

Intrinsic and extrinsic influences on African large herbivore assemblages and implications for their conservation

by

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Abstract

Understanding the intrinsic and extrinsic influences that affect large herbivore assemblages are important for protected area managers, especially if their current rate of population decline in Africa continues. I aimed to determine how large herbivore species in African grazing ecosystems, respond to intrinsic and extrinsic influences, and the implications of these influences for their conservation.

Conservation planners struggle to reliably reconstruct grazer assemblages for ecological restoration into areas from which they were extirpated, because of the lack of historical distribution data for their regions. Large herbivore population trends in Mkambati Nature Reserve were investigated in order to determine how well grazing herbivores established since introduction, how the success of the introduction was influenced by facilitation and competition, and what the conservation implications are for the ecological restoration. Reconstructing species assemblages for ecological restoration, using biogeographic and biological information, could potentially provide the opportunity for a grazer assemblage which included beneficial facilitatory effects. A well-packed grazer assemblage in turn could potentially lead to an ecosystem which is able to maintain its grazer assemblage structure.

I investigated the factors influencing forage patch use behaviour in Mkambati Nature Reserve. A limited set of traits yielded different patch use rules for different species. Patch use was influenced by anthropogenic impacts such as poaching and changed fire regimes.

Environmental heterogeneity, species' traits, water availability as well as anthropogenic influences, affected large herbivore behaviour. The dominant movement behaviour of large herbivores was Brownian motion, with one to four exponential distributions. When animals faced the trade-off between forage quality and quantity during the dry season, they moved further between forage areas and water sources in order to get to better forage. The number of movement scales, i.e. exponential

step length distributions, increased in more heterogeneous areas, and home range size and fences had a significant affect on the number of movement scales.

Finding suitable forage patches in a heterogeneous landscape, where patches change both spatially and temporally, poses challenges to large herbivores for maintaining energy budgets. I tested whether large herbivores used visual cues to gain *a priori* knowledge about potential higher value foraging patches at a habitat-patch scale. Large grazing herbivores did not use visual cues but rather adapted their movement behaviour to the heterogeneity of the specific landscape.

In conclusion, I demonstrated that intrinsic factors, including individual species' traits can influence the way large herbivores interact with their environment. These factors, in turn, determine how large herbivores react to extrinsic factors such as poaching, fire, artificial water holes and fences which are important to consider in the conservation management of protected areas.

Preface

The work described in this dissertation was carried out in the School of Life Sciences, University of KwaZulu-Natal, Westville Campus, Durban from July 2009 to June 2014 under the supervision of Prof Rob H. Slotow (University of KwaZulu-Natal) and Prof Herbert H.T Prins (Wageningen University and University of KwaZulu-Natal).

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others, it is duly acknowledged in the text.



Jan A. Venter

20 August 2014

DECLARATION 1 - PLAGIARISM

I, Jan Adriaan Venter declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
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DECLARATION 2 - PUBLICATIONS

Details of contribution to publications that form part and/or include research presented in this thesis.

Publication1: VENTER, J.A., PRINS, H.H.T., BALFOUR, D.A., SLOTOW, R., (2014). Reconstructing grazer assemblages for protected area restoration, PLoSONE, 9(3) e90900. (see Appendix A)

Publication2: VENTER, J.A., NABE-NIELSEN, J., PRINS, H.H.T., SLOTOW, R., (2014) Forage patch use by grazing herbivores in a South African grazing ecosystem. Acta Theriologica 59:457–466 (see Appendix A)

Publication 3: VENTER, J.A., PRINS, H.H.T., MASHANOVA, A., DE BOER, W.F., SLOTOW, R., (submitted for review) Surface-water, heterogeneity, large herbivore traits, interspecific competition and fences influence the scales at which large African herbivores move.

Publication 4: VENTER, J.A., PRINS, H.H.T., MASHANOVA, A., SLOTOW, R., (submitted for review) Large grazing herbivores do not use visual cues to find forage patches at a habitat patch scale.

Authors contributions:

JV collected data, processed and analysed the data, and designed and wrote the manuscripts. JN and AM assisted with data analysis. DB and WD provided additional data. HP, RS, DB, JN, AM, WD provided valuable comments on the manuscripts.



Signed:

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Chapter 1: Introduction

1.1 INTRODUCTION

Understanding how intrinsic and extrinsic factors influence the movement and behaviour of large ungulates is important for protected area managers, as these could influence individual species survival abilities as well as have effects on other species and the ecosystem. With many of Africa's large herbivore populations currently in decline (Vie et al. 2009, Craigie et al. 2010), understanding the spatial interaction between animals, the environment and anthropogenic influences is key to the long-term conservation of these populations (Bailey et al. 1996, Viswanathan et al. 1999, Owen-Smith et al. 2010). This is especially important because large herbivore population declines in the last three decades are mainly attributed to anthropogenic (human) impacts (Vie et al. 2009, Craigie et al. 2010).

In this chapter I review the different concepts related to intrinsic and extrinsic influences on African large herbivore assemblages and conservation. I describe how different large herbivores are classified according to their different traits. I also describe the known effect of facilitation and competition on large herbivore population structure and species richness. I introduce the concept of heterogeneity and scale in relation to large herbivore foraging and movement. I introduce patch foraging behaviour to the considerations of this study. I detail animal search movement behaviour in recent and past literature, and how animal movement is affected by predation as well as anthropogenic effects such as poaching, artificial water sources and fences. I introduce the background, status and management practice of protected areas in South Africa. I state the research question, describe the research aim and objectives, and indicate the significance of the study. Finally, I provide an outline of the thesis.

1.2 LARGE MAMMALIAN HERBIVORE FEEDING TYPES

African ecosystems are well known for their exceptional diversity of large mammalian herbivores, of which a large proportion are ruminant bovids with a few non-ruminant equids (Grange et al. 2004). Early studies identified a variety of feeding patterns or feeding type categories among large herbivores (Lamprey 1964, Hofmann and Stewart 1972, Gordon 2003). Broader feeding type categories classify large herbivores into grazers, mixed feeders preferring grass, mixed feeders

preferring browse and browsers (Grunow 1980, McNaughton and Georgiadis 1986, Gordon 2003). The feeding type categories classify ruminants into concentrate selectors, intermediate types and grass/roughage eaters (Hofmann 1989), and non-ruminants as non-selective roughage eaters (Bell 1971).

The feeding strategy of ruminants relies on efficient extraction and use of protein and energy with an inability to maintain a high intake rate and processing capability, resulting in them needing to select for high protein plant components (Bell 1971, Duncan et al. 1990). The non-ruminant is much more tolerant of poor quality forage but must maintain a high rate of intake to be able to survive on this type of food (Bell 1971, Duncan et al. 1990, Bailey et al. 1996). The selectivity of a non-ruminant is considered to be much less intense than that of a ruminant (Bell 1971). In areas with much moribund vegetation, grazing ruminants face particular constraints because nearly all vegetation biomass has a low quality, which reduces food intake rates or increases the need for selectivity (Drescher et al. 2006a, Drescher et al. 2006b, van Langevelde et al. 2008). Some concentrate selectors are morphologically adapted to be very selective at times when suitable forage is scarce (Gordon and Illius 1988, Schuette et al. 1998). Non-ruminants by contrast, are considered to be more tolerant of fibrous food and are less selective (van Soest 1982).

The feeding type of a large herbivore is, therefore, an intrinsic constraint on the habitat that they can effectively use, and provides an understanding as to how one species may be more or less constrained than another in a particular set of environmental conditions. I will include the species' foraging type as one of the intrinsic factors I consider through the thesis.

1.3 FACILITATION AND COMPETITION

Resource competition and facilitation could have a significant effect on the structure and species-richness of large mammal assemblages (Gordon and Illius 1996, Prins and Olf 1998a, Arsenault and Owen-Smith 2002, Olf et al. 2002). Allometric relationships between body size and metabolic rate, and body size and gut capacity, predict that large grazers can survive on lower quality forage but

require higher bulk intake diets, while smaller grazers require higher quality forage, but can cope with lower quantities of it (Demment and Soest 1985). This suggests that, for species within the same guild, those that are more similar in size are likely to occupy a similar niche (Gordon and Illius 1996, Prins and Olf 1998a, Kleynhans et al. 2011). This increases the likelihood of competitive interactions (Wilmshurst et al. 2000, Arsenault and Owen-Smith 2002, Mishra et al. 2002) even though this interaction is modified by the type of digestive system of these ungulates, as ruminants of larger sizes could directly compete with smaller non-ruminants (Illius and Gordon 1992). Ultimately competitive interactions between species could lead to the extinction of the poorer competitor (Prins and Olf 1998a, Olf et al. 2002). When the abundance of one herbivore species decreases its competitive influence declines, and competitive release of other species may occur (Kareiva 1982). This competitive release can cascade into lower trophic levels, as the forage species composition shifts in response to changed foraging behaviour of the released herbivore species (Ripple et al. 2001, Fortin et al. 2005, Lagendijk et al. 2012).

Hutchinson's weight ratio theory predicts that character displacement among sympatric species leads to sequences in which each species is twice the mass of the next (Hutchinson 1959). The higher the species diversity in an area the closer the species packing will be (i.e., difference between body mass amongst species) (Prins and Olf 1998a, Olf et al. 2002, Klop and Prins 2008, Namgail et al. 2010). Closer species packing is expected in complex or highly heterogeneous systems (May 1973) as is the case in African grazing ecosystems (Prins and Olf 1998a, Cromsigt and Olf 2006, Bonyongo and Harris 2007). Grazing by larger animals decreases the grass biomass as they are better suited to handle high biomass/low nutrient quality forage (Bell 1971, Illius and Gordon 1987, Bailey et al. 1996, Prins and Olf 1998a, Murray and Illius 2000). Furthermore, grazing often increases quality and decreases the stem-leaf ratio, thus facilitating improved food intake (Drescher et al. 2006a, Drescher et al. 2006b). These two processes lead to facilitation for smaller grazers (McNaughton 1976, Prins and Olf 1998a), which would maximize both production and utilization in the grass layer (Vesey-FitzGerald 1960, Bell 1971, McNaughton 1976). Such facilitation could result in a higher total grazer biomass in an area, and result in closer species packing (Prins and Olf 1998a, Cromsigt and Olf 2006, Cromsigt et al. 2009).

Extrinsic factors such as competition and facilitation, and the intrinsic effect of body size, therefore have important effects on the structure and species-richness of large mammal assemblages. I will consider the extrinsic factors of competition or facilitation among species, in combination with the intrinsic factor of body size (and its allometric consequences), as to how they affect large herbivore assemblages in the context of protected area restoration.

1.4 HETEROGENEITY AND SCALE

Large herbivores react to spatial patterns in topography and forage distribution i.e. to changes in environmental heterogeneity (Bailey et al. 1996). Resource heterogeneity occurs at different spatial and temporal scales, which make it difficult to predict at which particular scale resource selection by large herbivores might occur (Senft et al. 1987a, Bailey et al. 1996). Scales are defined by rates of foraging processes and ecosystem processes, and the boundaries between units at each scale are defined by animal behaviour (Senft et al. 1987a). The spatial scales of resolution range from the chemical composition of individual plant parts, to the habitat patch, the landscape and the regional system which contains the entire distribution range of a particular animal (Senft et al. 1987a, Bailey et al. 1996). The temporal scale is equally broad, ranging from the amount of time spent feeding on a particular plant to the seasonal shift in range and foraging behaviour (Wilmshurst and Fryxell 1999, Ager et al. 2003). Patch selection is scale-dependent, and although herbivores can often afford to be selective on a fine scale (plant part or species), this may not be the case at coarse scales (habitat scale) due to energetic constraints (van Beest et al. 2010).

Resource heterogeneity at different spatial and temporal scales is an essential extrinsic factor to consider and may influence animals in different ways. For example, in behaviour related to the way large herbivores move to find suitable forage. I will consider the extrinsic factors of heterogeneity and scale with intrinsic factors such as body size on movement behaviour of large herbivores in the context of protected areas and grazing ecosystems.

1.5 PATCH FORAGING BEHAVIOUR

Grazing ungulate's food occurs in discrete patches (Prins 1996, Bailey and Provenza 2008, Prins and Van Langevelde 2008b) that are reasonably homogeneous with respect to some environmental feature (Bailey et al. 1996, Bailey and Provenza 2008, Owen-Smith et al. 2010). Large herbivores feed within forage patches and then move through areas where no or little acceptable food is encountered (Bailey et al. 1996, Prins 1996, Owen-Smith 2005). They use high-value food by adjusting their movements to habitat structure (Fortin 2003, de Knegt et al. 2007). They accelerate when moving between forage patches (Shiple et al. 1996) and spend more time in more rewarding patches (Distel et al. 1995, Courant and Fortin 2012). Normally feeding is the dominant activity within a forage patch, even though ungulates engage in other activities such as walking, resting and drinking (Green and Bear 1990, Ryan and Jordaan 2005, Shannon et al. 2008).

Acceptable forage or habitat patches might not be discernible from a distance, may change with influence from other herbivores (Arsenault and Owen-Smith 2002, Kohi et al. 2011), and/or their location may shift continuously as forage quality changes due to abiotic circumstances (e.g., fire, rainfall or flood recession) (Olf et al. 2002, Archibald and Bond 2004, de Knegt et al. 2008, van Beest et al. 2010). Herbivores are, therefore, faced with a challenge of how to find and choose good quality forage patches in a landscape where the location and quality of such patches are continuously changing (Senft et al. 1987a, Bailey et al. 1996). Large herbivores may use a range of behaviours to enhance their foraging efficiency (Beekman and Prins 1989, Bailey et al. 1996). They may use *a priori* knowledge for memory (from a previous visit to the patch)(Edwards et al. 1996, Dumont and Petit 1998, Fortin 2003, Brooks and Harris 2008) or find new patches through visual cues (Edwards et al. 1997, Howery et al. 2000, Renken et al. 2008). If the presentation of the forage resource is complex (e.g. when forage patches are not well defined), or the distribution of forage patches are likely to change continuously (e.g. when a patch is grazed or the grass sward becomes less suitable for grazing due to ageing), then recalling the location of forage patches may be of limited value (Edwards et al. 1997). In such heterogeneous situations, i.e. in both space and time, the capacity to recognise and assess the potential reward from different forage patches at a distance through visual cues, would promote foraging success (Edwards et al. 1997). A number of field based studies have

linked movement patterns to the use of memory by large herbivores to locate or revisit suitable forage patches (Ramos-Fernandez et al. 2003, Brooks and Harris 2008).

Extrinsic factors could potentially influence patch use behaviour of large herbivores. In addition, the way different species with varied intrinsic traits deals with these factors could be different. This in turn could have impacts on ecosystems and more specifically protected areas. I will consider the influence of extrinsic factors linked to intrinsic traits on patch use behaviour of large herbivores.

1.6 ANIMAL SEARCH MOVEMENT

Animal movement is a core mechanism that influences a number of ecological processes at individual (e.g., home ranges, foraging), population (e.g., metapopulation connectivity, invasion dispersal), community (e.g., assemblages, species coexistence), and ecosystem levels (nutrient cycling, spread of disease, seed dispersal, trampling) (Turchin 1996, Fryxell et al. 2008, Nathan 2008, Delgado et al. 2009). Animal movement matrices can be used to provide perspective on complex biological interactions between individuals and the environment they exist in (Shannon 2005, Birkett et al. 2012, Delsink et al. 2013, Jachowski et al. 2013)

Animal search movements consists of a discrete series of displacements (i.e. step lengths) separated by successive re-orientation events (i.e. turning angles)(Bartumeus et al. 2005). Foraging and searching behaviour have been described using two different types of random movement behaviours, namely random walks (Brownian motion) and Lévy walks (Viswanathan et al. 1996, Viswanathan et al. 1999, Bartumeus et al. 2005, Edwards et al. 2007). Random walks reflect essentially similar steps (on the same spatial scale) separated by orientation and changing turn angles (Viswanathan et al. 1999). Lévy walks reflect clusters of shorter steps that are connected by rare large steps (Edwards et al. 2012). Lévy walkers can outperform Brownian random walkers as they revisit patches far less often, and because the larger steps potentially increase the probability of finding new patches (Viswanathan et al. 1999, Raposo et al. 2009, Viswanathan 2010).

More recently the composite Brownian motion emerged as a strong alternative model to the Lévy walks (Benhamou 2007, de Jager et al. 2011, Schultheiss and Cheng 2011, Jansen et al. 2012, Reynolds 2013), whereby animals switch between two or more Brownian walks, each characterised by an exponential step-length distribution (Jansen et al. 2012, Reynolds 2013). In heterogeneous environments, Brownian walks, at two different scales (composite Brownian motions), e.g., a small-scale area-restricted search (within patches) mixed with a set of large movements (between patches), can be close to optimal (Benhamou 2007). The composite Brownian walk closely resembles a Lévy motion and could also be considered as more optimal or efficient than ordinary Brownian motion (Schultheiss and Cheng 2011, Reynolds 2013).

These recently developed movement models, with the more robust statistical methodology, opened a new avenue to investigate animal movement behaviour. I will use these new models to test a number of hypothesis related to extrinsic and intrinsic factors in large herbivore behaviour.

1.7 ANTHROPOGENIC EFFECTS ON ANIMAL MOVEMENT

Human activities have an influence on animal movement behaviour in various ways including poaching, providing artificial water holes and erecting fencing:

a. Poaching

In Africa, poaching has substantial effects on large herbivore behaviour, population densities, spatial distribution and movement (du Toit 1995, Fischer and Eduard 2007, Vie et al. 2009, Waltert et al. 2009, Craigie et al. 2010). Poaching can cause large herbivores to respond in the same way as they do to predation risk (Morgantini and Hudson 1985, Manor and Saltz 2003, Blom et al. 2004, Proffitt et al. 2009), especially in areas with high poaching incidence (Fischer and Eduard 2007, Hayward 2009b).

Large herbivores avoid becoming prey to predators, by responding to predation risk (Kie 1999, Creel et al. 2005, Fortin et al. 2005, Creel et al. 2008, Valeix et al. 2009b). They display a variety of behavioural responses to predation risk, which may be additive on, or

compensatory for, its effects (Creel et al. 2008). Responses to predation includes altering time budgets (Brown and Kotler 2004, Fortin et al. 2004, Marion et al. 2009, Pays et al. 2011), habitat choice (Festa-Bianchet 1988, Creel et al. 2005, Fortin et al. 2005), grouping (Marion et al. 2009), sensitivity to environmental conditions (Winnie et al. 2006), and diet (Christianson and Creel 2007). Forage resources in risky areas need to be worth the risk in order for herbivores to make use of such areas. Herbivores may choose to ignore predator risk when deciding where to forage, and focus on quality of forage resources and/or other factors instead (Prins 1996). However, they may also respond by avoiding predators (Creel et al. 2005, Valeix et al. 2009a) or by moving out of harm's way when predators are encountered (Fischhoff et al. 2007, Winnie and Creel 2007).

b. Artificial water holes

Abiotic factors such as surface water supplies are the primary determinants of large-scale distribution patterns of large herbivores in Africa and act as constraints within which they have to interact with biotic features such as forage resources (Bailey et al. 1996, Redfern et al. 2003, Smit et al. 2007). In historic times, natural lakes, rivers and streams served as water sources to large herbivores. With the increased presence of man, large herbivore populations in Africa are increasingly confined to protected areas (Carruthers 2008). Early protected area management approaches tended to be "agricultural" in nature (Carruthers 2008), with artificial water holes being established in many parks to provide water for wildlife use, and to maximize access to forage resources in areas with little natural water supplies, especially during the dry season (Owen-Smith 1996, Chamaille-Jammes et al. 2007). Excessive numbers of artificial water holes can, however, potentially have negative effects by: favouring water-dependent ungulates at the expense of rarer species; increasing predator impacts on prey populations; increasing vegetation degradation; worsening animal mortalities during droughts; and decreasing ecosystem stability as well as biodiversity loss (Owen-Smith 1996).

