalist feeders [1, 2], we predicted that springbok respond more strongly in their dietary niche than gemsbok when facing a shortage of food sources. We predicted that during drought years springbok include food items that have been avoided during periods of good primary productivity. We used stable carbon and nitrogen isotope ratios to provide quantitative information on the relative contribution of different food resources to the diet of gemsbok and springbok across nineteen months, corresponding to one and a half seasonal cycle, of variable resource availability [23, 30]. Many desert plants differ in their stable carbon isotope ratios depending on their metabolic pathway of CO₂ fixation, which is either the C₄ and CAM (grasses and *Euphorbia* respectively) or the C₃ (trees and shrubs) photosynthetic pathway [31, 32, 33]. Since stable isotope ratios in tissues of gemsbok and springbok vary according to whether they consume grass, euphorbia, leaves of trees and shrubs or a combination of them, we used a stable isotope approach in our study. In particular, we analysed stable carbon and nitrogen isotope

ratios to provide quantitative information on the relative contribution of food resources to the diet of gemsbok and springbok across three years of variable resource availability. The information gathered in this study might shed light on the mechanisms of resource partitioning between these two species and provide important knowledge for local wildlife management plans.

METHODS

Study site

This study took place from November 2010 to June 2012 in the southern part of the Kunene region of Namibia ($-20^{\circ} 12' 58.59''$ N, $+14^{\circ} 4' 6.24''$ E), a 3,500 km² area that is managed by the Torra Conservancy under the premise of sustainable use of natural resources. Gemsbok and springbok represent one of the main protein sources from wildlife for local communities. The local ecosystem consists of outcrops of basaltic mountain ranges, rocky and gravel plains, dry riverbeds and deltas formed by the ephemeral Huab and Springbok rivers. The annual precipitation usually ranges between 100 and 150 mm and the ambient temperature may reach up to 50°C during the dry season [29]. In 2010, the area received less than 80 mm of rain while in 2011 it received more than 500 mm (Torra conservancy, Damaraland Camp Weather station, [34]). In 2012, annual precipitation returned to less than 180 mm of rainfall (Torra conservancy, Namibian Weather Network [34]). Vegetation ranges from scarce open grasslands with bushes to plain rocky and/or sandy desert [29].

Study species

Gemsbok are large ungulates (180 to 240 kg) that have a geographical distribution from South Africa to northern Namibia and the southern parts of Botswana [2]. Springbok are smaller in body size (30 to 44 kg) and occur from the northwestern part of South Africa through the Kalahari Desert into Namibia and Botswana [2]. The distribution range of both gemsbok and springbok includes various habitats including savannahs, woodlands and deserts [2].

Sample collection

Our work was carried out under the Research Permits number 1534/2010 and 1676/2012 issued by the Ministry of Environment and Tourism of Namibia and has been approved by the Internal Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Re-search (IZW) of Berlin. Also, the Torra Conservancy had granted us the right to

conduct our research on the Torra Conservancy communal land, on behalf of the conservancy members.

We collected and analysed the stable isotope ratios of potential food sources and three types of tissues (blood, liver, muscle) from both species. We first collected plant and animal tissues samples from November 2010 to February 2011, which corresponded to a period of severe drought, labelled as “2010” in our study. We continued our sample collection from April 2011 to August 2011, time period associated with heavy rainfalls and increased primary productivity. This time period was labelled “2011” in our study. Our third fieldwork session was performed from February 2012 to June 2012, which corresponds to another drought period, labelled as “2012” in our study.

Collected plant species were selected according to the known diet of the springbok and gemsbok [2], direct observations or based on information from local game guards. We also collected samples from plants from which feeding observations by ungulate were not recorded and from plants of poor availabilities, scarcely distributed in the environment. From each plant, we collected about 2 g wet mass of leaves. Samples were dried in the sun before storing them in 1.5 ml Eppendorf vials. We obtained samples from the following species; Trees (C3): *Colophospermum mopane* (leaves; n = 26), *Boscia albitrunca* (leaves; n=26), *Faidherbia albida* (leaves) (n = 14), *Acacia erioloba* (leaves, flowers and pods; n = 27), *Acacia tortilis* (leaves, flowers and pods; n = 33), *Terminalia prunoides* (fruits and leaves; n = 22), *Tamarix usneoides* (leaves; n = 18); Bushes and shrubs (C3): *Calicorema capitata* (leaves and flowers; n = 14), *Boscia foetida* (leaves; n = 25), *Salvadora persica* (leaves; n = 13), *Cyperus marginatus* (leaves; n = 34), *Petalidium spiniferum* (leaves; n = 39), *Cadaba shroepelli* (leaves; n = 35), *Phaeoptilum spinosum* (leaves; n = 18); Grasses (C4): *Stipagrostis damarensis* (n = 12), other *Stipagrostis sp.* (n = 42) and *Eragrostis sp.* (n = 53) and succulent plants (CAM): *Euphorbia damarana* (fruits and branches; n = 26), *Salsola sp* (leaves; n = 11) and *Zygophyllum simplex* (leaves; n = 11). Additionally, we collected material from a few ephemeral bushes and flowers during the unusually heavy rainy season of 2011, including samples of *Petalidium halimoides* (n = 10), *Pegolettia oxydonta* (n = 6), *Geigeria alata* (n = 6), *Trichodesma africanum* (n = 6), *Lotononis sp.* (n = 6), *Cleome foliosa* (n = 6) and *Heliotropium oliveranum* (n = 6) as well as *Indigofera adenocarpa* (n = 6). Samples from the same species were collected from various habitats such as riverbeds, plains, valleys, hills and mountain slopes to cover most of the important habitats of the area in which gemsbok and springbok populations lived. In total, we collected 551 plant samples from 29 species.

Tissues of springbok and gemsbok (herein after referred to as consumer tissues or

materials) were collected during the communal hunting of the Torra community-based conservancy or from fresh carcasses found in the field. Animals were not killed for the purpose of this study; we were granted the right to collect samples from hunt products by the Torra Conservancy. Under Namibia's Community Based Natural Resource Management Program [35], conservancies are given annual quotas to kill selected mammals as a source of revenue for community projects and food to households. During the study period, we collected samples (2 g muscle tissue, 2 g liver tissue and 1 ml blood) from 56 gemsbok and 55 springbok individuals. From gemsbok, we collected samples from 6 males and 3 females in 2010, from 18 males and 20 females in 2011 and from 4 males and 5 females in 2012. From springbok, we collected samples from 2 males and 4 females in 2010, from 17 males and 26 females in 2011 and from 4 males and 2 females in 2012. All samples were dried in the sun and then stored in 1.5 ml plastic vials. Plant and tissue samples were shipped to the stable isotope laboratory at the Leibniz Institute for Zoo and Wildlife Research in Berlin, Germany. In the laboratory, all samples were washed with distilled water, dried in an oven (Heraeus Function Lab, Thermo Electron Corporation, 63505 Langensbold, Germany) until constant mass, and then powdered using a mortar grinder (RETSCH GmbH milling machine). An aliquot sample of 1.5 and 2 mg and 0.3-0.4 mg, for plant and consumer materials respectively were loaded into tin capsules (COSTECH Analytical Inc.).

Samples were combusted and the resultant gases (N_2 and CO_2) were sequentially measured in a CE 1110 elemental analyzer connected via a continuous flow system to a Thermo Finnigan Delta Plus isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany). The sample isotope ratios were compared with international gas standards (USGS-24 and IAEA-N1) [36]. Isotope ratios were expressed in the δ notation in parts per thousand (‰) [37]. We used stable carbon isotope ratio of Vienna Pee Dee Belemnite limestone and the nitrogen isotope ratio of air as reference. The precision of measurements was better than 0.1‰ (one standard deviation) for both elements.

Statistical analysis

To delineate the feeding habits of gemsbok and springbok, we used isotope mixing models that included information about $\delta^{13}C$ and $\delta^{15}N$ for both consumer and food material [38, 39, 40]. We also controlled for variable concentrations of C and N in focal plants [41, 42, 43, 44, 45]. The use of stable isotopic techniques to study animal diets requires a priori estimates of isotope discrimination within the tissues of interest ($\Delta^{13}C$ and $\Delta^{15}N$, also called discrimination factors), which represent the differences in isotopic composition between

animal tissues and the animals' diet. Since we did not know the species-specific discrimination factors for our study species, we referred to discrimination factors for blood, liver and muscle of mammalian species according to Caut and colleagues [46] for blood and liver, and to the work of Sutoh [47] and Codron and colleagues [38] for muscle. Hence, we corrected raw stable isotopic ratios of carbon and nitrogen of blood by -1.3 ‰ and 2.7 ‰, of liver by -0.69 ‰ and 3.3 ‰, of muscle by 1.5 ‰ and 2.9‰ ($\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$, respectively). We used the Monte Carlo Mapped Power (MCMP) isotope mixing models from the package SIAR version 4.1.3 [48] of the free statistical software R (R Development Core Team, 2010) to assess the relative contribution of plant resources to the diet of our two study species. Furthermore, we report the estimated proportions of food sources to the gemsbok and springbok diets given by the most likely source mixture solutions calculated by the Bayesian isotope mixing models [39, 43, 49]. The range of variation in ‰ was sufficiently high to warrant a high resolution in the estimate of the plants' relative contribution to the overall diet of gemsbok and springbok, e.g. > 10 ‰ in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Fig. 2) [50]. We selected *a priori* eleven plant groups as potential food sources and categorized them according to their photosynthetic pathway and their similarity or apparent differences in stable carbon and nitrogen isotope ratios. The potential food sources were clustered as followed: “*Stipagrostis*” (n = 54) and “Grass” (n = 53) for the C4 plant type; “*Euphorbia*” (n = 26) and “Other succulents” (n = 22) for the CAM plant group and “*Calicorema*” (n = 14), “Weed & others” (n = 14), “Shrub” (n = 78), “Tree” (n = 52), “*Boscia*” (n = 16), “*Salvadora*” (n = 13), “*Cyperus*” (n = 27) for the C3 plant group, which summed up to 369 plant samples used.

Since we sampled plant species or plant groups during three field trips over a period of nineteen months in the same environment, we performed a MANOVA, including “year” as fixed factor, for C3, C4 and CAM plant categories separately, to assess whether the isotopic composition of each clustered food resources differed between years and between them. We then performed a pairwise comparison MANOVA, excluding the year of sampling as co-parameter and including plant groups as factor, to test whether these defined groups were isotopically different.

Using MANOVA, with “year” included as fixed factor, we tested whether the isotopic composition of the two species differed and whether it varied among years. We performed Mann Whitney pairwise comparisons to delineate between the potential effects of the different years of sampling on the mean tissues stable carbon and nitrogen isotopic compositions of gemsbok and springbok.

RESULTS

Plant stable isotope composition

In general, $\delta^{13}\text{C}$ of plants followed a bimodal distribution, consistent with the isotopic contrast between C3, C4 and CAM plants (Table 1). $\delta^{15}\text{N}$ values were more evenly distributed (Table 1). Stable carbon and nitrogen isotope ratios of potential feeding plants with a C3 photosynthetic pathway did not differ among years ($F_{2,203} = 0.37$; Pillai = 0.007; $p = 0.83$) but differed between a priori defined plant categories ($F_{6,203} = 19.6$; Pillai = 0.73; $p < 0.001$). These differences were consistent over years ($F_{11,203} = 2.9$; Pillai = 0.27; $p < 0.001$). We therefore pooled data of different years for each element and plant category in this C3 plant group.

We observed that “*Boscia*” and “*Salvadora*” had similar isotopic signatures ($F_{1,35} = 0.66$; Pillai = 0.037; $p = 0.52$). “*Boscia*” and “*Salvadora*” also shared a similar isotopic signature with “Weed & others” ($F_{1,37} = 0.06$; Pillai = 0.0033; $p = 0.94$ and $F_{1,26} = 0.19$; Pillai = 0.015; $p = 0.82$; respectively). Stable isotope ratios of the categories “Tree” and “Shrub” were similar ($F_{1,140} = 2.65$; Pillai = 0.037; $p = 0.073$). “*Boscia*” and “Tree” differed in their isotopic composition ($F_{1,85} = 5.33$; Pillai = 0.11; $p = 0.0066$). Moreover, “Tree” differed from “*Salvadora*” ($F_{1,74} = 5.37$; Pillai = 0.13; $p = 0.0066$) and “Weed & others” ($F_{1,101} = 14.45$; Pillai = 0.22; $p < 0.001$). “*Boscia*” differed from “Shrub” ($F_{1,76} = 4.56$; Pillai = 0.11; $p = 0.013$). Hence, we grouped “*Boscia*”, “*Salvadora*” and “Weed & others” in the category “C3a” ($n = 43$) and “Shrub” and “Tree” in the category “C3b” ($n = 130$). Following this, the isotopic mixture of “C3a” differed from “C3b” ($F_{1,192} = 21.11$; Pillai = 0.18; $p < 0.001$), from “*Calicorema*” ($F_{1,64} = 15.68$; Pillai = 0.33; $p < 0.001$) and “*Cyperus*” ($F_{1,65} = 33.7$; Pillai = 0.33; $p < 0.001$). “C3b” also formed an independent cluster from “*Calicorema*” ($F_{1,154} = 32.8$; Pillai = 0.3; $p < 0.001$) and “*Cyperus*” ($F_{1,155} = 90.47$; Pillai = 0.54; $p < 0.001$). Lastly, “*Calicorema*” and “*Cyperus*” were found to be significantly different ($F_{1,27} = 12.24$; Pillai = 0.48; $p < 0.001$) (Fig.1).

Our MANOVA analysis revealed that stable carbon and / or nitrogen isotope ratios of C4 potential plant sources differed between years ($F_{2,143} = 3.47$; Pillai = 0.092; $p = 0.009$) and between a priori defined plant categories ($F_{3,143} = 22.49$; Pillai = 0.64; $p < 0.001$). Our analysis indicated that these differences were consistent over years ($F_{6,143} = 2.43$; Pillai = 0.18; $p = 0.005$). We therefore performed MANOVA pair-wise comparisons to test if these C4 and CAM defined groups were isotopically different within years. Moreover, when comparing C4 and CAM plant categories for 2010, we found that “*Stipagrostis*” had a similar isotopic composition compared with “Other succulents” ($F_{1,29} = 0.14$; Pillai = 0.010; $p = 0.86$)

(Fig. 1A). Consequently, we pooled these two potential food sources as “C4a1” (n =31) and recalculated our model (Fig. 1A). According to this analysis, “C4a1” differed from “Grass” ($F_{1,45} = 9.50$; Pillai = 0.30; $p = 0.0004$) and “*Euphorbia*” ($F_{1,44} = 5.05$; Pillai = 0.19; p -value = 0.011). “*Euphorbia*” and “Grass” also differed from each other ($F_{1,29} = 7.82$; Pillai = 0.35; $p = 0.002$) (Fig. 1A).. For 2011, we found that “*Stipagrostis*” had a similar isotopic composition with “Other succulents” ($F_{1,14} = 3.40$; Pillai = 0.34 $p = 0.065$) and that ”*Euphorbia*” and “Grass” also shared similar isotopic compositions. Consequently, we pooled “*Stipagrostis*” and “other succulents” potential food sources as “C4a2” (n = 16) and “*Euphorbia*” and “Grass” as “C4b2” (n = 19). Plants of the category “C4a2” differed from those of “C4b2” ($F_{1,33} = 62.85$; Pillai = 0.79; $p < 0.0001$) (Fig. 1B). In 2012, “*Stipagrostis*” differed from “Other succulents” ($F_{1,20} = 4.56$; Pillai = 0.32 $p = 0.024$), from “Grass” ($F_{1,40} = 25.68$; Pillai = 0.56; $p < 0.001$) and “*Euphorbia*” ($F_{1,30} = 12.75$; Pillai = 0.46; $p = 0.00010$). The isotopic composition of “Grass” differed also from “Other succulents” ($F_{1,24} = 21.30$; Pillai = 0.64; $p < 0.0001$) and from “*Euphorbia*” ($F_{1,34} = 23.13$; Pillai = 0.58; $p < 0.0001$). “Other succulents” and “*Euphorbia*” differed from each other as well ($F_{1,14} = 27.60$; Pillai = 0.80; $p < 0.0001$) (Fig. 1C).

To summarize, categories “C3a”, “C3b”, “*Calicorema*”, “*Cyperus*” and “C4a1”, “Grass1”, “*Euphorbia*1” (“2010”; Fig. 1A). “C4a2” and “C4b2” (“2011”; Fig. 1B) and “*Stipagrostis*3”, “Grass3”, “Other succulents3” and “*Euphorbia*3” (“2012”; Fig. 1C) differed significantly in their mean stable carbon and nitrogen isotopes ratios (Table 1). Thus, we documented thirteen resources with distinct mean stable carbon and / or nitrogen isotopes values (Table 1; Fig. 1). Mean values and standard deviations for stable isotope ratios were used in our stable isotope mixing models (Table 1).

Isotopic composition of consumer tissue

The mean isotopic mixtures of collected tissues from gemsbok and springbok varied among years ($F_{2,105} = 5.42$; Pillai = 0.48; $p < 0.0001$; Fig. 2). Gemsbok and springbok differed in their respective isotopic signatures ($F_{1,105} = 250.92$; Pillai = 0.94; $p < 0.0001$; Fig. 1 & 2) and this difference was consistent over years ($F_{2,105} = 5.1$; Pillai = 0.46; $p < 0.0001$; Fig. 1 & 2).

Results of our study showed that the mean stable carbon isotope ratio of gemsbok tissues differed between 2010 and 2011 ($W = 282$; $p = 0.0028$; Fig. 2 A), between 2010 and 2012 ($W = 69$; $p = 0.0013$; Fig. 2A) but not between 2011 and 2012 ($W = 157$; $p = 0.72$; Fig. 2A). Data analysis further indicated that the mean nitrogen isotope ratios of gemsbok did not differ

between 2010 and 2011 ($W = 142$; $p = 0.45$ Fig. 2B), or between 2010 and 2012 ($W = 38$; $p = 0.86$; Fig. 2B) or between 2011 and 2012 ($W = 176$; $p = 0.91$; Fig. 2B). With respect to the springbok population, our model revealed that the mean stable carbon isotope ratios of the three tissues (blood, liver and muscle) differed between 2010 and 2012 ($W = 33$; $p = 0.015$), and between 2011 and 2012 ($W = 195$; $p = 0.043$), but not between 2010 and 2011 ($W = 163$; $p = 0.31$). Moreover, mean values of nitrogen stable isotope ratios differed between 2010 and 2011 ($W = 245$; $p < 0.0001$), between 2010 and 2012 ($W = 5$; $p < 0.041$) as well as between 2011 and 2012 ($W = 0$, $p < 0.0001$). Simultaneously, we observed a large range of deviating isotopic values within each distinct gemsbok population (Fig 2A, 2B). Accordingly, we calculated mixing models for both species and for each year separately instead of pooling isotopically similar data from 2011 and 2012.

Relative contribution of potential food sources to the animal diet

Using isotopic mixed models (SIAR) for each of the collection years, we estimated the relative contribution of the major food sources to the diets of gemsbok (Fig. 3 A, B & C) and springbok (Fig. 3E; 3F; 3G). For gemsbok, the best model explained 90% of the variation in stable isotope ratios. This model suggested that gemsbok fed on average on $68 \pm 21.7\%$ of C4/CAM and on $21 \pm 14.2\%$ of C3 plants (Fig. 4 A). Our best model for springbok explained 96% of the variation in stable isotope ratios. According to this analysis, springbok included $65 \pm 8\%$ C3 and $29 \pm 1.5\%$ C4/CAM plants in their diet (Fig. 4 B) (Mean \pm SD of the three year mode for each species). However, our results regarding gemsbok indicate a shift in food resource utilization between dry and wet years. Gemsbok diet included 93% C4/CAM and 5% C3 plants sources in 2011, whereas the diets of 2010 and 2011 were more balanced with respect to the relative contributions of plant types (Fig. 3 A, B & C; Fig.4 A). Our data also suggest that springbok diets were less variable than those of gemsbok. Indeed, the pattern of resource utilization for springbok did not change from wet to dry years (Fig. 4 B). Our model revealed that the isotopic signature of springbok tissues matched a broad range of plant, with a constant mixed use of C3 and C4 / CAM sources and with a preference for C3 plants.

DISCUSSION

We studied the effect of increased food availability following an intense rain period on the feeding habits of gemsbok and springbok in the arid Kunene region of Namibia. We found that (1) the stable isotopic compositions of C4 and CAM plant sources varied at a local and restricted geographical scale, between years of extreme drought and exceptional rainfall.

Further, (2) stable isotope ratios in consumer tissues differed between gemsbok and springbok and respective isotopic compositions of these tissues varied annually according to resource availability. In addition, (3) annual changes reflected the severity of the drought. Lastly, the study indicated that (4) gemsbok were flexible in their diet but specialist feeders when preferential food resources were available. In contrast, springbok were constant generalist feeders. In the next paragraphs, we discuss each finding in detail.

Plant isotopic compositions

The stable isotopic ratios of C4/CAM plants categories varied between years of extreme drought and the intermediate year of unusual rainfall at a local scale. Similar variations in isotopic compositions of plant species have been previously recorded at a much larger spatial scale, encompassing environments with different precipitation patterns [33, 51, 52, 53, 54, 55]. In our study, the variations in C4/CAM plant isotopic signatures were possibly related to the fluctuations in rainfall intensity during the study period. The observed variations in plant isotope compositions were mostly related to variation in $\delta^{15}\text{N}$ of C4/CAM plants, since $\delta^{13}\text{C}$ values of C4 plants are not known to correlate with water availability (e.g. the extent of precipitation) [52, 53]. The large range of ^{15}N enrichments in plant matter might be related to varying levels of aridity. Also, $\delta^{15}\text{N}$ might differ between C4/CAM plant species [55, 56, 57, 58]. In our study, we also showed that the perennial *Stipagrostis sp.* (including the endemic *Stipagrostis damarensis*) were enriched in ^{15}N compared with less resistant, more ephemeral grass species such as *Eragrostis sp.* This might reflect the fact that *Stipagrostis* is better adapted to grow during relatively dry conditions [54, 55, 56, 58]. Using a combination of *a priori* categories that were based on knowledge and *post hoc* categories that were based on statistical criteria [42, 44], we defined C4/CAM plants categories for each year of the study period. In contrast to C4 and CAM plants, we did not record any inter-annual variations in C3 plant isotope compositions. On the regional scale, C3 plants of arid environment exhibited higher $\delta^{15}\text{N}$ than C3 vegetation of wetter areas [52, 57, 58, 59]. Since we subsumed several species in the various C3 plant categories, it is possible that the resulting higher variation in stable isotope ratios may have obscured inter-annual differences in isotope compositions for the C3 plant categories [52, 53, 55]. Moreover, intra-specific variation in isotopic composition might have also occurred between individuals collected from different micro-habitats, such as river beds, rocky plains or mountain slopes [60, 61]. Yet, we could not control for these effects in our data analysis because the number of putative interfering factors was large in relation to the sample size of our study.

Animal tissues compositions and inferred diets

Long-term climate data confirmed that the Torra conservancy of the Kunene region faced a five year drought that ended in early 2011 (Torra Conservancy, Namibian Weather Network [34], Damaraland Camp Weather station). Prior to March 2011, the local ecosystem received only little rain (< 80 mm per year) and temperatures reached up to 50°C at sun-exposed places. During such conditions, only a few patchily distributed and dry perennial grasses persist above ground and are thus accessible to ungulates. According to the variation in ¹³C enrichment in animal tissues over the nineteen months study period, gemsbok included more plant resources during the dry than during the wet years. The gemsbok population of the Torra conservancy used leaves from perennial bushes such as *Boscia foetida*, *Calicorema capitata*, *Salvadora persica* but seemed to rely more on the resistant evergreen *Cyperus marginatus*. However, the inferred diet of gemsbok included mostly C4/CAM plants with a predominance of *Euphorbia damarana* and a mixture of high ¹⁵N grasses and succulent plants. Succulent plants are well adjusted to adverse conditions [62] and may represent a useful resource for ungulates during dry periods, because they are rich in water [24]. Yet, our study is the first to demonstrate the significant use of succulent plants by gemsbok (up to 40% of the overall diet), which may explain why gemsboks are relatively independent from drinking water during extended periods of drought. Most interestingly, gemsbok predominantly fed on the evergreen *Euphorbia damarana* during the dry years. This euphorbia is highly toxic and endemic to our study area [63]. Other *Euphorbia* species are used by other herbivores as well, such as browsing Kudu *Tragelaphus strepsiceros* [64], black rhinoceros *Diceros bicornis bicornis* [65] or small antelopes [66] but have never been documented to be utilized by an ungulate that is traditionally considered a grazer. Hence, our result suggests that the gemsbok population of the Kunene region may have evolved physiological abilities that allow them to process or tolerate the highly toxic secondary compounds of *Euphorbia damarana* and consequently to benefit from its high water and nutritious content. In 2011, during our second study period, the local ecosystem received unusually heavy rainfall (>500 mm within two months; Torra conservancy, Damaraland Camp Weather station, [34]). As a consequence, we observed a large increase in flowering perennial and ephemeral grasses with high and low ¹⁵N values; respectively, which were almost uniformly distributed across various habitats of our study area. During this time, gemsbok consumed these available and relatively easily palatable plants, an observation that is in agreement with earlier studies [67, 68]. However, during the rainy year, gemsbok did not include *Euphorbia damarana* in their diet. Instead,

they seemed to feed on a mixture of grasses and succulents.

In 2012, when rainfall decreased in intensity by more than half, we observed an increase in ^{13}C enrichment in the gemsbok tissues. From this, our stable isotope mixing model inferred an increased contribution of *Euphorbia damarana* and succulent plants to the gemsbok diet. Our stable isotope mixing model suggested an intermediate use of C4/CAM and C3 plants as food, meaning that although animals are using both resource types, their diets are biased toward C4 and CAM plants. The evergreen *Cyperus marginatus* as well as *Calicorema capitata* and other perennial shrubs such as *Boscia foetida* and *Salvadora persica* were used as food; probably in response to the shortage in *Stipagrostis sp.* and low ^{15}N , less resistant grasses. Similar to 2010, *Euphorbia damarana* represented one of the most utilized food items for gemsbok.

The diet of springbok was more constant over the nineteen months of our study period, with fewer variations in C3 versus C4/CAM resource contributions between years. However, we observed an enrichment of ^{13}C and a depletion of ^{15}N in the mean isotope tissue compositions between 2010 and 2011. This can be explained by a dietary switch from *Cyperus marginatus* / *Calicorema capitata* mixture in 2010 to plants of the category C3b (shrubs & trees) in 2011. The depletion of springbok tissue in ^{15}N during 2011 could be explained by the much larger proportion of plants from the categories “C4a2” (*Stipagrostis sp.* & succulent plants) and “C4b2” (low ^{15}N grasses & *Euphorbia damarana*) in the diet of springbok. Both C4 and CAM categories had lower $\delta^{15}\text{N}$ values in contrast to *Calicorema capitata* and *Cyperus marginatus* food sources. In 2012, we observed that springbok tissues were enriched in ^{13}C and depleted in ^{15}N compared to 2010 and 2011. This indicated the combined and predominant use of *Cyperus marginatus*, *Calicorema capitata*, C3a and C3b food source categories as grasses availability decreased.