In many cases, large herbivores select different habitats and show a variety of movement patterns during times of low versus high resource availability (Ager et al. 2003, Venter and Watson 2008, Cornélis et al. 2011, Birkett et al. 2012). This is because they become

nutritionally stressed during the dry season when both forage quality and quantity are reduced (Prins 1996). In addition, surface water sources can dry up which influences the trade-off foragers face between nutritional requirements and surface-water constraints when forage quantity is reduced (Redfern et al. 2003). Forage quality and quantity are most affected near water sources, as animals tend to congregate in these areas due to water dependency (Redfern et al. 2003). The reduced forage quantities during dry years forces large herbivores to travel further from water sources to meet their nutritional requirements (Redfern et al. 2003, Venter and Watson 2008). The trade-off between nutritional requirements and surface-water constraints that species face varies according to their water dependence, size, feeding preference and digestive system (Redfern et al. 2003, Smit et al. 2007). For example, in Kruger National Park grazers were found to be more dependent on artificial water sources than browsers and mixed-feeders which were more dependent on rivers (Smit et al. 2007).

c. Fences

Fences are constructed to delineate land ownership, control access, contain animals, prevent the spread of disease and to protect livestock and crops (Boone and Hobbs 2004, Grant 2008). Fences and other barriers to animal movements can effectively limit larger migratory movements of large herbivores (Boone and Hobbs 2004, Loarie et al. 2009, Naidoo et al. 2012), thereby influencing their movement behaviour and altering space use patterns (Vanak et al. 2010). By limiting mobility of large herbivores, fenced areas become fragments within the landscape (Boone and Hobbs 2004). Fences may also entangle or electrocute herbivores, excise important resources needed by species, and allow resident populations to become too dense and potentially cause degradation of the vegetation (Boone and Hobbs 2004).

Extrinsic factors, especially those caused by humans, may have a substantial influence on animal behaviour. This is especially the case in protected areas where managers need to be aware of the possible unintended anthropogenic impacts on large herbivores. I will consider these anthropogenic extrinsic factors and how they relate to large herbivore intrinsic features and behaviour.

1.8 SOUTH AFRICAN PROTECTED AREAS

The Fifth World Parks Congress in Durban, South Africa, announced in September 2003 that the global network of protected areas covers 11.5% of the earth's land surface and provides an invaluable service in shielding ecosystems from destructive use and reducing biodiversity loss (Rodrigues et al. 2004). In South Africa protected areas were conceptualised by the end of the 19th century, due to the seriously depleted state of the wildlife populations caused by unsustainable hunting practises (Carruthers 2008). Since then a large number of formal protected areas have been created which currently covers 6.5% (790 km²) of South Africa's land-surface area (Jackelman et al. 2008). South Africa also has a substantial number of private protected areas and game ranches (van der Waal and Dekker 1998, Lindsey et al. 2009). A private protected area is a property of any size that is managed for the protection of biodiversity and owned or otherwise secured by individuals, communities, corporations, or non-governmental organisations (Jones et al. 2005). During the past 30 years, South Africa's wildlife industry, mainly in the form of private protected areas and game ranches, has developed into a multimillion dollar industry with positive benefits for employment creation, ecotourism and biodiversity (van der Waal and Dekker 1998, Sims-Castley et al. 2005). In South Africa both formal and private protected areas as well as game ranches play an important role in the conservation of large ungulates (van der Waal and Dekker 1998, Sims-Castley et al. 2005) which is reflected in their growing population numbers (Craigie et al. 2010).

1.9 PROTECTED AREA MANAGEMENT

Protected areas are an efficient way of protecting wild animals (Balmford et al. 1995), and, therefore, is an important conservation strategy many countries adopt (Bertzky et al. 2012; Hockings 2003). However, protected areas face an era of great change because they are facing increasingly complex challenges in understanding and conserving their biodiversity features (Venter et al. 2008), which are in mostly driven by anthropogenic influences (Venter et al. 2008, Biggs et al. 2011). Challenges facing protected areas include: alien plant and animal invasions, uncontrolled fires, bush encroachment, artificial water sources, dam building, disease, erosion, land invasion, land use change, solid waste management, mining, isolation, poaching, purposeful species eradication, resource utilization, siltation and tourism (Goodman 2003). Venter et al., (2008) describes the all-encompassing challenge for protected area management as: "To be confident that management

actions taken today are underpinned by reliable information and sound thinking, so that today's actions have a good chance of being successful in future ecological and social climates”.

There is a positive relationship between protected area management planning and performance (Goodman 2003). Systematic conservation planning assists in defining biodiversity conservation targets, evaluate how protected area networks perform with respect to these targets, identify additional areas that might be needed to meet these targets, as well as zoning land use and infrastructure planning within protected areas (Goodman 2003, Holness and Biggs 2011). Strategic protected area management planning, in turn, deals with protected area operations, i.e. day-to-day management actions to achieve operational and organizational goals (Biggs and Rogers 2003). Both these type of management planning processes require a great deal of information and understanding of ecosystem patterns and processes, as well as knowledge on technical management methodologies for implementation (Biggs and Rogers 2003, Goodman 2003).

Adaptive protected area management have been taking a foothold in more prominent protected areas in South Africa over the last decade (Biggs and Rogers 2003, Venter et al. 2008). Adaptive management involves management within certain ecosystem thresholds, which allows management to respond if the set ecosystem threshold is crossed (Biggs and Rogers 2003, Venter et al. 2008, Biggs et al. 2011). Thresholds of potential concern (TPC's) are used as a tool which explicitly set these thresholds, which allows protected area managers to measure when management action needs to be adapted or not (Venter et al. 2008, Biggs et al. 2011, Gaylard and Ferreira 2011). Biophysical and social sciences are critical for TPC formulation, as socio-ecological information forms the cornerstone of its implementation, and protected area management cannot be expected to understand the management meaning clearly, without understanding of the inter-linkages between these (Biggs et al. 2011, Gaylard and Ferreira 2011).

It is, however, important to understand ecological systems within protected areas in order to implement effective conservation action. My study will attempt to improve knowledge about large

herbivore ecology and make a contribution to improve conservation management of large herbivores in protected areas.

1.10 PROTECTED AREA RESTORATION

In many protected areas, the management interventions are intended to restore ecological patterns and processes that have been affected by anthropogenic disruption (Heinen 2002, Suding et al. 2004, Hayward 2009a). A common element of these interventions is to reintroduce 'suitable' species to, or remove 'undesirable' species from protected areas (Griffith et al. 1989, Novellie and Knight 1994, Fischer and Lindenmayer 2000, Atkinson 2001, Gusset et al. 2008). The reintroduction of indigenous herbivores to an ecosystem reintroduces natural disturbance and processes that are thought to support or promote the re-establishment of local diversity (Simenstad et al. 2006). A reintroduction is considered to be successful if it results in a self-sustaining population (Griffith et al. 1989). Reintroductions of large mammals to protected areas have had various levels of success over the last few decades (Griffith et al. 1989, Novellie and Knight 1994, Fischer and Lindenmayer 2000). Conservation authorities opt to use a precautionary approach when deciding which species to introduce or maintain in protected areas, as non-indigenous species are potentially harmful to habitats in which they did not evolve (Spear and Chown 2009, Spear et al. 2011). A critical aspect of this restoration process is the selection of species that are 'suitable'. In many instances, the past is used to determine which species are suitable, assuming that indigenous species are the most appropriate to achieve restoration objectives (List et al. 2007, Hayward 2009a, Boshoff and Kerley 2010).

Incorrect predictions of grazing assemblages not suitable for the restoration of protected areas could potentially have a detrimental influence on biodiversity. My study will attempt to improve methodology to predict the right grazer assemblages for effective protected area restoration.

1.11 PROBLEM STATEMENT

The behaviour ecology of large mammalian herbivores reflects the choices they make expressed in the form of changes in behaviour (Gaillard et al. 2010). Foraging theory concerns activities related to the acquisition of food (Owen-Smith et al. 2010) and this addresses a herbivore's decisions regarding where to search, when to feed, which food types to consume, and when to terminate feeding and move on (Stephens and Krebs 1986, Owen-Smith et al. 2010). The interaction between herbivores and their environment can be detected in their movement behaviour (Frair et al. 2005) which takes place at several scale levels: from steps between foraging stations, to daily movement in home ranges, to seasonal migratory movements (Prins and Van Langevelde 2008a). Advances in GPS tracking (telemetry) technology have made the acquisition of high quality fine scale movement data possible (Hebblewhite and Haydon 2010, Owen-Smith et al. 2010).

Fine scale movement tracking data are useful in studies on habitat selection (Creel et al. 2005, Galanti et al. 2006), home range behaviour (Shannon et al. 2006, Massé and Côté 2012), animal migration (Boone et al. 2006, Hebblewhite and Merrill 2011), ecology and conservation of species (Royer et al. 2005, Hays et al. 2006), conservation impacts (Proffitt et al. 2009, Phipps et al. 2013) and projecting impacts of climate change (Durner et al. 2009). However, many of these studies are characterized by either a focus on the spatial and temporal aspects of the species behaviour, i.e. where and when animals move, or deal with predator-prey or herbivore-forage interactions, and the vast majority deal with a single species only (Fortin et al. 2005, Frair et al. 2005). There are also a myriad of publications that focus on defining search efficiency in movement behaviour (Viswanathan et al. 1996, Viswanathan et al. 1999, Bartumeus 2005, Benhamou 2007, Edwards et al. 2007, Bartumeus 2009, Edwards et al. 2012, Jansen et al. 2012). However, there are few studies which compare movement behaviour among species to understand how their movements are responses to intrinsic and extrinsic influences (Underwood 1983).

Intrinsic factors such as body size, muzzle width, digestive system and feeding type, can influence the way large herbivores interact with their environment (Bell 1971, Bailey et al. 1996, Gordon and Illius 1996, Clauss and Hummel 2005, Prins and Van Langevelde 2008b, Hopcraft et al. 2011). These

factors in turn determine how large herbivores react to extrinsic factors such as seasonal changes of forage resources, competition, predation, poaching, fire, artificial water holes and fences (Prins 1996, Boone and Hobbs 2004, Fischer and Eduard 2007, Creel and Christianson 2008, Valeix et al. 2009a, Waltert et al. 2009, Parrini and Owen-Smith 2010, Sensenig et al. 2010, Vanak et al. 2010, Hassan and Rija 2011). Many studies have focused on either intrinsic or extrinsic factors (see references above) but only few studies have managed to link the two sets of factors, and to then apply it to real-time conservation practice and implications for management (Vanak et al. 2010, Delsink et al. 2013, Jachowski et al. 2013).

This study falls within the 'Conservation Biology Domain' and focuses on determining how different African large herbivore species, affected by various intrinsic factors, respond through movement behaviour, to extrinsic factors in protected areas. I will apply the understanding gained to improve conservation practice and management.

1.12 AIMS AND OBJECTIVES

The aim of the study was to determine how selected African large herbivore species, constrained by various intrinsic factors, respond to key extrinsic factors in protected areas.

The study therefore had the following objectives and sub-objectives:

- 1) To determine how well grazing herbivores have become established since introduction to the main study area, how this was influenced by facilitation and competition (extrinsic factors), and what the implications are for ecological restoration. The sub-objectives were:
 - a. To investigate grazer diversity for the protected area under different conceivable assemblages based on biological principles and/or management practise.
 - b. To assess the results against a separate established grazer assemblage.
 - c. To critically evaluate current conservation management policy regarding wildlife introductions and removals.
 - d. To make recommendations for a future management approach.

- 2) To determine what factors influenced forage patch use behaviour of large herbivores. The sub-objectives were:
 - a. To determine how two species of large herbivores with contrasting feeding type (intrinsic factor), used forage patches in a landscape of nutrient poor, moribund grassland (extrinsic factors), with a mosaic of higher quality forage patches (extrinsic factor), under a gradient of higher and lower poaching risk (extrinsic factor) .
 - b. To determine the differences in patch choice of two species, of differing physiology and anatomy (intrinsic factors), by assessing their choices according to burnt and unburnt patches, poaching risk, distance from previous patch, patch size and patch age (extrinsic factors).
- 3) To determine what factors affected scale of movement of large herbivores. The sub-objectives were:
 - a. To test whether eight African large herbivore species, with a variety of morphological traits (intrinsic factors), coming from landscapes of varying heterogeneity (extrinsic factor), showed a difference in step length distributions and number of scales at which movement takes place.
 - b. To determine if season, morphological traits, home ranges and fencing affected movement scale

To establish if large herbivores with different morphological traits (intrinsic factors) use visual cues when searching for new patches at a habitat patch scale. The aim and objectives deals with extrinsic and intrinsic factors influencing large herbivores and their conservation. As a conservation practitioner (I am an ecologist in a conservation agency), I tried to address relevant and current issues that I deal with on a day-to-day basis, hence, the relatively broad aim. I believe that addressing these questions will produce a valuable piece of work which will contribute to large herbivore conservation.

1.13 SIGNIFICANCE OF THE STUDY

There have been alarming declines in large mammal populations in protected areas in Africa in the last three decades, which are mainly attributed to habitat loss as well as to consumptive use (Vie et al. 2009, Craigie et al. 2010). Effective conservation management of African large ungulates is thus

crucial as conservation managers attempt to simulate natural processes and maintain heterogeneity of ecosystems to promote conservation outcomes in protected areas (Grant et al. 2011). Many studies have focused on intrinsic or extrinsic factors affecting large herbivores (Prins 1996, Boone and Hobbs 2004, Fischer and Eduard 2007) but only few studies have managed to link the two sets of factors and apply this to conservation management practise (Vanak et al. 2010, Delsink et al. 2013, Jachowski et al. 2013). My study focuses on understanding how animals are responding to their environment, whether through community richness, population success, or through different scales of behaviour (patch use or movement path). Importantly, I separate how intrinsic factors expressed through behaviour can influence large herbivores' reactions to extrinsic factors. In addition, the study links the findings to conservation practice and considers the implications for conservation management.

Protected area management agencies often struggle to reliably reconstruct grazer assemblages because of the lack of historical distribution data for their regions. Incorrect predictions of grazing assemblages could potentially affect biodiversity negatively. The linking of ecological patterns and processes to historical distribution data is mentioned by several authors (Boshoff and Kerley 2001, Bernard and Parker 2006), but few examples exist where this was actually done (List et al. 2007, Kuemmerle et al. 2012). This would suggest that conservation authorities are not using the full set of available tools when making management decisions for protected area restoration, especially when historical distribution data are lacking. This is a concern, as depauperate herbivore assemblages could have negative implications for biodiversity and associated patterns and processes (Chapin et al. 2000), both of which are goals for protected area conservation management (Venter et al. 2008). My study addresses this critical flaw in conventional approaches of reconstructing grazer assemblages for protected area ecological restoration and describes a method to overcome this.

Environmental heterogeneity such as in water or forage availability, species traits, as well as anthropogenic influences have a substantial effect on the ecological patterns and processes that shape the distribution of large herbivores (Boone and Hobbs 2004, Loarie et al. 2009, Vanak et al. 2010, Cornélis et al. 2011, Duffy et al. 2011). Understanding how different species in a system vary

their behaviour to meet their biological needs and how they deal with anthropogenic impacts such as poaching, artificial water sources and fences, should underpin such conservation management strategies, as their responses could influence individual species' ability to persist, as well as effecting on other species and the ecosystem (Fortin et al. 2005, Ripple and Beschta 2007). My study addresses an information gap regarding the influence of anthropogenic impacts such as poaching, artificial water sources and fences on large herbivores movement behaviour, contrasted across a number of species. When these factors are ignored by conservation management, this could have negative consequences for protected areas and the biodiversity they contain.

Large grazing herbivores have to deal with a range of challenges in their daily quest for survival. For example, finding a forage patch in a heterogeneous landscape where patches differ in suitability, poses a challenge, especially if individuals have no *a priori* knowledge of the location of the most suitable patches (Senft et al. 1987a, Bailey et al. 1996, Prins 1996). In such heterogeneous situations, in both space and time, the ability to recognise and assess different forage patches at a distance through visual cues, would promote foraging success (Edwards et al. 1997). A number of field based studies have linked movement patterns to the use of memory by large herbivores to locate or revisit suitable forage patches (Ramos-Fernandez et al. 2003, Brooks and Harris 2008), but none have tested if large herbivores use visual cues to find forage patches at a habitat patch scale. My study addresses this question, and provides evidence on the importance of visual cues in foraging at a habitat patch scale.

Information regarding large herbivore movement behaviour and how it is linked to intrinsic and extrinsic factors is essential for effective protected area management (Biggs et al. 2011, Gaylard and Ferreira 2011, Grant et al. 2011), because protected area managers cannot be expected to plan conservation action effectively without understanding cause-and-effect impacts of large herbivore assemblages on ecosystems (Delsink et al. 2013, Jachowski et al. 2013). This study provides important information which could benefit conservation management of large herbivores in protected areas.

1.14 STUDY OUTLINE

The study is presented in six chapters, of which chapters three to six are all written in the format for publication in peer reviewed journals:

Chapter 2: Study areas and species. This chapter described the nature reserves and study species which were investigated during the study. More detail was provided on Mkambati Nature Reserve, where the bulk of my study was performed.

Chapter 3: Reconstructing grazer assemblages for protected area restoration. This part of the study addressed Objective 1, to determine how well grazing herbivores have become established since introduction to Mkambati Nature Reserve, how this was influenced by facilitation and competition, and what the implications are for ecological restoration. I present a situation analysis of the large ungulate introduction and persistence history of Mkambati Nature Reserve, which, in addition, also addressed the conservation management challenge of effectively reconstructing grazer assemblages for protected area restoration purposes.

Chapter 4: Forage patch use by grazing herbivores in a South African grazing ecosystem. Objective 2, to determine what factors influence forage patch use behaviour of large herbivores is addressed. The chapter investigated the factors that influence forage patch use behaviour in Mkambati Nature Reserve. I investigated how non-ruminant zebra (*Equus burchelli*), and ruminant red hartebeest (*Alcelaphus buselaphus camaa*), used burnt patches in a landscape mosaic of forage patches of different nutritional quality, size, inter-patch distances and proximity to poaching risk.

Chapter 5: Extrinsic and intrinsic factors affecting large African herbivores movements. The chapter addressed Objective 3, to determine what factors effect scale of movement of large herbivores. I tested whether eight different African large herbivore species, with different feeding niches and digestive strategies, coming from landscapes of varying heterogeneity, show a difference in step length distribution and movement scale complexity. In addition, I also investigated whether seasonality and anthropogenic influences such as fences, influence movement scale.

Chapter 6: Large grazing herbivores don't use visual cues to find forage patches at a habitat patch scale. Chapter six addressed Objective 4, to establish if large herbivores used visual cues when searching for new patches at a habitat patch scale. I tested whether three large grazing herbivores

with a variety of different traits, improve efficiency when foraging at a heterogeneous habitat patch scale, by using visual cues to gain *a priori* knowledge about potential higher value foraging patches.

Chapter 7: Conclusion. The concluding chapter highlighted the main research findings and how these have addressed the research aim and objectives. I also provided conservation management recommendations and listed potential future research focus areas.

Chapter 2: Study areas and species

2.1 INTRODUCTION

This chapter describes the protected areas and study species which were investigated during the study. More detail is provided on Mkambati Nature Reserve and its associated study species where the bulk of the study was performed.

2.2 STUDY AREAS

All the study areas were formal or private conservation areas in South Africa. They are all managed with two main objectives, i.e. the conservation of biodiversity and providing benefits for employment creation, ecotourism as well as economic development.

2.2.1 Mkambati Nature Reserve

Mkambati Nature Reserve is situated on the coast of Pondoland, in the Eastern Cape Province, South Africa (31°13'-31°20'S and 29°55'-30°04'E). The reserve lies between Port Edward (30 km to the north east) and Port St Johns (59 km to the south west) (Shackleton 1989). The Reserve covers an total area of 7720 ha The reserve forms part of the Pondoland Centre of Plant Endemism, one of 235 sites identified globally as having important botanical biodiversity features (de Villiers and Costello 2013). The reserve is thus regarded as being of both regional and national conservation significance and contains an unique combination of plant species, many of which are rare or endemic to the area (ECPB 2009, de Villiers and Costello 2013). The Mtentu River to the north, the Msikaba River in the south, and approximately 12 km of coastline in the east form the natural boundaries of the reserve. All the surrounding land is owned by communities (Amadiba communities to the north, Lambasi communities to the south and Mkhambati communities to the west) (ECPB 2009). The only non-natural boundary is the border fence to the west.

The climate is sub-tropical with a relatively high humidity (Shackleton et al. 1991). The coastal location adjacent to the warm Agulhas Current provides for minimal differences between minimum and maximum daily temperatures (de Villiers and Costello 2013). The average rainfall is 1 200mm per annum, with the majority falling during spring and summer (September to February) (Shackleton

et al. 1991). On average, June is the driest month with a mean of rainfall 48 mm, and March is the wettest with a mean rainfall of 155 mm (Shackleton et al. 1991). A minimum of 50 mm rain is expected every month. Strong winds can occur with dominant winds blowing from the south-west or north-east (Shackleton et al. 1991).

The surface rock formations of the region are primarily sandstone of marine origin with localised dolerite intrusions (ECPB 2009, de Villiers and Costello 2013). An “island” of this sandstone, extending in a narrow band (15 km wide) from the uMzimkhulu River in southern KwaZulu-Natal to the Mbotyi region, is home to numerous plant species which are uncommon or absent from surrounding substrates (de Villiers and Costello 2013). The dominant soil forms in the reserve are Mispah (65%), Clovelly (16%), Champagne (7%) and Pinedene (2%) (Shackleton 1989) (Figure 2.1A). The soils are also generally deep (> 1.2 m) (Shackleton 1989). Mkambati falls within the Indian Ocean Coastal Belt Biome but also contains small pockets of the Forest Biome (Rutherford et al. 2006b). The two major vegetation types present in Mkambati are Scarp Forest (Mucina and Geldenhuys 2006) and Pondoland-Ugu Sandstone Coastal Sourveld (Mucina et al. 2006d). It consists of approximately 490 ha. of wetland, 662 ha. forest, 40 ha. scrubland and 6250 ha. grassland habitat (Shackleton et al. 1991).

More than 80 % of Mkhambati Nature Reserve is grassland, and it is the only conservation area in the Eastern Cape incorporating a portion of the Pondoland–Natal Sandstone Coastal Sourveld veld type (Mucina et al. 2006d). Shackleton (1991) described six dominant grassland communities within Mkambati (Figure 2.1B). These communities are the *Tristachya leucothrix* - *Loudetia simplex* short grassland community; *Tristachya leucothrix* - *Athrixia phyllicoides* short grassland community; *Festuca costata* - *Albuca setosa* medium grassland community; *Stoebe vulgaris* - *Athanasia calva* short shrub grassland community; *Cymbopogon validus* - *Digitaria natalensis* medium grassland community; and the *Aristida junciformis* - *Helichrysum mixtum* short grassland community (Shackleton et al. 1991). The grasslands are considered to be nutrient poor (Shackleton et al. 1991, Shackleton and Mentis 1992).

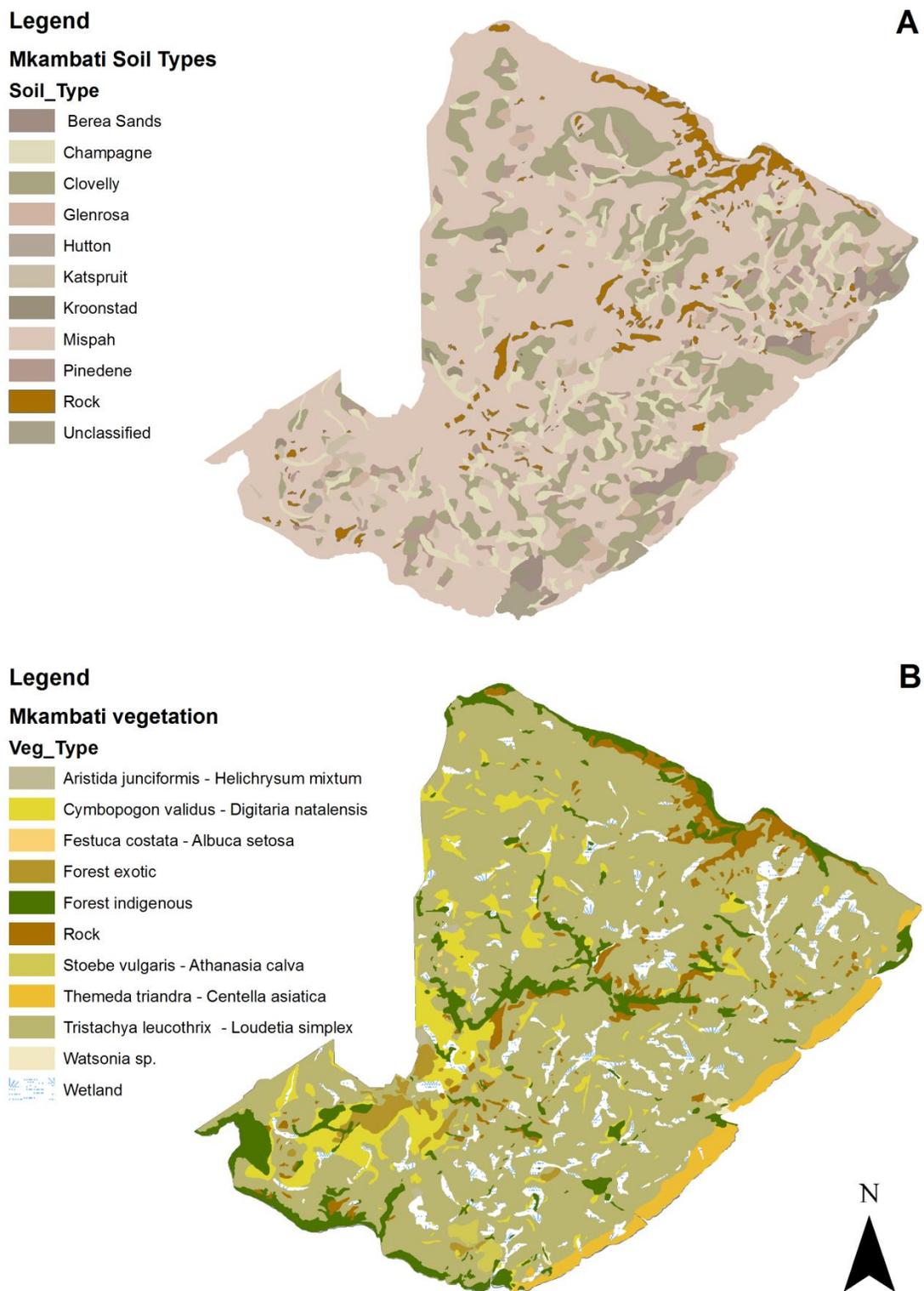


Figure 2.1: The soils (A) and vegetation (B) in Mkambati Nature Reserve (Shackleton 1989)

Fire plays an important ecological role in the grasslands of Mkambati (Shackleton 1989, 1990, Shackleton et al. 1991, Shackleton and Mentis 1992). Grassland fire stimulates temporary regrowth high in crude protein (8.6% compared to 4.6%, in older grassland); phosphorus concentrations (0.1% compared to 0.05%, in older grassland) and dry matter digestibility (38.6% compared to 27.1%, in older grassland) (Shackleton 1989). Nutrient concentrations remain elevated for up to 6 months post burn, by when they are comparable to surrounding unburned grassland (Shackleton and Mentis 1992). Frequent fires cause a continuously changing landscape mosaic of nutrient-rich burnt patches within a matrix of older, moribund grassland and older burnt patches (Figure 2.2). Most fires are ignited by poachers with the aim of attracting animals to certain areas once the new grass starts to grow.

Poachers cross the two major rivers, i.e. the Mtentu river (on the north-eastern boundary) and the Msikaba river (on the south-western boundary), to poach wildlife in Mkambati. Security patrols and field ranger records show that poachers use rifles, dogs and snares, and poaching intensity decreases away from the two major rivers (Eastern Cape Parks and Tourism Agency, unpublished data). This results in concordant danger and fire gradients within Mkambati. There are also prescribed management burns, but due to the high poacher driven fire incidence this rarely takes place. Lightning also causes fires, but only few have been recorded on Mkambati, and none during the study period (Eastern Cape Parks and Tourism Agency, unpublished data).

There are several large herbivore species present in Mkambati, but no large predators (Peinke et al. 2010) (Table 2.1). In total 1 344 medium to large herbivores were introduced to Mkambati in 1979 to create a hunting ranch that was aimed at attracting international clientele (de Villiers and Costello 2013). Species introduced in 1979 were blesbok (*Damaliscus pygargus phillipsi*), blue wildebeest (*Connochaetes taurinus*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazelle*), eland (*Tragelaphus oryx*), red hartebeest (*Alcelaphus buselaphus camaa*), Hartmann's mountain zebra (*Equus zebra hartmannae*), plain's zebra (*Equus burchelli*) and giraffe (*Giraffa camelopardalis*) (de Villiers and Costello 2013).

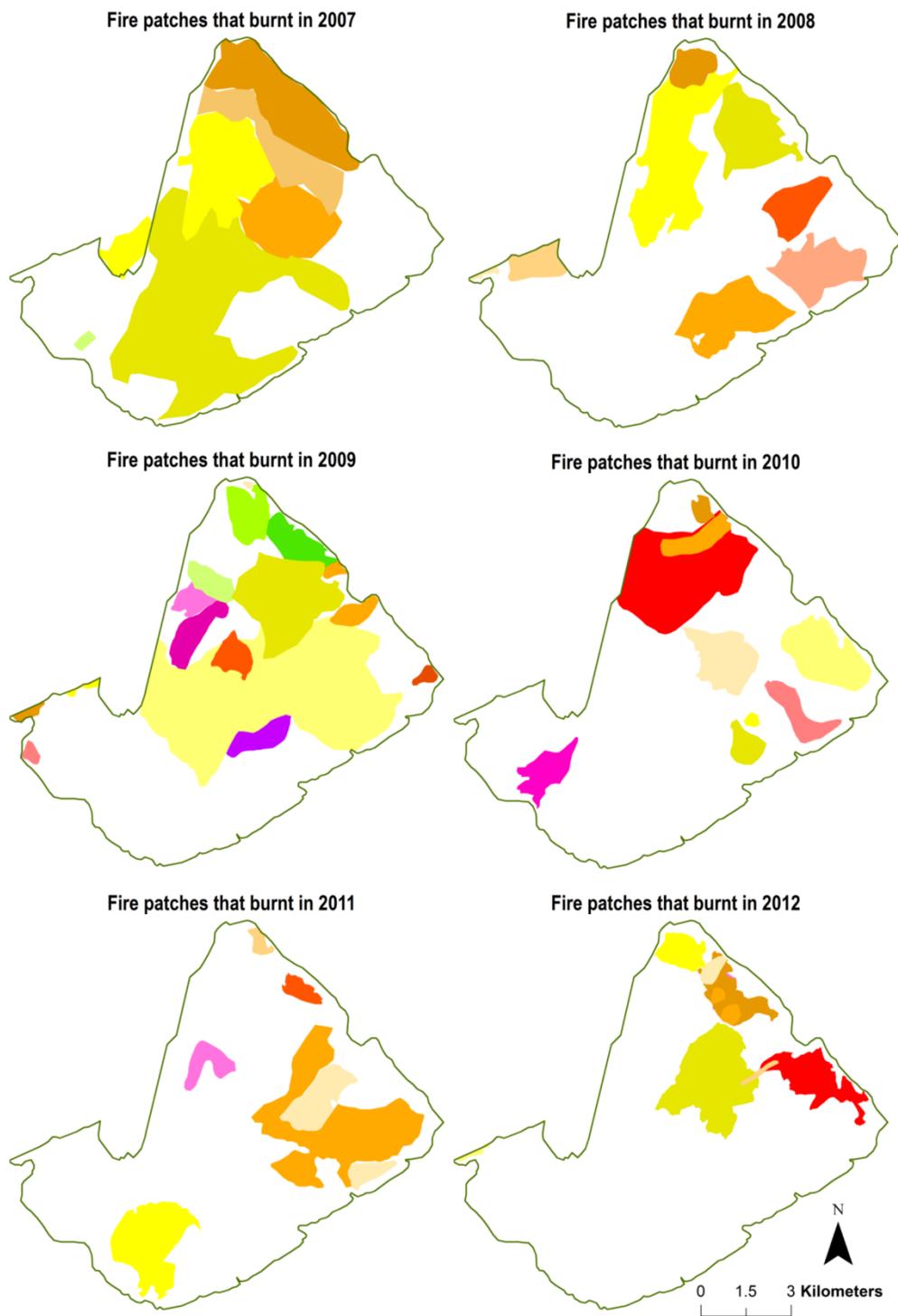


Figure 2.2: The fires recorded in Mkambati Nature Reserve during the study period.

The animals originated mainly from the Kwazulu-Natal Province in South Africa, as well as from Namibia (de Villiers and Costello 2013). Approximately 30% (427) of the introduced animals died shortly after introduction (Sunday Times, South Africa, 24 August 1980) and the cause was attributed to “stress and starvation” (de Villiers and Costello 2013). The hunting venture failed commercially, after which Mkambati’s status was changed to nature reserve (de Villiers and Costello 2013).

Mkambati’s main management objective is to conserve biodiversity and to provide sustainable benefits to local communities through natural resource use and tourism (ECPB 2009). The large mammalian herbivores play a significant role in both these stated objectives.

Table 2.1: The species and population sizes of ungulates present in Mkambati Nature Reserve during the 2010 game census (Peinke et al. 2010).

Species	Mean \pm Standard deviation	Coefficient of variation
Blesbok (<i>Damaliscus pygargus phillipsi</i>)	379 \pm 10	3
Blue wildebeest (<i>Connochaetes taurinus</i>)	2 \pm 0	0
Bushbuck (<i>Tragelaphus scriptus</i>)	6 \pm 3	46
Common duiker (<i>Sylvicapra grimmia</i>)	1 \pm 1	100
Eland (<i>Tragelaphus oryx</i>)	129 \pm 3	2
Impala (<i>Aepyceros melampus</i>)	1 \pm 2	115
Kudu (<i>Tragelaphus strepsiceros</i>)	9 \pm 4	48
Red hartebeest (<i>Alcelaphus buselaphus camaa</i>)	239 \pm 5	5
Southern reedbuck (<i>Redunca arundinum</i>)	25 \pm 17	67
Springbok (<i>Antidorcas marsupialis</i>)	11 \pm 3	30
Plains zebra (<i>Equus burchelli</i>)	328 \pm 28	9

2.2.2 Baviaanskloof Nature Reserve

The Baviaanskloof Nature Reserve (33°26'-33°53' S and 23°35'-24°59' E) is situated in the west of the Eastern Cape Province, South Africa extending from Uitenhage near Port Elizabeth to Willowmore on the Western Cape provincial boundary. The reserve is 211 476 ha. in size and covers most of the Kouga and Baviaanskloof mountain ranges, part of the Tsitsikamma Mountains in the south, and part of the Grootwinterhoek and Elandsrivier Mountains to the east (Venter et al. 2010). The topography of the reserve consists of vast mountain ranges cut by deep river valleys running from east to west. The reserve is situated between the arid Steytlerville karoo and the mesic southern Cape coast. The bulk of the reserve falls within the eastern part of the Fynbos biome (Rutherford et al. 2006b). The northern areas of the reserve fall within the Nama-karoo biome (Mucina et al. 2006b) while the eastern areas mostly fall within the Albany-thicket biome (Hoare et al. 2006). The Forest biome (Mucina and Geldenhuys 2006) is represented in the narrow river valleys and the Grassland biome (Mucina et al. 2006a) on the plateaus of the old African land surface in the Kouga and Baviaanskloof mountain ranges.

The average rainfall varies between the west and the east, with the driest months being January and February and the wettest months being July and August. Several large herbivore species are also present and leopard (*Panthera pardus*) is the only large predator present in the reserve (Reeves et al. 2011). There are currently a small population of Cape mountain zebra (*Equus zebra*)(23 ± 4 ; CV = 16) and medium sized population of African buffalo (*Syncerus caffer*)(244 ± 33 ; CV = 13) present on the reserve (Reeves et al. 2011). Other herbivore species include red hartebeest (*Alcelaphus buselaphus*), eland (*Tragelaphus oryx*), kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*), Cape grysbok (*Raphicerus melanotis*), mountain reedbuck (*Redunca fulvorufula*), grey rhebuck (*Pelea capreolus*), klipspringer (*Oreotragus oreotragus*) and black rhino (*Diceros bicornis*) (Reeves et al. 2011).

2.2.3 Kruger National Park

Kruger National Park (22°20'-25°32' S and 30°53'-32°02' E) is located in the north-eastern South African lowveld spanning the provincial border between the Mpumalanga and Limpopo Provinces (Venter et al. 2003). The national park is approximately 2 300 000 ha. in size, which includes private and provincial reserves; Manyeleti, Makuya, Balule, Letaba, Klaseri, Timbavati, Umbabat and Sabi Sands and stretches from the Crocodile River in the south up to the Levuvhu River in the north (Venter et al. 2003, Delsink et al. 2013). On average, it lies 300 m above sea level and consists mainly of plains with a low to moderate relief (Venter et al. 2003). Kruger falls within two climate zones: the lowveld bushveld zone in the south (rainfall 500-700 mm per annum) and the arid bushveld zone in the north (rainfall 300-500 mm annually)(Venter et al. 2003). Kruger falls within the summer rainfall zone and peaks in January/February (Venter et al. 2003). The whole of Kruger lies within the Savanna biome (Rutherford et al. 2006b), which can be broadly divided into two main ecological types: broad-leaved savanna which occupies approximately 75% and fine-leaved savanna which occupies the remaining 25% (Venter et al. 2003). The savanna varies in structure and composition at the local scale, and the factors that determine its heterogeneity are related mostly to soil, fire, climate and herbivory (du Toit 2003, Venter et al. 2003). The elephant population in Kruger National Park approached a total estimated number of 13 000 in 2006 (Owen-Smith et al. 2006). There is also a large number and variety of ungulate species in the park. The large predators in the park include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), wild dog (*Lycaon pictus*) and brown hyena (*Parahyaena brunnea*) (Pienaar 1969).