In this study, we demonstrated a high dietary plasticity of gemsbok during times of fluctuating primary productivity and water availability. Indeed, the gemsbok populations in our study area ingested a broad range of plants, including mostly C3 and C4/CAM plants during years of extremely low rainfall (2010 and 2012) but specialized on grasses during the year of exceptional heavy rainfall (2011) with high primary productivity. Hence, the reduced availability of grass plant matter during prolonged dry periods clearly led gemsbok to supplement their diet with alternative food sources. Contrary to our predictions, gemsbok was able to successfully expand their dietary niche when needed and thus did not move away from our study area. We also observed a large range of deviating isotopic values in stable isotope ratios for gemsbok, possibly suggesting some individual feeding preferences or movements

on a larger scale. As aridity increased and food resource availability decreased, animals might have travelled excessively and avoided aggregations [69]. Consequently, individuals from the same population might have visited different habitats with contrasting isotopic baselines [69, 70]. Individuals of the same population may have therefore specialized on a specific food mixture during the drought period in order to reduce intra-specific competition. Since sample sizes were low for animal tissues in 2010 and 2012, we were not able to elucidate better the underlying causes for isotopic variation within a given year. Hence, further studies, including a larger number of samples per individual over an extended lapse of the animal lifetime are needed to explicitly document this potential phenomenon of individual isotopic specialization. Springbok were mixed, intermediate feeders of C3 plants. However, the important shift of their mean tissues isotopic composition from one year to another, in conjunction with the small standard deviation of the overall C3, C4 and CAM resources used revealed a lower dietary plasticity in response to changes in precipitation patterns. Additionally, the smaller range of deviating isotopic values implies that individuals of the local population were mostly feeding on the same mixture of plants. In contrast to our expectation, springbok seem to have a lower dietary plasticity than gemsbok possibly for the simple reason that they might not need it.

In this study we observed distinct dietary strategies in two ungulate species with different body size. Gemsbok and springbok preferred different food sources at any time of our study period and do not necessarily overlap in resource use. This mechanism of resource partitioning may facilitate the coexistences of these two ungulate species [71]. Moreover gemsbok might facilitate the access to high quality grasses during increased primary productivity by cropping off dried plants, allowing springbok to easily access low height young green sprouts, which in turn stimulate plants to grow faster and higher [72, 73, 74]. Possibly gemsbok are then rewarded with a freshly grown plant source with adequate palatable height. To conclude, we inferred from stable isotope ratios of plants and animal tissues the contrasted diets of gemsbok and springbok in the arid Kunene environment. We successfully demonstrated a radical shift in gemsbok diet between years of different precipitation rhythms, while springbok diet remained constant, but intrinsically varied.

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Table 1: Summary of the Mean \pm s.d. values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for thirteen food sources.

Source (n=369)	Type	"Year"	$\delta^{13}\text{C}$ (Mean \pm s.d.) (‰)	$\delta^{15}\text{N}$ (Mean \pm s.d.) (‰)
C3a (n=43)	C3	2010, 11 & 12	-25.6 \pm 2.2	11.5 \pm 4.8
C3b (n=130)	C3	2010, 11 & 12	-25.9 \pm 1.9	7.8 \pm 3.9
<i>Calicorema</i> (n=14)	C3	2010, 11 & 12	-21.4 \pm 2.2	13.1 \pm 4.5
<i>Cyperus</i> (n=27)	C3	2010, 11 & 12	-26.5 \pm 3.3	20.8 \pm 6.9
C4a1 (n=31)	55% C4 - 45% CAM	2010	-14 \pm 1.8	9.3 \pm 1.8
Grass1 (n=16)	C4	2010	-14 \pm 1	4.3 \pm 1.2
<i>Euphorbia</i> 1 (n=15)	CAM	2010	-12.9 \pm 1.7	7 \pm 1.1
C4a2 (n=16)	56% C4 - 44% CAM	2011	-14.1 \pm 1.7	13.7 \pm 1.3
C4b2 (n=19)	84% C4 - 16% CAM	2011	-13.9 \pm 0.6	4.2 \pm 0.7
Stipagrostis3 (n=19)	C4	2012	-14.1 \pm 0.6	8.2 \pm 1.2
Other succulents3 (n=3)	CAM	2012	-14.1 \pm 1.5	13 \pm 5.4
Grass3 (n=23)	C4	2012	-14.0 \pm 0.9	4.1 \pm 1.1
<i>Euphorbia</i> 3 (n=13)	CAM	2012	-12.9 \pm 0.7	7.4 \pm 1

FIGURE CAPTIONS

Figure 1: Isotopic projections along the nitrogen and carbon axes (all in delta notation) of the thirteen major potential food sources (Mean; 95%CI) in A) 2010, B) 2011 and C) 2012 plotted with the mean values of the three metabolically active tissues (blood, liver and muscle) of gemsbok and springbok sampled in A) 2010, B) 2011 and C) 2012.

Figure 2: Mean (\pm s.d) of the yearly mean stable carbon isotope tissue composition of A gemsbok and C springbok. B and D represent the yearly mean nitrogen isotope composition of gemsbok and springbok tissues, respectively. The levels of significant differences are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$)

Figure 3: Relative contribution of the potential food sources to the diets of gemsbok (A,B,C) and springbok (D, E, F) , as determined by our SIAR isotope mixing model relative to the mean composition of the three metabolically active tissues analysed (blood, liver, muscle) for 2010 (A and D); 2011 (B and E) and 2012 (C and F). The boxplots show the relative proportions of each food source with 95% (dark grey), 75%, 25% and 5% (lightest grey) credibility intervals.

Figure 4: : Relative contribution of the potential food sources to the diets of gemsbok (A) and springbok (B) , as determined by our SIAR isotope mixing model relative to the mean composition of the three metabolically active tissues analysed (blood, liver, muscle) and for our three focal years. The boxplots show the relative proportions of each food source with C3 plant source (dark grey), C4/CAM plant source and the remaining explained part of the diets (lightest grey).

Figure 1

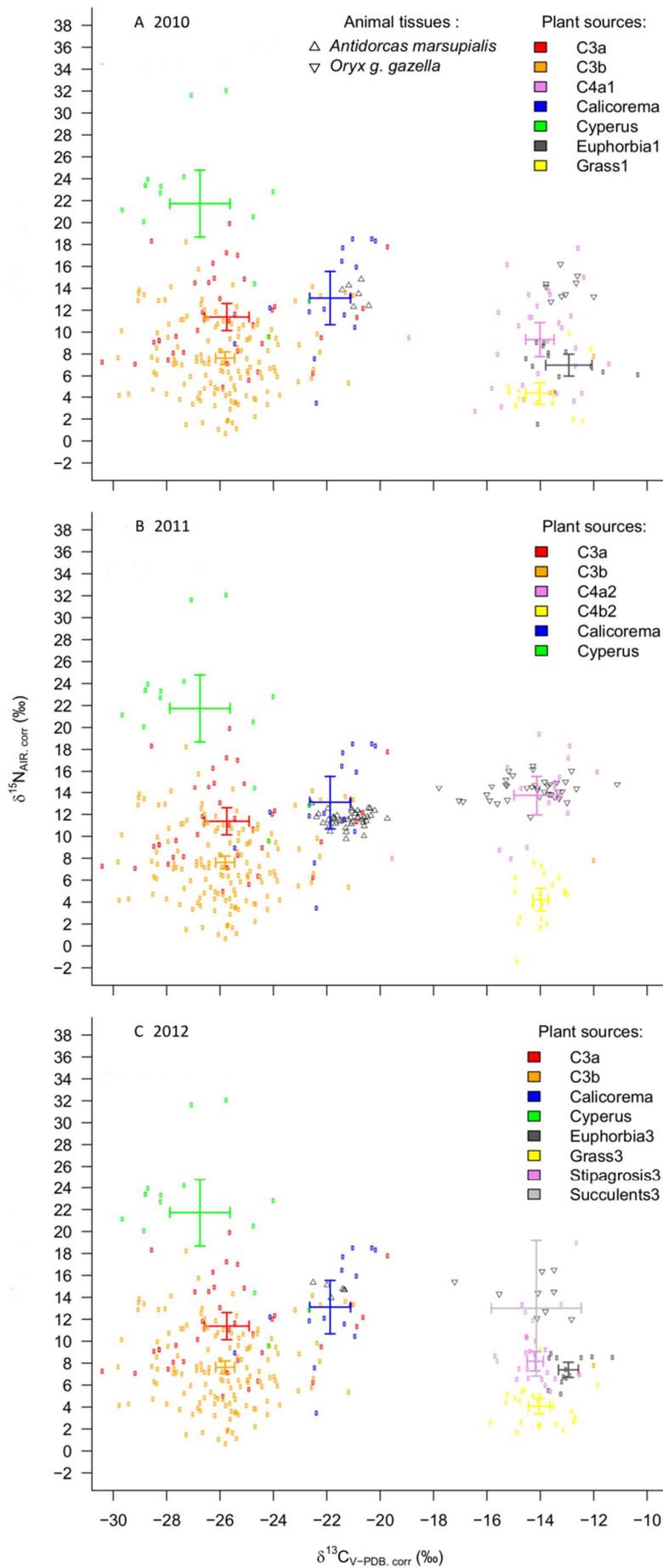


Figure 2

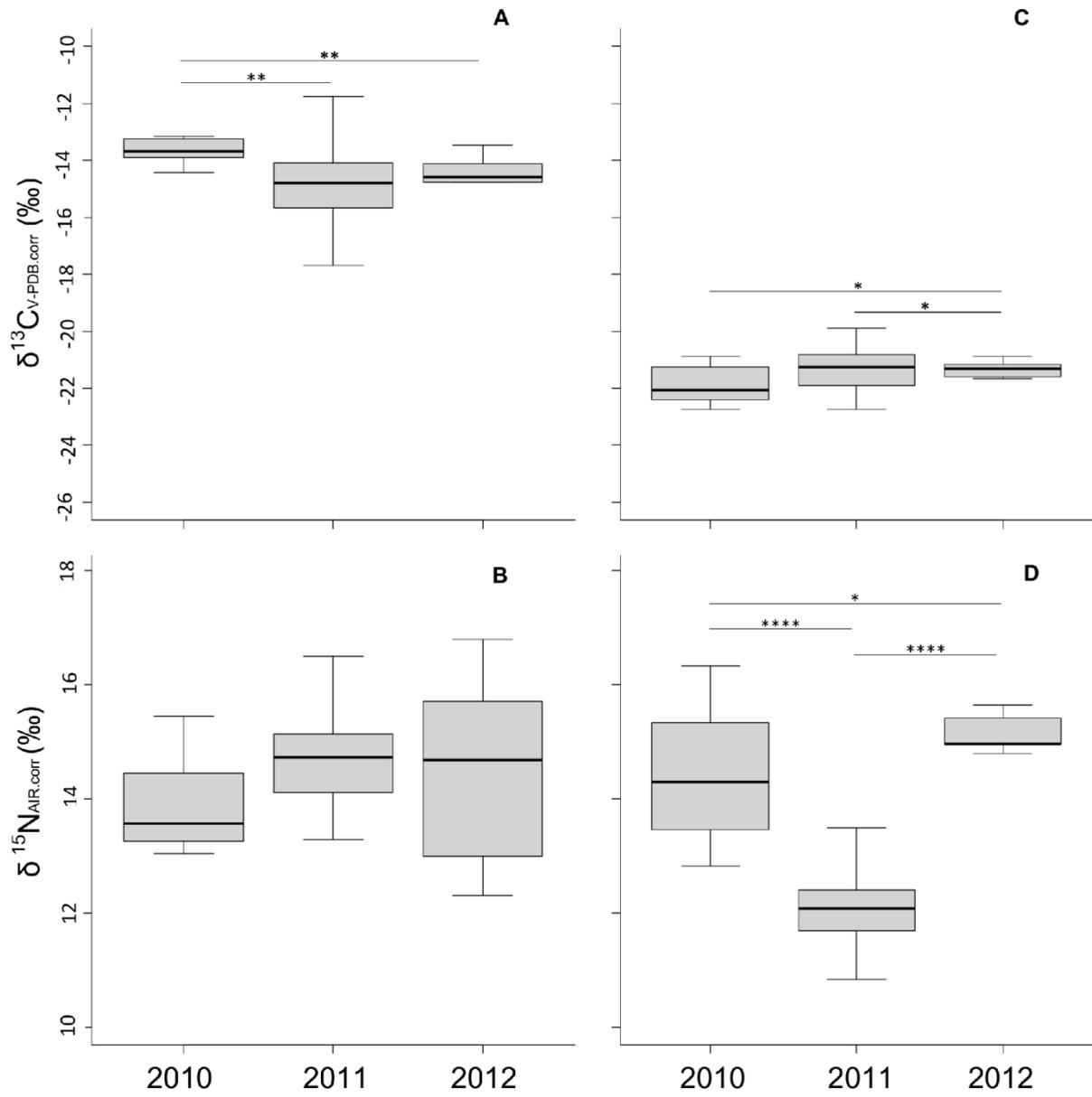


Figure 3

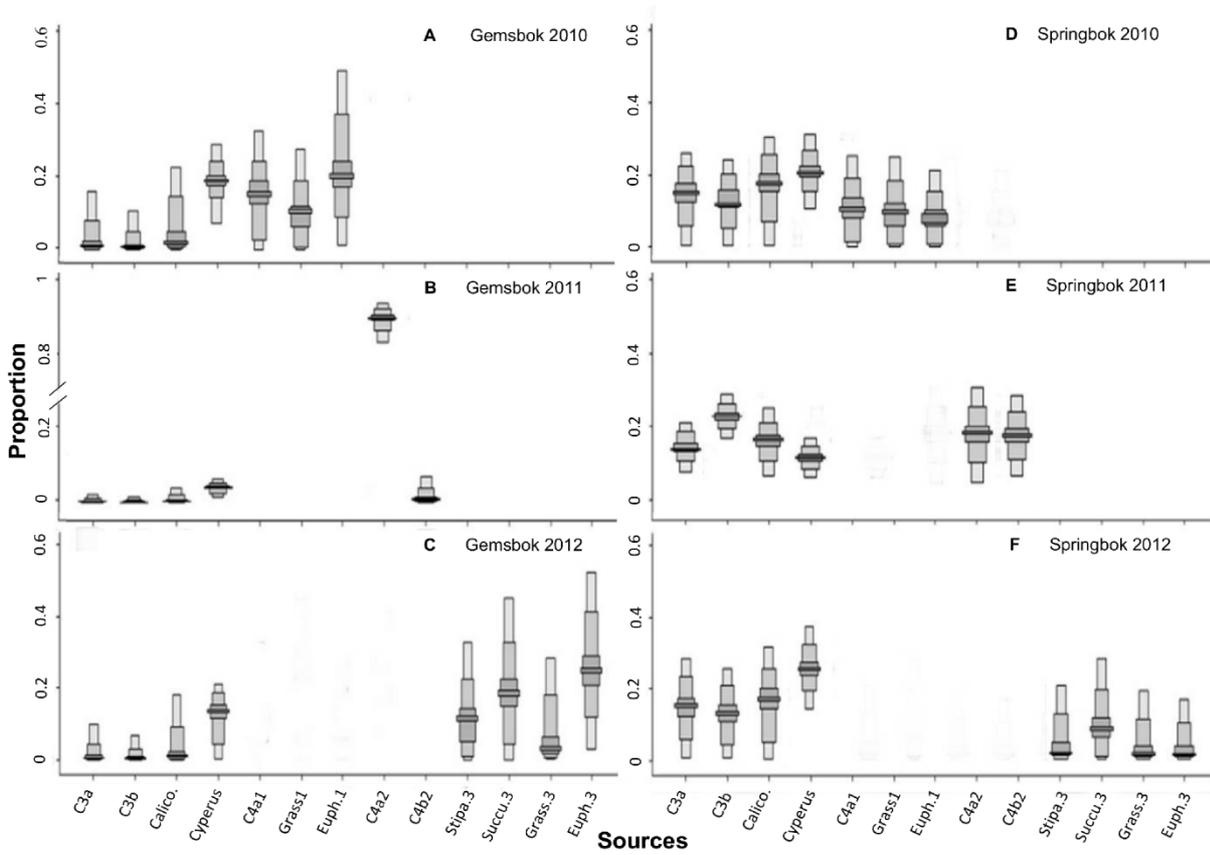
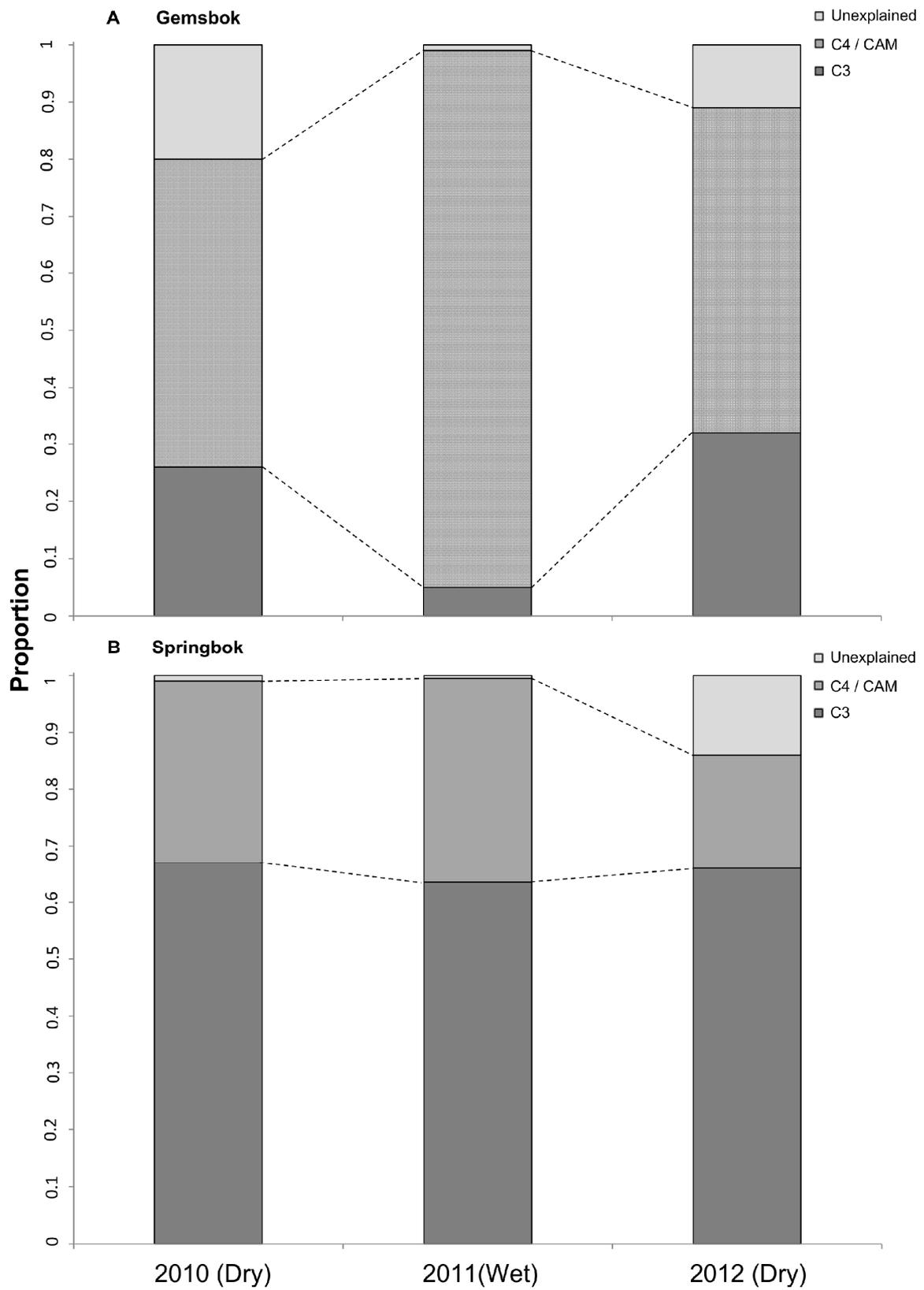


Figure 4



CHAPTER III

Individual variation of isotopic niches in grazing and browsing desert ungulates

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Author contributions: DL and CCV developed the original idea. DL, EG and CB established logistic. DL and EG conducted fieldwork. DL analysed the data. DL, JKEM and CCV wrote the manuscript.

Key words: Desert; resources availability; individual isotopic niche space; dietary strategy, spatial behaviour, tail hair; stable isotope analyses; NDVI values; *Oryx g. gazella*; *Antidorcas marsupialis*; Kunene; Namibia.

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Abstract. Ungulates often adjust their diet when food availability varies over time. However, it is poorly understood when and to what extent individuals change their diet and, if they do so, if all individuals of a population occupy distinct or similar dietary niches. In arid Namibian Kunene Region, we studied temporal variations of individual niches in grazing gemsbok (*Oryx g. gazella*) and predominantly browsing springbok (*Antidorcas marsupialis*). We used variation in stable carbon and nitrogen isotope ratios of tail hair increments as proxies to estimate individual isotopic dietary niches and their temporal plasticity. Isotopic dietary niches of populations of the two species were mutually exclusive, but similar in breadth. Isotopic niche breadth of gemsbok was better explained by within-individual variation than by between-individual variation of stable isotope ratios, indicating that gemsbok individuals were facultative specialists in using isotopically distinct local food resources. In contrast, inter- and intra-individual variations contributed similarly to the isotopic niche breadth of the springbok population, suggesting a higher degree of individual isotopic segregation in a more generalist ungulate. In both species, between-individual variation was neither explained by changes in plant primary productivity, sex, geographical position nor group size. Within species, individual dietary niches overlapped partially, suggesting that both populations included individuals with distinct isotopic dietary niches. Our study provides first evidence for isotopic dietary niche segregation in individuals of two distinct desert ungulates. Similar, yet isotopically distinct dietary niches of individuals may facilitate partitioning of food resources and thus individual survival in desert ecosystems.

INTRODUCTION

Mammalian herbivores such as ungulates select food resources according to various factors. For example, ungulates may choose food according to the availability of plants in space and time, endogenous digestive capabilities (du Toit 2003) and social constraints like individual ranks in a group (Appleby 1980, Côté 2000). Yet, many ungulates are also flexible in their feeding habits, for example when food abundance varies over time (Owen-Smith 2008, Lehmann et al. 2013). The dietary niche of an animal is typically defined by the overall range of food resources contributing to its diet. Since variation in primary productivity often follows precipitation patterns, and since a dietary niche of an animal species is influenced by the local quantity, quality and accessibility of available food resources (Macdonald, 1983; Spalinger and Hobbs, 1992; Sih and Christiansen, 2001), dietary niches of populations are expected to expand or shrink in response to the availability of the animals' preferred food items (Codron et al. 2007; Owen-Smith et al. 2013). At the population level, such expansions or constrictions in dietary niche width have been confirmed for sable antelopes (*Hippotragus niger*; Owen-Smith et al. 2013), zebras (*Equus quagga*; Owen-Smith et al. 2013) and moose (*Alces alces*) (Dungan and Wright 2005). Yet, past studies neglected that the feeding ecology of local ungulate populations might result from the additive effect of individual food selection and consequently by the extent of individualized dietary niches. Accordingly, dietary niches of animals may be better inferred from the sum of individual feeding preferences within a given population (Bolnick et al. 2003, 2007). For example, individuals within a population of dietary generalists might largely overlap in their use of food resources, or each individual might be highly specialized towards a subset of food resources (Roughgarden 1972). Individual dietary specialization has been confirmed for apex marine predators (Matich et al. 2010; Kim et al. 2013) and other predatory fishes (Quevedo, Svanbäck and Eklov 2009), for birds (Inger et al. 2006; Martinez del Rio et al. 2009), and for reptiles (Vander Zanden et al. 2010). Dietary specialization of individuals may be driven by seasonal and yearly or inter-habitat differences in resource availability or by energy requirements or habitat choices at specific life stages (Estes et al. 2003; Svanbäck and Persson 2004; Darimont, Paquet and Reimchen 2009). Overall, studies on individual dietary strategies of mammals are scarce and mainly limited to top predators (Urton and Hobson 2005), omnivores (Newsome et al. 2007), primates (Watts 1984; Dammhahn and Kappeler 2014) or mega-herbivores (Codron et al. 2012). Thus far, no study has considered dietary specialization in individual ungulates, and none has investigated individual specialization in antelopes of deserts.

Many desert plants differ in their stable carbon isotope ratios depending on their metabolic pathway of CO₂ fixation, which is either the C₄ and CAM (for example grasses and succulents such as members of the family Euphorbiaceae, respectively) or the C₃ (trees and shrubs) photosynthetic pathway (Bender 1971; Osmond 1978; Tieszen et al. 1979). Thus, stable carbon isotopes differentiate C₃ and C₄/CAM plants. In addition, using stable nitrogen isotope ratios of C₃, C₄ and CAM plants may further refine the differentiation of plants at the species levels within the aforementioned plant groups (Lehmann et al. 2013). Indeed, in a previous study, we observed that nitrogen ratios distinguished between grasses and succulent species of similar stable carbon isotope composition. As well, we were able to discriminate between trees and shrub species based on their nitrogen isotope ratios (Lehmann et al. 2013). Based on stable isotope ratios in metabolically active tissues (blood, liver and muscle), we showed that local populations of gemsbok (*Oryx g. gazella*) and springbok (*Antidorcas marsupialis*) varied in their dietary choice according to temporal changes in precipitation, (Lehmann et al. 2013). Our findings highlighted that gemsbok populations exhibit relatively flexible dietary habits (Lehmann et al. 2013), i.e. they consume a mixture of potential food plants, including more than 30% of C₃ plants during drought periods, but almost exclusively C₄ and CAM plant types when food is plentiful. During drought periods, the diet of gemsbok consisted presumably of up to 25% of *Euphorbia damarana*, an endemic CAM plant that is rich in toxic plant secondary compounds. In contrast, the studied springbok population consisted of more generalist feeders, which consumed a higher proportion of C₃ than C₄/CAM plants, independent of changes in environmental conditions (Lehmann et al. 2013). The ranges of such variations may therefore be used to infer the isotopic niche breadth at both individual and population levels in the two-dimensional ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) environmental isotopic space of the study site. The isotopic niche breadth therefore reflects the overall range of isotopically contrasted food resources consumed by an individual or a species. Although our previous findings provided important insights into how syntopic ungulates overcome unpredictable shortages in biomass productivity, individual isotopic niche breadths and their temporal plasticity still remained unexplored. Here, we go beyond the population level approach and ask how isotopic variation of individual gemsbok and springbok may contribute to the isotopic dietary niches of populations.

Stable isotope ratios of incrementally growing inert tissues such as teeth (including ivory), horns, whiskers or tail hairs have been increasingly used to infer temporal changes in both dietary isotopic niches of individuals and population (Cerling et al. 2009; Newsome et al. 2009; Codron et al. 2012, 2013; Kim et al. 2013). This is because such continuously growing

tissues record temporal variations in stable carbon and nitrogen ratios that directly reflect the range of isotopically contrasting food resources consumed over time. Specifically, we aimed to evaluate the isotopic dietary niche breadths of individual ungulates and their variation in time and position within the two-dimensional isotopic food space of our study site. We characterized the individual isotopic dietary niche breadths as the surface area enclosed within the boundaries of the 95% confidence interval of Bayesian ellipses within the two-dimensional ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) isotopic space of the food resources (Newsome et al. 2007; del Rio et al. 2009; Flaherty and Ben-David 2010). Accordingly, we estimate the isotopic dietary niche breadth of an animal by the metric size of the area occupied in the dietary isotopic space (Newsome et al. 2007, 2012). These ellipses were calculated and drawn from the varying values of the combined stable carbon and nitrogen isotopic compositions of tail hair of individual ungulates over a period of almost two years, encompassing two annual cycles that differed markedly in food and water availability. We asked if individual isotopic niches varied within and between populations of generalist and facultative specialists. We also asked if and how isotopic dietary niche breadths of individuals vary in response to temporal changes in resource availability. We hypothesized that the isotopic niche breadths of springbok and gemsbok ought to differ when plant productivity changes. Yet, we are aware that a distinction between isotopic and realized niches still remains. Therefore, based on the previously observed isotopic ratios of potential food resources and their temporal variations in the arid environment of the Kunene Region of Namibia (Lehmann et al. 2013), we set the variation of isotopic values of tail hair, recorded as Bayesian ellipse areas, in relation to the realized dietary niche of individual gemsbok and springbok.

For springbok we predicted that the isotopic dietary niche breadth remains constant and thus independent of fluctuating plant primary productivity, which is consistent with our previous findings that this ungulate species is an opportunistic intermediate feeder of C3 and C4/CAM plant resources (Lehmann et al. 2013). In contrast, we predicted that individuals of gemsbok, a facultative dietary specialist species in the arid Kunene Region of Namibia (Lehmann et al. 2013), have narrow isotopic dietary niches during periods of high primary productivity but broad ones when food resources become scarce. This pattern would indicate that both ungulate species are flexible in their feeding habits, allowing animals to adjust their diets to the food availability of a heterogeneous habitat, which on the long run may enhance their survival during periods of extreme food shortage, such as during prolonged droughts. Furthermore, intra and inter-species competition for resources may as well influence habitat selection in ungulates (Hensman et al. 2013). Accordingly, high levels of individual niche

variations in desert-dwelling ungulates would indirectly reflect mechanisms of habitat and resource partitioning in time and space among individuals and populations.