2.2.4 Pilanesberg National Park

Pilanesberg National Park (25°8'-25°22' S and 26°57'-27°13' E) is located in the remains of an extinct volcano, in the North-west Province, South Africa (Slotow and Van Dyk 2004). The national park is approximately 55 000 ha. in size. The topography consist of hilly savanna terrain and the vegetation consists of Acacia and broad-leaf bushveld which have thicket to open grassland patches (Slotow and Van Dyk 2004). There is one major river system running southeast through the central part of the park, with one large dam in the centre of the park, and a number of smaller dams scattered throughout the park (Slotow and van Dyk 2001). Rainfall is approximately 630 mm per

annum, and falls in summer, which are very hot (mean temperature 28–31 °C) while the winters are cold (minimum temperature 1–5 °C)(Slotow and van Dyk 2001). The park was proclaimed in 1979, and since then, approximately 6 000 individuals from a variety of wildlife species have been reintroduced to the park (Slotow and van Dyk 2001). The large predators include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), wild dog (*Lycaon pictus*) and brown hyena (*Parahyaena brunnea*) (van Dyk and Slotow 2003).

2.2.5 Mkhuze Game Reserve

The Mkhuze Game Reserve (27°33'–27°48'S and 32°08'–32°25' E) is situated located on the coastal plain east of the Lebombo Mountains in the Kwazulu-Natal Province, South Africa (White and Goodman 2010). The reserve is approximately 45 200 ha. in size. The climate is warm to hot, humid sub-tropical, with two distinct seasons: a warm, dry winter from April to September and a hot, humid summer from October to March (Balme et al. 2010). The average annual rainfall is 550 mm p.a., and the mean monthly temperatures range from 33 °C in January to 19 °C in July (Balme et al. 2010). The dominant habitat type is broad-leafed woodland interspersed with grasslands and wooded grasslands, whith a similar composition throughout the reserve (van Rooyen and Morgan 2007). The reserve supports a number of ungulate species which includes blue wildebeest (*Connochaetes taurinus*), eland (*Tragelaphus oryx*), plains zebra (*Equus burchelli*), and African elephant (*Loxodonta africana*).

2.2.6 iSimangaliso World Heritage Site

The iSimangaliso World Heritage Site (32°20'–32°56' E and 26°51'–28°28' S) is situated on the southeastern coast of Kwazulu-Natal, South Africa (Kwazulu-Natal Nature Conservation Service 1999). The park is 239 566 ha (Kwazulu-Natal Nature Conservation Service 1999) and has a subtropical climate with warm, moist summers (mean annual temperatures exceed 21 °C), and mild dry winters (Kwazulu-Natal Nature Conservation Service 1999). Rainfall at the coast varies from 1 200 to 1 300 mm per annum, with 60% of the rainfall in summer (November to March) and the rest in winter (May to September) (Kwazulu-Natal Nature Conservation Service 1999). The vegetation of the Park is exceptionally diverse, and contains a mosaic of forest, thickets, woodlands, grassland and several

wetland types, the distribution of which is largely determined by topography, moisture regimes and edaphic conditions (Kwazulu-Natal Nature Conservation Service 1999). There are 18 large herbivore species present in the park (Kwazulu-Natal Nature Conservation Service 1999). The large predators in the park include, leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*) and brown hyena (*Parahyaena brunnea*) (Xander Combrink pers. com.).

2.2.7 Mapungubwe National Park

The Mapungubwe National Park (22°10'-22°17' S and 29°08'-29°32'E) is located on the South African side of the confluence of the Shashe and Limpopo rivers in the Limpopo province, South Africa (SANPARKS 2012). The park is 28 168 ha in size (SANPARKS 2012). Mapungubwe comprises an scenic semi-arid landscape with various geological (SANPARKS 2012). The winter is mild with an average daily temperature of 20 °C while summer temperatures can reach up to a maximum of 45 °C (Shrestha et al. 2012). Most rainfall occurs in the summer with an annual mean of 300–400 mm (Shrestha et al. 2012). The main vegetation types that occur in the parks are Musina Mopane Bushveld, Limpopo Ridge Bushveld (Rutherford et al. 2006a) and Subtropical Alluvial Vegetation (Mucina et al. 2006c). Diverse plant communities occur on rocky outcrops surrounded by *Commiphora-Colophospermum* veld on the undulating terrain (Götze 2002). River- and floodplain-associated vegetation includes *Acacia xanthophloea*, *Hyphaene petersiana* palmveld, *Salvadora australis* shrubveld on the floodplains, and *Acacia stuhlmanni* communities on old agricultural fields (Götze 2002). Herbivores in the park include eland (*Tragelaphus oryx*), gemsbok (*Oryx gazella*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymnus*), blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus burchelli*), African elephant (*Loxodonta africana*) and white rhino (*Ceratotherium simum*) (SANPARKS 2012, Shrestha et al. 2012).

2.2.8 Welgevonden Private Game Reserve

Welgevonden Private Game Reserve (24°10'-24°25' S and 27°45'-27°56' E) is a privately owned wildlife reserve, 33 000 ha. in size, situated in the Waterberg region of the Limpopo province, South Africa (Kilian and Bothma 2003). The topography consist of mountainous areas with a number of

plateaus and open plains (Kilian and Bothma 2003). The reserve is situated in a warm and temperate summer rainfall area with a mean annual rainfall of 670 mm (Kilian 2003). The mean annual maximum temperature is 26.5 °C and the mean annual minimum temperature is 11 °C (Kilian 2003). The main vegetation types that occur in the reserve are Central Sandy Bushveld, Western Sandy Bushveld and Waterberg Mountain Bushveld (Rutherford et al. 2006a). The leached, acidic, sandy soils give rise to nutrient-poor, low quality sour veld that cannot support large numbers of herbivores (Kilian 2003). The reserve supports a number of ungulate species which includes blue wildebeest (*Connochaetes taurinus*), red hartebeest (*Alcelaphus buselaphus*), eland (*Tragelaphus oryx*), plains zebra (*Equus burchelli*), white rhino (*Ceratotherium simum*), and African elephant (*Loxodonta africana*) (Kilian 2003). The large predators on the reserve include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*) and brown hyena (*Parahyaena brunnea*) (Kilian 2003, Kilian and Bothma 2003).

2.2.9 Asante Sana Private Game Reserve

Asante Sana Private Game Reserve (32°15'-32°21' S; 24°52'-25°04'E) is a privately owned hunting and game reserve 10 700 ha. in size, situated near the town of Graaff-Reinet, Eastern Cape province, South Africa (Kok 2011). Prior to the establishment of the game reserve, the land use was small livestock farming (Kok 2011). In 1995, the stock farms were converted into a private game reserve (Kok 2011). Thereafter, various species like kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), lechwe (*Kobus leche*), springbok (*Antidorcas marsupialis*), African elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), and giraffe (*Giraffa camelopardalis*) were introduced onto the reserve (Kok 2011, Shrestha et al. 2012). The mean annual precipitation for a ten-year period (2001-2010) was 287 mm (Kok 2011). Rainfall peaks during the warm summer months of January to March and is at its lowest during June to August (Kok 2011). The winters are cold with an average 24 hr. temperature of 13 °C and the summer hot with maximum ambient temperatures of 38 °C (Shrestha et al. 2012). The reserve is mountainous and altitudes range between 980 m to 2 320 m above sea level (Kok 2011). The vegetation consists of two major vegetation units, Karoo Escarpment Grassland and Camdeboo Escarpment Thicket (Mucina et al. 2006b). These vegetation units roughly coincide with the altitudinal

ranges found throughout the park. The Karoo Escarpment Grassland is associated with higher (> 1300 m) altitude and Camdeboo Escarpment Thicket with lower (< 1300 m) altitudes (Kok 2011).

2.3 STUDY SPECIES

A number of species with different intrinsic traits, i.e. feeding type, digestive strategy and muzzle width have been included in the study in order to achieve the research objectives. The species included in this study were the impala, red hartebeest, blue wildebeest, eland, African buffalo, plains zebra, Cape mountain zebra and African elephant.

2.3.1 Impala (*Aepyceros melampus*)

The impala (*Aepyceros melampus melampus*, Lichtenstein 1812) is one of six subspecies of which only two occur in southern Africa (Skinner and Chimimba 2005). The other subspecies in this region is the black-faced impala (*A. melampus petersi*) (Skinner and Chimimba 2005). Impala are distributed widely in the eastern woodlands of Africa, from central Kenya to South Africa (Skinner and Chimimba 2005). Impala associate with open woodland (Skinner and Chimimba 2005) and they are classified as intermediate mixed feeders (Hofmann 1989) which make use of both graze and browse (Okello et al. 2002). The amount of browse and graze consumed is dependent on seasonal rainfall patterns and the associated availability of green grass (Skinner and Chimimba 2005). They are ruminants with a relatively selective foraging strategy that is associated with a high foraging efficiency, cropping rate and low intake rate (Okello et al. 2002). They are water dependent and rarely move far from surface water (Young 1972, Skinner and Chimimba 2005).

2.3.2 Red hartebeest (*Alcelaphus buselaphus*)

The red hartebeest (*Alcelaphus buselaphus*, Pallas, 1766) is one of two species of the *Alcelaphus* genus (Skinner and Chimimba 2005). Several subspecies are recognized i.e. *A. b. swayni* from Ethiopia; *A. b. tora* from Sudan, Eritrea and Ethiopia; and *A. b. major* from West Africa (Skinner and Chimimba 2005). In southern Africa, they occur in Namibia, Botswana, Zimbabwe and South Africa. Red hartebeest are considered to be predominantly selective grazers that will make use of browse

under limited resource conditions (Kilian, 1993; Murrey, 1993). Red hartebeest prefer open habitat and mainly occur in grasslands of various types (Skinner and Chimimba 2005). In areas with much moribund vegetation, grazing ruminants such as the red hartebeest face particular constraints because nearly all vegetation biomass has a low quality, which reduces food intake rates (Drescher et al. 2006a, Drescher et al. 2006b, van Langevelde et al. 2008). The hartebeest is an example of a concentrate selector; its skull morphology is specially adapted to be very selective at times when good forage is scarce (Schuette et al. 1998).

2.3.3 Blue wildebeest (*Connochaetes taurinus*)

The blue wildebeest (*Connochaetes taurinus*, Burchell 1823) belongs to the tribe Alcelaphini with two species in the genus that also include the black wildebeest *C. gnou* (Skinner and Chimimba 2005). Blue wildebeest are widespread and occur in most of the savanna areas of Africa (Skinner and Chimimba 2005). They are associated with woodlands and the availability of shade and drinking water are considered to be important for their survival (Skinner and Chimimba 2005). Blue wildebeest move on a seasonal basis in order to find suitable forage in the form of short grass (Ben-Shahar and Coe 1992, Skinner and Chimimba 2005) and mass migrations in search of suitable grazing are not uncommon (Bell 1971). They are predominantly grazers with a preference for short green grazing lawns (Attwell 1977, Skinner and Chimimba 2005). Their ability to make use of short grass is reflected in their wide muzzle and efficient tongue which make them capable of cropping short grass but less effective in tall grass environments (Ego et al. 2003).

2.3.4 Eland (*Tragelaphus oryx*)

The eland, (*Tragelaphus oryx*, Pallas, 1766) belongs to the tribe Tragelaphini (spiral-horned antelope), with three subspecies of the common eland being listed, *T. o. oryx* occupying the southern parts of the distribution range (South Africa, Botswana and Namibia), *T. o. livingstoni* the central parts (Angola, Zambia, Democratic Republic of the Congo, Zimbabwe, Mozambique and Malawi) and *T. o. pattersonianus* occupying the northern parts extending into the Somali arid areas (Ansell 1972). Eland have a wide distribution in Africa, ranging from south-eastern Sudan and south-western Ethiopia southwards (Skinner and Chimimba 2005). Historically eland occurred throughout the

Eastern Cape including the former Transkei area (Boshoff et al. 2007, Skead 2007). Eland are considered to be mixed feeders preferring browse (Hofmann and Stewart 1972, Watson and Owen-Smith 2000). Due to their ability to utilize a wide variety of food resources and their independence of surface drinking water they are able to make use of several different habitats (Watson and Owen-Smith 2000).

2.3.5 African buffalo (*Syncerus caffer*)

The African buffalo (*Syncerus caffer*, Sparrman 1779) is the only extant member of the *Syncerus* genus (Kingdon 1997). Three subspecies are recognized: the large black Cape buffalo, *Syncerus caffer caffer*, the small red forest buffalo, *Syncerus caffer nanus*, and an intermediate form from West Africa, *Syncerus caffer brachyceros* (Kingdon 1997). A fourth subspecies, *Syncerus caffer mathewsi*, the relic "mountain buffalo" is recognized by some authorities (Kingdon 1997). It is reported that there is considerable intergradation of the different subspecies where their distribution ranges overlap (Skinner and Chimimba 2005). Buffalo's former range, before the influence of European settlers, stretched over most of southern Africa and Angola, through central and east Africa to the southern borders of Sudan and Ethiopia (Sinclair 1977). African buffalo are still present in most of the southern African countries such as Namibia, Botswana, Zimbabwe, Mozambique and South Africa (Winterbach 1998). The digestive system of a buffalo is typical of bulk and roughage grazers, and is not suitable for a diet of browse (Hofmann 1989), but they will occasionally take browse (Novellie et al. 1991, Venter and Watson 2008).

2.3.6 Plains zebra (*Equus burchelli*)

The plains zebra (*Equus burchelli*, Gray, 1824) represents one of four species in the genus which forms part of the family *Equidae* under the order *Perissodactyla* (Bronner et al. 2003). The species occurs in most parts of southern Africa where it has been introduced in various protected areas and game farms (Skinner and Chimimba 2005). Plains zebra are gregarious, organized in small family groups headed by a stallion with a number of mares and their foals (Skinner and Chimimba 2005). They are water dependent and normally stay within 10-12 km from the nearest water source (Skinner and Chimimba 2005). Plains zebra are described as a savanna species which prefer more open

areas in woodland habitats (Skinner and Chimimba 2005). It is well known that they undertake daily and seasonal movements in order to find suitable forage areas (Skinner and Chimimba 2005). Zebras are considered to be grazers, but they do take browse occasionally (Prins and Olf 1998a, Gagnon and Chew 2000). Zebras are non-ruminants and they are much more tolerant to poor quality forage but must maintain a high rate of intake to be able to survive on this type of food (Bell 1971, van Soest 1982, Okello et al. 2002).

2.3.7 Cape mountain zebra (*Equus zebra zebra*)

The mountain zebra (*Equus zebra*) are characterized by the more numerous dark stripes on the head and body in contrast to those found in the plains zebra (*Equus burchelli*). A distinctive characteristic of the mountain zebra is that they, unlike most equids, have a dewlap (Penzhorn 1988). In the Cape mountain zebra (*Equus zebra zebra*, Linnaeus 1758) the upper two to three stripes on the hindquarter are very broad as opposed to those that are less broad in the Hartmann's mountain zebra (*Equus zebra hartmannae*) (Penzhorn 1988). Historically, the Cape mountain zebra historically occurred in the mountainous regions of the Cape Province of South Africa, extending from the Amatole Mountains in the Cathcart District to the Kamiesberg in Namaqualand (Millar 1970, Skead 2007). Cape mountain zebras are non-ruminants and in Mountain Zebra National Park they prefer grassland vegetation communities moving from plateaus with stands of *Themeda triandra* grass in the summer to mountain slopes in the winter (Novellie et al. 1988, Winkler 1992). These movements are generally associated with change in diet quality (Novellie et al. 1988). Cape mountain zebras are predominantly grazers, but might occasionally take browse in times when the quality and quantity of the grazing layer declines (Novellie et al. 1988).

2.3.8 African elephant (*Loxodonta africana*)

The African elephant (*Loxodonta africana*, Blumenbach 1797) represents one of two species on the African continent, the other being the forest elephant *L. cyclotis* (Skinner and Chimimba 2005). Elephants historically occurred throughout Africa south of the Sahara desert (Carruthers et al. 2008). They are non-ruminants and mixed feeders, preferring either grass or browse depending on the season (Codron et al. 2006, Shannon et al. 2013). Elephants concentrate their foraging within areas

of high forage availability that are sufficiently close to water and large enough to optimize the efficiency of movement and foraging (De Knegt et al. 2011). Surface-water is a strong determinant of elephant spatial use and may take precedence over the role that landscape heterogeneity plays in their movement (de Beer and van Aarde 2008, De Knegt et al. 2011). Conflict between elephants and humans is common in areas where rural human settlements and elephant ranges overlap, and elephants change their movement behaviour and habits in an attempt to avoid interacting with humans (Van Aarde et al. 2008).

2.4 SUMMARY

This chapter reviewed the protected areas included in this study as well as the animals that were studied. The bulk of this study was performed on Mkambati Nature Reserve where red hartebeest, eland and plains zebra were studied. The results in Chapters 3, 4 and 6 are focused on this protected area. A comparison was also done of grazer assemblages between Mkambati Nature Reserve and iSimangaliso World Heritage Site in Chapter 3. Chapter 5 investigated several large mammalian herbivore species in a number of wildlife areas. These include African buffalo and Cape mountain zebra in Baviaanskloof Nature Reserve; African elephant in Mkhuze Game Reserve, Pilanesberg National Park and Kruger National Park; blue wildebeest and plains zebra in Welgevonden Private Game Reserve; and eland, blue wildebeest and impala in Asante Sana Private Game Reserve and Mapungubwe National Park. Mkambati Nature Reserve was described in detail, but only short descriptions were made of the other study areas to provide sufficient information related to the research objectives of Chapter 3 and 5. In addition, a short description of each species was also provided.

**Chapter 3: *Reconstructing grazer assemblages
for protected area restoration***

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ABSTRACT

Protected area management agencies often struggle to reliably reconstruct grazer assemblages due to a lack of historical distribution data for their regions. Incorrect predictions of grazing assemblages could potentially affect biodiversity negatively. The objective of the study was to determine how well grazing herbivores have become established since introduction to the Mkambati Nature Reserve, South Africa, how this was influenced by facilitation and competition, and how indigenous grazer assemblages can best be predicted for effective ecological restoration. Population trends of several grazing species were investigated in order to determine how well they have become established since introduction. Five different conceivable grazing assemblages reflecting a range of approaches that are commonly encountered during conservation planning and management decision making were assessed. Species packing was used to predict whether facilitation, competition or co-existence were more likely to occur, and the species packing of the different assemblages were assessed using ANCOVA. Reconstructing a species assemblage using biogeographic and biological information provides the opportunity for a grazer assemblage that allows for facilitatory effects, which in turn leads to an ecosystem that is able to maintain its grazer assemblage structure. The strength of this approach lies in the ability to overcome the problem of depauperate grazer assemblages, resulting from a lack of historical data, by using biogeographical and biological processes, to assist in more effectively reconstructing grazer assemblages. Adaptive management of grazer assemblage restoration through reintroduction, using this approach would further mitigate management risks.

3.1 INTRODUCTION

There have been alarming declines in large mammal populations in protected areas in Africa in the last three decades, which are mainly attributed to habitat loss as well as to consumptive use (Vie et al. 2009, Craigie et al. 2010). In southern Africa, protected areas have been more successful in maintaining their large mammal populations due to effective conservation management (Owen-Smith and Mills 2006, Craigie et al. 2010). In many of these protected areas, the management interventions are intended to restore ecological patterns and processes that have been affected by anthropogenic disruption (Heinen 2002, Suding et al. 2004, Hayward 2009a). A common element of these interventions is to reintroduce 'suitable' species to, or remove 'undesirable' species from, protected areas (Griffith et al. 1989, Novellie and Knight 1994, Fischer and Lindenmayer 2000, Atkinson 2001, Gusset et al. 2008).

The reintroduction of indigenous herbivores to an ecosystem, reintroduces natural disturbance and processes that are thought to support or promote the re-establishment of local diversity (Simenstad et al. 2006). A reintroduction is considered to be successful if it results in a self-sustaining population (Griffith et al. 1989). Reintroductions of large mammals to protected areas have had various levels of success over the last few decades (Griffith et al. 1989, Novellie and Knight 1994, Fischer and Lindenmayer 2000). Most of the unsuccessful reintroductions are attributed to unsuitable habitat (Castley et al. 2001), animals being non-indigenous (outside of their historical distribution range) (Novellie and Knight 1994), and to behavioural problems of the reintroduced animals (Slotow and van Dyk 2001, Venter 2004). Often, however, these explanations are either tautological, or based on suppositions. Conservation authorities opt to use a precautionary approach when deciding which species to introduce or maintain in protected areas, as non-indigenous species are potentially harmful to habitats in which they did not evolve (Spear and Chown 2009, Spear et al. 2011). A critical aspect of this restoration process is the selection of species that are 'suitable'. In many instances, the past is used to determine which species are suitable, assuming that indigenous species are the most appropriate to achieve restoration objectives (List et al. 2007, Hayward 2009a, Boshoff and Kerley 2010). This piecing together of the past is frequently based on historical mammal distribution data (historical records in diaries, journals and correspondence of early explorers, settlers, hunters, missionaries or naturalists as well as from archaeological records and rock paintings) thus leading to

the reconstruction of local historic animal assemblages (Heinen 2002, Bernard and Parker 2006, List et al. 2007, Boshoff and Kerley 2010). But the process of deciding which species is 'suitable' or 'undesirable' is not an exact science and is open to criticism (Bernard and Parker 2006, List et al. 2007).

Resource competition and facilitation could have a significant effect on the structure and species-richness of large mammal assemblages (Prins and Olf 1998a, Arsenault and Owen-Smith 2002, Olf et al. 2002). Allometric relationships between body size and metabolic rate, and body size and gut capacity, predict that larger grazers can survive on lower quality forage but require higher bulk intake diets (Demment and Soest 1985, Kramer and Prins 2010). Conversely, smaller grazers require higher quality forage, but can cope with lower quantities of it (Demment and Soest 1985). This suggests that for species within the same guild, the more similar in size the more similar a niche they would occupy (Prins and Olf 1998a, Kleynhans et al. 2011). This increases the likelihood of competitive interactions (Wilmshurst et al. 2000, Arsenault and Owen-Smith 2002, Mishra et al. 2002), despite this interaction being modified by the type of digestive system of these ungulates because ruminants of larger sizes could directly compete with smaller non-ruminants (Illius and Gordon 1992). Ultimately competitive interactions between species could lead to the extinction of the lesser competitor (Prins and Olf 1998a, Olf et al. 2002). When the number of one of the herbivore species decreases, competitive release of other species may occur as the effect of a competing herbivore species' declines (Kareiva 1982). This competitive release can cascade into lower trophic levels, as the forage species composition shifts in response to changed foraging behaviour of the released herbivore species (Lagendijk et al. 2012).

Hutchinson's weight ratio theory predicts that character displacement among sympatric competing species leads to sequences in which each species is twice the mass of the next (Hutchinson 1959). The higher the species diversity in an area the closer the species packing will be (i.e., reduced difference in body mass among species) (Prins and Olf 1998a, Olf et al. 2002, Klop and Prins 2008, Namgail et al. 2010). Closer species packing is expected in complex or highly heterogeneous systems (May 1973) as is the case in African grazing ecosystems (Prins and Olf 1998a, Croomsigt

and Olf 2006, Bonyongo and Harris 2007). The grazing by larger grazers decreases grass biomass as they are better suited to handle high biomass/low nutrient quality forage (Bell 1971, Bailey et al. 1996, Prins and Olf 1998a, Murray and Illius 2000). Furthermore, grazing often increases forage quality and decreases the stem-leaf ratio thus facilitating food intake (Drescher et al. 2006a, Drescher et al. 2006b). These two processes lead to facilitation for smaller grazers (McNaughton 1976, Prins and Olf 1998a), which would maximize production and subsequent utilization of the grass layer (Vesey-FitzGerald 1960, Bell 1971, McNaughton 1976). Such facilitation will result in a higher total grazer biomass in an area, and in closer species packing (Prins and Olf 1998a, Cromsigt and Olf 2006, Cromsigt et al. 2009).

The linking of these type of ecological patterns and processes to historical distribution data is mentioned by several authors (Boshoff and Kerley 2001, Bernard and Parker 2006), but few examples exist where this was actually done (List et al. 2007, Kuemmerle et al. 2012). This would suggest that conservation authorities are not using the full set of available tools when making management decisions for protected area restoration, especially when historical distribution data are lacking. This is a concern, as depauperate herbivore assemblages could have negative implications for biodiversity and associated patterns and processes (Chapin et al. 2000), both of which are goals for protected area conservation management (Venter et al. 2008).

The aim of this study was to determine how well grazing herbivores established since introduction, how it was influenced by facilitation and competition, and how indigenous grazer assemblages can best be predicted for ecological restoration. The objectives of the study were therefore to: (1) investigate the role of facilitation and competition on species persistence for eight grazing species post re-introduction; (2) investigate grazer diversity for the protected area under different conceivable assemblages based on biological principles and/or management practice; (3) assess our results against a separate, established, grazer assemblage; (4) critically evaluate current conservation management policy regarding wildlife reintroductions and removals in protected areas and (5) make recommendations for a future management approach.

3.2 STUDY AREA

Mkambati Nature Reserve is a 77-km² provincial nature reserve situated on the east coast of the Eastern Cape Province, South Africa (31°13'-31°20'S and 29°55'-30°04'E). The reserve was established in 1977, before which it was communal grazing land. The stated objective for the current management of the reserve is the conservation of Mkambati's unique biodiversity features (ECPB 2009). The reserve lies within the Indian Ocean Coastal belt bio-region (Rutherford et al. 2006b) and Pondoland centre of plant endemism (Conservation International and South African National Biodiversity Institute 2010), and has a mild sub-tropical climate with relatively high rainfall (1200 mm) and humidity (Shackleton 1990, de Villiers and Costello 2013). Soils originates from the Natal Group sandstones and are acidic, dystrophic and sandy (Shackleton 1989). Small forest fragments occur in the reserve, and wetland patches are abundant. Some 80 % of the reserve consists of Pondoland–Natal Sandstone Coastal Sourveld Grassland (Mucina et al. 2006d). Fires, ignited mainly by poachers, are frequent, which causes a landscape mosaic with nutrient-rich grass patches within a matrix of older, moribund grassland (Venter *pers. observation*), which are considered to be nutrient poor (Shackleton et al. 1991, Shackleton and Mentis 1992).

A total of 1 344 medium to large herbivores were introduced to Mkambati in 1979 to create a hunting ranch that aimed at an international clientele (de Villiers and Costello 2013). Species introduced were blesbok (*Damaliscus pygargus phillipsi*), blue wildebeest (*Connochaetes taurinus*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazelle*), eland (*Tragelaphus oryx*), red hartebeest (*Alcelaphus buselaphus camaa*), Hartmann's mountain zebra (*Equus zebra hartmannae*), plain's zebra (*Equus burchelli*) and giraffe (*Giraffa camelopardalis*) (de Villiers and Costello 2013). The animals originated mainly from the Kwazulu-Natal Province in South Africa, as well as from Namibia (de Villiers and Costello 2013). Approximately 30% (427) of the introduced animals died shortly after introduction (Sunday Times, South Africa, 24 August 1980), with the cause being attributed to "stress and starvation" (de Villiers and Costello 2013). The hunting venture failed commercially, after which Mkambati's status was changed to nature reserve (de Villiers and Costello 2013). In 2002 a culling program was initiated, initially to reduce animal numbers, but later (2004 onwards) to remove species that were considered to be non-indigenous from the reserve (ECPB 2010). The removals were based on recommendations

derived from historical mammal distribution data (Boshoff et al. 2004, Skead 2007), which later shaped the development of a large mammal management policy (ECPB 2010). Up to 2013, there were still no large predators present in Mkambati Nature Reserve.

3.3 METHODS

To determine how well grazing herbivores established in Mkambati since introduction population data were collected from various sources in order to establish population fluctuations from 1979 (when introductions took place) to 2010 (when the most recent game census was carried out) (Shackleton 1989, Feely 2005, Peinke et al. 2007, Venter 2007, Peinke et al. 2010, de Villiers and Costello 2013). The counting methods over the years varied between known group counts (on foot), to single aerial counts and triplicate aerial counts (using a helicopter) in the later years (Venter 2007). We have limited our investigation to mammalian species > 2 kg in mass that have grass as an important component (> 10%) in their diet. Species mass and feeding type data were sourced from literature (Prins and Olf 1998a, Gagnon and Chew 2000, Skinner and Chimimba 2005). Some of the species investigated (e.g., eland and impala), are mixed feeders (Watson and Owen-Smith 2000, van der Merwe and Marshal 2012), which allowed for a different kind of niche differentiation (grazer/browser), but the study was simplified by only considering them as grazers, as was done by Prins and Olf, (1998a) and Olf et al., (2002).

Five conceivable assemblages were investigated, and although assemblages one to four are specific to the circumstances of Mkambati, they do reflect a range of approaches that are commonly encountered during conservation planning and management decision making elsewhere (Table 3.1).

Assemblage 1 – 'Introduction': This assemblage was based on the nine grazer species that were introduced to Mkambati in 1979 together with three species already present at that time (Table 3.1). The assemblage reflects objectives that were understood to be economic ('consumptive use') rather than biological (ecological or biogeographic), and implemented at a time when experience with the restoration of African large herbivore assemblages was still limited.

Assemblage 2 – ‘Status quo’: This assemblage was based on all grazer species that were still present in Mkambati by the year 2010 (Table 3.1). The assemblage reflects the outcome of the original decision, the subsequent culling (2002) and decision to remove what was considered to be non-indigenous species (2004), and the performance of the remaining species up to 2010.

Assemblage 3 – ‘Current policy’: This assemblage was based on all grazer species that would be present in Mkambati if the currently approved large mammal management policy (ECPB 2010) were implemented (Table 3.1). Assemblage 3 was similar to Assemblage 2, but took into account recommendations based only on historical records (Boshoff et al. 2004) to modify the assemblage. All species that were considered to be non-indigenous are removed, and additional species that were considered to be indigenous, but which do not occur in 2010, are reintroduced.

Assemblage 4 – ‘Biogeographic’: This assemblage was based on all grazer species that would be present in Mkambati if a biogeographic approach were followed (Table 3.1). There is good evidence (Griswold 1991, Minter et al. 2004, Rutherford et al. 2006b) that Mkambati falls within the same biogeographic region as the Kwazulu-Natal and southern Mozambique coast, which is confirmed by recent new empirical evidence (Linder et al. 2012). Based on the above evidence, we accumulated historical distribution data for the Indian Ocean coastal belt bioregion (Rutherford et al. 2006b) in order to produce a comprehensive species list which included all species that were recorded to have occurred within this region in the past (Rowe-Rowe 1994, Plug 2004, Skead 2007, Uys 2012, Fisher et al. 2013).

Assemblage 5 – ‘iSimangaliso’: This assemblage was based on the grazer assemblage present in the coastal sections of the iSimangaliso World Heritage Site (van Rooyen 2004) (in Kwazulu-Natal Province), which falls within the same biogeographic region as Mkambati, namely the Indian Ocean coastal belt (Rutherford et al. 2006b)(Table 1). iSimangaliso has similar rainfall patterns (1200 -1300 mm p.a.) (Kwazulu-Natal Nature Conservation Service 1999) and soil characteristics (nutrient poor and well leached) when compared with Mkambati (Witkowski and Wilson 2001, Mucina et al. 2006d). Programmes aimed at the re-establishment of locally extinct species have been implemented in the park (Kwazulu-Natal Nature Conservation Service 1999). In particular, there have been successful introductions of buffalo *Syncerus caffer*, waterbuck *Kobus ellipsiprymnus* (Kwazulu-Natal Nature Conservation Service 1999). The assemblage reflects an external reference point from

within the same biogeographical region, with a well-established indigenous grazer assemblage, of which most have persisted naturally.

Species packing was determined to assess the role of facilitation and competition on species persistence for all assemblage's following the method of Prins and Olf, (1998a) and Olf et al., (2002), in which the natural logarithm of body mass was regressed against rank number, with the smallest species in the assemblage ranked one, the next species ranked two, etc. When the natural logarithm of species body weight is plotted against the rank number, the slope is predicted to be $\ln 2 (= 0.693)$ if there is a sequence where each species is exactly twice as heavy as the next (Prins and Olf 1998a). Under such circumstances, the weight ratio WR equals $e^{\ln 2}$ is 2. Therefore, the natural logarithm of body weight of the i -th species (W_i) is expected to depend on the rank number (R_i) where the regression line follows the function:

$$\ln(W_i) = aR_i + b$$

where W_i is the body mass of the i -th species in the assemblage and R_i its rank number (Prins and Olf 1998a). The WR is then obtained by the function

$$WR = e^a$$

Based on Hutchinson's hypothesis, [21] predicted that in a functional group, facilitation is more likely to occur at a weight ratio $WR > 2$, competition at $WR < 2$, while co-existence will occur at $WR = 2$. They predicted that when species body mass are too far apart; the larger grazers will keep the grass in a state of utilization in which the vegetation quality is too low for small herbivores, in which case facilitation will not occur. They further predicted that when species are similar in body mass, they might not gain enough from facilitation, and competition will increase (Prins and Olf 1998a). Based on this a weight ratio of $WR \geq 2$ was considered optimal for allowing facilitatory processes needed in an optimal grazer assemblages. Species packing for conceivable assemblages one to four were compared first in order to investigate differences in historical, current and proposed conceivable assemblages within Mkambati.

Table 3.1: The five different grazer assemblages used during the study. For each assemblage species body weights were ranked with the smallest species ranked one, the next largest species ranked two, etcetera.

Species	Common name	Mass (kg)#	Assemblage ranks				
			1 Introduction assemblage	2 Status quo assemblage	3 Current policy assemblage	4 Bio- geographical assemblage	5 iSimangaliso assemblage
<i>Pronolagus crassicaudatus</i>	Natal red rock rabbit	2.2	1	1	1	1	
<i>Lepus saxatilis</i>	Shrub hare	2.5	2	2	2	2	1
<i>Ourebia ourebi</i>	Oribi	15			3	3	2
<i>Redunca fulvorufula</i>	Mountain reedbuck	29.5				4	3
<i>Antidorcas marsupialis</i>	Springbok	33	3	3			
<i>Aepyceros melampus</i>	Impala	51	4	4		5	4
<i>Redunca arundinum</i>	Southern reedbuck	58	5	5	4	6	5
<i>Damaliscus pygargus</i>	Blesbok	64	6	6			
<i>Phacochoerus africanus</i>	Warthog	73.5				7	6
<i>Damaliscus lunatus</i>	Tsessebe	131					7
<i>Alcelaphus buselaphus</i>	Red hartebeest	150	7	7	5	8	
<i>Connochaetes taurinus</i>	Blue wildebeest	189	8	8		9	8
<i>Oryx gazella</i>	Gemsbok	195	9				
<i>Kobus ellipsiprymnus</i>	Waterbuck	201				10	9
<i>Equus burchelli</i>	Plain's zebra	235	10	9		11	10
<i>Equus zebra</i>	Hartmann's mountain zebra	262	11				
<i>Tragelaphus oryx</i>	Eland	511	12	10	6	12	11
<i>Syncerus caffer</i>	Buffalo	544			7	13	12
<i>Ceratotherium simum</i>	White rhinoceros	1875				14	13
<i>Hippopotamus amphibius</i>	Hippopotamus	1900				15	14
<i>Loxodonta africana</i>	African elephant	3550			8	16	15

#Body weight data (average of both sexes) from Prins & Olff (1998), Gagnon & Chew (2000) and Skinner & Chimimba (2005)

A one-way analysis of co-variance (ANCOVA) was conducted to determine if there was a significant difference in the degree of species packing for conceivable assemblages one to four. The proposed 'biogeographic' assemblage was then compared to an external reference point, i.e. 'iSimangaliso', in order to assess accuracy of the predicted grazer assemblage. To determine if there was a difference in species packing for assemblage four and five, a t-test was used. Statistical analysis was conducted using IBM SPSS Statistics for Windows, Version 19.0. (Armonk, NY: IBM Corp.). We compared grazer species abundance among the five different conceivable assemblages according to weight, by generated weight ranges, in which each weight range is more or less half the mass of the next heavier weight range (see (Hutchinson 1959, Prins and Olf 1998a)). The weight ranges were: mini grazers (2-10 kg), small grazers (11-30 kg), small-medium grazers (31-100 kg), medium grazers (101-200 kg), medium-large grazers (201-500 kg), large grazers (501-1000 kg), mega-grazers (1001-2000 kg) and mega+ -grazers (> 2000 kg).

3.4 RESULTS

Dealing with the assumed local indigenous species (Boshoff et al. 2004) first, the population of red hartebeest had an initial weak decline ($F(1,13) = 4.160$; $P = 0.062$) until culling of blesbok and blue wildebeest started in 2002, from when population growth showed an upward trend ($F(1,4) = 37.973$; $P = 0.004$) (Figure 3.1). The number of southern reedbuck remained relatively stable at between 20 - 50 individuals ($F(1,3) = 1.252$; $P = 0.345$) (Figure 3.1). Numbers of eland fluctuated between 100 - 200 individuals before and during times when culling took place ($F(1,12) = 42.781$; $P = 0.062$ and $F(1,5) = 0.455$; $P = 0.30$) (Figure 3.1).

For the assumed non-indigenous species, numbers of blesbok declined initially after introduction, where-after their numbers fluctuated between 500 - 800 individuals ($F(1,13) = 0.120$; $P = 0.735$ and $F(1,5) = 1.437$; $P = 0.284$). Blue wildebeest showed a strong population growth initially ($F(1,13) = 7.966$; $P = 0.014$) (Figure 3.1). The population started declining in 2002 due to culling, and was totally removed by 2011 ($F(1,4) = 37.401$; $P = 0.0004$) (Figure 3.1). The numbers of plain's zebra steadily increased to, and stabilized between 300 and 400 animals by 2010 ($F(1,13) = 39.096$; $P < 0.005$ and $F(1,4) = 16.026$; $P = 0.016$) (Figure 3.1). The

number of Hartmann's mountain zebra started declining after introduction and the species was extinct on Mkambati by 2000, 20 years post-introduction ($F(1,5) = 36.845$; $P = 0.002$)(Figure 3.1). The numbers of gemsbok declined straight after the introduction until the species went extinct in 1999 ($F(1,11) = 52.783$; $P < 0.005$)(Figure 3.1). The population of impala declined after introduction, and crashed to < 30 animals ($F(1,12) = 17.162$; $P = 0.001$) (Figure 3.1), with only a few (3) being alive in 2010 ($F(1,3) = 1.452$; $P = 0.315$). The springbok numbers grew initially until 1992 (± 60 individuals) when the population started to decline ($F(1,12) = 0.006$; $P = 0.939$) (Figure 1), and by 2012 there were only 11 animals left ($F(1,4) = 0.954$; $P = 0.384$). None of the springbok population changes were statistically significant. Of the supposedly indigenous species, some did well after introduction and some less so, and, of the supposedly non-indigenous species, the same can be said (Table 3.2).