METHODS

Study site and species

Field work took place in June 2011 in the southern part of the Kunene Region of Namibia ($-20^{\circ} 12' 98.3''$ N, $+14^{\circ} 04' 15.2''$ E), a 3,500 km² area that is managed by the Torra conservancy under the premise of sustainable use of natural resources (Fig. 1). The local ecosystem consists of outcrops of basaltic mountain ranges, rocky and gravel plains, dry riverbeds and deltas formed by the ephemeral Huab and Springbok rivers. The annual precipitation usually ranges between 100 mm and 150 mm and the ambient temperature may reach up to 50°C during the dry season (Digital Atlas of Namibia, 2002). Precipitation may vary largely in this area and therefore plant availability is mostly unpredictable. Vegetation ranges from few, scarce open grasslands with bushes to plain rocky and/or sandy desert.

Gemsbok are relatively large ungulates (body mass of 180 to 240 kg) that have a geographical distribution from South Africa to northern Namibia and the southern parts of Botswana (Skinner and Chimimba 2005). Springbok body mass (30 to 44 kg) is lower than that of gemsbok. Springbok occur from the north-western part of [South Africa](#) through the Kalahari Desert into [Namibia](#) and [Botswana](#) (Skinner and Chimimba 2005). The distribution range of both species is largely overlapping and includes various habitats such as savannahs, woodlands and deserts (Skinner and Chimimba 2005).

Sample collections

Sample collection was authorised by the Ministry of Environment and Tourism of Namibia (Research permit numbers 1534/2010 and 1676/2012) and approved by the Institutional Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Research (IZW) of Berlin (Number 2009-10-01).

Under the Namibian program of community based natural resource management (NACSO 2012, Namibia Association of CBNRM Support Organizations), conservancies are given annual quotas for population control. We collected tail hairs of springbok and gemsbok hunted by conservancy members. In total, we collected tail hairs from 16 adult gemsbok (10 males and 6 females) and 30 adult springbok (17 males and 13 females). As the growth rate of gemsbok and springbok tail hair is unknown, we used data from closely related species of similar body size as the best estimate. We assumed that gemsbok tail hair has a similar growth rate as that of equids and large bodied bovid which both averages 0.7 mm per day (Domestic

horse *Equus caballus*: Ayliffe et al. 2004; West et al. 2004; Ponies: Dunnett and Lees, 2005 and domestic cow *Bos taurus*: Schwertl et al. 2003). As the best proxy for the growth rate of springbok tail hair, we referred to a study on the similar sized impala (*Aepyceros melampus*) (Saitoh et al. 1969; Sponheimer et al. 2003) that indicated a tail hair growth rate of 1 cm per month. We collected on average 35 ± 6 cm (Mean \pm SD) of tail hair from gemsbok individuals and 16 ± 6 cm from springbok individuals. Accordingly, we assumed that the stable isotope ratios of tail hair of both species integrated over the food consumption of a maximum of 22 months (from Nov. 2009 to 15th Jun. 2011, i.e. the day of the hunt).

We recorded the specific locations where animals were hunted (location), as well as the identity and size of the group from which it was collected (group identity and size). Springbok and gemsbok were harvested by game guards from two areas in the Torra conservancy. In the Western part of the conservancy, we collected samples from animals roaming around at four localities at a distance of about 8 ± 6 km (mean \pm one standard deviation) from each other (Euclidian distance, Table S1, Fig. 1). In addition, we collected samples from animals near Spaartwater, around 40 km North from the central position of the four others locations (Euclidian distance, Table S1, Fig. 1). These two areas are situated within the Etendeka mountain range and are similar in habitat characteristics; a set of rugged hills interlacing with open grassland, flood plains and herbaceous uplands as well as with more wooded riverbed and drainage lines. Springbok were sampled from twelve groups of eight group sizes. Gemsbok individuals were sampled from nine distinct groups of six group sizes. The identity of groups, their respective sizes at the time of the hunt and locations are reported beside numbers and sex of individuals in Table S1. We collected mean values of NDVI, Normalized Distributed Vegetation Index, (One month composite NDVI, NASA MODIS 13B, National Aeronautics and Space Administration Moderate-resolution Imaging Spectroradiometer) from the Torra conservancy as a measure for vegetation growth that corresponds to variations in plant primary productivity during the 22 months preceding the communal hunt. High NDVI values occurred after rainfall events while low values indicated drought periods, when vegetation growth rates are minimal or null. However, since these variations in plant primary productivity are unpredictable in the arid environment of the Kunene region, the pattern is not consistent with the conventional definition of a yearly seasonal cycle.

Our estimations of monthly rainfall in our study site were not reliable and therefore could not be used in this study. Based on discontinuous records of local precipitation and weather stations from tourist camps and neighbouring conservancies, we estimated yearly amounts of rainfall in Torra conservancy. In 2009, rainfall occurred in February-March and October-

November and amounted in total about 60 mm. In 2010, the area received less than 80 mm of rainfall from January to March and November to December. In 2011, local habitats received more than 500 mm of rainfall with an intense rainy period between January and April (Torra conservancy, Damaraland Camp Weather station, Namibian Weather Network). Since NDVI measures green vegetation, it takes into account the retention of green matter through dryer times, allowing a more accurate observation of the temporal changes in food resources availability than rainfall (Chirima et al. 2013).

All tail hairs were cleaned with water, dried in the sun and stored in plastic bags. Hair samples were shipped to the stable isotope laboratory at the IZW in Berlin, Germany under the export permit number M.E.T 85197 issued on 30 Aug. 2011.

Laboratory preparation

We cut tail hairs into series of 1 cm intervals, which summed up to 557 samples for gemsbok and 453 samples for springbok. Tail hair sections were obtained from a single individual hair to avoid potential signal blurring that could arise when using clumps of multiple hair strands (Remien et al. 2014). We obtained on average 34.8 ± 5.6 hair sections from each gemsbok individual and 15.1 ± 6.0 from each springbok individual. The soft tissue root of each hair was removed using a scalpel to avoid sample contamination by non-keratinous material. All samples were wiped with 96 % alcohol to remove potential oil residues and dirt that could have biased the stable carbon isotopic values. We did not use a 2:1 chloroform-methanol solution to further extract lipids from the hairs since the effects of lipid extraction seems to have no or little effects on $\delta^{13}\text{C}$ in lipid-poor tissues (such as keratinous materials, see Tieszen and Boutton, 1989).

All samples were then repeatedly cleansed with distilled water and dried in a drying oven (Heraeus Function Lab, Thermo Electron Corporation, 63505 Langensbold, Germany). Samples were then powdered using a mortar grinder (RETSCH GmbH milling machine). An aliquot sample of 0.3 to 0.4 mg of each hair section was hereafter loaded into tin capsules (COSTECH Analytical Inc.) and combusted. The resultant gases (N_2 and CO_2) were sequentially measured in a CE 1110 elemental analyser which was connected to a Thermo Finnigan Delta Plus (Thermo Finnigan, Bremen, Germany) isotope ratio mass spectrometer via continuous flow. The sample isotope ratios were hereafter compared with international gas standards; USGS-24 (U.S. Geological Society graphite) uses the stable carbon isotope ratio of Vienna Pee Dee Belemnite limestone as reference and IAEA-N1 (International Atomic Energy Agency ammonium sulphate) refers to the nitrogen isotope ratio of air (Gonfiantini et

al. 1995; Voigt et al. 2003). Stable isotope ratios were expressed following the δ notation with parts per mil (‰) as the unit of measurement (Slater et al. 2001). According to repeated measurements of laboratory standards, precision was always better than 0.1‰ (one standard deviation) in both elements.

Statistical analyses

Animal hair isotopic compositions

To project the compositions of tail hairs of gemsbok and springbok in an isotopic space, we required a priori estimates of isotopic trophic discrimination of the tissues of interest. Trophic discrimination of stable isotopes refers to the differences in isotopic composition between animal tissues and that of the animals' diet. Since we did not know the species-specific discrimination factors for our study species, we used discrimination factors for keratinous materials that have been observed in other ungulate species before (Cerling and Harris 1999, 2003; Sutoh et al. 1987). Accordingly, we corrected raw stable carbon and nitrogen isotopic ratios of tail hair by subtraction of 3.1‰ (Cerling and Harris 1999) and 2.9‰ respectively (Sutoh et al. 1987).

To inform whether the isotopic compositions of segmented tail hairs varied significantly among and within individuals of both species and among groups and locations, we performed linear mixed effect models. To do so, we nested the identity of an individual within the group identity from which it belonged, which was nested within its original location; e.g.: $\text{lmer}(\text{Carbon} \sim 1 | \text{Location}/\text{GroupID}/\text{ID})$.

To assess the influence of NDVI on within- and between- individual variations in isotopic concentration, we used the method described by van de Pol and Wright (2009) since NDVI values were linked to specific tail hair sections according to the respective hair growth rate of each species. We defined two different covariates for NDVI: one is providing the mean values for NDVI in each individual and one is providing a proxy for temporal deviations from this mean value (NDVI-Mean_NDVI) for each measurement of an individual. In the remainder of the text, we refer to this deviation as Residual_NDVI. Accordingly, the regression coefficient associated with the first covariate quantified the effect of between-individual isotopic variations of tail hairs and the one associated with the second covariate measures the effect of NDVI on within-individual variation of stable carbon and nitrogen isotopes ratios (van de Pol and Wright, 2009). Thus, to explain the inter- and intra-individual variation in stable carbon and nitrogen isotope ratios in both species, we considered Mean_NDVI, Residual_NDVI, and sex and group size as fixed factors to be included in two additional models, one for each

stable isotope and species; e.g.: $\text{lmer}(\text{Carbon} \sim \text{Mean_NDVI} + \text{Residual_NDVI} + \text{Sex} + \text{GroupSize} + (1|\text{Location}/\text{GroupID}/\text{ID}))$.

Each factor (Mean_NDVI, Residual_NDVI, group size, sex) was added one by one and models were compared using one-way analysis of variance based on AIC criterion. We then selected the model with the lowest value of AIC, i.e the model which explained best the isotopic variation for each species and element. We performed one model per isotope per species. The model residuals were tested for normal distribution using Q-Q plot. Model outputs provided estimates of the influence of factors in explaining inter- and intra- individual range of stable isotope ratios of tail hairs. We hereafter refer to these estimates of inter- and intra-individual isotopic range as $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$. We used 1,000 parametric bootstraps to obtain the 95% confidence intervals of the effects of fixed and random factors on the variation of tail hair isotopic ratios within and between individuals. All tests were performed with R (version 3.0.2; R Development Core Team 2013) using the function *lmer* and *confint* from the package “lme4” (version 1.0.5) ([Bates](#) et al. 2013) for linear mixed effect models.

To assess whether changes in food resource availability influenced the variations of springbok and gemsbok individual isotopic niches, we clustered NDVI values according to periods of high and low primary productivity; namely NDVI+ (Jun.-Feb. 2011 and May-Feb. 2010) and NDVI- (Jan. 2011 – Jun. 2010 and Jan. 2010 – Aug. 2009).

Isotopic niches

Isotopic dietary niche metrics were calculated and plotted using SIBER routines (Jackson 2011, Parnell and Jackson 2013) from SIAR and CAR packages using R (version 3.0.1; R Development Core Team 2013). The limits of the isotopic niche were statistically defined as Bayesian standard ellipses drawn in bivariate plots ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the local isotopic space of plant resources. Since stable isotopes ratios of gemsbok and springbok were converted to diet coordinates, we regarded the generated ellipses as being representative of the respective isotopic dietary niche in the isotopic space of the Torra conservancy; which is defined by the stable carbon and nitrogen isotope compositions of the food resources potentially consumed by animals. SEA values were corrected for small sample size (SEAc) using ‘Stable Isotope Bayesian Ellipses in R’ (SIBER; Jackson et al. 2011) from the ‘SIAR package, version 4.2, in R (R Development Core Team 2013). We defined the 95% confidence intervals of these niches as the actual boundaries of individual isotopic dietary niches during the study period (see Jackson et al. 2012). We then used 1,000 parametric bootstraps to create Bayesian estimations of SEAc (SEA.B), which allowed calculations of isotopic dietary niche overlaps by comparing 95% confidence intervals (CI). Accordingly, we

estimated isotopic niche overlap among individuals (and populations) by looking at the extent at which ellipses overlapped. Ellipses were first estimated for each individual of both gemsbok and springbok across the study period, which summed up to 46 ellipses ($n = 46$ individuals). To observe the degree of individual isotopic specialization, we calculated the overlap of an individual's isotopic dietary niche with niches of all other conspecifics. We then estimated the mean total overlap for each individual with all other conspecifics. We calculated the proportional overlap between two ellipses based on total area of the corresponding ellipses involved. Thus, we obtained the extent of total mean overlap that ranged from 0 to 100% for each individual, with values closer to 100% suggesting almost complete isotopic dietary niche overlap and implying that individuals of the study population occupy the exact same isotopic dietary niche. The mean isotopic composition of females and males were calculated for each species as four ellipses, thereby allowing SIBER pair-wise comparisons between the ellipses of males and females in each species. Finally, population ellipses were also calculated, allowing isotopic niche comparisons between our two focal species. Using a pair-wise niche comparison approach based on SIBER, we calculated and compared ellipses for each sex and population for periods of NDVI+ and NDVI - to assess co-variation in isotopic dietary niche breadth with plant productivity.

RESULTS

Isotopic composition of tail hairs

The tail hair isotopic compositions of 16 gemsbok averaged $-15.6 \pm 1.2\text{‰}$ for $\delta^{13}\text{C}$ (range: -18.1 to -12.2‰ ; Fig. 1A) and $14.1 \pm 0.8\text{‰}$ for $\delta^{15}\text{N}$ (range: 12.4 to 15.5‰ ; Fig. 1B). The stable isotopic compositions of tail hair analysed from 30 springbok averaged $-21.8 \pm 1.2\text{‰}$ for $\delta^{13}\text{C}$ (range: -24.1 to -17.3‰ ; Fig. S1C) and $13.3 \pm 1.3\text{‰}$ for $\delta^{15}\text{N}$ (range: 10.4 to 16.3‰ ; Fig. S1D). For gemsbok, the best models explaining isotopic variations within and between individuals included Mean_NDVI and Residual_NDVI as fixed factor for both elements (Table S2.a). Our models indicated that stable carbon and nitrogen isotope ratios of tail hairs significantly differed among individuals (inter-individual differences hereafter referred to as $\Delta^{13}\text{C}$ or $\Delta^{15}\text{N}$), since the estimate for random effect (ERE; 0.5‰) fell within the 95% CI [0.2 to 0.8‰] for carbon ($\Delta^{13}\text{C}$) and for nitrogen ($\Delta^{15}\text{N}$: ERE = 0.5‰ , 95% CI = [0.2 to 0.8‰]). Our models also revealed larger variations within than between individuals for both stable isotopes ratios ($\Delta^{13}\text{C}$: ERE = 1.1‰ , 95% CI = [1.05 to 1.2‰]; $\Delta^{15}\text{N}$: ERE = 0.8‰ , 95% CI = [0.7 to 0.8‰]). Stable carbon and nitrogen isotope ratios varied only little between gemsbok groups of the same location ($\Delta^{13}\text{C}$: ERE = 0.8‰ , 95% CI = [0.07 to 1.02‰]; $\Delta^{15}\text{N}$:

ERE = 0.6‰, 95% CI = [0.02 to 1.04‰]). In addition, our models suggested that isotope ratios varied between gemsbok individuals from different locations ($\Delta^{13}\text{C}$: ERE = 0.2‰, 95% CI = [0.1 to 1.3‰]; and $\Delta^{15}\text{N}$: ERE = 0.001‰, 95% CI = [0.01 to 0.9‰]).

For gemsbok, our models further indicated that sex and group size did not explain inter-individual variations in stable carbon and nitrogen isotope ratios. Furthermore, the model suggested that a difference in Mean_NDVI by 0.1 is equivalent to an average isotopic difference among individuals of 0.7‰ for carbon and of 1.7‰ for nitrogen. However, Mean_NDVI had a wide range of effects on inter-individual isotopic variations and, therefore, its impact cannot be generalized for the gemsbok population (95% CI = [-3.9 to 5.3‰] for carbon, 95% CI = [-1.9 to 5.7‰] for nitrogen), indicating that NDVI+ or NDVI- had no effect on the isotopic differences between individuals. In addition, we observed that as Residual_NDVI increased by 0.1, isotopic compositions of individual tail hairs increased by 0.1‰ for stable carbon isotopes (95% CI = [0.04 to 0.2‰]) and by 0.09‰ for nitrogen isotopes (95% CI = [0.02 to 0.1‰]), suggesting a significant effect of Residual_NDVI on isotopic composition within individuals.

For springbok, the best models explaining isotopic variations within and between individuals included Mean_NDVI and Residual_NDVI but did not include group size and sex for both stable carbon and nitrogen isotope ratios (Table S2.b). Both models revealed that stable carbon and nitrogen isotope ratios differed significantly among individuals ($\Delta^{13}\text{C}$: ERE = 0.8‰, 95% CI = [0.5 to 1.1‰]; $\Delta^{15}\text{N}$: ERE = 1.0‰, 95% CI = [0.6 to 1.2‰]). We also observed high isotopic variations within individuals ($\Delta^{13}\text{C}$: ERE = 1.3‰, 95% CI = [1.2 to 1.4‰]; $\Delta^{15}\text{N}$: ERE = 1‰, 95% CI = [0.9 to 1.1‰]). Similar to gemsbok, isotopic composition of springbok did not vary between groups ($\Delta^{13}\text{C}$: ERE = 0.001‰, 95% CI = [0.05 to 1.1‰] for carbon; $\Delta^{15}\text{N}$: ERE = 0.001‰, 95% CI = [0.03 to 1.04‰]). As for gemsbok, the isotopic compositions of springbok varied only little between locations ($\Delta^{13}\text{C}$: ERE = 0.07‰, 95% CI = [0.01 to 0.7‰]; $\Delta^{15}\text{N}$: ERE = 0.2‰, 95% CI = [0.1 to 0.8‰]). Since group size and sex were not selected as fixed parameters based on AIC criterion, we assumed that these factors had no effect on the stable carbon and nitrogen isotopes ratios of tail hair sections within and between springbok individuals. Our models showed that a difference in Mean_NDVI by 0.1 is equivalent to an isotopic difference in tail hair among individuals by 0.6‰ in ^{13}C and of 1.5‰ in ^{15}N . However, Mean_NDVI had a wide range of effects on inter-individual isotopic variations and its impact can therefore not be generalized for the springbok population (95% CI = [-0.5 to 1.8‰] for carbon, 95% CI = [-0.2 to 1.4‰] for nitrogen), indicating that NDVI + or NDVI - had no effect on the isotopic differences between springbok. Also our models

revealed that as Residual_NDVI increased by 0.1, within individual stable isotope compositions decreased by 0.2‰ for stable carbon isotopes (95% CI = [-0.3 to -0.05‰]) and by 0.5‰ for nitrogen isotopes (95% CI = [-0.6 to -0.4‰]), suggesting a significant effect of Residual_NDVI on isotopic composition within springbok individuals.

Breadth and overlap of isotopic niches

At the individual level, we observed variations in the areas of ellipses ($2.5 \pm 1 \text{ ‰}^2$; Fig. 2A) and an average overlap of $18.8 \pm 8.7\%$ across all studied gemsbok individuals (Fig. 2A, Fig. 3A). Our results showed a similar extent of overlap between springbok individuals ($21 \pm 7.6\%$; Fig. 2A). The sizes of the isotopic surface area occupied by springbok within the dietary isotopic space varied greatly among individuals ($3.8 \pm 2.8 \text{ ‰}^2$, Fig. 3A). On average, isotopic niches of male and female gemsbok overlapped by 55% (Fig. 2B), with isotopic dietary niches of males being wider along the nitrogen axis than those of females. In contrast, females exhibited a broader isotopic dietary niche along the carbon axis than males (Fig. 2B). Male and female gemsbok showed similar sizes in isotopic dietary niche areas as defined by standard Bayesian ellipses (SEA.B; male = 2.3 ‰^2 ; female = 2.2 ‰^2 ; $p = 0.33$; fig. 3B). In springbok, females exhibited significantly smaller isotopic dietary niches than males (females: SEA.B = 1.9 ‰^2 ; males: SEA.B = 4.2 ‰^2 ; $p = 0.041$; Fig. 2B, 3B), i.e. the isotopic niche of male springbok encompassed the isotopic niches of female springbok, yet only 43% of male isotopic niche was overlapping with the female isotopic niche (Fig. 2B).

We calculated the isotopic dietary niche of both species, using the mean stable carbon and nitrogen isotope ratios of tail hair increments of individuals of the respective species. Isotopic niches of the two species were completely separated at the population level (Fig. 2B), yet both isotopic niches were of similar size (gemsbok SEA.B = 2.4 ‰^2 ; springbok SEA.B = 3.1 ‰^2 ; $p = 0.26$; Fig. 3C).

We further asked if changes in primary productivity, recorded here as NDVI+ and NDVI-, would affect the isotopic niches of individuals and, thus, populations of both species. Also, we asked if isotopic niche size and breadth of males and females changed in response to primary productivity. At the individual level, only five out of sixteen gemsbok (31% of individuals) showed significant decreases in isotopic niche sizes as primary productivity increased (Table S3a). Similarly, six out of thirty springbok individuals (20% of individuals) showed decreases in isotopic niche sizes following increased primary productivity (Table S3b).

Gemsbok individuals had similar isotopic niche breadths in times of high and low primary productivity (NDVI + / NDVI -; $p = 0.5$) and isotopic niches of males and females overlapped largely during both periods (Table 1). Springbok individuals, however, had a narrower isotopic dietary niche during the NDVI + period than during the NDVI - period ($p = 0.018$). The overlap of isotopic niches of springbok between both periods averaged 34% (Table 1). The isotopic dietary niche of gemsbok males did not differ in size during periods of higher plant source availability (NDVI +) from that realised during periods of lower primary productivity (NDVI -) ($p = 0.78$; Table 2), yet overlap was only small (Table 2). Also, males and females had similar isotopic niche sizes during periods of higher vegetation growth, i.e. during periods of NDVI + ($p = 0.88$). Female isotopic niche breadths did not differ between periods with contrasting NDVI values ($p = 0.88$) but overlapped largely (Table 2). In contrast, niche breadth of male springbok decreased as primary productivity increased ($p = 0.032$) and overlapped only little between periods of NDVI + and NDVI - (Table 3). The niche breadths of female springbok were similar in times of high and low primary productivity and overlapped only little ($p = 0.68$, Table 3). Niche breadth was larger in males than in female springbok during times of low primary productivity ($p = 0.004$; Table 3).

DISCUSSION

We assessed the isotopic niches of individual gemsbok and springbok in the arid Kunene Region of Namibia by measuring the stable carbon and nitrogen isotopes ratios in tail hair increments. We were interested in the variation of individual isotopic dietary niches in response to temporal changes of food availability. Our study revealed for gemsbok that within-individual variation of stable isotope ratios explained the isotopic niche breadth of the study population better than between-individual variation. In contrast, inter- and intra-individual variation in stable isotope ratios contributed equally to the isotopic niche breadth of springbok. We observed that the isotopic surface areas of study animals, characterized in our study by Bayesian ellipses, fell within the local isotopic space defined by the stable isotopic composition of the food resources they consumed potentially. Therefore, we inferred that the limits of these ellipses reflected the extent of the isotopic dietary niche occupied by an individual. Further, we demonstrated that populations of both species consisted of individuals with distinct isotopic dietary niches. In contrast to our prediction, we found that the size of gemsbok isotopic niches did not differ between periods of low and high primary productivity, whereas springbok individuals reduced their isotopic dietary niche breadth during periods of high primary productivity. Lastly, we showed that isotopic dietary niches of springbok and

gemsbok populations were similar in breadth but did not overlap in the isotopic space of local habitats.

Variation of isotopic niches in individual ungulates

Our study suggests non-overlapping isotopic dietary niches of individuals in the studied gemsbok and springbok population. Relatively high levels of within- and between-individual variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of tail hair sections, and thus a high degree of individual isotopic food specialization, have also been found in previous isotopic studies on e.g. carnivores (Cherel et al. 2009, Matich et al. 2010), omnivores (Newsome et al. 2009) and non-mammalian herbivores (Murry and Wolf, 2013). Yet, our findings contrast with those from African mega-herbivores, namely elephants, where intra-individual isotopic variations caused by seasonal changes in plant productivity explained almost all inter-individual variation in stable carbon, nitrogen and oxygen isotopes (Codron et al. 2013).

We speculate that the difference of isotopic dietary niches among individuals of desert ungulates is best explained by a combination of individual preferences for a specific food type and also by specific movements of individuals across various habitats in response to changing environmental conditions. With respect to the dietary strategy, our previous study indicated that the two study species prefer distinct food resources in the Kunene Region of Namibia. This clear dietary segregation between gemsbok and springbok echoed with the results of this study because the respective isotopic dietary niches of gemsbok and springbok individual did not overlap. Furthermore, the stable isotopic compositions of both gemsbok and springbok populations observed in the current study matched with the stable isotopic compositions recorded before across a nineteen months period within the entire geographical range of the Torra conservancy (Lehmann et al. 2013). Therefore, we assume that the gemsbok sampled in this study followed the relatively flexible feeding habits as it was demonstrated in our earlier study (Lehmann et al. 2013); where gemsbok included 30% of C3 plants and up to 25% of *Euphorbia damarana* during drought periods, but fed almost exclusively on C4 grasses and discreet CAM plants when food was plentiful. Hence, the results of the present study suggest that the breadth of the realized dietary niche of the gemsbok population might be represented by the sum of the distinct, non-overlapping, isotopic dietary niches of individual conspecifics. We therefore conclude that individual variation in isotopic dietary niche arises from individual specialization in gemsbok. The studied springbok population consumed a mixture of C3 and C4/CAM plants, irrespective of changes in environmental conditions (Lehmann et al. 2013). Thus, the high level of isotopic dietary niche segregation observed among

individual springbok suggested that the population of this dietary generalist is in fact composed of relatively specialized individuals, similar to what previous studies found in populations of other species, e.g. reptiles and fishes (Bolnick et al. 2007; Vander Zanden et al. 2010), mammalian predators (Newsome et al. 2009) and mammalian herbivores (McEachern et al. 2006). In both our study species, isotopically distinct individual dietary niche may mitigate the intensity of intra-specific resources competition.

Influence of sociality, age, sex and plant primary productivity on individual use of isotopic niche

Typically, increases in NDVI values at a local scale reflect an overall increase in both C3 and C4/CAM biomasses. However, the availability of C4 plants seemed to be more related to rainfall than that of C3 plants (Lehmann et al 2013). For example, evergreen C3 plants such as *Cyperus sp* and *Acacia sp.* and also CAM plants, e.g. the endemic *Euphorbia damarana* might represent the most available food resources during periods of low NDVI values; i.e. drought. *Stipagrostis sp* (C4 grass) also persists at a relatively high density during both wet and dry periods and may therefore provide a continuously available forage even during severe droughts. In our previous study, we collected 30 different plant species that included potential food resources for gemsbok and springbok in the study area. Based on stable carbon and nitrogen isotope ratios, these plants species were grouped into 13 different food types (Lehmann et al. 2013). C3 plants biomasses was mainly present in riverbed habitats and their isotopic compositions remained constant from drought to wetter periods, while C4 and CAM food resources mainly occurred in open-field habitats (grassland, flood plains and herbaceous uplands). In contrast to C3 plants, $\delta^{15}\text{N}$ values of some C4/CAM plant species such as, *Zygophyllum simplex* (CAM) and *Eragrostis sp* (C4) varied with the extent of drought, and thus between periods of high and low NDVI values, at the local geographic scale of the Torra conservancy (Lehmann et al. 2013). In this study, we observed that both gemsbok and springbok move over relatively large areas (pers. observation, unpublished data); which suggests, given the short distances between our collection sites, that individuals of this study were equally likely to cross the interlacing set of habitats (riverbeds, open-field and hillsides) that characterized our study area. Therefore, we argue that individual ungulates of our study were subject to similar spatial and temporal variations in food plant availability and isotopic compositions. Furthermore, we did not observe any differences in isotopic compositions of the two study species between populations of the two study sites (at 40 km distance), suggesting that vegetation structures and availabilities might have been similar in both of our sampling areas.