When the ANCOVA was performed we first determined that there was a linear relationship between log mass and rank number for each conceivable assemblage, by visually assessing the scatterplot (Figure 3.2). There was heterogeneity of regression slopes as the interaction term was statistically significant, ($F(3,37) = 4.051$; $p = 0.014$), but with visual inspection of the scatterplot it was concluded that this would have a minor effect on the results because the interaction occurred at the very lower end of the scatterplot (Figure 3.2) see (D'Alonzo 2004). Standardized residuals for the conceivable assemblages and for the overall model were normally distributed, as assessed by Shapiro-Wilk's test ($p > 0.05$). There was homoscedasticity and homogeneity of variances, as assessed by visual inspection of a scatterplot and Levene's test of homogeneity of variance ($p = 0.008$), respectively. There were no outliers in the data, as assessed by no cases with standardized residuals greater than ± 3 standard deviations. There was a statistically significant difference between the different conceivable assemblages, ($F(3,40) = 4.994$; $p = 0.005$). *Post hoc* pairwise analysis performed with a Bonferroni adjustment indicated a significant difference between the 'Introduction' and 'biogeographical' assemblages versus the 'current policy' assemblage (Table 3.3). The result of the t-test indicated that there was no significant difference in species packing between the 'biogeographic' and 'Simangaliso' assemblages ($t(1,2) = -0.321$, $p = 0.750$). The *WR* for the 'status quo' and 'current policy' assemblages were < 2 , indicating lower species packing and thus higher potential for competitive grazing interactions (Table 3.4 and Figure 3.2). The *WR* for the

'introduction', 'biogeographical' and 'iSimangaliso' assemblages were > 2 , indicating higher species packing and thus higher potential for facilitation among grazing species (Table 3.4 and Figure 3.2).

In order to assess the different species' ability to persist post introduction we needed to compare 'introduction' assemblage with the 'status quo' assemblage. The number of species within the small grazer, mega grazer and mega+ grazer body weight ranges, were depauperate in both 'introduction' and the 'status quo' assemblages (Figure 3.3). There was a decrease in the number of species in the medium (-2) and medium-large (-1) grazer weight ranges in the period between 1979 and 2010 (i.e., time period between 'Introduction' and the 'status quo' assemblages)(Figure 3.3).

There were no species present in the medium-large and mega grazer weight ranges for the 'current policy' assemblage (Figure 3.3). In addition there was only one species per range for the small, small-medium, medium, and mega+ grazer weight ranges (Figure 3.3). There were between 2 and 3 species for all weight ranges in the 'biogeographical' assemblage, except the mega+ weight range, which only had one species (Figure 3.3). The species packing results for the 'introduction', 'biogeographical' and 'iSimangaliso' assemblages indicate a facilitation assemblage, achievable with a suite of 12; 16 to 15 grazing species, which are relatively evenly spread over all weight ranges, except for the 'introduction' assemblage which did not have representative species in the very large weight ranges. The 'biogeographical' and 'iSimangaliso' assemblages were similar, except for a depauperate mini grazer weight range in the 'iSimangaliso' assemblage (Figure 3.3).

Table 3.2: A summary of the population trends of the large herbivores based on their presumed status of indigenous versus non-indigenous, from when they were introduced to Mkambati Nature Reserve in 1979, until the latest game census in 2010.

Presumed status (Boshoff et al. 2004)	Number of species	Increasing population trend	Decreasing population trend	Stable population trend
Indigenous	3	2	0	1
Non-indigenous	7	2	3	2

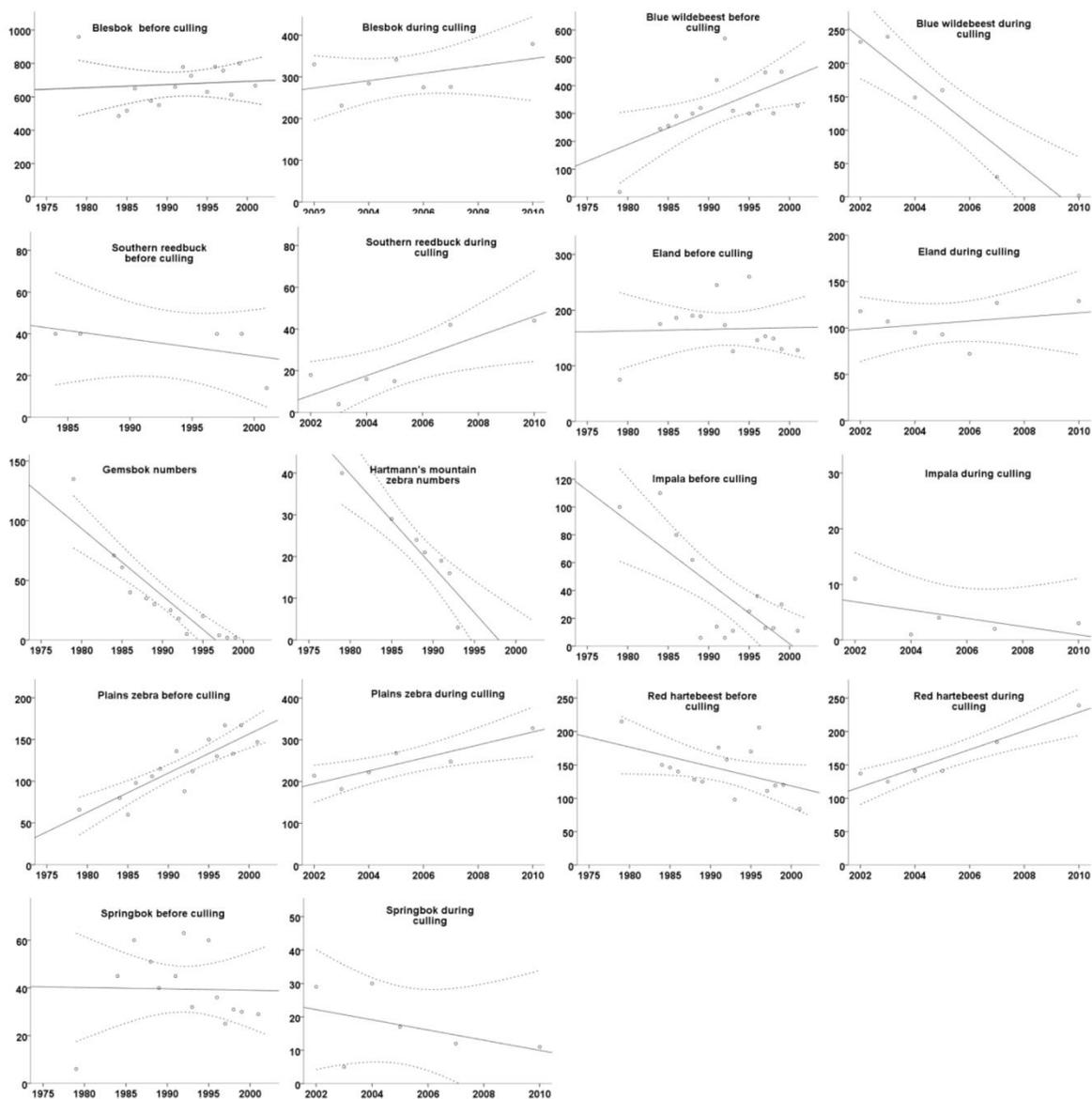


Figure 3.1: Linear regression lines indicating the population growth/decline of red hartebeest, southern reedbuck, eland, blesbok, blue wildebeest, plains zebra, Hartmann's mountain zebra, gemsbok, impala and springbok in Mkambati Nature Reserve before and during culling. Species that were culled were blesbok and blue wildebeest. Dashed lines indicate the 95% CI of the predicted mean.

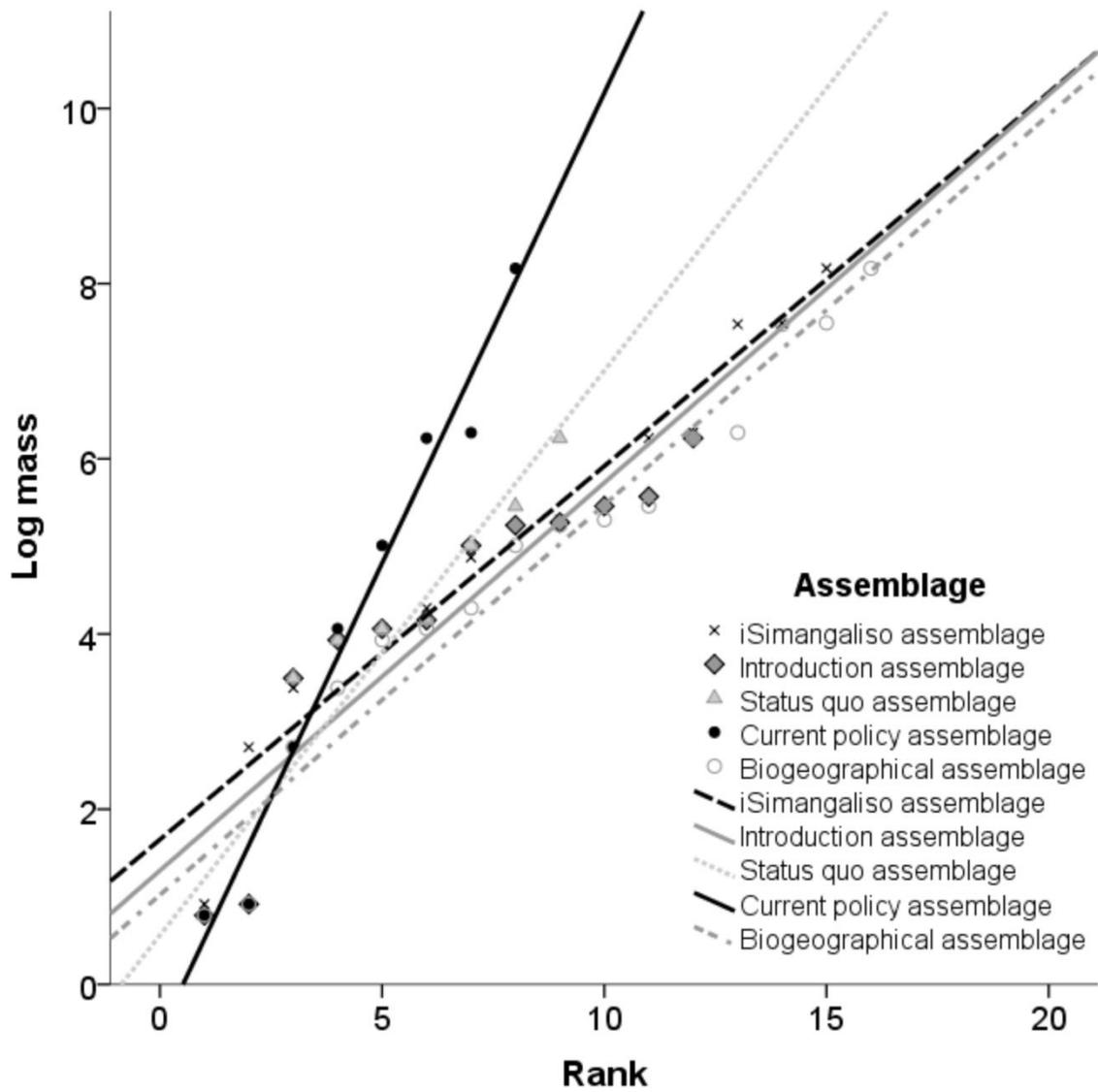


Figure 3.2: Linear regression lines with the natural logarithm of species' body mass is plotted against the rank number to indicate the degree of species packing for the 'Introduction', 'Status quo', 'Current policy', 'Biogeographic', and 'iSimangaliso' grazer assemblages.

Table 3.3: Post-hoc pairwise comparisons indicating the differences between species packing amongst the different conceivable assemblages

Assemblage	Mean Difference*	Std. Error	Sig.	95% Confidence Interval for Difference	
				Lower Bound	Upper Bound
Introduction assemblage versus Status quo assemblage	-0.371	0.382	1.000	-1.433	0.691
Introduction assemblage versus Current policy assemblage	-1.116	0.398	0.047	-2.222	-0.010
Introduction assemblage versus Biogeographical assemblage	0.393	0.336	1.000	-0.539	1.324
Status quo assemblage versus Current policy assemblage	-0.745	0.418	0.493	-1.904	0.415
Status quo assemblage versus Biogeographical assemblage	0.764	0.379	0.303	-0.288	1.815
Current policy assemblage versus Biogeographical assemblage	1.509	0.398	0.003	0.404	2.614

*A negative value indicates that the first assemblage have a higher species packing than the second

Table 3.4: The degree of species packing for the different conceivable assemblages in Mkambati Nature Reserve.

Assemblage	Number of species	R²- value	Weight ratio (WR)
'Introduction'	12	0.837	3.669
'Status quo'	10	0.895	1.751
'Current policy'	8	0.975	1.751
'Biogeographic'	16	0.952	2.773
'iSimangaliso'	15	0.949	5.207

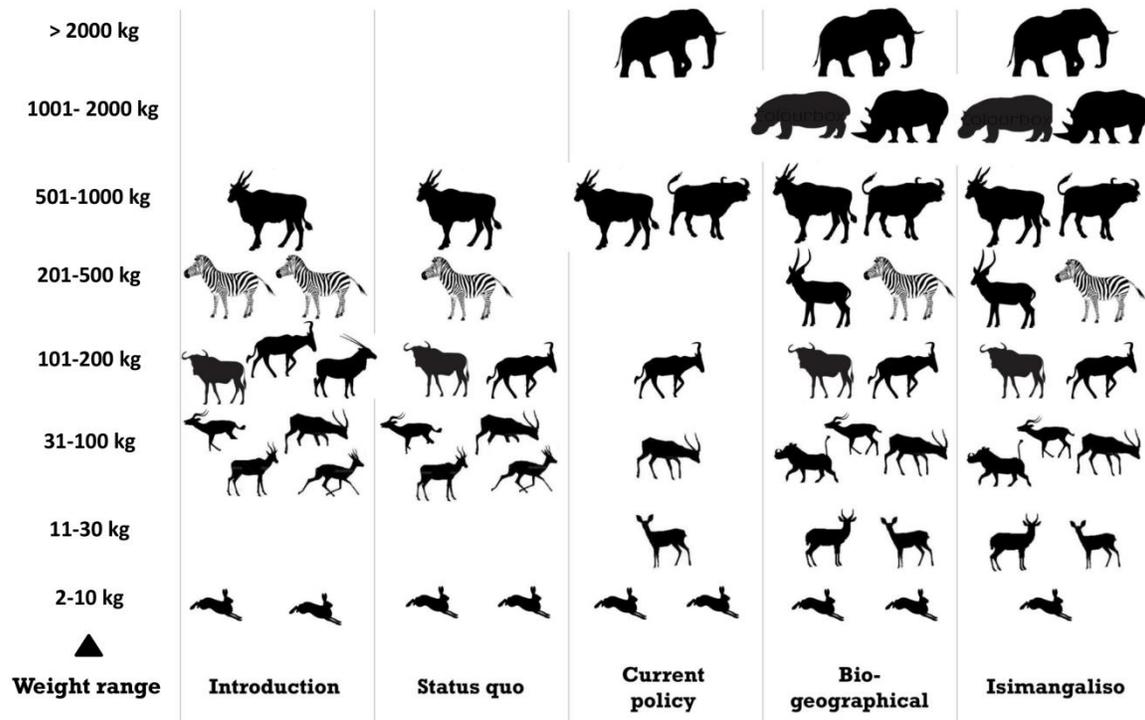


Figure 3.3: The weight ranges for the grazing species under the five different conceivable assemblages investigated during the study. Weight ranges were grouped as mini grazers (2-10 kg), small grazers (11-30 kg), small-medium grazers (31-100 kg), medium grazers (101-200 kg), medium-large grazers (201-500 kg), large grazers (501-1000 kg), mega grazers (1001-2000 kg) and mega+ grazers (> 2000 kg). Conceivable assemblages 'biogeographic' and 'Isimangaliso' are considered best. Each species is represented by a silhouette.

3.5 DISCUSSION

Forage quality, in many cases, decreases with increasing grass biomass, which imposes an important constraint on net nutrient and energy intake by grazers (Prins and Olf 1998a, Olf et al. 2002), which is also the case in Mkambati (Shackleton 1990, Shackleton and Mentis 1992). The presence of larger grazers can decrease grass biomass (because they are better suited to handle high biomass/low nutrient quality forage)(Bell 1971, Bailey et al. 1996, Prins and Olf 1998a), and increase quality as well as decrease stem-leaf ratio of forage, thereby facilitating food intake for smaller grazers (McNaughton 1976, Prins and Olf 1998a, Drescher et al. 2006a, Drescher et al. 2006b).

In the case of Mkambati the evidence suggests competitive exclusion resulting in local extinction of some species. This is supported by the species packing values that were <2 , as well as evidence of population decline of species in certain weight ranges in the time period that lapsed between the 'introduction' and the 'status quo' assemblage. Shorter term effects that may in addition indicate competitive exclusion can also be seen in the increased population growth of red hartebeest (from 2002 onwards) after the decline of blue wildebeest due to the culling program. Although the 'introduction' assemblage showed a facilitation scenario, we reason that it happened in the lower weight ranges, and there was a general lack of facilitation within higher weight ranges, i.e. large and mega grazers upwards. In high rainfall areas (≥ 750 mm p.a.) mega grazers such as the white rhino and hippopotamus act as influential ecosystem engineers, creating and maintaining short grass swards, which alter habitat for other grazers and change the fire regime (Owen-Smith 1987, Truett et al. 2001, Waldram et al. 2008). Elephant, through trampling effect rather than grazing, are probably also able to facilitate availability of grazing resources in dense overgrown areas (Vesey-FitzGerald 1960). This ecosystem engineering role cannot be replicated by smaller grazers (Waldram et al. 2008). The lack of facilitation effects could thus be linked to the evidence of competition driven species decline in "overpopulated weight ranges" in, especially, the larger, i.e. medium and medium-to-large weight ranges. It can reasonably be argued, in the case of gemsbok and Hartman's zebra, which normally occur in more arid areas (Coetzee 1969), that poor habitat suitability and their non-indigenous status could have been the main factor responsible for the species demise (Novellie and

Knight 1994, Castley et al. 2001). This argument could, however, be tautological in that the conclusions are made once the species fails to establish. We argue that, in addition to failure to establish due to a habitat suitability disadvantage, these grazing species may also have been less competitive. Had there been fewer effective competitors and increased facilitation from larger grazers, these species may have been able to overcome the habitat suitability disadvantage and persisted. Our argument, based on missing biological processes, is strengthened by the data showing a prolonged period (20 years) of decline of the said species.

The 'current policy' assemblage produced the lowest equal degree of species packing (lowest WR), with a resulting increase of likelihood for interspecific competition. In this case, facilitation is unlikely, as there were several gaps in the larger weight ranges (medium-large and mega grazers) of the grazer assemblage. There are two noteworthy observations regarding the 'current policy' assemblage. Firstly, a small grazing species assemblage of only eight species in a grass dominated ecosystem is unusual compared to larger species assemblages in other African ecosystems (Mean = 20; ± 3 SD; $n = 8$) (Rowe-Rowe 1994, Boshoff and Kerley 2001, Bonyongo and Harris 2007, Klop and Prins 2008). Secondly the lack of 'mega' grazers in the assemblage is contrary to the expected assemblage of more abundant mega grazers in high rainfall (Fritz et al. 2002) or high biomass/nutrient poor regions (Bell 1982). The 'current policy' assemblage, although intended to have a restoration and thus biodiversity conservation objective, may prove to carry the highest risk. In this assemblage, the removal of species might trigger, and could already have triggered, competitive release which may affect lower trophic levels, and cause forage species composition shifts, in response to changed foraging behaviour of the released herbivore species, which could potentially affect biodiversity patterns and processes (Chapin et al. 2000, Zavaleta et al. 2001, Legendijk et al. 2012). The risk to biodiversity could further increase due to a higher fire frequency, caused by fuel load build-up when grass biomass is not effectively cropped by grazers (Bond and Keeley 2005, Fuhlendorf et al. 2009, Leonard et al. 2010). This could effectively keep Mkambati in a 'fire trap', which currently seems to be the case (Venter, *personal observation*). Furthermore, the lack of larger grazers creates an ecosystem devoid of facilitatory effects which in turn leads to an ecosystem which is unable to maintain its herbivore assemblage structure (Prins and Olff 1998a).