Springbok are usually gregarious, roaming in small herds during dry time but aggregating in much larger groups when primary productivity increases (Child and Le Riche, 1969). Therefore, we expected similar isotopic dietary niche in individuals of the same group. In contrast, our findings of relatively high isotopic dietary niche segregation of individuals during both dry and wet periods indicate that animals partition their food resources even when grazing or browsing in a group. This is also supported by the fact that group size did not explain intra- or inter-individual isotopic variations in this study. However, group compositions may vary over time in both species following a fission-fusion pattern (Jarman 1974) and might therefore still explain some of the isotopic differences found among members of the same core group. We only considered adult individuals in our study, but were not able to include age as a factor. Therefore, we were not able to evaluate if age correlates with some isotopic niche breadth. Age-related changes in dietary requirements have already been observed in other taxa, including herbivorous mammals (Lindström, 1999). Therefore, some of the unexplained variation in isotopic data may be attributable to age-specific feeding habits. Also, intrinsic physiological conditions may have varied among conspecific individuals and this may have influenced their food resources selection and spatial movements.

With respect to sex-specific differences in isotopic niche size of ungulates, we observed differences between individuals of the studied gemsbok and springbok population. We observed a twofold broader isotopic dietary niche in male springbok than in female springbok, suggesting that males included a broader range of isotopically contrasting plant resources in their diet. This might have been caused by sex-specific differences in the movement behaviour. Like other ungulates of Southern Africa, springbok and gemsbok females usually form groups; whereas males are more loosely associated with members of the same or opposite sex and have typically larger home-ranges (Estes 1991, Skinner and Chimimba 2005). Possibly, springbok males utilized larger territories, thereby encountering a larger number of isotopically different food items. Male and female gemsbok did not differ in absolute sizes of their respective isotopic niche breadths, but we observed differences in isotopic locations of their niches, with females exploiting a broader range of plants with different $\delta^{13}\text{C}$ values. In contrast, males selected plants with similar $\delta^{13}\text{C}$ values but with more variable $\delta^{15}\text{N}$ values. Sex-specific differences in isotopic dietary niches may also reflect sex-specific differences in the use of local habitats. Indeed, the isotopic dietary niches of female gemsbok seem to include more C3 plants than that of males. In the Torra conservancy, we recorded C3 plants mostly along ephemeral riverbeds, suggesting that female groups preferred

this habitat. Possibly, they were capable of doing so because as a group they were better able to be vigilant against predators (Jarman 1974) even in dense *Colophospermum mopane* forests with large *Acacia* trees and thick bushes (e.g. *Salvadora persicata* and *Cyperus marginatus*), which lowered the visibility of predators (Thaker et al. 2011).

Accordingly, group-living could enable female gemsbok to exploit other plants compared with solitary males. The latter may prefer open grassland and uplands where they can better detect and avoid predators. Additionally, the shape of the isotopic dietary niche of males, which was broad along the $\delta^{15}\text{N}$ scale but narrower along the $\delta^{13}\text{C}$ scale, may also reflect the preferential use of open habitat food types, i.e. the larger range of $\delta^{15}\text{N}$ values of male isotopic niche is consistent with the observation of $\delta^{15}\text{N}$ variation (around 2‰) in the most available C4/CAM plants, such as *Stipagrosis sp.*, *Eragrostis sp.*, *Zygophyllum simplex* (Lehmann et al. 2013). In summary, we conclude that the variations in isotopic compositions of males may reflect the variations in isotopic compositions of C4/CAM plants across varying environmental conditions; i.e. from drought to wetter time. Lastly, the observed differences in isotopic dietary niche variations between males and females might also be related to sex-specific energy demands due to the allometric correlation of metabolism and body size, which might lead to both foraging and habitat segregations (reviewed by du Toit in Ruckstuhl and Neuhaus, 2005). In general, female ungulates increase the selection of high quality food resource, to enhance their digestion rate and to compensate for the physiological costs imposed by maternal care (Ruckstuhl et al. 2003). Thus, we hypothesized that the stable carbon isotopic variations observed in females reflect a dietary shift from C4/CAM to C3 plant foods to fuel the high energetic costs of gestation and lactation, since C3 food resources were more available over time than C4 plants and because C3 plants contain in general more nutrients than C4 plants (Barbehenn et al. 2004). Also, females may reduce their consumption of CAM plant food resources during reproductive periods, since the high concentration of secondary plant metabolite in these plants may have adverse effects on the foetal and ontogenic development of the offspring. Dietary shift from C4/CAM to C3 plant resources may also explain some of the more pronounced intra-individual isotopic variations observed in reproductively active female gemsbok.

We predicted that the isotopic dietary niche breadth of gemsbok would decrease with increasing primary productivity. Although this trend of isotopic dietary niche reduction was observed it was only statistically significant for five individuals, representing 30% of all gemsbok studied. For springbok, we predicted that the isotopic niche breadth remains constant irrespective of changes in plant productivity. However, we observed a reduction in

isotopic dietary niche breadth size in six individuals, representing 20% of our springbok data set. The tail lengths of five springbok were too short to allow a statistical comparison of their respective isotopic compositions between periods of low and high plant production. Since these variations among some individuals followed fluctuations of plant primary growth that unpredictably occurred in the arid environment of the Kunene region; the observed pattern of isotopic dietary niche constriction from drought to wetter time is therefore not consistent with the conventional definition of a yearly (periodic) or seasonal (semi-periodic) cycle. However, these results suggest that individuals of both species exhibited different dietary tactics to cope with changes in plant productivity. This variation in the feeding habits of individuals has to be considered when investigating the impacts of food resource abundance on both distribution and dietary niches of ungulate species in desert environment (Hopcraft et al. 2012).

Conclusion

In this study, we observed high levels of dietary segregation within populations of two desert ungulate species that differed in body size and feeding habits. We showed that populations of gemsbok and springbok exhibited isotopically distinct dietary niches and argue that individually distinct isotopic niches within populations of the same species reflect dietary preference of individuals, which can also be potentially influenced by their specific spatial behaviour and intrinsic physiological requirements. The observed flexibility in the breadth of the dietary niche of desert ungulates may help to increase survival and co-existence of individuals during adverse periods such as drought. Moreover, we demonstrated that males and females of both species occupied distinct, albeit overlapping, isotopic niche, which may reflect sex-specific differences in habitat utilization. In conclusion, stable isotope ratios of tail hair increments indicated that isotopic dietary niches were distinct and overall separated from each other in individuals of gemsbok and springbok co-existing in an arid environment of the Kunene Region in Southern Africa.

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CHAPTER III: INDIVIDUAL VARIATION OF ISOTOPIC NICHES

Table 1: SEA.B areas ($\%^2$) and niche overlap (%) of population of both species during periods of high (NDVI+) and low (NDVI-) primary productivity.

Population	Gemsbok (n =16)		Springbok (n = 30)	
	Size SEA.B	Overlap	Size SEA.B	Overlap
NDVI +	2.7	77.2	3.2	52.8
NDVI -	3.0	69.7	4.9	34.8

Table 2: SEA.B areas ($\%^2$) and niche overlap (%) of male and female gemsbok during periods of high (NDVI+) and low (NDVI-) primary productivity.

Gemsbok	Male (n =10)		Female (n = 6)	
	Size SEA.B	Overlap	Size SEA.B	Overlap
NDVI +	1.8	52	1.9	76.7
NDVI -	2.9	31	3.0	49

Table 3: Summary of the SEA.B areas ($\%^2$) and niche overlap (%) of male and female springbok during periods of high (NDVI+) and low (NDVI-) primary productivity.

Springbok	Male (n =17)		Female (n = 13)	
	Size SEA.B	Overlap	Size SEA.B	Overlap
NDVI +	3.4	54.6	2.6	32.1
NDVI -	7.0	26.7	1.9	44.0

1 Figure 1: Diptych map. Distribution ranges of gemsbok and springbok across the Southern Africa (right). Springbok distribution is reported in
2 yellow. Gemsbok distribution is represented in orange. Note that both animal distributions largely overlap. The black rectangle delimits the limits of
3 this study in the Kunene Region of Namibia. The distribution ranges were taken from IUCN (International Union for Conservation of Nature; *Oryx*
4 *gazelle* & *Antidorcas marsiupialis*. Version 2014.3. The IUCN Red List of Threatened Species). The enlarged and topographic map of the study
5 area (left) details the Torra conservancy where this study took place. The two major locations from which our focal animals were sampled are
6 indicated by blue circles. Both sampling areas were located within the Etendeka Mountain chain (red). Map built from topographic satellite imagery
7 (ASTER GDEM https://lpdaac.usgs.gov/data_access_freely_accessible)

8

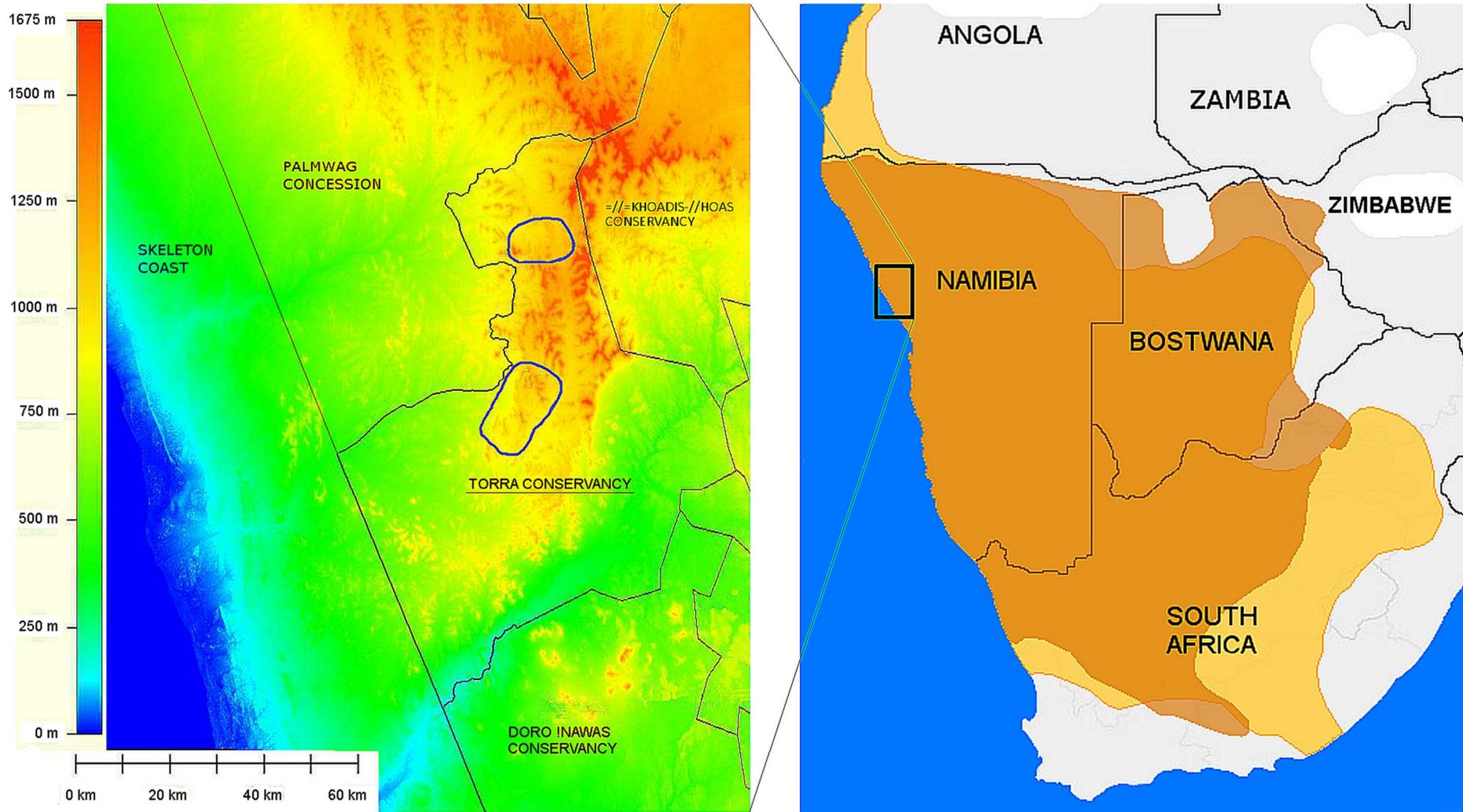
9 Figure 2: Bivariate plot of stable carbon and nitrogen isotope ratios (mean \pm one standard deviation) in tail hair of individual gemsbok and
10 springbok. Raw isotopic data were corrected for trophic discrimination. Each Bayesian standard ellipse was calculated based on all data points of a
11 given individual (A) or for males and females of both species separately (B).

12

13 Figure 3: Isotopic niche sizes of gemsbok and springbok individuals (A) of males and females of the corresponding species (B) and of the two
14 species (C) estimated by the area of ellipses ($\%o^2$) in the two-dimensional isotopic space. Black dots represent the mode; grey squares represent the
15 true population values. The shaded boxes indicate the 50%, 75% and 95% credible intervals from dark to light grey.

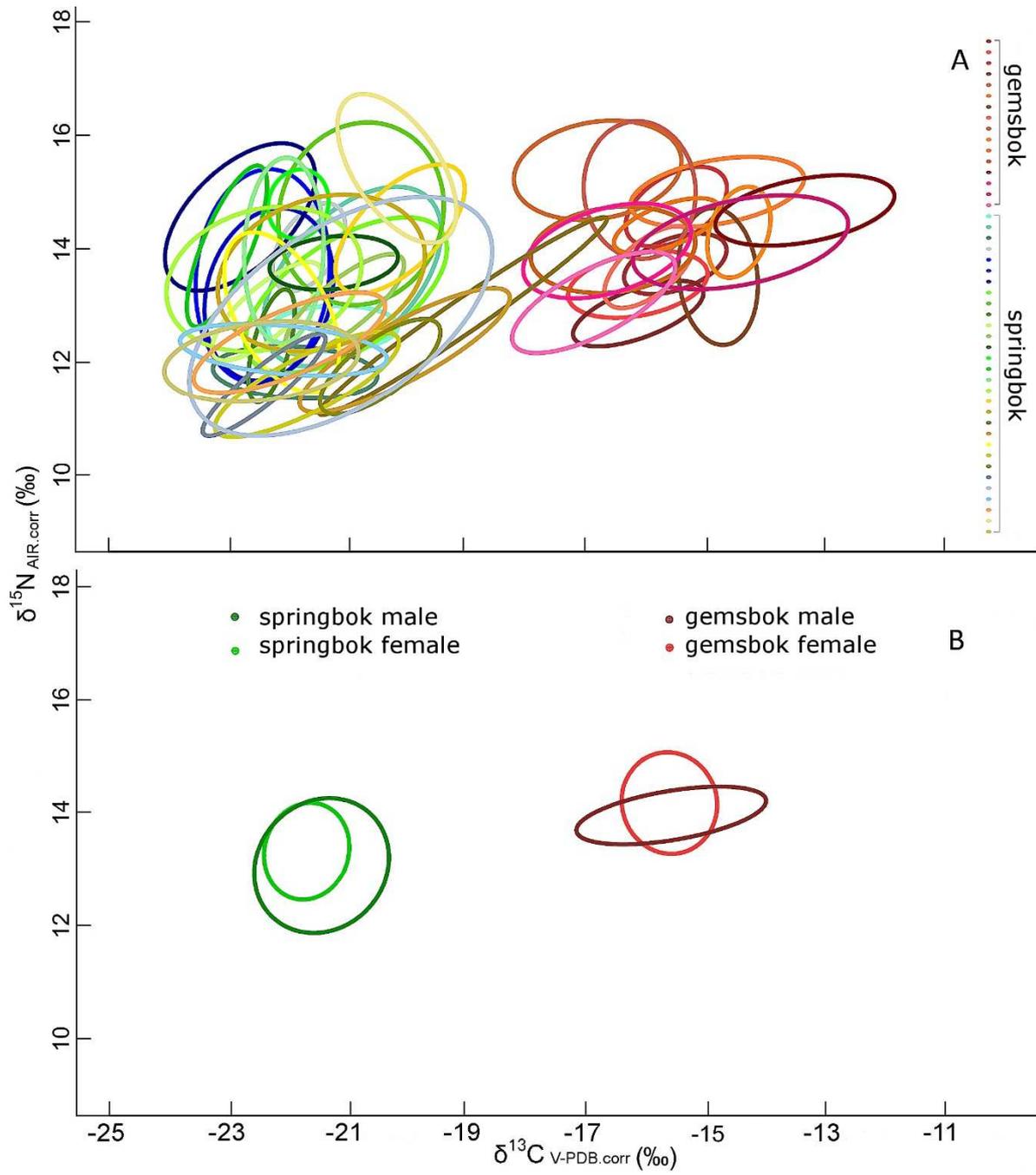
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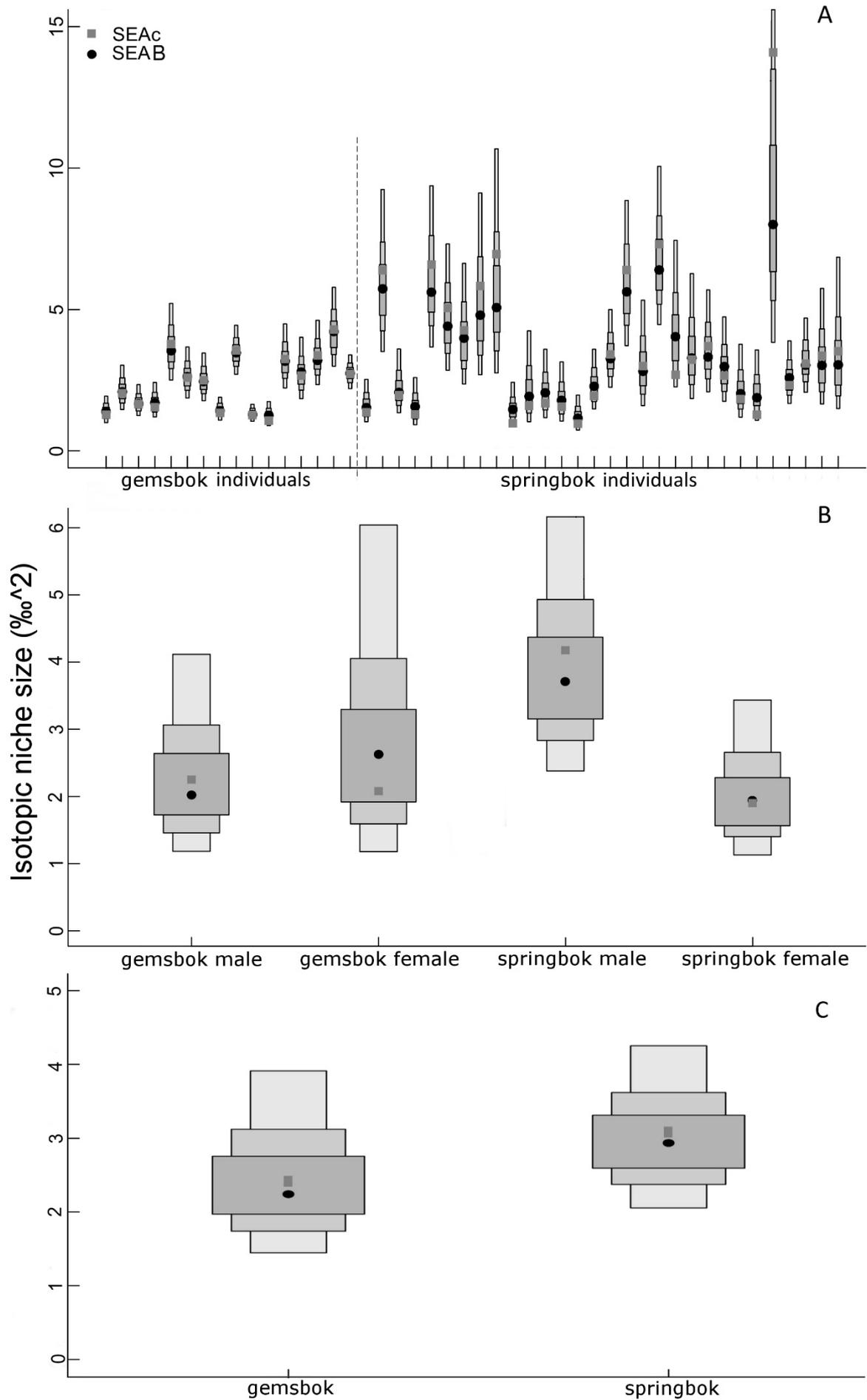
CHAPTER III: INDIVIDUAL VARIATION OF ISOTOPIC NICHES



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Electronic supplementary material: Additional tables

Individual variation of isotopic niches in grazing and browsing desert ungulates

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Key words: Desert; resources availability; individual isotopic niche space; dietary strategy, spatial behaviour, tail hair; stable isotope analyses; NDVI values; *Oryx g. gazella*; *Antidorcas marsupialis*; Kunene; Namibia.

Author Contributions: DL, JKE, CB and CCV developed the original idea. DL, EG and CB established logistic. DL and EG conducted fieldwork. DL analysed the data. DL, JKE and CCV wrote the manuscript.

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Electronic Supplementary Materials:

Table S1: The identity of distinct groups sampled. Their respective sizes and locations are reported besides individual sex for a) gemsbok and b) springbok.

a) Gemsbok	Group	Group-size	Location	Female (n)	Male (n)
	Ag	30	Spaarwater	3	0
	Bg	1	Jebico	0	1
	Cg	3	Spaarwater	0	1
	Dg	15	Driefontein	0	1
	Eg	13	Zinkfontein	2	1
	Fg	2	Spaarwater	0	1
	Gg	2	Spaarwater	0	2
	Hg	2	CollinsRoadSpring	0	2
	Ig	15	CollinsRoadSpring	1	1
b) Springbok	As	120	Driefontein	4	2
	Bs	25	Jebico	1	1
	Cs	18	Zinkfontein	1	1
	Ds	1	CollinsRoadSpring	0	1
	Es	12	CollinsRoadSpring	1	1
	Fs	150	CollinsRoadSpring	1	3
	Gs	30	Zinkfontein	2	0
	Hs	25	Jebico	0	1
	Is	25	Spaarwater	0	1
	Js	90	CollinsRoadSpring	3	1

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Ks	10	Zinkfontein	0	1
Ls	25	Spaarwater	0	4

a)	Fixed factors	Random factors	AIC	ΔAIC
Gemsbok				
Carbon	Mean_NDVI + (Residual_NDVI-Mean_NDVI)	(1 Location/GroupID/ID)	1791.9	0
	Mean_NDVI + (Residual_NDVI-Mean_NDVI) + Sex	(1 Location/GroupID/ID)	1793.8	1.9
	Mean_NDVI + (Residual_NDVI-Mean_NDVI)+ GroupSize	(1 Location/GroupID/ID)	1793.9	2
	Mean_NDVI + (Residual_NDVI-Mean_NDVI) + Sex + GroupSize	(1 Location/GroupID/ID)	1795.8	3.9
	1	(1 Location/GroupID/ID)	1797.7	5.8
Nitrogen	Mean_NDVI + (Residual_NDVI-Mean_NDVI) + GroupSize	(1 Location/GroupID/ID)	1361.2	0
	Mean_NDVI + (Residual_NDVI-Mean_NDVI)	(1 Location/GroupID/ID)	1361.5	0.3
	Mean_NDVI + (Residual_NDVI-Mean_NDVI) + Sex	(1 Location/GroupID/ID)	1362.9	1.7
	Mean_NDVI + (Residual_NDVI-Mean_NDVI) + Sex + GroupSize	(1 Location/GroupID/ID)	1363.1	1.9
	1	(1 Location/GroupID/ID)	1367.1	5.9
b)				
Springbok				
Carbon	Mean_NDVI + (Residual_NDVI-	(1 Location/GroupID/ID)	1555.8	0

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	Mean_NDVI)			
	Mean_NDVI + (Residual_NDVI- Mean_NDVI)+ GroupSize	(1 Location/GroupID/ID)	1556	0.2
	Mean_NDVI + (Residual_NDVI- Mean_NDVI) + Sex	(1 Location/GroupID/ID)	1556.7	0.9
	Mean_NDVI + (Residual_NDVI- Mean_NDVI) + Sex + GroupSize	(1 Location/GroupID/ID)	1557.1	1.3
	1	(1 Location/GroupID/ID)	1563.2	7.4
Nitrogen	Mean_NDVI + (Residual_NDVI- Mean_NDVI)	(1 Location/GroupID/ID)	1388.7	0
	Mean_NDVI + (Residual_NDVI- Mean_NDVI) + Sex	(1 Location/GroupID/ID)	1390.2	1.5
	Mean_NDVI + (Residual_NDVI- Mean_NDVI) + Sex + GroupSize	(1 Location/GroupID/ID)	1391.1	2.4
	1	(1 Location/GroupID/ID)	1457.6	68.9
	Mean_NDVI + (Residual_NDVI- Mean_NDVI) + GroupSize	(1 Location/GroupID/ID)	1556.7	168

Table S2: List of candidate linear mixed effect models for the stable carbon and nitrogen isotope compositions of individual tail hairs for a) gemsbok and b) springbok. The best supported models according to the AIC criterion are reported in front row for each isotope of each species.

Table S3: Summary of the SEAc areas (%²) of gemsbok a) and springbok b) individuals during periods of low (NDVI-) and high (NDVI+) primary productivity. Significant differences are given by SIMPER pairwise comparison (*p < 0.05. **p < 0.01. ***p < 0.001).

a) Gemsbok	NDVI- SEAc	NDVI+ SEAc	SIMPER (p)
	1.3	1.2	0.42
	1.4	2.3	0.75
	2.4	0.9	0.01 **
	1.6	1.2	0.24

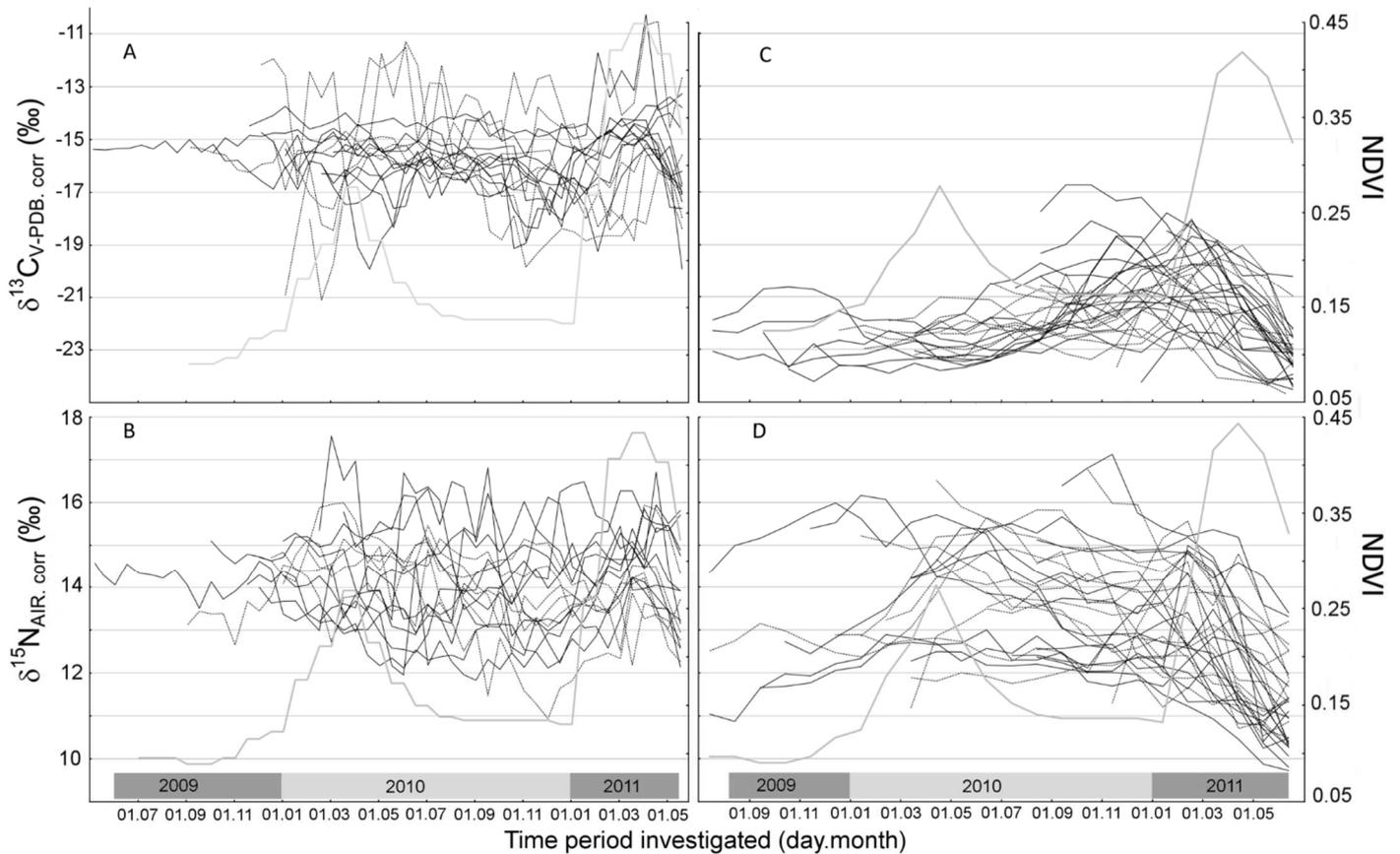
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	6.1	1.9	0.01 **
	2.4	0.8	0.02 *
	1.5	0.8	0.12
	1.5	0.7	0.10
	1.6	2.0	0.49
	0.7	1.5	0.82
	1.7	0.8	0.09
	2.2	0.9	0.03 *
	4.9	1.4	0.01 **
	2.3	1.9	0.31
	0.8	1.8	0.87
	2.3	3.3	0.74
b) Springbok	0.3	0.9	0.40
	8.4	0.7	0.004 ***
	1.3	0.1	0.09
	1.6	0.8	0.02 *
	1.7	3.6	0.53
	2.0	1.0	0.12
	2.1	1.2	0.16
	2.2	2.1	0.14
	3.1	1.9	0.23
	0.4	0.6	0.55
	0.6	5.4	0.90

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1.5	0.3	0.055
0.5	0.7	0.18
0.5	0.4	0.16
4.0	1.0	0.01 **
0.4	1.0	0.38
4.7	3.5	0.40
2.9	0.2	0.03 *
7.5	2.1	0.11
2.2	0.4	0.09
3.1	0.5	0.04 *
0.8	1.0	0.62
0.5	0.3	0.23
3.5	0.1	0.02 *
1.3	0.3	0.13
10.3	0	0.26
0.9	0	0.67
5.0	0	0.07
0.6	0	0.46
2.1	0	0.50

Figure S1: Stable carbon and nitrogen isotope ratios in tail hair increments of 16 gemsbok (A, B) and 30 springbok (C, D) in relation to day of year (day, month) when corresponding tail increments grew. Tail hairs were cut into 1-cm pieces and converted into the retrospective time period by assuming species-specific growth rates. Sequences of male individuals are represented by full lines, those of females by dotted lines. Raw isotopic data were corrected for diet-tissue discrimination factor. NDVI values are plotted for reference. NDVI records represent the variations in plant primary productivity in the general geographic region over the length of time represented by the hair isotope record. The two marked picks in NDVI values occurred after rainfall events. Each pick represents an increase in plant green growth while low NDVI values represent drought times, when the vegetation growth is minimal or null.



CHAPTER IV

Movements of desert dwelling gemsbok (*Oryx g. gazella*) in response to spatio-temporal variations in plant productivity

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Author Contributions: DL and CCV developed the original idea. DL, JC and CB established logistic. DL, JKEM, EG, JC, OHKA, SK, LM and CCV conducted fieldwork. DL analysed the data. DL, JKEM and CCV wrote the manuscript.

Key words: Desert; resources availability; home range; spatial movement behaviour, habitat suitability, plant productivity, satellite imageries; *Oryx g. gazella*; Kunene; Namibia.

Unpublished

Abstract. Ungulates often adjust their habitat use when food availability varies over time, by switching between forage or by migrating. However, it is poorly known how sedentary desert ungulates respond towards shortages in plant availability. In the arid Kunene Region of Namibia, we studied the temporal variation of home ranges and habitat use of gemsbok equipped with GPS collars. During our study, gemsbok did not migrate when food productivity decreased drastically. Home-range sizes did not vary with local Normalized Differenced Vegetation Index; a proxy for local plant productivity. Gemsbok selected their habitat according to plant primary productivity and resource accessibility, topography and estimated risk of predation. We argue that inter-individual variation in home-range and habitat uses reflect dietary preferences, but may also be influenced by individual life history stages. Gemsbok responded to resource fluctuations by using a combination of interlacing habitats that differ in plant productivity, plant composition, topography and vegetation cover. Gemsbok exploit local resources efficiently and thus survive when facing temporal and unpredictable food shortages. Our study help community-based wildlife management by providing important information about gemsbok habitat preferences, which facilitate the development of refuge habitats for gemsbok and other ungulates where hunting wildlife and grazing livestock are forbidden.

INTRODUCTION

Understanding what factors influence distribution and thus abundance of animals and how animal populations move and select habitats in their natural environment is of fundamental importance to both ecological research and conservation efforts (Simcharoen et al., 2014, Mateo-Sánchez et al., 2014). Movements of animals are often constricted to specific home ranges (Stamps 1995), and animals usually select their preferred habitats based on several criteria such as species-specific preferences for food items, competition for resources, the availability and accessibility of habitats, predation risk or human disturbances among others (Johnson, 1980; Senft et al., 1987; Johnson et al., 2014).

The size of home ranges is largely influenced by the specific energetic requirements of animals which are a function of body size and life history stage, such as growth or reproduction (Harestad & Bunnell 1979; Lindstedt, Miller & Buskirk 1986; Carbone et al., 2005). However, home range sizes may also vary within species beyond factors such as size and life-history stage (Kie et al., 2002, Börger et al., 2006). For example, the spatial behaviour of individuals may be affected by an interplay of temporal changes in resource abundances (seasonal: Dussault et al., 2005a or daily: Rivrud, Loe & Mysterud 2010) and intrinsic life history traits (Cederlund & Sand 1994; Börger et al., 2006). For example, van Beest and colleagues (2011) showed that reproductive status was the most important factor explaining differences in home ranges among individual moose (*Alces alces*), with female-calf pairs using smaller areas than gravid or non-gravid individuals. Furthermore, they demonstrated that individual home ranges and their variations were strongly related to temporary fluctuations of food abundance and quality. On top of that, anthropogenic factors such as roads or hunting pressure largely influence movements, site selection and home range boundaries of wildlife species (e.g. in American Black Bear *Ursus americanus*, Lewis et al., 2011; Roe deer *Capreolus capreolus*, Benhaiem et al., 2008;).

For ungulates, temporal variations of habitat characteristics may lead to seasonal shifts between distinct home ranges (Börger et al., 2006), or to varying levels of resource exploitation in the core areas of home ranges (Kernohan et al., 2001). Environmental stochasticity, such as temporal variation in ambient temperature, precipitation, occurrence of flash floods or the temporary presence of ephemeral water bodies might as well influence individual movement patterns, as for example in moose (*Alces alces*; van Beest et al., 2011) and sable antelopes (*Hippotragus niger*; Hensman et al 2013). Lastly, intra- and inter-specific competition of wildlife species with similar ecological niches, interactions with potential

predators and human hunting pressure may also influence the spatial movement patterns and home range sizes (Gaston, 1991; Verlinden et al., 1998; Chirima et al., 2013).

In deserts, fluctuations in food availability may be the most prominent stressor responsible for changes in ungulate movements. Species of arid or semi-arid environments face severe challenges when resources are vanishing, for example during extended periods of drought (Lehmann et al., 2013). Gemsbok (*Oryx g. gazella*) of the Kunene Region in Namibia vary their diet with increasing drought, i.e. even though gemsbok are considered to be strict grazers, they may include more than 30% of forage from shrubs and bushes in their diet when ambient conditions are dry. However, during periods of high plant productivity, they consume almost exclusively grass and succulent plants. Interestingly, in the Kunene region of Namibia they may also include up to 25% of *Euphorbia damarana*, an endemic succulent plant that is rich in nutrients and water but also in toxic secondary compounds (Lehmann et al., 2013). Thus, temporal fluctuations in available plants and their productivity may strongly influence the spatial distribution and behaviour of desert gemsbok. Other studies used indirect measures of vegetation productivity such as the Normalized Difference Vegetation Index to study habitat selection of ungulates (NDVI; e.g. Wiegand et al., 2008; Mueller et al., 2008; Pettorelli et al., 2011; Hurley et al., 2014). NDVI values have been found to be positively related to grass greenness in the field and to rainfall (Verlingen & Masago, 1997). NDVI values explained partially the habitat selection process of migratory grazers in the semi-arid Kalahari ecosystem (e.g., wildebeest *Connochaetes taurinus* and hartebeest *Alcelaphus buselaphus*, Verlinden & Masogo 1997). But NDVI alone may not be ideal in to explaining habitat selection and spatial behaviour of non-water dependant antelopes, such as gemsbok (Nagy, 1994), inhabiting heterogeneous environments (Verlinden & Masogo, 1997). Hence, additional biotic and abiotic factors to NDVI have to be considered to understand and explain the spatial behaviours and habitat selection of water independent, non-migrating, ungulates in arid mountain ecosystems such as the Kunene Region of Namibia.

Here, we investigated the spatial movements of female gemsbok (*Oryx g. gazella*) equipped with GPS collars in the arid environment of the Kunene Region of Namibia, specifically in the Palmwag concession. Gemsbok are of crucial importance for local communities, not only as a source of protein for local communities, but also as a source of income when local conservancies engage in managed trophy hunting and meat sales. In the conservancies neighbouring our study site, ungulates are hunted under the premise of a sustainable management that defines annual quotas for each species and site (NACSO 2012). Understanding the spatial behaviour and the factors underlying the selection of habitats by

ungulates might therefore provide important insights for refining the annual quota that are set for each conservancy, and help to define protected sites within the conservancies. In our study, we used empirical data of habitat and vegetation characteristics and satellite pictures to evaluate the relevance of three major habitat types for gemsbok; i.e. open-fields, riverbeds and hillsides. We describe local habitats according to the following parameters: composition and cover of vegetation, temporal fluctuations of green plant matters, topography, and likelihood of detecting large predators according to visibility. We recorded changes in plant primary productivity during three years and obtained information on the spatial movement of gemsbok from individuals equipped with GPS collars.

We predicted that gemsbok select grasslands during periods of high primary productivity. Grasslands may be open or part of more complex ecosystems such as savannah or plateaus which are also rich in herbs. When grass resources decrease, we expected gemsbok to select habitats with relatively high abundance of alternative food sources, such as shrubs and bushes or *Euphorbia damarana*. We also predicted that gemsbok select open habitats with high levels of visibility since this would facilitate predator detection and increase the likelihood of escaping from them successfully. Further, we expected gemsbok core areas to increase in size as primary productivity decreases while their overall home range should remain similar. In concordance with observations in other African ungulates, we expected home ranges of neighbouring individuals to overlap to some extent (e.g. African buffalo *Syncerus caffer*, Cornélis et al., 2011; Sable antelopes *Hippotragus niger*, Hensman et al., 2013). We expected therefore that neighbouring individuals share similar habitat types within their respective home ranges and face similar environmental variations leading to convergent patterns in their spatial behaviour. However, if gemsbok individuals are plant specialists, we expected them to select different plant species when sharing the same habitat with other conspecifics to avoid or reduce competition for food sources. Hence, we expected to observe differences between individual spatial movement behaviours, habitat selection, home range sizes and associated variations. Finally, since the study population seems to be well adapted to overcome even strong shortages of food sources (Lehmann et al., 2013), we also expected gemsbok not to move outside the area during prolonged periods of drought.

METHODS

Study area

The Palmwag concession is located in the Kunene Region of north-west Namibia (19°52'54"S- 13°56'46"E) between the Etendeka Concession, Etosha National Park and the

Skeleton National Park. It includes a 5,500 km² area almost void of human settlements and thus anthropogenic impact on wildlife. Hunting is not allowed within the concession and only about 900 km² is accessible for tourists. The climate shows an overall annual rainfall between 100 and 150 mm and the ambient temperature may reach up to 50°C during the hot-dry season (Digital Atlas of Namibia, 2002). The local ecosystem consists of outcrops of basaltic mountain ranges, rocky and gravel plains, dry riverbeds and deltas formed by ephemeral rivers. Metamorphic and granitic stones with a thin and compacted sedimentary crust only retain a substrate poor in nutrients for primary productivity. Vegetation therefore ranges from none to open grassland and sparse savannah, with more wooded area concentrated around ephemeral riverbeds.

Gemsbok are relatively large bodied ungulates (body mass of 180 to 240 kg, Skinner and Chimimba 2005). Their distribution ranges from South Africa to northern Namibia and the southern parts of Botswana (Skinner and Chimimba, 2005). Gemsbok use various habitats throughout their geographic distribution range, such as savannahs, woodlands and deserts (Skinner and Chimimba 2005), suggesting that this animal is capable of adjusting to a broad range of environmental conditions (Lehmann et al., 2013).

Immobilisation of animals and GPS collaring

For our study, we selected only female gemsbok because they may provide information on the habitat preferences of herds. Male gemsbok often forage solitary. Moreover, females are more important than males from a management perspective. Between 1st and 4th of April 2011, we immobilized seven adult females from seven different herds in the recreational area of Palmwag, and equipped each with IRIDIUM GPS collars (VECTRONIC aerospace, Berlin GmbH). One additional collar was placed on another female in February 2013. Immobilization attempts took place between 6 a.m. - 12 a.m. and 3 p.m. - 5 p.m to avoid the peak temperatures. Gemsboks were darted from the ground, using single-use pressurised darts filled with 7 mg M99, 10 mg Medetomidine and 100 mg Azaperone. Darted females rapidly fell asleep after within 12 ± 3 minutes (mean \pm SD) on average. Individuals were then transferred to the shade of a bush or tree and moisten with water to reduce the effects of solar radiation and to avoid overheating. Individuals remained immobilized for an average of 19 ± 3 minutes (mean \pm SD). Drug effects were reversed using an intravenous injection of 12 mg M5050 mixed with 50 mg Naltraxone and 5 ml Yohimbine or Atisidane. GPS collars were programmed with 7 hours rollover schedules; meaning that one location was recorded every 7 hours independently of the time of the day. This method allowed a more

complete overview of the daily activity rhythm of our focal, radio-collared, individuals and the coverage of the whole 24 hours of a day when GPS worked for several months. GPS fixes were automatically transmitted via satellite to a computer.

Capture using immobilizing drugs were conducted by the Namibian state veterinarian and authorised by the Ministry of Environment and Tourism of Namibia (Research permit numbers 1534/2010 and 1676/2012). The conditions of the immobilization procedure were approved by the Institutional Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Research (IZW) of Berlin (Number 2009-10-01). During the course of this project, we lost three animals: One was lost to predation, i.e. the animal was killed by lions (as revealed by field investigation). Another female was most likely poached and one died from unknown natural causes other than predation as its carcass was found in a seemingly intact state and un-scavenged (pers. observation Dr. Philipp Stander). From these individuals, we only collected 1938 (06-04-2011 to 23-08-2012), 950 (04-04-2011 to 13-11-2011) and 647 (04-04-2011 to 18-08-2011) spatial locations, respectively. Of the five remaining individuals we collected 3,396 (06-04-2011 to 31-08-2013), 3,220 (05-04-2011 to 31-08-2013), 3,227 (03-04-2011 to 31-08-2013), 3,173 (04-04-2011 to 31-08-2011) and 676 (15-02-2013 to 31-08-2013) GPS locations. In sum, we obtained a total of 15,487 GPS data points between the 04th of April 2011 and the 31th of August 2013.

Habitat empirical characterization

We used two complementary approaches to characterize suitable habitats for gemsbok individuals equipped with GPS collars. First, we visually assessed distinct habitat categories such as riverbeds, hillsides and open-fields as well as substrates, topographies and dominant vegetation types in order to describe the overall distribution of plant resources as a function of habitat specificity. Secondly, we selected 78 spots within the boundaries of the recreational tourist zone of the Palmwag Concession (33 spots in open-fields type habitats, 15 in riverbeds environments and 30 in hillside/mountainous habitats). At each of these spots, two transects of 20 meters that crossed in the middle were laid, and discrete and continuous data on vegetation were recorded using a mixed point / line-intercept method (Floyd & Anderson, 1987). Vegetation types, dominant plants, percentage of cover, greenness, percentage of grass and shrub and substrate were recorded (Manley et al., 1993; Sanchez-Rojas & Gallina, 2000; Johnson et al., 2002). In the four quotas formed by the cross-point intercept, we identified and measured the two nearest trees from the centre. Using a 1 by 1 m square with 16 compartments (four ropes being fitted between each parallel sides of the square) placed at the

centre and at the four edges of each transect, we assessed the percentage of soil cover (using the Braun-Blanquet cover-abundance scale; Braun-Blanquet, 1932) and fine-scale percentage green, grass and shrub. The estimates of the 16 compartments were then pooled for one square, averaged and expressed as percentage values. In each square, we furthermore measured the height of grass. Percentage of visibility at each plot was assessed as a measure of predation/competition detection and calculated using a 1.5 m pole painted with 10 cm alternating white and red stripes. This pole was placed at five random locations per sampling site and at a distance of 25 to 30 meters from the centre. The stripes that were visible from the point intercept were counted and expressed as percentage of visibility. Suitability of the habitat for gemsbok is likely varying unpredictably in this environment between years or seasons. To determine changes in habitat characteristics over time, we conducted two repeated measures between subsequent years covering high (15th July 2011 to the 2nd August 2011) and intermediate primary productivity times (27th March 2012 to 28th April 2012). Unfortunately, we could not investigate these sites during the lowest primary productivity period of 2013. To detect differences of these estimates within and between habitats, we used Wilcoxon signed-rank test and Mann-Whitney U Test for independent samples, respectively.

Satellite imagery and habitat modelling

A map of three major habitats types (open-fields, riverbeds and hillsides) from the study area was drawn using a combination of satellite imageries from LANDSAT (50 meters resolution; <http://earthexplorer.usgs.gov/>), MODIS Terra (250m resolution, MOD13Q1; https://lpdaac.usgs.gov/data_access) and ASTER topographic visualization (30 meters resolution; ASTER Global DEM; https://lpdaac.usgs.gov/data_access) as well as from the data obtained from field work on the ground. We digitized polygons around these three available habitats and confirmed that all our 78 spots were encompassed within the habitat types originally assigned to them, which therefore validated our empirical habitat assessment. The defined habitat polygons were then converted to shapefiles.

Simultaneously, we used NDVI data to estimate vegetation density. We downloaded 62 NDVI raster maps from MODIS Terra with 250 meters resolutions from two-week intervals to track changes in primary productivity during the study period (Johnson et al., 2002; Brown et al., 2006; Mueller et al., 2008). To assess whether changes in food source availability influenced the spatial behaviour and habitat selection of gemsbok in the Palmwag concession, we defined three periods with contrasting plant primary productivity: High (06-03-2011 to 24-08-2011; NDVI = 2859 ± 754), Intermediate (25-08-2011 to 31-05-2012; NDVI = 1553 ± 85) and Low (01-06-2012 to 31-08-2013; NDVI = 1329 ± 61). NDVI values were then used to

estimate variations in food resource availabilities across time within and between habitat types. From the variations of NDVI values during our study period, we defined three distinct intensities of plant productivity and referred to it as “season” in our model, acknowledging that the apparent unpredictability of plant productivity at our study site is not consistent with the conventional definition of a yearly seasonal cycle. Comparison of the plant greenness were made between the three habitat types, yet we noted that the tree layers of the riverbed environments might blurred the total primary productivity of this habitat, since variations in ground-based vegetation might be masked by tree canopies (Hensman et al., 2013). Our estimation of plant greenness was slightly different than the subjective estimation performed by Knigh 1991 and Verlinden & Masago (1997), where they defined six different point scales of the herbaceous layers greenness alone (no grass, grass without green, slightly green, yellow-green, green-yellow, and totally green). In contrast, we visually estimated the percentage greenness relative to the entire plant cover present at each plot; including both grasses and shrubs species since previous study had shown that gemsbok do not exclusively feed on grass species in this environment (Lehmann et al., 2013). Indeed, riverbeds harbours many potential food sources, such as *Cyperus sp.*, *Stipagrostis damaranensis* and succulent plant species that are used by gemsbok during prolonged periods of drought (Lehmann et al., 2013). We therefore controlled for potential NDVI biases in primary productivity of riverbeds by visually assessing the greenness of its ground-based plants and took into account the implications of such potential biases while interpreting our gemsbok habitat selection model output.

Further, we downloaded shapefiles of the primary (gravel roads) and secondary roads (usually non-gravel) crossing the concession, the drainage lines, the major tributaries and the ephemeral riverbeds (freely accessible online via the website of the Environmental Information Service Namibia, <http://www.the-eis.com/>).

Data analysis

We first converted all latitude and longitude coordinates (UTC) to the UTM coordinate system using the WGS 1984 UTM 33 south projection. We also converted UTC day time of recorded locations to Namibian local time.

We included only GPS locations that were marked as “validated” in the offset transmitted via IRIDIUM satellite into our dataset, meaning that the recorded geographic location was accurate to five meters or less. Additionally we removed burst, points that were time stamped at a closer interval than initially specified and spatially auto-correlated locations (Getz et al.,

2007, Mueller et al., 2008). Consequently, we reduced our overall dataset from 15,487 to 13,190 GPS data points. From this data pool, we calculated the 95% (total home range area) and 50% (core home range area) isopleths for both Kernel and MCP home ranges (Ha) (Worton 1987, Jennrich & Turner 1969), using the R library 'adehabitat' (Calenge 2006). We only referred to the Kernel estimates in the following text. Kernel estimates of individual home-ranges were log-transformed to yield data with normal distribution. We used student t-test for paired samples to assess differences in the overall and core area home-range sizes between three periods of contrasting plant resources abundances (high, intermediate, and low plant primary productivity).

Further, as we lost three individuals during the course of this study we did not obtain the same number of data points for each individual. Consequently, our total dataset of gemsbok spatial locations was biased against these less represented individuals. To control for this bias, we randomly resampled a more homogeneous amount of gemsbok locations between each individual during each primary productivity time period and for each day and night (Fieberg 2007a, Fieberg 2007b). We then obtained a definite data base of 10,000 GPS locations to which 5 individuals contributed with 80 % and the three killed animals with 20% of data points. For each GPS location of each individual, we extracted the corresponding NDVI value from the nearest two-week NDVI raster data. Using ArcGIS 9.3.1 Proximity Analysis-230 Near-tool, we calculated for each GPS point the nearest distance to a road and riverbed (including major tributaries and drainage lines). These parameters are referred to in the remainder of the text as Dist_Road and Dist_RB. Using ASTER topography imagery at 30 meters resolution of the Palmwag concession, we extracted elevation values for each individual GPS location. Additionally, using our habitat map, we attributed to each GPS point one of the three major habitat types. Finally, we calculated the differences between individual NDVI_indiv. values of each point location with the MeanNDVI of its total home range at a given time, providing a proxy for temporal deviations from this mean value (NDVI_indiv.-MeanNDVI) for each spatial locations of an individual, which will be referred to as DfNDVI in the following. Simultaneously, DfNDVI reveals the range of primary productivity preferred by individual gemsbok. Also, in order to define whether animals used the environment depending on daytime hour, we included Day-Night as co-parameters. Therefore, to assess whether a location was reached by an individual according to specific environmental and temporal conditions, we randomly permuted the time data within individuals keeping location constant. Thus, we created a simulated dataset where animal locations were randomly re-allocated in time of year and day ensuring that our focal individuals were not located at this

particular spatial position at this specific time. For this simulated dataset we also extracted elevation, NDVI of each individual at every single location reached at a specific time and calculated the differences in primary productivity with the mean primary productivity of the individual entire home range (DfNDVI), distance to nearest road and riverbeds as well as habitat and season. We therefore obtained an absence versus presence binomial dataset where the observed GPS locations are represented by 1 and the simulated GPS points by 0 (Mueller et al., 2008). The absence versus presence of gemsbok individual at a specific location at a given time is referred in the remaining of the text as Response. Therefore, each individual contributed with both “observed” and “simulated” point locations to the data analysis, which summed up to an overall dataset of 20,000 GPS locations.

To explain variation in geographical locations selected by an individual and to test for hypothetical differences in spatial behaviours among individuals inhabiting the same area but with individualized, albeit overlapping home ranges, we considered MeanNDVI, DfNDVI, elevation, Day-Night, habitat, season and year as fixed factors to be included in a binomial generalized mixed effects model as used vs. available resource selection. In this analysis, we included individual ID as random factor intercept to account for residual patterns of each fixed effects that could occur from repeated measure of our focal gemsbok (Pinheiro & Bates 2000; Börger et al., 2006). Our general model would therefore take the following form e.g.: $glmer(\text{Response} \sim \text{Dist_Road} + \text{Dist_RB} + \text{Day-Night} + \text{MeanNDVI} + (\text{Elevation} + \text{Habitat} + \text{DfNDVI}) * \text{Season} + (1|\text{ID}), \text{family} = \text{binomial})$. Accordingly, the regression coefficient associated with MeanNDVI covariate of each GPS point quantified the effect of between-individual variations in site selection. The regression coefficient of DfNDVI of each GPS point was associated with the covariate measures of the effect of NDVI on within-individual variation in habitat selection (van de Pol and Wright, 2009).

Model outputs provided estimates of the influence of factors in spatial movement behaviours between and within individual. We used 1,000 parametric bootstraps to obtain the 95% of confidence intervals of the effects of fixed and random factors on the variation of habitats selection within and between individuals. All tests were performed with R (version 3.0.2; R Development Core Team 2013) using the function *glmer* and *confint* from the package “lme4” (version 1.0.5) (Bates et al., 2013).

Lastly, we conducted Spearman correlation two-sided tests to observe whereas the mean of individual proportions of habitats occupancy across our study period were related to the individual mean -range sizes. We also conducted Spearman correlation two-sided tests on the standard deviation of these individual habitat occupancy estimates to observe whether

individual proportion shift in habitat used across our study period were related to total and core home-range sizes.

RESULTS

Habitats characterizations and vegetation surveys

The three focal habitats of our study area are characterized in Table 1 and their geographical distribution is described in Fig. 1. Open habitats such as gravel and flood plains, sparse savannahs and grasslands were dominated by the following plants: *Eriagrostis sp.* and *Stipagrostis sp.* (both grasses), *Boescia foetida* (shrub), *Euphorbia damarana* (succulent), *Petalidium spiniferum* (shrub), *Calicorema capitata* (shrub), *Zygophyllum simplex* (succulent), and *Salsola sp.* (succulent) as well as *Boecia albitrunca* (tree). *Heliotropium oliveranum*, *Indigofera adenocarpa*, *Petalidium halimoides* and *Sesamothamnus guerichii* were also observed and are reported as ‘other’ in Table 1. *Euphorbia damarana* (n = 13) averaged 5.8 ± 2.7 m in plant circumferences and 1.98 ± 0.68 m in height while *Boescia albitrunca* (n = 5) averaged 1.2 ± 0.65 m in circumferences and 4.7 ± 1.6 m in height. Open-field substrates were composed of 70% basaltic rock, 20% gravel and 10% of a mixture of compacted earth and sand.