The use of only vegetation types in combination with historical distribution data to predict grazer distribution patterns (Boshoff and Kerley 2001, Boshoff et al. 2004) could thus potentially provide inaccurate results (Bernard and Parker 2006, List et al. 2007). Examples exist where older historical distribution predictions were later proven inaccurate when new evidence was produced (Goodman and Tomkinson 1987, Cramer and Mazel 2007). For these reasons, we predict that the current policy approach will not be able to optimally achieve Mkambati's stated biodiversity conservation purpose (ECPB 2010). The weakness in this approach lies inherently in the lack of a full grazer assemblage, planned for by using insufficient historical data.

Biogeographic regions are better defined by combining vertebrate data with vegetation data due to a large degree of congruence in distributions caused by the effect of vertebrate distributions (Linder et al. 2012). Plant species tend to be responsive to localized environmental conditions, while animal species respond to the broader vegetation structure (i.e. biogeographical regions), which could be a spatially more coherent representation of the floristic patterns (Linder et al. 2012). Medium to large grazers in Africa are well known for their ability to move/migrate over large distances, driven by regional seasonal changes in forage conditions (Bell 1971, McNaughton 1985, Drent and Prins 1987, Fryxell et al. 2005, Skead 2007), which further supports the use of broader, biogeographical, rather than a narrower vegetation type approach. The 'biogeographic' assemblage thus seems to be the more appropriate model to use. This assemblage is similar to an established grazer assemblage in 'iSimangaliso' in the same biogeographic region.

The 'biogeographic' assemblage, with a full, evenly spread (equal number of species for each weight class) grazer species assemblage, provides the opportunity for a grazing ecosystem that allows for facilitatory effects, that leads to an ecosystem that is able to maintain its herbivore assemblage structure. This in turn maximizes production and utilization in the forage layer which could increase grazer biomass. It would also allow Mkambati to escape from its current 'fire trap' of a very high fire return rate. When an assemblage exists where there is a lack of sufficient historical data, the biogeographic approach could be considered to be the more responsible conservation management approach. Furthermore this approach has the highest likelihood of achieving Mkambati's stated

purpose and restoration objectives. The strength of this approach lies in the ability to overcome the problem of depauperate grazer assemblages, caused by a lack of historical data, by using biogeography and ecological processes, to assist in more effectively restoring grazer ecosystems. The proposed approach however, is still very simplistic in nature and various additional factors could be considered. Mouth anatomy, sexual dimorphism, season and population density, for example, could be important factors that contribute to niche overlap and ecosystem engineering effects (Arsenault and Owen-Smith 2008, Kleynhans et al. 2011). Size scaling as hypothesised by (Prins and Olf 1998a) still needs to be convincingly proved as fact. In addition there is also a limitation that a decision is always required as to which historical stage any reconstruction is aiming to match. Current ecological conditions may not equate to those at a chosen time and it may be impossible to recreate a herbivore assemblage from a particular historical time. The biological approach could address this issue partially but less so for the biogeographical approach.

3.6 MANAGEMENT IMPLICATIONS

It remains important that non-indigenous species are not introduced into formal protected areas due to the potential risk associated with such an action (Atkinson 2001, Castley et al. 2001, Spear and Chown 2009). When there is no confirmation from historical data that a species was present in the immediate vicinity of the protected area, but biological or biogeographical patterns contradicts the historical assessment, reintroduction should be planned using a strategic adaptive management approach (Biggs and Rogers 2003). This approach should take cognisance of all the potential risks (Castley et al. 2001, Spear and Chown 2009) and be focussed on improving incomplete understanding and reducing the identified risks. This should take place through an iterative process of setting reintroduction objectives, implementing reintroduction actions and evaluating the implications of their outcomes for future management action (Biggs and Rogers 2003, Gaylard and Ferreira 2011, Roux and Foxcroft 2011). This could involve re-introducing certain species (as identified through biogeographical and biological assessment tools), setting thresholds of potential concern (TPC's)(Biggs et al. 2011), intensively monitor the species' effect on the ecosystem and the grazer assemblage, later deciding to remove or maintain them, depending on conclusions derived from set TPC's. A protected area restoration strategy that aims to simulate the natural processes and heterogeneity of a system should thus make full use of all the tools available to reconstruct past

species assemblages. These tools are not limited to historical distribution data but include biogeographic and biological approaches. The model proposed in this study should not be seen as the ultimate solution for predicting large herbivore assemblages but rather as a contribution to the development of more scientifically robust and defensible protected area restoration methodology.

3.7 CONCLUSION

We conclude that it is the larger grazers missing from the Mkambati grazer suite, thus creating an ecosystem devoid of facilitatory effects exerted by these species, which in turn leads to an ecosystem that cannot maintain its herbivore assemblage structure. If certain species are excluded from the system purely based on assumptions derived from local colonial history and early explorer travel habits, the scientific validity of the assessment of their non-indigenous status should be questioned, especially when biological or biogeographical patterns contradict the historical assessment. The functioning of grazing ecosystems is driven by various patterns and processes, and excluding certain species, weight ranges or guilds, could potentially be just as detrimental to biodiversity as including non-indigenous species.

**Chapter 4: Forage patch use by grazing
herbivores in a South African grazing ecosystem**

Jan A. Venter, Jacob Nabe-Nielson, Herbert H.T. Prins & Rob Slotow

ABSTRACT

Understanding how different herbivores make forage patch use choices explains how they maintain an adequate nutritional status, which is important for effective conservation management of grazing ecosystems. Using telemetry data, we investigated non-ruminant zebra (*Equus burchelli*), and ruminant red hartebeest (*Alcelaphus buselaphus* subspecies *camaa*), use of burnt patches in a landscape mosaic of nutrient poor, old grassland interspersed with young, recently burnt, nutrient rich grass patches. The Mkambati Nature Reserve landscape on the east-coast of South Africa provided large grazers with a challenge in finding and using appropriate patches in which to forage to meet their nutritional requirements. In Mkambati, grassland fires, mostly ignited by poachers, induce re-growth of young nutrient rich grass, which subsequently attract grazers. Using MANOVA we tested if the study animals foraged more in burnt patches than in the unburned grassland and whether burnt patch use was related to the distance to the previously visited burnt patch, burnt patch size, burnt patch age and distance to areas with high poaching risk. In general, zebra moved faster than red hartebeest, and both species moved faster in unburnt grassland than in burnt patches. Red hartebeest and zebra patch selection were influenced by inter-patch distance, patch age, patch size and poaching risk. A limited set of intrinsic traits, i.e. body mass, digestion strategy and muzzle width, may cause different patch use rules for the two species. Large ungulates patch use behaviour varied among species and across conditions, and was influenced by anthropogenic impacts such as poaching and changed fire regimes. This could potentially affect biodiversity negatively and needs to be factored into management of conservation areas.

4.1 INTRODUCTION

In protected areas, conservation managers attempt to simulate natural processes and maintain heterogeneity of ecosystems to promote conservation outcomes (Grant et al. 2011). For large African ungulates, whose populations have declined over the last three decades (Craigie et al. 2010), effective conservation management is crucial (Carbutt and Goodman 2013). Understanding how species in a system vary their behaviour to meet their biological needs and deal with anthropogenic impacts should underpin such conservation management strategies (Gibbs et al. 1999). This paper presents the results of a study that investigated the patch use behaviour of two different grazing ungulate species.

Large herbivores feed within forage patches and in doing so, move through areas where no or little acceptable food is encountered (Bailey et al. 1996, Prins 1996, Owen-Smith 2005), and utilize high-value food by adjusting their movements to habitat structure (Fortin 2003, de Knegt et al. 2007). They accelerate when moving between food items (Shipley et al. 1996) and they spend more time in more rewarding patches (Distel et al. 1995, Courant and Fortin 2012). Normally, feeding is the dominant activity within a forage patch, although large herbivores engage in other activities such as walking, resting and drinking (Green and Bear 1990, Ryan and Jordaan 2005, Shannon et al. 2008). Acceptable forage or habitat patches might not be discernible from a distance, and their location may shift continuously as the forage quality changes due to abiotic circumstances (e.g., fire, rainfall or flood recession) (Olf et al. 2002, Archibald and Bond 2004, de Knegt et al. 2008, van Beest et al. 2010), or influences from other herbivores (Arsenault and Owen-Smith 2002, Kohi et al. 2011). Herbivores are, therefore, faced with the challenge of how to find and choose good quality forage patches in a landscape where the location of suitable patches is continuously changing (Senft et al. 1987a, Bailey et al. 1996). Understanding how different herbivores make these choices explains how they maintain an adequate nutritional status, which is important for effective conservation management of grazing ecosystems.

Grazing ungulate food occurs in discrete patches (Prins 1996, Bailey and Provenza 2008, Prins and Van Langevelde 2008b), and these patches are reasonably homogeneous with respect to some

environmental feature(s) (Bailey et al. 1996, Bailey and Provenza 2008, Owen-Smith et al. 2010). Patch selection is scale-dependant, and although herbivores can often afford to be selective on a fine scale (plant part or species), this may not be the case at coarse scales (habitat patch) due to the energetic constraints of having to moving further without reward (van Beest et al. 2010). The quality of a patch, and the likelihood that it is selected by an animal, will be influenced by various factors, such as patch size and inter-patch distance (Gross et al. 1995, Sibbald and Hooper 2003, Wallace 2008).

In addition, herbivores also need to avoid becoming prey to predators, and do so by responding to predation risk (Kie 1999, Creel et al. 2005, Fortin et al. 2005, Creel et al. 2008, Valeix et al. 2009b). Foragers may choose to ignore predator risk when deciding where to forage, and focus on the quality of forage resources and/or other factors (Prins 1996). However, they may also respond by avoiding predators (Creel et al. 2005, Valeix et al. 2009a) or by moving out of harm's way when predators are encountered (Fischhoff et al. 2007, Winnie and Creel 2007). Human disturbance can cause large herbivores to respond in the same way as they do to natural predators (Morgantini and Hudson 1985, Manor and Saltz 2003, Blom et al. 2004, Proffitt et al. 2009), especially in areas with high poaching incidence (Fischer and Eduard 2007, Hayward 2009b).

An area where patch forage behaviour may be particularly important is the fire-prone, nutrient poor grasslands on the east coast of South Africa. Here, grassland fires induce re-growth of young nutrient rich grass (Shackleton and Mentis 1992), which may subsequently attract grazers (Parrini and Owen-Smith 2010, Allred et al. 2011). In these coastal grasslands, the biomass productivity is very high, and the grazing pressure is often too low to prevent the accumulation of moribund grass (Shackleton 1990). The moribund, low nutrient grassland are interspersed with young, recently burned, nutrient rich grass patches (Shackleton and Mentis 1992). This landscape provides large grazers with a challenge in finding the appropriate forage patches, from which they can consume suitable food to maintain or surpass their nutritional requirements. The east coast grasslands of South Africa thus form a good model system to study grazer-forage interactions that are typical for the many under-grazed savanna grasslands.

Our study aim was to determine which factors influence forage patch use behaviour of large herbivores. We investigated how two species of large herbivores zebra (*Equus burchelli*) and red hartebeest (*Alcelaphus buselaphus*) with contrasting intrinsic traits, used forage patches in a landscape of nutrient poor, moribund grassland, with a mosaic of higher quality forage patches, under a gradient of higher and lower poaching risk. The differences in patch choice between the two species were investigated to establish any differences as a result of their intrinsic traits, i.e. their physiology and anatomy. This was done by assessing: (1) whether burnt patches were selected as preferred forage habitat; (2) the confounding effects of poaching risk; (3) effects of distance from the previous patch, patch size and patch age (time since burnt), on choice, and, (4) contrasting patch choice between zebra and red hartebeest. In order to test for poaching and fire effects we also tested whether there was concordant danger and fire gradients within Mkambati, with risk decreasing from the boundary rivers.

4.2 STUDY AREA

The Mkambati Nature Reserve (Mkambati) is a 77-km² provincial nature reserve situated on the east coast of the Eastern Cape Province, South Africa (31°13'-31°20'S and 29°55'-30°04'E). The climate is mild sub-tropical with a relatively high humidity (de Villiers and Costello 2013). The high rainfall (1 200 mm annually), mild mean daily temperatures (18 °C winter and 22 °C summer), and presence of abundant streams and wetlands, results in a landscape that is not water limited in any season. Forests occur in small patches (mostly in fire refuge areas). More than 80 % of Mkambati consists of Pondoland–Natal Sandstone Coastal Sourveld grassland (Mucina et al. 2006d). The grassland communities are considered to be nutrient poor (Shackleton et al. 1991, Shackleton and Mentis 1992).

Grassland fire stimulates temporary regrowth high in crude protein (8.6% compared to 4.6%, in older grassland), phosphorus concentrations (0.1% compared to 0.05%, in older grassland) and dry matter digestibility (38.6% compared to 27.1%, in older grassland) (Shackleton 1989). Nutrient concentrations remain elevated for up to 6 months post burn, by which time they are comparable to

surrounding unburned grassland (Shackleton and Mentis 1992). Frequent fires cause a continuously changing landscape mosaic of nutrient-rich burnt patches within a matrix of older, moribund grassland and older burnt patches. Most fires are ignited by poachers with the aim to attract animals to certain areas. Poachers cross the two major rivers, i.e. the Mtentu river (on the north-eastern boundary) and the Msikaba river (on the south-western boundary), to poach wildlife in Mkambati. Security patrols and field ranger records show that poachers use rifles, dogs and snares (Eastern Cape Parks and Tourism Agency, unpublished data). There are also prescribed management burns, but due to the high poacher fire incidence this rarely takes place. Lightning also causes fires, but only few have been recorded on Mkambati, and none during the study period (Eastern Cape Parks and Tourism Agency, unpublished data). Several large herbivore species are present in Mkambati but no large predators (Peinke et al. 2010).

In our study area, the two most dominant grazers are plains zebra (*Equus burchelli*) and red hartebeest (*Alcelaphus buselaphus camaa*). In areas with much moribund vegetation, grazing ruminants such as the red hartebeest face particular constraints because nearly all vegetation biomass has a low quality, which reduces food intake rates (Drescher et al. 2006a, Drescher et al. 2006b, van Langevelde et al. 2008). The hartebeest is an example of a concentrate selector; its skull morphology is specially adapted to be very selective at times when good forage is scarce (Schuette et al. 1998). The non-ruminant zebra, in contrast, is much more tolerant to poor quality forage but must maintain a high rate of intake to be able to survive on this type of food (van Soest 1982, Okello et al. 2002). We therefore expected two possible scenarios: that zebra are better able to use more fibrous, older grassland patches than are red hartebeest (Sensenig et al. 2010), or that hartebeest, with their ability to be so selective due to special anatomy, could use the same older grassland, but there would be differences in selection strategies within patches.

4.3 METHODS

All poaching incidents recorded by Mkambati field rangers between 2008 and 2010 were mapped and the distance to the nearest major river calculated in metres using ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute).

Seven zebra (6 female and 1 male) and nine red hartebeest (8 female and 1 male) were fitted with GPS-UHF collars (Africa Wildlife Tracking CK., RSA), active from September 2008 to August 2011. All animals were darted by an experienced wildlife veterinarian from a Robinson 44 helicopter. The work was approved by, and conducted in strict accordance with, the recommendations in the approved standard protocols of the Animal Ethics Sub-committee of the University of Kwazulu-Natal. All field work was conducted by, or under the supervision of the first author, a staff member of the Eastern Cape Parks and Tourism Agency, as part of the operational activities of the appointed management authority of Mkambati (Eastern Cape Parks and Tourism Agency Act no. 2 of 2010, Eastern Cape Province, South Africa). The animals were in separate harems or herds when they were collared. The collars were set to take a GPS reading every 30 min, and data were downloaded via UHF radio signal. The collars remained functional between four and 16 months depending on various factors, including loss of animals to poaching (11% of N=26), lost collars (23% of N=26) natural mortality (3% of N=26), and malfunction (23% of N=26). We suspected that the collars lost could also be attributed to poaching which would increase potential poaching effects to 34%. Data downloaded from the collars were converted to geographical information system (GIS) format, after which it was manually screened for missing values. Sections of the data with missing values were removed and not used in the analysis.

All grassland fires in Mkambati from January 2007 (18 months before first collars were deployed) to August 2011, were mapped by Mkambati field rangers. Each burnt patch was given a unique ID number, and all unburnt patches (patches that have not burned post-2007) were given the same unique ID number. The patch ID number was linked to the collar data using ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). Patch visits were defined as the period from when an individual animal entered a burnt patch or unburnt grassland until it left again. Movement speed S (metre per hour) was calculated using the equation:

$$S = d/t$$

(1)

Where time spent t per visit was the sum of 30 min intervals (GPS-UHF data) per visit, and the cumulative distance d covered over that time was the total distance (m) travelled per patch visit.

To compare factors influencing the use of burnt patches, visits to these areas were identified from the GPS data. For this analysis, the location data in unburnt patches was not used. We measured: (1) the distance (m) to the nearest major river which served as a proxy for poaching risk; (2) the distances (m) between burnt patch centroids; (3) burnt patch sizes (ha); and (4) time (days) since burn. A control was established by also measuring the four different factors for all the available burnt patches not visited at the time of each choice. The distance from the previous patch (m) was calculated by measuring the distance between the centroid of the burnt patch that the animal had departed to the centroid of the new burnt patch entered. Due to the nature of the data used in the analysis, i.e. burnt patch visits rather than consecutive 30 min GPS points there was no risk of autocorrelation (Dray et al. 2010).

4.4 DATA ANALYSIS

First we used a linear regression analysis to test whether there was a relationship between number of poaching incidents and distance from the major rivers. The linear regression analysis was performed using IBM SPSS Statistics for Windows, Version 19.0. (Armonk, NY: IBM Corp.). We tested whether animals preferred foraging in burnt patches than in the unburned grassland by assessing time spent per visit and speed travelled per visit, using a MANOVA. To separate species effects from random variations among individuals, the independent variables included both a species identifier and a habitat variable describing whether the animal was in a burnt patch or in unburnt grassland and adding an individual animal identifier as a covariate. Both the time spent and speed travelled variables were log transformed and a total of 11 extreme outliers identified through box-plots were removed from the data set in order to avoid them materially affecting the result. We tested whether the animals' burnt patch use was related to the distance to the previously visited burnt patch, burnt patch size, burnt patch age (i.e., time since burn in days) and distance to areas with high poaching risk (near the major rivers) using MANOVA. The dependent variables were distance to the previously visited burnt patch, burnt patch size, time since burn, and distance to the nearest major river. The

independent variables was whether the patch was visited or not and species, and the covariate was an individual animal identifier. We did not separate the sexes in the analysis because there was only one male per species. The MANOVA's was performed using IBM SPSS Statistics for Windows, Version 19.0. (Armonk, NY: IBM Corp.). The MANOVA was complemented with a logistic regression analysis to assess if the probability that a patch was entered depended on the distance to the patch from the previous patch, the size of the patch, the days since it burned, and distance to major river. The logistic regression analysis were done using the R-Statistics package version 2.11 (R-Development-Core-Team 2011).