Riverbed habitats included ephemeral rivers, major tributaries, drainages lines and canyons and were dominated by *Colophospermum mopane* (tree), *Acacia torticollis* (tree) and *A. erioloba* (tree) as well as *Faidherbia albida* (tree). Ground vegetation included *Cyperus marginatus* (classified here as shrub), *Stipagrostis sp.* and *Stipagrostis damarensis* as well as *Eriagrostis sp.* *Terminalia prunoides* were always observed in drainage lines and *Salvadora persicata* (shrub) were present at high density along riverbeds. Also, *Trichodesma africanum*, *Welwitschia mirabilis*, *Pegolettia oxydonta*, *Geigeria alata*, *Cleome foliosa* and various weed species were also frequently encountered (reported as ‘other’ in Table 1). We could not quantify the height and width of *Acacia sp.*, *Faidherbia albida* and Mopane trees as they were too high (> 4.5 m). However *Terminalia prunoides* (n = 7) averaged 3.6 ± 2.1 m in circumferences and 3.2 ± 1.8 meters in height. *Salvadora persicata* (n = 4) averaged 6.7 ± 2.8 m and 2.6 ± 0.78 meters respectively. The substrate of this habitat was composed of about 30% gravel, 30% rock, 30% sand and 10% of a mixture of sand and mud.

Hillside habitats included ridges, cliff and steep slopes as well as herbaceous plateaus and were dominated by *Eriagrostis sp.*, *Stipagrostis sp.*, *Petalidium spiniferum*, *Boescia albitrunca*, *Sesamothamnus guerichii* (tree) and *Commiphora wildii* (tree). *Geigeria alata*, *Pachypodium lealii*, *Lotononis sp.*, *Euphorbia virosa* and *Adenia pechuelii* were also present

in this environment and reported as 'other' in Table 1. *Boeascia albitrunca* (n = 6) averaged 3.9 ± 1.4 m in height and 1.8 ± 0.72 m in circumference, and *Sesamothamnus guerichii* (n = 7) 1.8 ± 0.93 m and 1.2 ± 0.65 m respectively. Hillsides were formed of about 80% basaltic rocks, 10% gravel and 10% compacted earth.

The three defined time periods differed in plant primary productivity. The period of high plant productivity differed from that of intermediate and low productivity (W = 198, $p < 0.0001$ and W = 330, $p < 0.001$; respectively); and the latter two differed as well (W = 538, $p < 0.0001$). Primary productivity estimated from NDVI values of these habitats decreased between the two periods investigated in the field (Table 1). As expected, primary productivity was always higher in riverbeds, albeit only slightly compared with open-fields and hillsides (W = 635, $p = 0.005$ and W = 1270.5, $p = 0.0015$; respectively, Table 1). Plant primary productivity was similar across time between open-field and hillsides habitats (W = 2111, $p = 0.52$, Table 1). Percentage plant covers was always close to or lower than 50 % in all three habitats investigated (Table 1), which means that the bare ground was almost not covered by vegetation. The percentage of ground covered by plants, representing the density of ground surface plants, decreased as primary productivity decreased in both open-fields and hillsides habitat (Table 1). Percentage greenness relative to the overall vegetation cover increased only in open-field areas between high and intermediate plant productivity periods (Table 1).

Open-fields and hillsides included the highest vegetation cover throughout the study period. Vegetation cover of these two habitats were of similar amplitude (W = 1843.5, $p = 0.42$). Riverbed areas harboured less vegetation than open-fields (W = 1321, $p = 0.0011$) and hillsides (W = 499, $p = 0.0089$). Visibility rates across time were higher in open-fields and hillsides than in riverbeds (W = 1757.5, $p < 0.001$ and W = 90, $p < 0.001$; respectively). Open-fields provided better visibility than hillsides (W = 2088.5, $p = 0.017$). Estimated visibility for gemsbok at 25 meters distance to central points did not differ in habitats over time; open-fields: High: 85.6 ± 17.3 %; Inter: 85.7 ± 26.0 %; W = 460.5, $p = 0.49$; riverbeds: High: 39.4 ± 17.92 %; Inter: 41.6 ± 23.8 %; W = 99, $p = 0.81$; hillsides: High: 78.2 ± 15.9 %; Inter: 79.77 ± 38.08 %; W = 434, $p = 0.81$.

Home range sizes and variations

The total home ranges (95% Kernel isopleths) of the 8 radio-collared gemsbok averaged $6,151 \pm 3,835$ ha (range: 683 -11,399 ha; Table 2; Fig. 1). The core area (50% Kernel isopleths) of gemsbok home ranges averaged $1,289 \pm 710$ Ha (range: 642 – 2,324 ha; Table 2;

Fig. 1) for the overall 13,190 GPS locations observed. Individual home ranges of gemsbok were sorted according to size in Table 2.

There were no significant differences in total home range sizes of gemsbok between periods of high and intermediate ($t = -0.68$, $df = 5$, $p = 0.52$; Fig. 2), periods of high and low ($t = -1.35$, $df = 4$, $p = 0.25$ Fig. 2) or periods of intermediate and low plant productivity ($t = -1.33$, $df = 4$, $p = 0.25$; Fig. 2). Although core areas appeared to be smaller during periods of high and intermediate primary productivity than during the period of low primary productivity, these differences were not significant ($t = -1.42$, $df = 4$, $p = 0.23$ and $t = -1.69$, $df = 4$, $p = 0.16$; respectively, Fig. 2). Furthermore, there were no significant differences in core area sizes between times of high and intermediate plant primary productivity ($t = -1.03$, $df = 5$, $p = 0.35$; Fig. 2). Individual core areas and their variations between periods of different plant productivity appeared to differ; i.e.; 95% and 50% home-range sizes differed across time within and between individual were summarized and drawn for qualitative visualisation (Fig. 3, Table 3).

Environmental parameters influencing spatial movement behaviours and habitat selections

Our model suggested that local gemsbok presence was not related to local NDVI values (Table 4) since gemsbok selected areas of intermediate plant growths during the period of highest primary productivity but preferred areas with the highest plant productivity during intermediate and low productivity periods (Table 4). Gemsbok selected areas of low elevation during periods of high primary productivity (Table 4), but selected habitats of high elevations during intermediate and low primary productivity periods (Table 4). Gemsbok predominantly used open-field habitats during our study period ($52.6 \pm 7\%$ occupancy against $26.4 \pm 2.5\%$ hillside and $21.1 \pm 5\%$ riverbeds; mean \pm SD) but significantly increased the use of riverbed environments when plant sources vanished elsewhere (Table 4, Fig 4). The relevance of hillside habitats increased as primary productivity decreased (Table 4, Fig. 4). Distance to riverbeds and roads did not affect the spatial behaviour of gemsbok (Table 4). Habitat selections differed significantly between individuals even when facing similar environmental variations (ID ($n = 8$), variance of random effect estimate = 0.025: SD = 0.16: 95% confidence interval to the standard deviation of the intercept [0 – 0.04]; Table 5). These different proportions of habitat occupancies among individuals was not correlated with both total and core area home range sizes for open-field (95% isopleths: $\rho = -0.38$, $p = 0.36$; 50 % isopleths: $\rho = -0.45$, $p = 0.27$; $n = 8$), hillside (95% isopleths: $\rho = 0.59$, $p = 0.13$; 50 % isopleths: $\rho = -0.59$, $p = 0.13$; $n = 8$) and riverbed habitats (95% isopleths: $\rho = 0.27$, $p = 0.51$; 50 %

isopleths: $\rho = 0.19$, $p = 0.65$; $n = 8$). Also, intra-individual variations of selected habitats among the three periods was neither related to both total nor to core area home-range sizes for open-field (95% isopleths: $\rho = -0.55$, $p = 0.17$; 50 % isopleths: $\rho = -0.24$, $p = 0.58$; $n = 8$), hillside (95% isopleths: $\rho = 0.07$, $p = 0.88$; 50 % isopleths: $\rho = 0.26$, $p = 0.53$; $n = 8$) and riverbed habitats (95% isopleths: $\rho = -0.12$, $p = 0.79$; 50 % isopleths: $\rho = -0.33$, $p = 0.43$; $n = 8$).

DISCUSSION

We assessed the movement ecology of gemsbok in the arid Kunene Region of Namibia using GPS locations of 8 females over a 29 months period. We described the habitat use of gemsbok in relation to three types of habitats which covered major elements of the local landscape and which contrasted in plant primary productivity, vegetation composition, greenness, plant cover, vegetation height and thus visibility, type of ground substrate and elevation. We were interested in how gemsbok would respond in their spatial behaviour to variations in food source availability and habitat characteristics, topography and human disturbances such as roads. Our study revealed that gemsbok did not perform seasonal (i.e. migration) or non-seasonal (temporal relocation) movements, even when plant productivity decreased drastically during periods of severe drought. Furthermore, gemsbok home ranges did not vary in size across the three periods of contrasting plant productivity. However, we observed differences in home-range sizes and spatial behaviour among individuals, suggesting that gemsbok follow distinct individual movement strategies even when encountering similar environmental conditions. In general, the extent of movements was not related to changes in Normalized Differenced Vegetation Index (NDVI) values, a proxy for the greenness of habitats. Instead, gemsbok selected patches with highest plant growth within habitats which they used only during periods of low primary productivity, and preferred areas of intermediate primary productivity when food sources were plentiful. Also, gemsbok always preferred open habitats. However, they also used increasingly riverbeds during periods of low plant productivity. Results further revealed that open-fields provided better visibility for gemsbok and thus a higher likelihood of escaping successfully from potential predators. Contrary to our expectation, we did not observe differences in habitat occupancies between day and night. Lastly, the proximity of roads did not influence the spatial behaviour of gemsbok.

4.1 Suitability of habitats in the Palmwag concession area of the Kunene Region for gemsbok

At our study site, we distinguished between three major habitat types based on abiotic (topographic profile and substrate types) and biotic features (primary productivity, community structures of plants and visibility), namely open-field, riverbed and hillside. NDVI values decreased in all environments from wet to dryer conditions at our study period. We observed the highest primary productivity in riverbeds compared with other habitats, probably due to large trees and evergreen bushes. Riverbeds included less grass species than open-fields and hillsides. The coverage of ground surface plants (excluding trees) decreased in open-fields and hillsides habitats with increasing dryness but not in riverbeds between these two time-periods. Only open-field habitats seemed to continue providing new green grasses forage when drought continued. Therefore, the open-field habitat may still provide high quality areas when overall available food sources decreased in the Kunene area. The higher protein crude content of fresh grass sprouts makes them better suitable for ungulates than dry forage (Cable & Shumway 1966, St-Louis & Côté 2014). Since gemsbok usually prefer fresh grass, and due to the relative resilience of grass greenness even in times of increased aridity (Knight 1991, Verlinden & Masago, 1997), open-field habitats might be preferred over riverbeds as drought periods progressed. In general, evergreen bushes, succulent and weed species and trees, including pods and fruits (Lehmann et al., 2013), were always more abundant in riverbeds than in open-field or hillside habitats. Riverbed plant communities were more stable across time, making riverbeds the most suitable habitat when grass species disappear elsewhere (Lehmann et al., 2013). However, foraging in riverbeds might increase the likelihood of predation, since dense *Colophospermum mopane* forests and thick *Salvadora persicata* and *Cyperus marginatus* bushes and high river banks may facilitate the hunting success of large predators (Thaker et al., 2011).

Open-field and hillside vegetation structures were dominated by grasses. These habitats were therefore more suitable during wetter time periods, since gemsbok almost exclusively feed on grasses when sufficiently available (Skinner and Chimimba, 2005; Lehmann et al., 2013). Additionally, open-field habitats encompass many *Euphorbia damarana* plants, a plant that may significantly contribute to the diet of gemsbok during drought periods (Lehmann et al., 2013). *Boescia sp.* was also abundant in open-fields and thus may have contributed to the overall attractiveness of this habitat for gemsbok (Eloff 1959, Lehmann et al., 2013). Also, gemsbok may travel easier on the smoother substrate and even topography of open-fields than on hillside terrain. The terrain structure of open fields may also better support the vigilance behaviour and thus escape success of gemsboks compared to more challenging habitats such

as hillsides or riverbeds. In conclusion, open-field habitats seem to be the most suitable landscape element for gemsbok, at least during high and intermediate primary productivity periods.

Home-range and habitat selection of gemsbok with increasing drought

We investigated the total home range and core areas of gemsbok in the recreational part of the Palmwag concession over 29 months, covering periods of varying drought. In general, gemsbok moved over relatively stable geographical ranges across time, which concords with the gemsbok population spatial behaviour in the arid Kalahari Transfrontier Park (Knight 1991, Verlinden & Masogo, 1997). As predicted, gemsbok total home ranges did not vary or shift across three different levels of plant productivity, suggesting that temporal changes in plant primary productivity did not fully explain gemsbok spatial behaviours (Verlinden & Masogo, 1997). Contrary to our prediction, core areas of gemsbok did not increase as plant primary productivity decreased. Therefore, gemsbok do not seem to roam across larger areas to follow shifts spatio-temporal variations in food sources, contrary to non-desert dwelling or migratory ungulates species when subject to seasonal environmental changes (Sinclair 1983, McNaughton 1985, Mueller et al., 2008; Owen-Smith & Goodall 2014).

We confirmed from our habitat selection model that NDVI values did not directly influence habitat selection of gemsbok. Gemsbok home-ranges did not shift largely in response to vanishing resources. Yet, gemsbok preferred mostly open-field habitats to riverbed and hillside during periods of high plant primary productivity. As expected, gemsbok selected a larger portion of riverbed habitats in search of food when drought progressed and grass availability decreased in open-field and hillside habitats. The ephemeral rivers of the Palmwag concession are “flash-flood” riverbeds and surface water runs only temporarily. However, the riverbed habitat still had small water bodies patchily distributed, as aridity increased, which may have increased the attractiveness of this habitat for gemsbok (Cain III et al., 2006). Lastly, the substrate of riverbed habitats allows a slower retention of water than the open-field and hillside grounds, which enhances growth of water-dependant plants as compared to grasses for example (Kemp et al., 1997). This could result in a higher density of alternative food sources for gemsbok than in the two other habitats. The use of hillside habitats increased slightly during periods of drought. Topography was one of the main factors linked to habitat selection of our study animals. The topography of hillside habitats seems to be much more challenging for moving gemsbok than open-field. Usually, gemsbok followed game trails which might have constrained their spatial range during foraging. Overall, a

hillside habitat were less attractive for foraging gemsbok than open-field habitats, but were generally preferred over riverbeds.

As predicted, home-ranges analyses and habitat selection model revealed significant differences between the spatial movements of individuals even though animals faced similar, albeit not exactly the same environmental variations. Study animals included all three habitat types in their home ranges and their home ranges also overlapped largely. We observed differences in size and variation of total and core home ranges among individuals. Previous studies on large ungulates illustrated that reproductive status was the main factor explaining differences in home ranges among individuals (Bertrand et al., 1996, Beest et al., 2011). All of our adult females equipped with GPS units were observed to be asynchronously gravid or lactating at least once during our study period, confirming that this species has no regular breeding season in the Kunene region (personal observations, Eloff 1959). These observations also suggest that females do not adjust reproductive effort in response to environmental variations, as it is the case in ungulates of the temperate zone or of more seasonal climates (Simard et al., 2014). In each specific herd of each focal female, calves ranging from a few weeks to several months in age were observed during the entire study period (pers. Observation. D. Lehmann). Unfortunately, we could not pair calves and cows in each group and thus estimates dates of birth or whether offspring were successfully weaned. Hence, we could not control for the potential influence of such life history traits and differences in energy requirements on individual home ranges. However, since all individuals were reproductively active, they shared similar reproductive costs. Therefore, calving cannot fully explain the differences in home-ranges and spatial movement behaviour observed during the overall study period. Alternatively, limits and variations of home ranges and habitat selections might have also been driven by gemsbok individual dietary specialization, with individual specialist being more prone to spatial displacement following the varying availability of their preferred food sources and thus covering larger portion of the environment, while more generalist individual feeding on a larger range of food plants could better exploit smaller areas.

Spatial data of the lion pride roaming in the Palmwag concession would be needed to shed light on the relationship between gemsbok movements and their main predator and to obtain a more comprehensive picture of gemsbok habitat selection criteria including predatory risks.

The tourist visitation rate is quit high throughout the year in this area, and gemsbok are sued to be exposed to human presence and related disturbances (such a noise and smell) throughout their whole lives. Hence, gemsbok showed great tolerance towards roads, which had

unsurprisingly no impact on their spatial behaviour and habitat selection. However, they remained shy towards cars attempting to approach them at close range and usually maintained a minimum distance of about 50 meters, in contrast to other African ungulates in fenced national parks (Sable antelope *Hippotragus niger*; 20 m tolerance to car, Hensman et al., 2013).

Implications for management and conservation

The results of the present study have important implications for management and conservation of ungulates and in particular gemsbok inhabiting the Palmwag Concession area of Kunene Region and its surrounding communal conservancies. Residency of gemsbok in the study area even during periods of drought suggests that management and conservation efforts should concentrate on ensuring that the habitats of gemsbok are maintained and not degraded by human activities. Preference of open-fields where gemsbok fed predominantly on grasses during periods of high primary productivity allows the rare and endemic *Euphorbia damarana* to grow, so that during periods of drought, there is plenty of alternative food available for gemsbok (Lehmann et al., 2013). Furthermore, grazing on open-field habitats during periods of high to intermediate primary productivity allows riverbeds to accumulate more biomass which is used during periods of low productivity; gemsbok spent more time in riverbed habitats during periods of lower plant growth. The conservancies should therefore encourage local communities to protect riverbed habitats; they should not destroy or cut down vegetation in riverbeds especially during periods of drought. The present study showed that total home ranges of gemsbok did not vary or shift over time even though food availability differed largely in time, i.e. gemsbok did not leave the study area even when resources were very low. This implies that gemsbok is predominantly resident in the concession area and hence an important component of the area as a source of income via tourism or hunting under conservancy management. However, conservancies should be encouraged to avoid livestock presence in gemsbok feeding refuges during periods of low primary productivity when food is scarce and not available in some areas such as open-fields to reduce pressure on these habitats. This would reduce the human-wildlife conflict and enable a quick recovery of these habitats following periods of strong drought. Finally, tourism is an important source of income to the local community-based conservancies owning the Palmwag concession. The fact that gemsbok resides permanently in this arid environment and that human disturbance (e.g. human presence, noise from cars) did not drive away local gemsboks indicates that this charismatic ungulate is an excellent wildlife species for tourists to observe.

Conclusion

In this study, we observed relatively few spatial movements of gemsbok related to strong decreases in plant primary productivity and availability in the Palmwag concession of the Kunene Region in Namibia. We showed that NDVI values were not related to the limits, extent and variations of gemsbok home ranges. We further demonstrated that gemsbok trade habitat use between local plant primary productivity, topography and resources accessibility as well as predatory risk. We argue that in-between individual variations in home-ranges and habitat use reflect dietary preference of individuals, which can also be potentially influenced by their specific reproductive status. In conclusion, gemsbok cope with drastic environmental changes by maximizing the utilization of interlacing habitats that differ in biotic and abiotic traits, such as plant community and productivity, topography and openness. The efficient use of these habitats may reduce fitness costs associated with increased spatial movements during times of decreasing plant availability. Thus, gemsbok seems particularly well adapted to survive in arid environments which are prone to unpredictable environmental changes. Our study also provides local community-based conservancies with important knowledge on gemsbok spatio-temporal habitat use, which could help mitigating resource competition with livestock and help conserving habitats in this extreme environment.

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Germany, shall be allowed to make the final draft post-refereeing of this scientific paper freely accessible to the general public on the Internet or in some other form 6 months after publication of the article.

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ASTER GDEM is a product of METI and NASA. The LANDSAT, MODIS TERRA MOD13Q1 and ASTER L1B data products were obtained through the online Data Pool at the NASA Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov/data_access).

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Tables

Table 1: Habitat specific characteristic, vegetation dominance and seasonal variations of the three main habitat types empirically investigated in the recreational area of the Plamwag concession. Percentage estimate of each plants category and greenness are relative to the overall vegetation cover of each habitat. We used Wilcoxon paired rank test to observe significant differences between season of each estimates and for each habitat. P values are listed as follow $p < 0.001$ ***, $p < 0.01$ ** and $p < 0.05$ *

Habitat types	Open-fields (n=33)		Riverbeds (n=15)		Hillsides (n=30)	
	15.07.2011 02.08.2011	28.03.2012 30.04.2012	15.07.2011 02.08.2011	28.03.2012 26.04.2012	16.07.2011 01.08.2011	27.03.2012 29.04.2012
Variables (Mean \pm SD)						
NDVI	1,769.5 \pm 202.5	1,449.6 \pm 269.1 ***	2,019.6 \pm 369.2	1,728.7 \pm 430.3 ***	1727.2 \pm 182.6	1434.9 \pm 209.2 **
Cover (%)	56.4 \pm 24.2	26.6 \pm 18 ***	28 \pm 20	17.3 \pm 14.9	47.5 \pm 25.7	26.3 \pm 20.4 *
Green (%)	7.6 \pm 9.5	42.2 \pm 32.5 ***	22.17 \pm 18.63	40.4 \pm 38.6	12.3 \pm 13.6	31.8 \pm 30
Grass (%)	78.2 \pm 24.6	78.8 \pm 34.2	18 \pm 24.5	18.9 \pm 27.6	64.7 \pm 25.8	65.6 \pm 37
Shrub (%)	10.3 \pm 17.1	9.2 \pm 16.3	51.8 \pm 35.8	54.5 \pm 38.9	30 \pm 24.9	26.9 \pm 26
Succulent (%)	2 \pm 6.6	1.8 \pm 9.6	4.2 \pm 2.9	6.1 \pm 5.2	0.2 \pm 1.4	0.8 \pm 4.6
Other (%)	3.6 \pm 12	0 \pm 0 *	0.6 \pm 2.2	1.7 \pm 6.4	1.6 \pm 8.9	0.3 \pm 2.1
Weeds (%)	0 \pm 0	0 \pm 0	8.2 \pm 3.9	0.3 \pm 1.3	0.6 \pm 3.4	0.3 \pm 1.9
Tree (%)	0.3 \pm 1	1.4 \pm 7	14.7 \pm 7.1	17.1 \pm 6.4	1.5 \pm 2.9	3.1 \pm 8.3
Euphorbia (%)	5.5 \pm 7.6	8.8 \pm 14.4	2.5 \pm 5.7	1.3 \pm 4	1.3 \pm 2.4	2.8 \pm 7
Grass Height (cm)	46 \pm 19	16.3 \pm 13.2 ***	61.5 \pm 31.8	42.5 \pm 34.1 *	45.3 \pm 13.8	19.7 \pm 10.5 ***

Table 2: Gemsbok home range sizes estimates from 4th April 2011 to the 31 August 2013 in the Palmwag concession of the Kunene Region in Namibia. The 95% isopleths represent the total area size used by individual and 50% isopleths the core area utilized by animals during this period.

Home range estimates	MCP (ha)		Kernel (ha)	
	95%	50%	95%	50%
ID -Time lapse				
9278 (03-04-2011 - 31.08.2013)	12223	2600	11398	2324
9259 (05-04-2011 - 31-08-2013)	10200	2844	10345	2252
9258B (15-02-2013 - 31-08-2013)	9389	1677	9773	1769
9215 (04-04-2011 - 31-08-2011)	6082	533	5046	642
9251 (06-04-2011 - 23-08-2102)	4175	831	4200	855
9284 (04-04-2011- 18-08-2011)	3546	1054	4102	877
9258(04-04-2011 to 13-11-2011)	3182	806	3543	902
9257 (06-04-2011 - 31-08-2013)	1045	10403	794	682

Table 3: Spatio-temporal variations of individual gemsbok home range sizes in the Palmwag concession of the Kunene Region. 95% isopleths represent the total area size used by individual. 50% isopleths represent the core area utilized by animals during this period. Home range estimates are reported in Ha for both MCP and Kernel isopleths. Individual 9258 was killed before the lowest plant productivity time period. Individual 9284 died before the intermediate season and individual 9258B was only equipped at the beginning of the lowest plant growth period.

Home-ranges estimates	MCP isopleths						Kernel isopleths					
	High		Intermediate		Low		High		Intermediate		Low	
NDVI time period	95%	50%	95%	50%	95%	50%	95%	50%	95%	50%	95%	50%
Animal ID	95%	50%	95%	50%	95%	50%	95%	50%	95%	50%	95%	50%
9215	2442	291	2339	417	5485	567	3170	388	2367	473	7035	900
9251	3056	790	3908	717	2658	1083	4367	902	4181	761	4261.71	1095
9257	7746	879	8530	981	9224	1055	7732	990	7267	947	7022.24	853
9258	1500	501	2532	610	NA	NA	1976	527	3810	788	NA	NA
9259	8815	2411	10713	2583	9819	2857	11415	2545	11000	2486	10953	2392

CHAPTER IV: SPATIO-TEMPORAL MOVEMENT PATTERNS

9278	5130	1697	8767	1886	11577	2810	6770	1764	9665	2067	13608	2786
9258B	NA	NA	NA	NA	9389	1677	NA	NA	NA	NA	9773	1769
9284	3546	1054	NA	NA	NA	NA	4102.06	877	NA	NA	NA	NA

Table 4: Fixed effects of logistic generalized mixed models explaining spatial movement behaviours of gemsbok from April 2011 to August 2013. Estimate, standard error. Z-value and 95% confidence interval of each factor are reported.

Fixed effects	Estimate	SE	Z-value	2.5%	97.5%
Day_Night	4.45e+00	2.87e+01	0.15	-0.05	0.06
DIST_RIVER	1.11e-02	8.19e-02	0.13	0.00	0.00
DIST_ROAD	-3.04e-03	1.25e-02	-0.24	0.00	0.00
DfNDVI	-9.03e-01	9.19e-02	-9.82	0.00	0.00
MeanNDVI	-9.51e-03	3.90e-02	-0.24	0.00	0.00
SeasonInt	-1.20e+03	8.32e+02	-1.44	-1.75	-0.67
SeasonLow	-9.59e+03	7.85e+02	-12.22	-10.00	-9.16
Elevation	-5.53e+00	7.11e-01	-7.79	-0.01	-0.01
HabitatOpenGrassland	3.48e+02	7.43e+01	4.69	0.22	0.48
HabitatRiverbed	-4.52e+02	1.05e+02	-4.31	-0.64	-0.27
DfNDVI:SeasonInt	8.88e-01	1.23e-01	7.23	0.00	0.00
DfNDVI:SeasonLow	9.46e-01	1.22e-01	7.74	0.00	0.00
SeasonInt:Elevation	1.48e+00	8.82e-01	1.67	0.00	0.00
SeasonLow:Elevation	1.03e+01	8.29e-01	12.42	0.01	0.01
SeasonInt:HabitatOpenGrassland	-4.67e+02	9.52e+01	-4.90	-0.64	-0.29
SeasonLow:HabitatOpenGrassland	-3.71e+02	9.00e+01	-4.12	-0.55	-0.20
SeasonInt:HabitatRiverbed	4.74e+02	1.27e+02	3729.00	0.28	0.72
SeasonLow:HabitatRiverbed	6.85e+02	1.21e+02	5.65	0.48	0.91

Table 5: Spatio-temporal variations of individual gemsbok habitats selection in the Palmwag concession of the Kunene Region. Habitat used by individual are reported in proportion (%), across three different plant primary productivities. OF represents open field, HS represents hillside and RB represents riverbed habitat.

NDVI period	High			Intermediate			Low			Total (mean \pm SD)		
Animal ID /Habitat	OF	HS	RB	OF	HS	RB	OF	HS	RB	OF	HS	RB
9278	47	18	35	41	24	36	47	39	14	45 \pm 4	27 \pm 11	28 \pm 13
9259	67	22	11	47	32	21	47	34	18	54 \pm 12	30 \pm 7	17 \pm 5
9258B	NA	NA	NA	NA	NA	NA	38	25	38	38 \pm 22	25 \pm 14	38 \pm 22
9215	83	14	3	63	26	11	40	15	45	62 \pm 22	18 \pm 7	20 \pm 22
9251	34	57	9	55	26	19	39	51	10	43 \pm 11	45 \pm 17	12 \pm 6
9284	39	23	38	NA	NA	NA	NA	NA	NA	39 \pm 23	23 \pm 13	38 \pm 22
9258	74	23	4	49	26	25	NA	NA	NA	61 \pm 38	24 \pm 14	14 \pm 14
9257	77	16	7	54	19	28	66	11	23	65 \pm 12	15 \pm 4	19 \pm 11

FIGURE CAPTIONS

Fig 1: Mapped distribution of three habitat types in our study area. Dark grey represents riverbeds habitat, grey represents open-fields habitat and light grey represents hillsides habitats. Riverbed, drainage lines and major tributaries are represented in dash lines. Cross lines represent roads. Total home ranges (95% Kernel isopleths) of 8 gemsbok individuals are represented in solid lines and their core areas (50% Kernel isopleths) are represented in dotted lines.

Fig 2: Spatio-temporal variation of gemsbok home range size across three distinct primary productivity time periods. Box plots are given for log-transformed 95% and 50% Kernel isopleths in hectares (ha).

Fig 3: The 50% home range Kernel isopleths of female gemsbok. Core areas for period of high primary productivity are represented with solid lines, for period of intermediate primary productivity in dash lines and for low primary productivity in dotted lines. Dark grey represents riverbeds habitat, grey represents open-fields habitat and light grey represents hillsides habitats. Riverbed, drainage lines and major tributaries are represented in dash lines. Cross lines represent roads. A, B, C, D and E represent individual that lived through the entire time span investigated. F represents home ranges of an individual for both high and intermediate primary productivity time period. G represents the individual home range only for the lowest primary productivity time period and H only for the highest primary productivity time period.

Fig 4: Change in the proportion of GPS locations in riverbeds (dark grey), open-fields (grey) and hillsides (light grey) habitats for height gemsbok individuals across three different time periods of primary productivity.

Figure 1



Figure 2

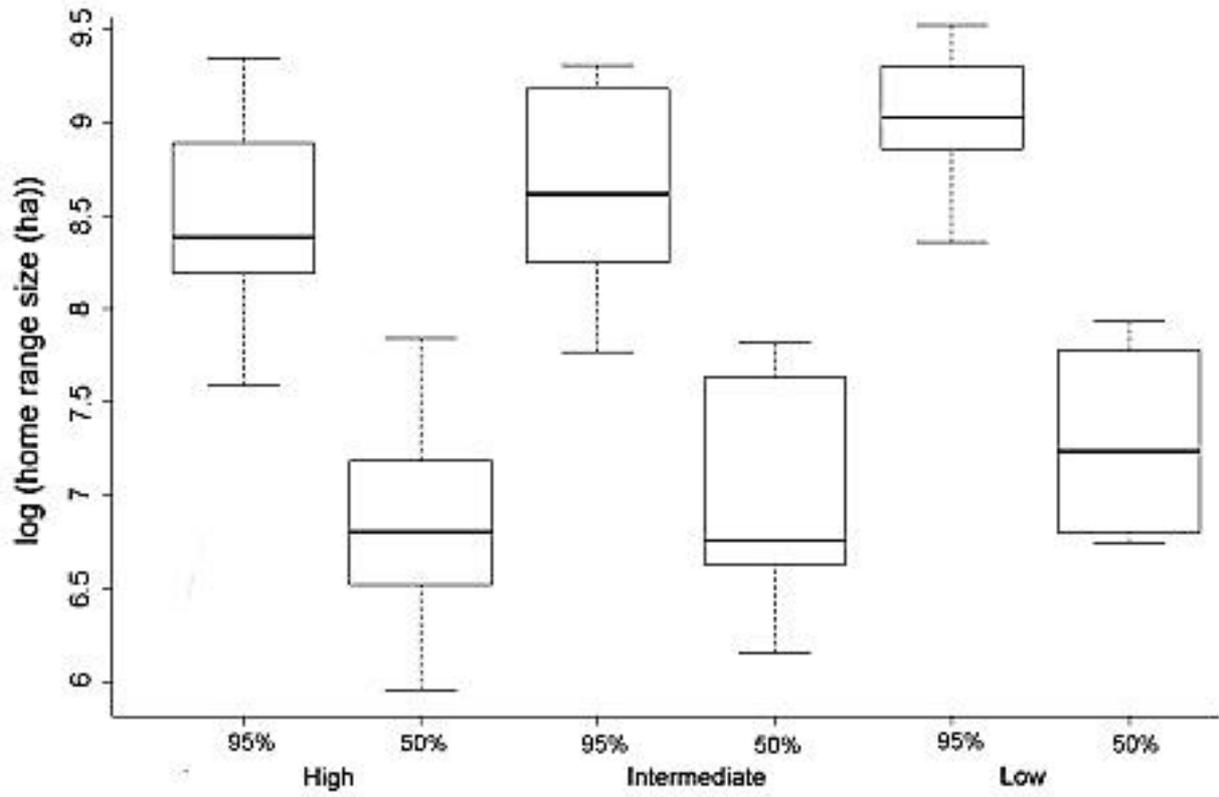


Figure 3

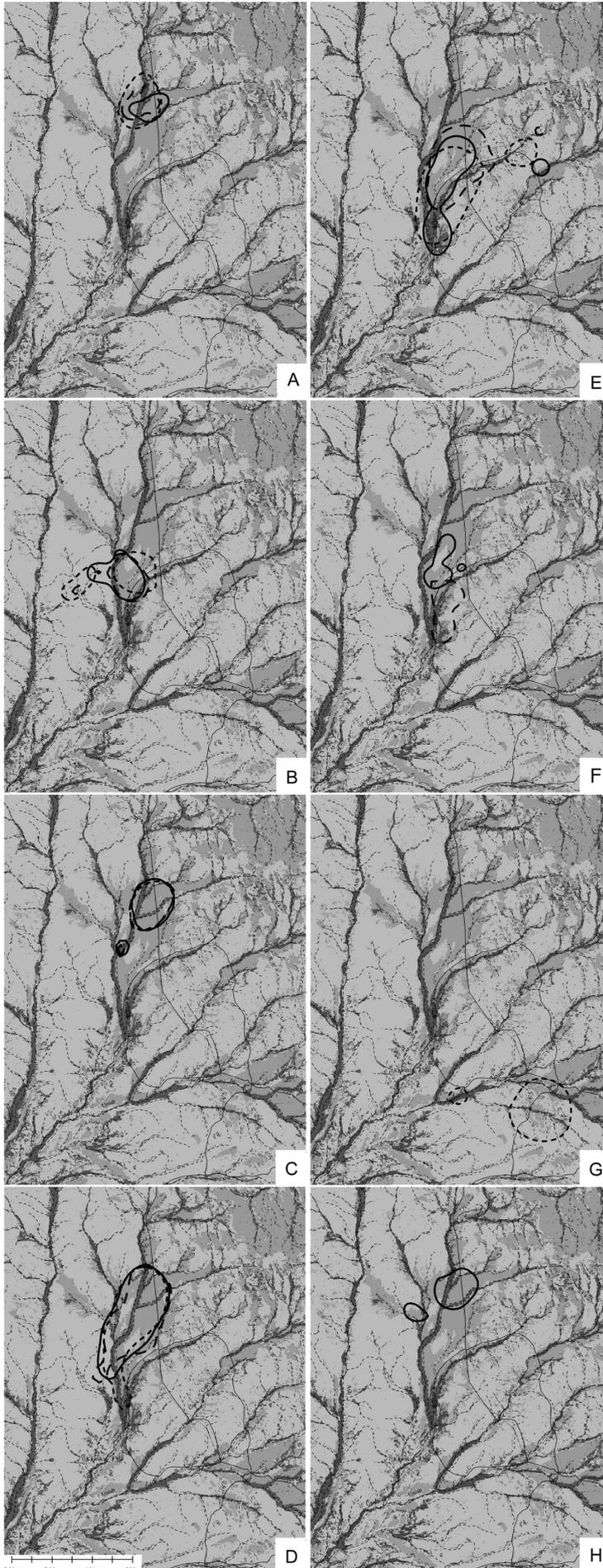
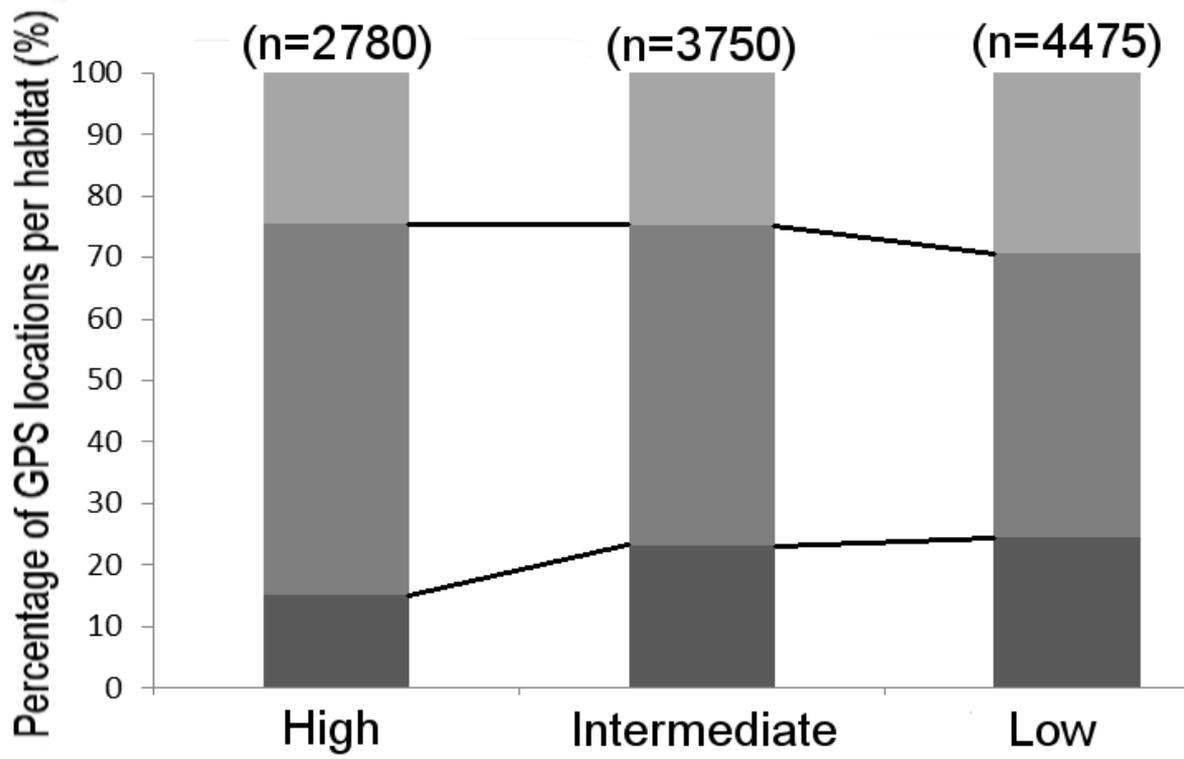


Figure 4



Supplementary material: Additional figure

Movements of desert dwelling gemsbok (*Oryx g. gazella*) in response to spatio-temporal variations in plant productivity

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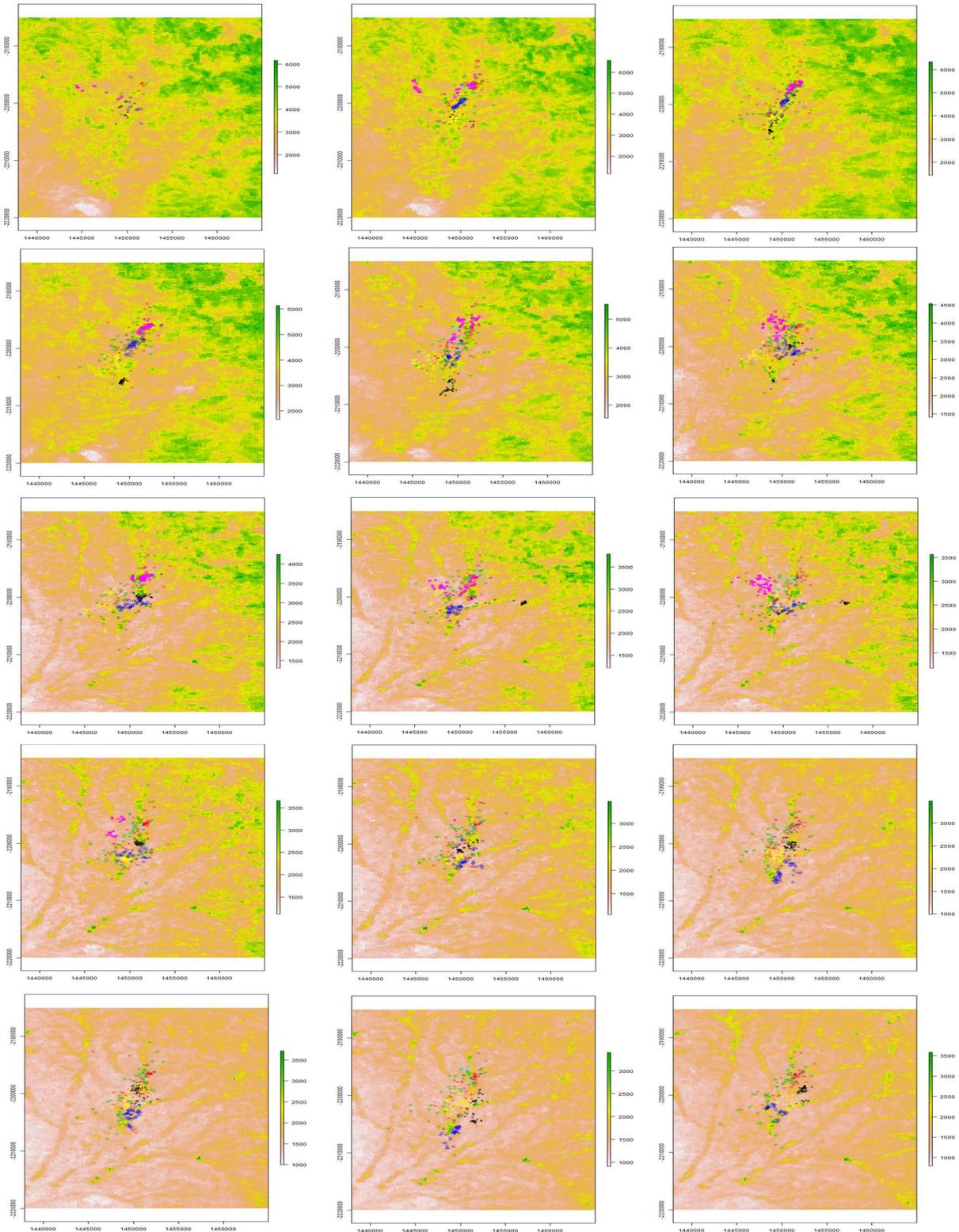
IZW, Alfred-Kowalk-Str. 17, 10315 Berlin, Germany.

Author Contributions: DL and CCV developed the original idea. DL, JC and CB established logistic. DL, JKEM, EG, JC, OHKA, SK, LM and CCV conducted fieldwork. DL analysed the data. DL, JKEM and CCV wrote the manuscript.

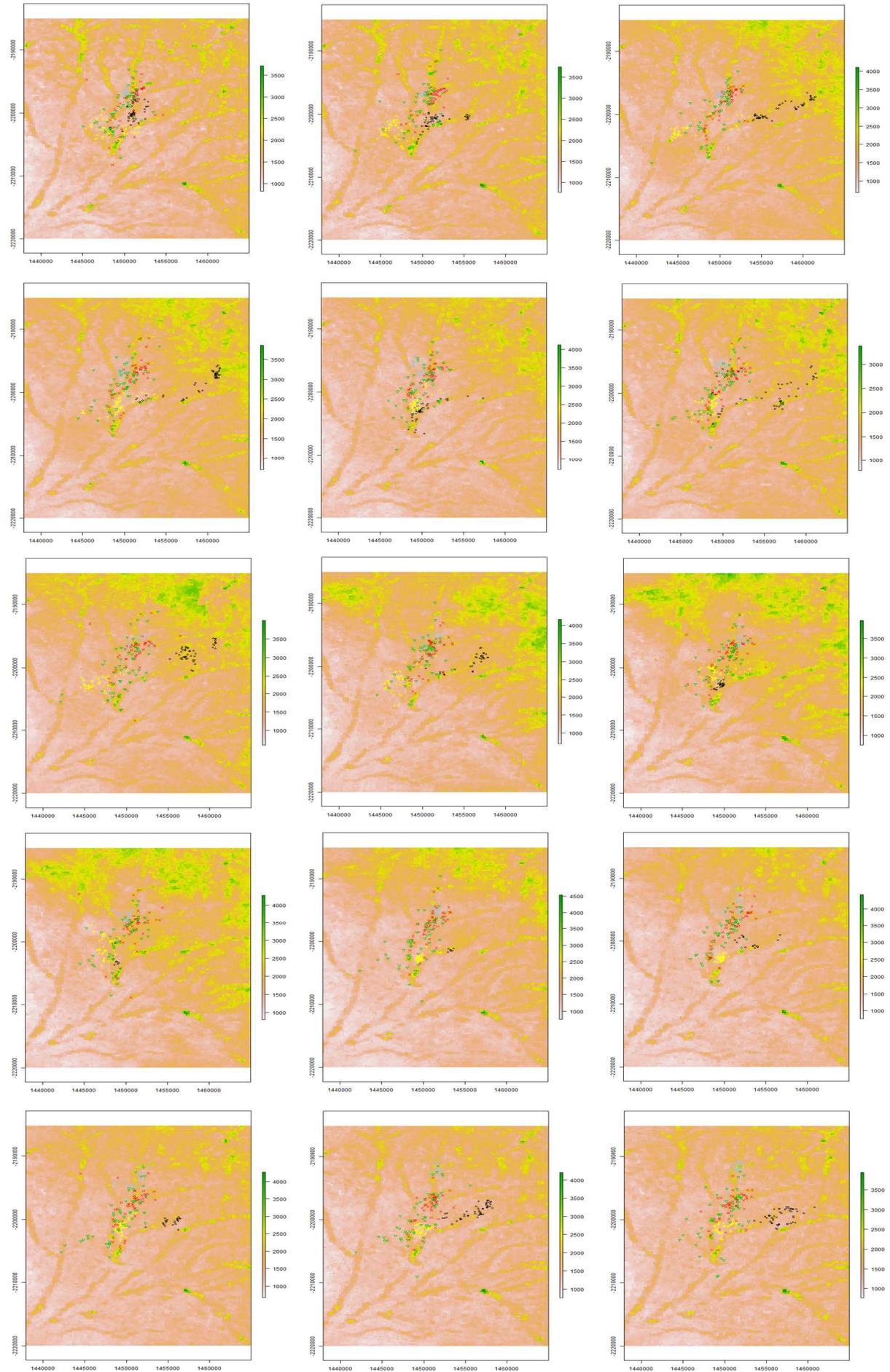
Key words: Desert; resources availability; home range; spatial movement behaviour, habitat suitability, plant productivity, satellite imageries; *Oryx g. gazella*; Kunene; Namibia.

Unpublished

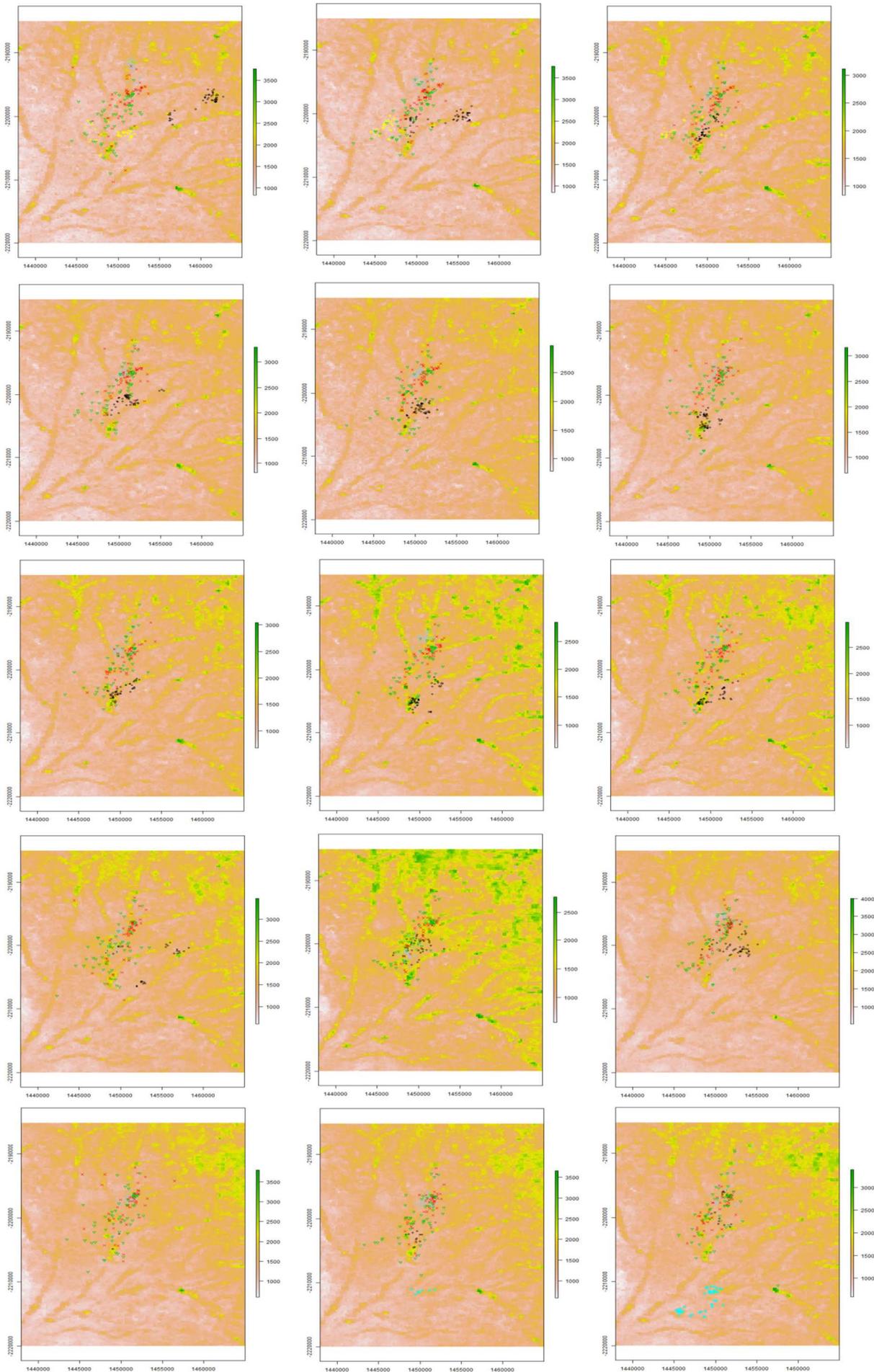
Figure 1: Relationship between movements of eight gemsbok in the Palmwag concession and changes in primary productivity as represented by shades of green. NDVI values of the area are time-spaced from one another by two weeks interval. GPS locations of each gemsbok were projected within the nearest two-week time window picturing NDVI values. The time window depicted in this figure through 59 pictures range from the 6th March 2011 to the 29th August 2013, from left to right, and covers the entire study period.



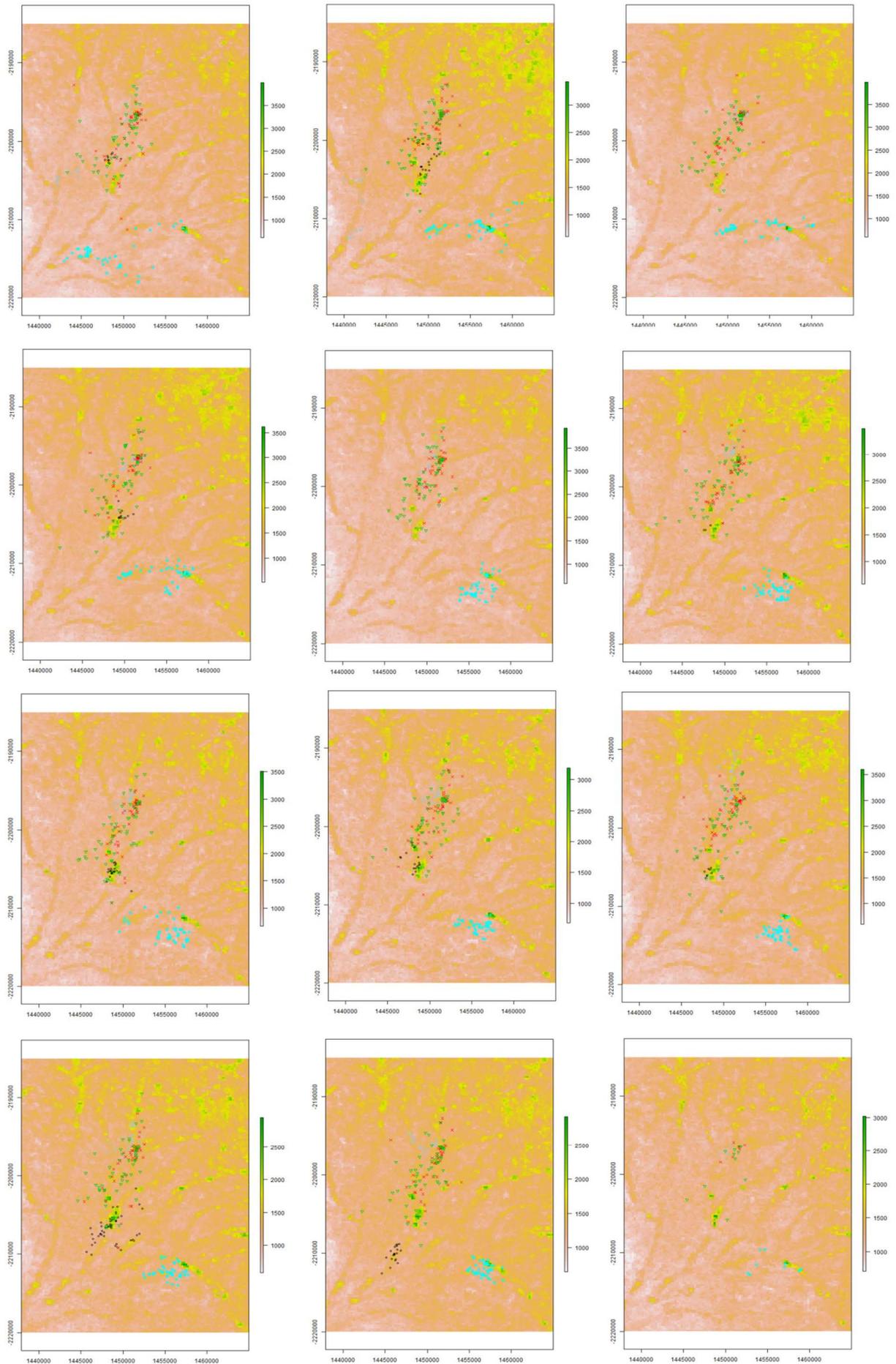
CHAPTER IV: SPATIO-TEMPORAL MOVEMENT PATTERNS



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CHAPTER V: GENERAL DISCUSSION

The general purpose of this dissertation was to gain insights into the dietary and spatial movements strategies of gemsbok and springbok to cope with unpredictable variations of food resources in the Northern section of the Namib Desert of Namibia, the arid Kunene Region. The arid environment of the Kunene region is characterized by erratic, unpredictable and short rainy period, with low and discontinues rainfall, high evaporation rate and high temperature amplitude from night to day. Desert ungulates face constant challenges upon their survival and reproductive success arising from very limited and highly variable food resources availability. In this thesis, I focused on the food resources and habitats used across drastic changes in environmental conditions, at both the population and individual levels, allowing gemsbok and springbok to survive, coexist and thrive in desert environments.

Dietary and spatio-temporal strategies of desert-dwelling ungulate populations in responses to drought

During this study, I inferred the underlying dietary strategies allowing gemsbok and springbok to survive and thrive in the Torra conservancy of the Kunene Region of Namibia from stable isotopes analyses of animal and plant tissues. I analyzed the stable isotope compositions of blood, liver and muscle from 56 gemsbok and 55 springbok across a nineteen months period with two periods of drought and an intermediate period with extreme rainfalls resulting in exceptional plant growth. To infer the diet of these two ungulates species, I collected 551 plant samples from 29 species and grouped them statistically in 13 different food resource types.

In Chapter II, I found that stable isotope ratios in consumer tissues differed between gemsbok and springbok and respective isotopic compositions of these tissues varied annually according to resource availability. The results of my doctoral work suggested that the gemsbok population was dietary plastic, a result that contrasts with previous work on this species in more temperate environment (Cerling *et al.*, 2003; Ambrose & DeNiro, 1986). During drought, gemsbok had a mixed diet of grass and succulent plants (60%), shrubs and trees (30%) and including around 10% of uncertainty, while during periods of intense rainfall, they fed almost exclusively on fresh grass (Chapter II). Interestingly, the results of my isotopic analyses also suggested that gemsbok also fed on *Euphorbia damarana* during dry periods (up to 25% of their diet), a plant which is rich in secondary plant compounds and thus toxic to most mammals. The uncertainties arising from the stable isotope mixing models reported in

Chapter II may be resulting from omitting identifying an alternative food resources during drought but are more likely to arise from missing or inadequate prior information to stable isotope analyses (see last part of this discussion: Limits and prerequisites of stable isotope mixing models). These results are in concordance with habitat use patterns of this species, which I found from data of 8 gemsbok individuals equipped with radio collars over a 29 months period. In Chapter IV I have characterized, using both extensive empirical assessments and computational habitat modelling via satellite imageries, three major habitat types, riverbed, open-field and hillside contrasting in plant primary productivity, vegetation composition, greenness, plant cover, vegetation height, type of ground substrate and topography. I have then found that during drought, these individuals increased their used of river habitat that embedded most of the shrubs and trees in the area, which concord with the observed radical shift of gemsbok toward C3 food resources (Chapter II), compared to period of high primary plant growth, when they extensively used open-field habitats covered with fresh C4 grass (Chapter IV). As well, Chapter IV revealed that gemsbok did not vacate the area when plant productivity decreased drastically during periods of severe drought and that their home-range sizes did not vary across different periods of contrasting plant productivity, suggesting that the extent of the gemsbok movements was not directly related to changes in habitats greenness (as inferred from NDVI values). Thus, the flexibility of gemsbok in adequately using an interlacing set of local habitats, based on a hierarchical selection of environmental parameters such as plant primary productivity and resource accessibility, topography and estimated risk of predation, supports the dietary plasticity of this population observed in Chapter I.

In contrast to gemsbok who adjusts its diet to the rainfall, springbok maintained a predominantly browser diet, independent of dryness, which is in accordance with previous studies using behavioral data (Van Zyl, 1965; Bigalke, 1972; Skinner & Louw, 1996). However, these studies did not provide quantitative estimates of the relative contribution of different food resources to the springbok diet. In this study, I was able to illustrate two distinct dietary strategies in gemsbok and springbok with different body size. Gemsbok and springbok use different types of food resources at any time of our study period, suggesting a segregation of their respective dietary niches (Chapter II). The result is further supported by the fact that isotopic dietary niches of springbok and gemsbok populations, albeit similar in breadth, did not overlap in the isotopic space of the local habitat (Chapter III). This might help avoiding, or reducing, competition for food resources between these two species, which would allow them to better co-exist and thrive in such arid environment (Hanley & Hanley 1982; Gordon

& Illius, 1989). Fundamentally, these results also refute the Jarman-Bell hypothesis (Bell, 1971; Jarman, 1974; Demment & van Soest, 1985; Hofmann, 1989), that expect small antelopes to be more specialised in their diet than larger bodied ungulates. In this doctoral work, I was also able to directly link the inferred gemsbok dietary plasticity (Chapter II) to its spatio-temporal behavior (Chapter III).

Individual dietary and spatio-temporal tactics of desert-dwelling ungulates in responses to drought

During the course of my doctoral work, I observed individual differences in spatial and feeding behaviors of gemsbok. I therefore decided to investigate whether individuals of both springbok and gemsbok population have similar feeding preferences, and whether these differences could be linked to individual spatio-temporal movement patterns in gemsbok (Chapter III & IV). In particular, I was interested to observe the extent of individual dietary variation in relationship to temporal changes in food resource availability. It is not yet fully understood when and to what extent individuals change their diet and, if they do so, if all individuals of a population occupy distinct or similar dietary niches. Using the isotopic compositions of one centimetre increment of one tail hair from 16 gemsbok and 30 springbok each as proxy, I therefore studied the temporal variation in individual isotopic niche space in both gemsbok and springbok (Chapter III). The results of Chapter III suggest that within-individual variation of stable isotope ratios in gemsbok tail hair increments better explained the isotopic niche breadth of the study population than between-individual variation. In contrast, inter- and intra-individual variation in stable isotope ratios contributed equally to the isotopic niche breadth of springbok. Further, the populations of both species consisted of individuals with distinct isotopic niches, suggesting a relatively high degree of individual isotopic specialization in both species, indicating that they might exhibit isotopically distinct dietary niches. At contrary that what I first expected, I found that the size of the isotopic dietary niche of gemsbok did not differ between periods of low and high primary productivity. However, this result concord with the invariability of home-range sizes across contrasting periods of plant primary productivity that I observed in Chapter IV. In contrast, springbok individuals reduced their isotopic dietary niche breadth during periods of high primary productivity, indicating that their apparent dietary generalization observed in Chapter II might in fact be obligate; meaning that they might narrow their dietary preferences towards a smaller set of the most available food resources during period of high primary productivity,

but that they must maintain a similar ratio of C3/C4 food resources in their diet, irrespectively of environmental conditions.

Typically, dietary specialisation can be interpreted as an individual tactic, which arises from the individual specific proprieties and constraints that condition its optimum feeding behavior (Le V. Dit Durell, 2000). Thus, individuals within a population of dietary generalists might largely overlap in their use of food resources, or each individual might specialize towards a subset of the available food resources (Roughgarden, 1972). Dietary specialization may therefore reflect the preferences of an individual and might directly be related to social status, individual ability and morphological or physiological adaptations, individual energy requirements and habitat choices at specific life stages (Le V. Dit Durell, 2000; Estes *et al.*, 2003; Svanbäck & Persson 2004). Such individual tactic might also be driven by seasonal and yearly or habitat differences in food resource availability (Darimont *et al.*, 2009). Individual dietary specialization has been thoroughly investigated and underlined in apex marine predators (Matich *et al.* 2010; Kim *et al.* 2013) and other predatory fishes (Quevedo *et al.*, 2009), for birds (Inger *et al.* 2006; del Rio *et al.* 2009), and for reptiles (Vander Zanden *et al.*, 2010). But the individual component in dietary tactic remain widely overlooked in mammals and mainly addressed predators (Urton & Hobson 2005), omnivores (Newsome *et al.*, 2007), primates (Oelze *et al.*, 2014) or mega-herbivores (Codron *et al.* 2012).

In this doctoral work, my results suggest for the first time the dietary specialisation of individual desert ungulates (Chapter III). For gemsbok, these findings are also supported by the data I obtained from GPS-collared individuals (Chapter IV). The observed differences among individuals in home-range sizes and use of the three major habitat types, riverbed, open-field and hillside, suggest that gemsbok follow distinct individual movement tactics (Chapter IV), in response to similar changes in environmental conditions. These dietary and habitat use specialization might be due to the individual ability of desert ungulates to assimilate different types of food resources and to respond to resource fluctuations by using a combination of interlacing local habitats that differ in plant productivity, plant composition, topography and vegetation cover. Indeed, animal that are able to process toxic secondary plant compounds are more likely to include larger proportion of *Euphoria damarana*, and thus utilize open-field habitat at greater rate than individuals that are unable to do so. Such feeding and spatial individual tactics might help partitioning scarce and unpredictably available food resources and reduce intra-specific competitions. They might also have consequences upon the whole populations, where individuals more prone to include C3 plants in their diets during drought would spend more time foraging in river bed habitat, where the visual detection of

predators by ungulates is made difficult from a dense cover of shrubs and trees (Chapter IV) and thus increase their risks of being predated upon large predators (such as lions). In contrast, individuals specializing in CAM plants during drought would spend relatively more time foraging open-field habitats, where the risk of predation is lower. However, these individuals might face the physiological costs of increased toxic secondary plant compounds in their diet. Therefore, differences in individual risk and benefits may result from their specific individual dietary and spatial tactics, and thus may lead to difference in individual reproductive success and survival in desert environment. In my study, I also observed that isotopic niche segregation occurred between sexes, which may indicate that males and females differ in their spatial and dietary responses to environmental variations.

Relationship between variation in stable isotopes compositions of desert plants and aridity

The analyses of the collected plant materials also provided important information on the variation in stable isotopic signatures of desert plants through drastic changes in aridity. Stable isotopic compositions of C₄ and CAM plant sources varied at a local and restricted geographical scale, between years of extreme drought and exceptional rainfall. Similar variations in isotopic compositions of plant species have previously also been recorded at a larger spatial scale, across environments largely differing in precipitation patterns and environmental conditions (Swap *et al.*, 2004; Liu *et al.*, 2005), with isotopic composition of C₃ plants such as tree and shrubs being mainly affected by seasonal changes. My results might provide important information on the long term proprieties on water use efficiency, stress and dependency of C₄ and CAM plants in such environment. Changes in stable carbon isotope composition of plant material are generally correlated to the ratio of intercellular to ambient CO₂ levels (Ehleringer *et al.*, 1992). This ratio varies according to temperature and aridity (Ehleringer *et al.*, 1992). Thus, the desert plants that significantly vary in their isotopic composition might be the plant species that depend the most on water input and temperature variations, such as the grass *Eriagrostis sp.* and the succulent plant *Zygophyllum simplex*, whereas evergreen shrubs and trees (C₃) as well as *Euphorbia Damarana* (CAM) and *Stipagrostis sp.* (C₄) may be more resistant to drought, since I did not record inter-annual variations in their stable isotope compositions. These findings are of crucial importance for reconstructing animal local diet using stable isotopes analyses. In fact, to obtain the most accurate dietary inferences from stable isotopic mixing models, we must obligatory associate

temporal isotopic signatures of food resources to the specific retrospective time window of the animal tissues investigated.

Adaptations to toxic plants

As aforementioned, gemsbok seem to feed substantially on toxic *Euphorbia damarana* during dry periods. This leafless stem succulent is a dominant evergreen perennial plant in the Kunene region. The photosynthetic pathway of Euphorbiaceae has been classified as crassulacean acid metabolism, a physiological adaptation allowing survival in arid environments (Ehleringer & Monson, 1993; Al-Turki *et al.*, 2014). Desert succulent plants have been described as being tolerant to drought by storing water bodies within its photosynthetic organs that help maintaining a positive daily carbon balance even when cell water content decrease drastically. Furthermore, this plant type avoids drought by physical adaptations maintaining tissue water concentration higher than in soil or ambient air (Levitt, 1980; Nobel, 1984; Mulroy & Rundel, 1977; von Willert, 1992). In contrast to *Zygophyllum simplex*, another dominant succulent species of this environment that stores water in its leaf and therefore more prone to evaporation and desiccation during extended drought period, *Euphorbia damarana* has a thick latex embedded in its branches that contains high concentrations of water, nutrients and plant secondary metabolite compounds.

Euphorbia damarana is well known as being extremely toxic, and inhabitants of the Torra conservancy avoid being in direct contact with the latex secreted by these plants when wounded. The high concentration of secondary metabolite compounds present in the latex of *Euphorbia sp* (such as flavonoids, tannins, alkanes, sterols, terpenoids, as well as skin-irritating and tumor-promoting substances (Acamovic & Brooker, 2005; Jassbi, 2006) is sought to deter herbivore and thus represent anti-predator mechanisms. Such secondary plant metabolite compounds might have negative effects on the physiology, health and reproductive success of animals feeding on plant with high concentration of secondary metabolite compounds (Dearing *et al.*, 2005; Acamovic & Brooker, 2005; Estell, 2010). Furthermore, the ingestion of plant secondary metabolite compounds increased water intake and urine output and decreased urine osmolarity in woodrats, suggesting that diuresis might be a prevalent consequence of secondary metabolites consumption in herbivorous species (Dearing *et al.*, 2001). One striking result of my doctoral thesis was the significant relative contribution of *Euphorbia damarana* to the gemsbok diet during drought time, when the availability of its preferred food sources, such as grass species was reduced. For gemsbok roaming the arid environment of the Kunene region, with temporal and spatial restrictions in accessing surface

water, the potentially increased need for water intake arising from the consumption of *Euphorbia damarana* may have influenced both dietary and spatial foraging behaviors observed during my doctoral work. During my doctoral work, I could not delineate whether individuals that fed more on that plant increased their water intake and consumption. Hence, I suggest to further analyses stable hydrogen and oxygen isotopes ratios in gemsbok and plant tissues, but also from spring, riverbed and rainfall, to observe the relationship between the variations in use of free standing water, preformed water contained in plant forages, water created by oxidizing fat deposits and the quantitative estimates of *Euphorbia damarana* assimilated in the diet of gemsbok during dry periods. The relative consumption of different water sources would then be compared with wetter times, when gemsbok focus almost exclusively on fresh grass growth as food resources. *Euphorbia* species have been known to be use by other herbivores as well, such as browsing Kudu *Tragelaphus strepsiceros* (Hofmann & Stewart, 1972), black rhinoceros *Diceros bicornis bicornis* (Luske *et al.*, 2009) or small antelopes (Prins *et al.*, 2006) but have never been found to be implemented in the diet of a traditionally thought specialist grazer ungulate. Thus, the studied gemsbok population of the Kunene region might have evolved physiological abilities allowing them to process or tolerate the highly toxic secondary compounds of *Euphorbia damarana* and thus, to potentially benefit from its high water and nutritious content.

Yet, it is relatively unknown how ungulates may counteract the negative effects of secondary plant metabolites. Potentially, the evolutionary pressures of the Kunene environment may have selected individual that are able to mitigate or inhibit the adverse effects of alkaloid with their saliva, as previously observed in moose (*Alces alces*) and European reindeer (*Rangifer tarandus*) feeding on the mutualistic association of foliar fungal endophyte *Epichloë festucae*, that produces ergot alkaloids, and its grass-host *Festuca rubra* (Tanentzap *et al.*, 2014). Increased food retention time through the rumen and physical breakdown via mastication may also help fractionating these metabolites, inhibiting their chemical effects on the body and increasing their excretion rates in the urine. The increased size of the renal system and associated loop of Henle characterize desert adapted ungulates and allow the retention and reabsorption of water while creating concentrated urine for excretion (Tracy & Walsberg, 2000; Ostrowsky *et al.*, 2002, 2006). This particular physiological adaptation may as well help counteracting the potential diuresis effects of the plant secondary compounds ingested.

I first suggest performing complete qualitative and quantitative analyses of the *Euphorbia damarana* secondary plant metabolite compounds. I further suggest a comparative experimental study measuring the effects these secondary plant compounds on water

consumption, urine volume, urine osmolarity, metabolic rate, and their effects on internal organs such as liver between two distinct captive gemsbok populations, one originating from the arid Kunene Region and one other originating from a more temperate environment. Such experiment would help shed light on the evolutionary mechanisms allowing gemsbok to successfully overcome toxicity included in its diet.

Implications for local and global management of desert dwelling antelopes

The results of this doctoral work have important implications for management and conservation of ungulates inhabiting desert environments.

The results of this doctoral work provide new insights on the dietary and spatial ecology of two of the most abundant wildlife species inhabiting the arid Kunene Region of Namibia. The complex dietary strategies and tactics of gemsbok and springbok and associated spatial movements of gemsbok, as highlighted in my work, would help managing the sustainable use of different habitat types and defining suitable pastures for livestock in order to reduce direct competition for food resources with wild species (as detailed in Chapter IV). The permanent residency of gemsbok in the area provides excellent wildlife sightings for tourists. Since tourism is a major source of income for the local people, the community-based conservancies must make sure that all habitat types of their environment remain suitable for gemsbok, and springbok, especially while experiencing prolonged period of drought (Chapter IV).

At a more global scale, the new knowledge on dietary and spatial strategies displayed to overcome challenging environmental events, as well as the individualized tactics suggested from the results of my doctoral work might help the conservation efforts of wild ungulates species in environments subject to the process of desertification. This study might also be of crucial importance for the translocation and reintroduction of endangered ungulates species in the wild or within the limits of a wildlife reserve. In general, the reintroduction of animals that were extirpated from their natural habitat into an unfamiliar, but *a priori* similar, environment is a complex operation and present high risks of failure; during which all reintroduced individual might perish (Short *et al.*, 1992; Fischer & Lindemayer, 2000). Previous works aimed toward increasing the success rate of such reintroduction efforts advocate an in-depth observation of the reintroduced animal (Fischer & Lindemayer, 2000; Armstrong & Seddon, 2008); where its ability to cope with the imposed trade-off between the exploration of the new environment and the exploitation of its food resources was closely monitored. The need of such extensive post-release monitoring has been successfully demonstrated in reintroduced

desert-adapted ungulates populations of Persian fallow deer (*Dama mesopotamica*) and Arabian oryx (*Oryx leucoryx*) (Berger-Tal & Saltz, 2014) and Sand gazelle (*Gazella subgutturosa marica*) and Arabian oryx (Islam *et al.*, 2014). However, the results of my doctoral work enhance the relevance of a complete pre-release ecological study of the targeted ungulates species to maximize the success of such operations, especially for species inhabiting these challenging environment that are deserts. The dietary and spatial strategies of ungulates species displayed toward changes of environmental conditions, vegetation structure and community, as well as its ability to reduce or avoid competition for food resources and habitat use with sympatric species must be assessed. Habitat types also need to be meticulously characterized in both natal and adoptive environments and their variations in suitability for the focal species across time must be compared. As well, since individual may differ in their preferred food resources and habitat uses, the degree of individual specialization within the reintroduced population must be investigated beforehand, allowing the selection of an environment that can provide sufficient food resource and habitat diversities to support the determined spectrum of individualized dietary and spatial tactics; and thus maximizing the survival of the entire reintroduced population.

Limits and prerequisites of stable isotope mixing models

Stable isotopes mixing model is one of the main tool used by ecologist to infer the quantitative contribution of food resources to an animal diet and was the main method used in my doctoral work. A simplistic approach of this model can be translated as follow: with two isotopically contrasting food resources (e.g., foods X, Y) and one stable isotope, we obtain an equation of two unknowns (p_X , p_Y) where p_X gives the contribution of the food source X and p_Y gives the contribution of food source Y to the animal diet. Assuming that $(p_X + p_Y) = 1$, such model can easily be solved. However, the degree of complexity of these models, and thus associated uncertainty, increases with the number of food resources, numbers of stable isotopes investigated and prior information such as isotopic discrimination factors (Phillips & Gregg, 2003). Despite the difficulty to match all prerequisites, as in any biological studies, I find it both relevant and informative to discuss them in the following paragraphs, while in Chapter II and III, I have already explained in details how some of these priors information were taken into account while performing stable isotope analyses. The extensive efforts displayed to understand the environmental dynamic of my study area, to define all potential food resources, to characterize habitats as well as the field based behavioral observations of both species, the large samples size of plant and animal tissues, the in-depth record of the

changes in environmental parameters across different periods of contrasting precipitation and plant primary productivity, and the accurate stable isotopes and statistical analyses performed during my doctoral work allowed me to be very confident with the robustness of my results.

Assumptions of stable isotope mixing models

The outputs of stable isotope mixing model infer the contribution of a mixture of assimilated diet, not ingested diet and will assume by default that all consumers have the same diet, that all food resources are equally available, that the turnover rate of consumer tissues match the time period investigated, that all potential food resources were included, and that their isotopic signatures were stable in time. Often, not all of these assumptions are met, but should be investigated prior to performing a mixing model. In Chapter II, I have already well explained how I tackled these assumptions.

Prior information to mixing models

Ideally, the use of stable isotope mixing to reconstruct or infer animal diets and trophic levels would require numerous prerequisites information. These a priori estimates mainly regard the isotopic fractionation between diet and animal tissue, isotopic routing that differ between different consumer tissues, the elemental concentration of each food resource, the assimilation efficiency and digestibility of food resources, as well as information gathered from gut contents, scat analysis or behavioral observations. Incorporating all these prior estimates into the stable isotope mixing model would lead to greater result robustness. However, they are not always available and thus, the inference of animal diet from the outputs of mixing models must always be reported with their uncertainties that potentially arise from missing priors.

Discrimination factors

Discrimination factors (referred as $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ for carbon and nitrogen stable isotopes), are also called fractionation factors and represent the differences in isotopic composition between an animal and its diet (e.g. Stable carbon isotope diet-tissue discrimination factor (ΔX) = $\delta\text{X}_{\text{tissue}} - \delta\text{X}_{\text{diet}}$; where X represents the stable isotope ratios investigated (Caut el al., 2009; Gustine et al., 2014). Isotope fractionation occurs during animal metabolic transformations of food resources during digestion processes. These discrimination factors may vary according to taxon, environment, tissues, ages, food resources and trophic levels (Caut el al., 2009; Lecomte et al., 2011). Due to mass differences between heavy and light stable isotopes, the relative abundance of stable isotopes naturally varies in food resources.

These differences in masses between different isotopes of the same atom cause these isotopes to behave differently in both physical processes and chemical reactions occurring during the assimilation of food nutrients in animal's body. The lighter isotopes (^{12}C and ^{14}N in my study) generally form weaker bonds leading to greater rate of physical fractionation and also react chemically faster than the heavier isotope (^{13}C and ^{15}N) (del Rio & Wolf, 2005). Consequently, heavier isotope excretion rate is smaller than that of lighter ones and typically leave the animal tissues enriched with heavier stable isotopes when compared to the isotopic signatures of its assimilated food resources (del Rio & Wolf, 2005). Thus, raw isotopic data of animal tissues must be corrected by isotopes and tissues specific discrimination factors prior performing stable isotopes analyses, as I did in Chapter II and III.

Dietary switch experiment, discrimination factors and tissue turnover rates

It is quit challenging to define appropriate discrimination factors specific to taxon, environment, animal tissues or food resources, and thus, they often taken from previous studies. Such factors are best defined when performing a dietary switch experiment, where a target species is fed a single or mixed diet of known isotopic signature for a time lapse long enough to allow the investigated tissue to reach a stable isotopic equilibrium state. At this point, the animal diet is switched to a second food resource with contrasting isotopic values. Depending on the turnover rate of the tissue investigated, the isotopic compositions of this tissue will eventually reach another isotopic plateau, from which we can subtract the isotopic value of the new food resources, and thus determine the stable isotope discrimination factor specific to this animal tissue (Lecomte et al., 2011). This method also allows determining the turnover rate of consumer tissues, which is relevant to replace the inferred diet within its corresponding time-window (Lecomte et al., 2011). Unfortunately during my doctoral work, it was not possible to perform such dietary switch experiment. I therefore used stable carbon and nitrogen isotopes discrimination factors specific to blood, liver and muscle of ungulates described by Caut and colleagues (2009). I choose these discrimination factors after performing sensitivity analyses on the raw isotopic values of each tissue of both gemsbok and springbok. However, dissimilarity between the discrimination factors used from literature and the true, unknown, discrimination factors might have occurred, and therefore contributed to uncertainties of the stable isotope mixing models reported in Chapter II.

Isotopic routing, assimilation and digestibility of food resources in animal tissues

Nutrients, and thus stable isotopes of food resources, might be assimilated differently within the animal body, depending on the tissue-specific metabolic assimilation and energy requirements that might vary due to variations in food resources availability (seasonality, changes in environmental conditions) and animals' intrinsic life history traits (fat gain or loss, reproductive status, ontogeny development) (del Rio & Wolf 2005; Gustine *et al.*, 2014). As a result, stable isotope ratios might differ from one tissue to another even though their cells are replaced during a period where the individual ingested the same mixture of food (Gustine *et al.*, 2014). Also, the degree of efficiency in assimilating food resources, as inferred via stable isotope analyses, might differ from the degree of food resource specific digestion rate, as inferred via visual, chemical or DNA food resources analysis in faeces. For example, the higher protein crude content of fresh grass sprouts makes them better suitable for ungulates than dry forage (Cable & Shumway, 1966; St-Louis & Côté, 2014) and we can assume that crude proteins are relatively easier to assimilate into the animal tissues. These two different types of food resources might have different assimilation efficiency, and their dietary isotopic signatures would therefore be incorporated into consumer tissues at different rates. In this doctoral work, it was not possible to determine the efficiency in assimilating different food resources by gemsbok and springbok. Hence, to control for discrepancies that might have occurred between food resources rates of assimilation, I combined three tissues of different turnover rates to obtain mean values in stable carbon and nitrogen isotope ratios that covered a time window relatively long enough to allow assimilation of all ingested food resources into the animal tissues, and thus providing better estimates of the actual diet (Chiaradia *et al.*, 2014). Both this method and the one described above to determine discrimination factors may serve as an alternative if studies face certain limitations leading to the inability to perform prior experiments or analysis. This may especially be important for studies on protected or rare species, or when funding is limited as it was the case during my doctoral work.

Elemental concentration dependence of food resources

Elemental concentration dependence of food resources also need to be determined prior to performing stable isotope mixing models, as the percentage of food resource contribution to the diet might not be the same for all elements examined (e.g., C & N) and these elemental concentrations may also vary between food resources (Phillips & Koch, 2002). Typically, food resources with high concentration of nitrogen contribute more nitrogen relative to carbon than do food resources with lower nitrogen concentration (Phillips & Koch, 2001). Thus, it is

important to incorporate these data into mixing models, as I did in Chapter II, while inferring the relative contribution of different food resources to an animal diet.

Conclusive remarks

In this thesis, I explored the dietary and spatio-temporal behaviors of desert dwelling gemsbok and springbok used to overcome drastic changes in environmental conditions in a desert ecosystem. I investigated the processes underlying dietary and habitat choices in a dynamic framework of population strategies and individualized tactics displayed to cope with the decreased availability of food resources during prolonged periods of drought. For this purpose, I used stable isotope analyses of plant materials and metabolically active and inert animal tissues, GPS telemetry data of gemsbok and both empirical and computational habitat characterizations. These analyses were coupled with complex statistical methods. The identified dietary plasticity of gemsbok driven by changes in food resource availability did not match previous conclusions from the existing literature. In fact, gemsbok has been described as an obligate specialist grazer. However, the results of my doctoral work suggested that this species may dramatically shift its diet from grass to browse and use significant proportion of CAM toxic plants when drought occur and preferred grass food resources are not available. Springbok however followed the predictions arising from previous works and may feed on a broad spectrum of available and contrasting food resources, irrespectively of changes in environmental conditions. Thus, my studies revealed two distinct dietary strategies allowing both species to survive and co-exist in a harsh and unpredictable desert environment.

My investigations of the dietary tactics used by individuals of both species suggested differentiation in diet selected among individual when facing similar environmental changes. Isotopic food niches of the two species were mutually exclusive, but similar in breadth. Within species, my results suggested, that individual of both species may have distinct isotopic niches; being the first time this is shown in ungulates species. This observation suggested an of individualized dietary niche mechanism that potentially reduce intra species competition for food resources and thus may facilitate ungulates' survival in desert environments. To support such complex dietary behaviors, I found that gemsbok responded to resource fluctuations by using an interlacing set of local habitats that differ in plant productivity and composition, topography and vegetation cover. The results of this thesis provide important insights on the complexities of intra- and inter- species relationship of sympatric ungulates species to food resources availability in an unpredictable and challenging environment. They should contribute to our understanding of the conflicts arising between

ungulates populations and within individuals of the same species toward habitats and food resources used to overcome drought. My work shed light on new behavioural processes having implications for both local and global management of desert dwelling antelopes.

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Berlin, den 13.01.2015

David Lehmann