4.5 RESULTS

The linear regression established that distance from major river could significantly predict number of poaching incidents, $F(1, 4) = 7.066$, $p = 0.05$ and it accounted for 64% of the explained variability in poaching incidents (Figure 4.1). The time animals spent in a patch depended on the habitat type, animal species, and individual animal (Table 4.1). The species-habitat type interaction was statistically significant (Table 4.1). Both zebra and red hartebeest spent more time during visits to burnt patches than to the unburned grassland (Figure 4.2). Red hartebeest generally spend more time in both burnt patches and old grassland compared to zebra (Figure 4.2). The speed animals moved at while in a patch depended on the habitat type, animal species, and individual animal (Table 4.1). For speed in a patch the species-habitat interaction were significant (Table 4.1). Both red hartebeest and zebra moved equally fast in both habitats, but zebra moved faster than red hartebeest (Figure 4.2). Compared to other available patches, both zebra and red hartebeest chose to enter patches closer to the one they last vacated and there was no difference between the two species in this regard (Table 4.2 and Figure 4.3). Both species entered younger burnt patches more frequently, but zebra were less likely to visit older burnt patches than red hartebeest (Table 4.2 and Figure 4.3). Although both species selected relatively large patches, zebra mostly used larger patches (Table 4.2 and Figure 4.3). Both species were more likely to enter patches further from the major rivers, but zebra were more likely to do so (Table 4.2 and Figure 4.3). The probability that a new patch was entered depended on the distance to the patch the animal previously visited, the size of the new patch, time since it burned, and the distance to the major river (Table 4.3).

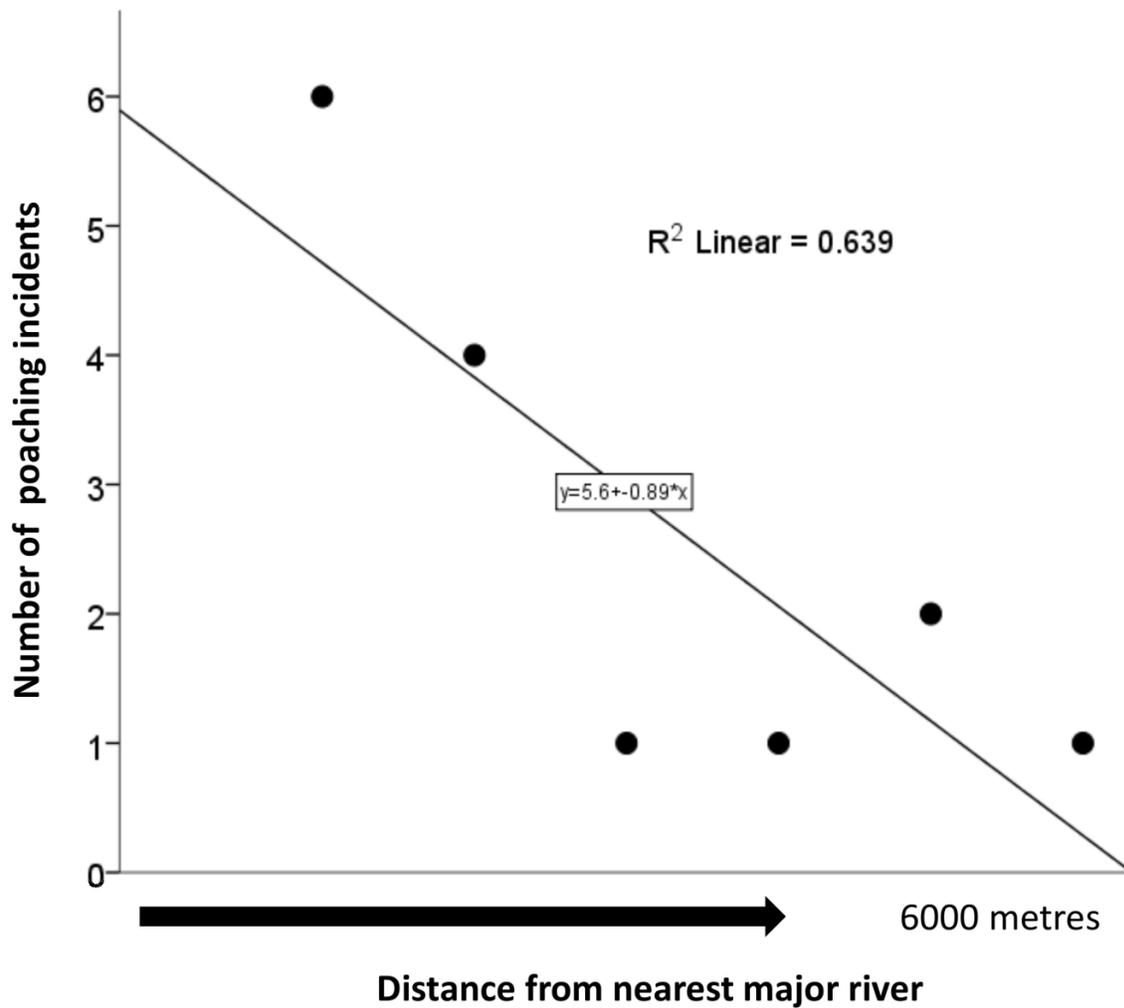


Figure 4.1: The relationship between number of poaching incidents (as recorded by field rangers on Mkambati from 2008 to 2010), and distance from the nearest major river.

Table 4.1: The results of the MANOVA test, testing for a) the difference between mean time spent within the unburnt grassland and the burnt patches; b) the difference between mean speed travelled within the unburnt grassland and the fire-patch mosaic.

Source	df †	F	P Value
a) Time spent			
Individual	1	1.672	0.196
Habitat	1	304.486	<0.0001
Species	1	8.338	0.004
Habitat * Species	1	7.292	0.007
Residuals	8523		
b) Speed travelled			
Individual	1	113.463	<0.0001
Habitat	1	13.401	<0.0001
Species	1	1122.71	<0.0001
Habitat * Species	1	5.182	0.023
Residuals	8523		

† Residual degrees of freedom in the model represent visits to forage patches

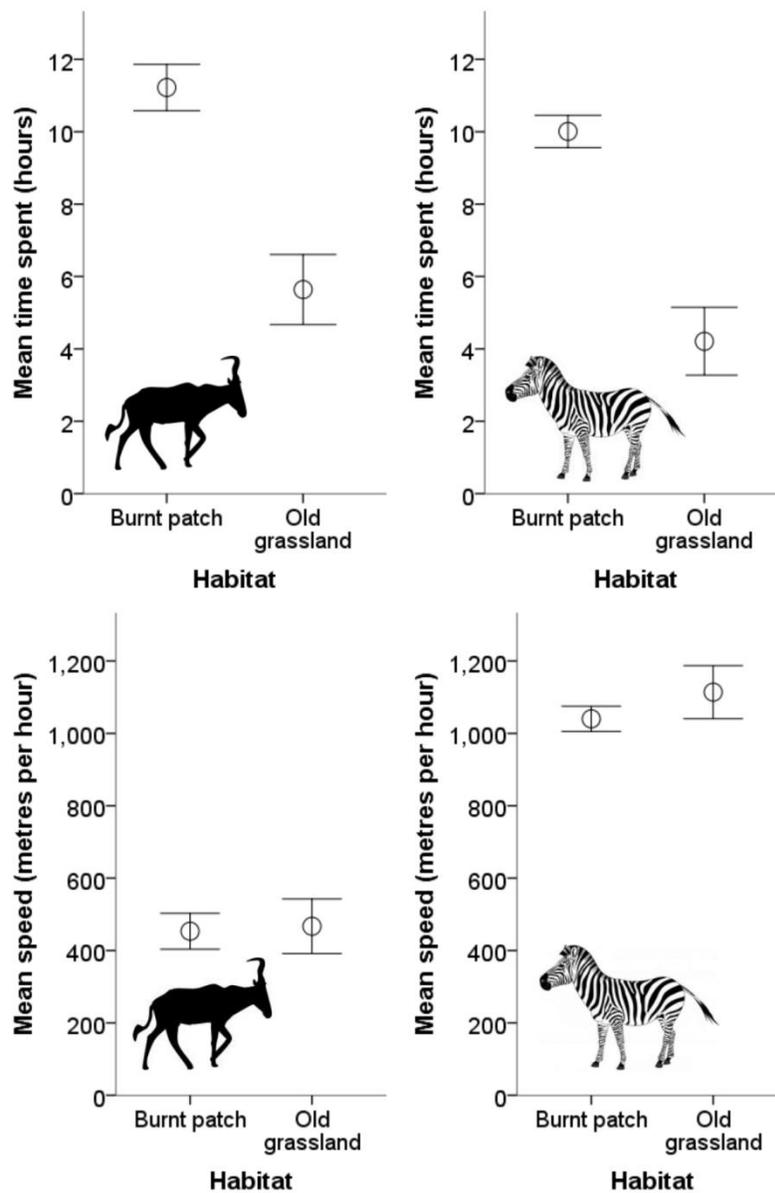


Figure 4.2: Time spent and movement speeds per visit to burnt patches and old grassland for zebra and red hartebeest. Error bars indicate upper and lower 95% CI. Silhouettes indicate species.

Table 4.2: The results of the MANOVA test, testing for: a) the distance between the fire-patch that the animal left and the new fire-patch an animal entered in comparison to the other patches it did not enter; b) the size of the patch of the new fire-patch an animal entered in comparison to the other fire-patches it did not enter; c) the time (days) since burning of the new patch an animal entered in comparison to the other fire-patches it did not enter and; d) the distance from nearest major river to the new fire-patch an animal entered in comparison to the fire-patches it did not enter

Source	df †	F	P value
a) Distance to previous patch			
Individual animal	1.000	0.029	0.864
Patch being entered	1.000	4170.870	<0.0001
Species	1.000	0.212	0.645
Patch being entered * Species	1	7.016	0.008
Residuals	138409		
b) Patch size			
Individual animal	1.000	4.322	0.038
Patch being entered	1.000	4459.201	<0.0001
Species	1.000	58.413	<0.0001
Patch being entered * Species	1.000	42.48	<0.0001
Residuals	138409		
c) Days since burn			
Individual animal	1.000	205.699	<0.0001
Patch being entered	1.000	244.943	<0.0001
Species	1.000	317.149	<0.0001
Patch being entered * Species	1.000	0.641	0.423
Residuals	138409		
d) Distance to river			
Individual animal	1.000	6.013	0.014
Patch being entered	1.000	3426.923	<0.0001
Species	1.000	7.461	0.006
Patch being entered * Species	1.000	38.11	<0.0001
Residuals	138409		

† Residual degrees of freedom in the model represent visits to forage patches

Table 4.3: The results of the logistic regression analysis to assess whether the probability that a new patch is entered depends on the distance from the burnt patch, the patch size, days since burn and the distance to a major river.

Interaction	Estimate	Std. Error	z-value	P-value
Intercept	-1.960	0.077	-25.518	<0.0001
Distance to previous patch	-5.71x10 ⁻⁴	1.2x10 ⁻⁵	-47.278	<0.0001
Patch size	8.79x10 ⁻⁴	1.9x10 ⁻⁵	45.321	<0.0001
Time since burn (days)	-1.67x10 ⁻³	6.1x10 ⁻⁵	-27.518	<0.0001
Distance to major river	3.67x10 ⁻⁴	1.4x10 ⁻⁵	26.183	<0.0001
Species	1.03	0.3	3.433	0.0005
Distance to previous patch x species	0.02x10 ⁻⁴	2.2x10 ⁻⁵	0.073	0.9418
Patch size x species	-2.44x10 ⁻⁴	3.7x10 ⁻⁵	-6.636	<0.0001
Time since burn x species	8.32x10 ⁻⁴	1.05x10 ⁻⁴	7.902	<0.0001
Distance to major river x species	-0.88x10 ⁻⁴	0.25x10 ⁻⁴	-3.471	0.0005

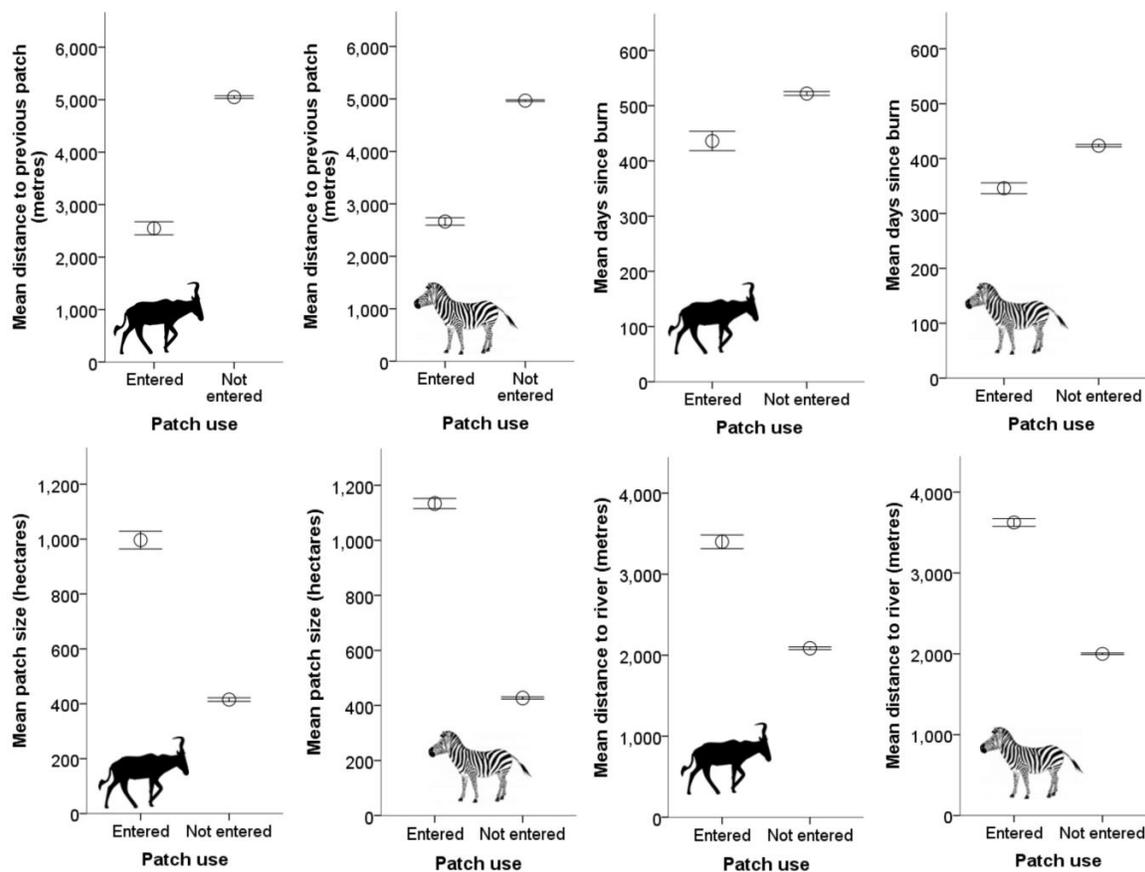


Figure 4.3: The effect of inter-patch distance; time since burn; patch size and; distance to major river, of fire-patches entered compared to fire-patches not entered, by red hartebeest and zebra. Error bars indicate upper and lower 95% CI. Silhouettes indicate species.

4.6 DISCUSSION

Red hartebeest moved slower and spend more time in patches compared to zebra. This was expected because being ruminants they have to spend more time resting while ruminating (Bell 1971). By having a more efficient digestive system red hartebeest thus moved slower through patches in the landscape compared to zebra. Contrary to expectations, red hartebeest used older burnt patches more than zebra. In east Africa, ruminants selected recently burnt patches more compared to non-ruminants (Sensenig et al. 2010). The east African grassland biomass is depleted seasonally at the onset of the dry season by high grazing pressure (McNaughton 1976). At Mkambati, grazing pressure is so low that significant accumulation of grass biomass occurs (Shackleton 1990), which, after a few months of growth, results in large quantities of moribund grass. Hartebeest have a specially adapted “long faced” skull morphology that enables them to graze scarce re-growth from between this moribund material when good forage is scarce (Schuette et al. 1998). This was evidenced by the abundant presence of “feeding holes” in moribund grass patches at Mkambati, made by the muzzle of red hartebeest, (*Pers obs.* Jan A. Venter). Although the patches lost their elevated nutritional value due to aging and the build-up of moribund material, this adaptation probably enabled red hartebeest to use older burnt patches more even though there were younger burned patches of better quality available elsewhere.

In contrast to red hartebeest, zebra should be more tolerant of fibrous food, but would have to sustain a much higher intake rate to maintain energy levels when feeding on low-quality forage (Bell 1971, Okello et al. 2002). Zebra moved faster and further than red hartebeest which is consistent with their higher food intake requirements associated with their digestive system. Higher movement rates by zebra compared to ruminants have also been observed in other recent studies (Owen-Smith and Goodall 2014). In hindgut fermenters (non-ruminants), faster throughput is an advantage that outweighs their lower digestive efficiency, particularly when feeding on poor quality foods (Illius and Gordon 1992). When other species of equids were faced with similar trade-offs their decisions depended on forage quality (Edouard et al. 2010). It is probable that zebra with their wider muzzle, are better able to exploit very short grass sprouting on recently burnt patches, and thus maximize bite size and intake rate on these swards (Gordon and Illius 1988) compared to red hartebeest which are not able to do so with equal efficiency. We thus showed that intrinsic traits, such as muzzle width,

could possibly carry over into patch use rules in an unexpected way. As muzzle width can evolve relatively independently of body mass, our results show how a very limited set of intrinsic traits (i.e. body mass, digestion strategy and muzzle width) may yield very different patch use rules for animals that rely on the same resource.

Red hartebeest and zebra in Mkambati selected patches closer to the one they came from, supporting other studies on patch selection (Gross et al. 1995, Sibbald and Hooper 2003). The red hartebeest and zebra in Mkambati chose to use larger burnt patches compared to other available burnt patches. Smaller burnt patches could have higher quality grass compared to larger burns, due to being maintained as closely cropped grazing lawns (Sensenig et al. 2010). In addition, smaller-bodied animals prefer smaller burns (Sensenig et al. 2010). Intensive grazing by smaller herbivores could change grazing conditions and potentially displace other large herbivores (Illius and Gordon 1992). Red hartebeest and zebra chose to visit larger habitat patches, which may be related to interspecific competition. If smaller patches are preferred by smaller grazers (Cromsigt et al. 2009, Sensenig et al. 2010), species such as blesbok (*Damaliscus pygargus phillipsi*) (61 kg as compared to 140 kg for red hartebeest and 210 kg for zebra), which were present in large numbers in Mkambati, would have the competitive advantage. By altering the vegetation state (being able to temporarily maintain very small burned patches as closely cropped grazing lawns) (Sensenig et al. 2010), we would predict blesbok to be able to competitively exclude the larger grazers like red hartebeest and zebra (Illius and Gordon 1987, Prins and Olff 1998b).

Both red hartebeest and zebra reduced the probability of encountering poachers by choosing to visit patches further away from major rivers. By focussing on suitable patches within areas of lower 'predation' (or poaching) risk (Gude et al. 2006, Thaker et al. 2010), rather than only reacting when 'predators' (or poachers) are encountered (Creel et al. 2005, Fortin et al. 2005, Kittle et al. 2008), hartebeest and zebra appear to have a cognitive approach to patch use at a habitat patch scale by actively avoiding high poaching risk areas. With ever increasing poaching in Africa (Hayward 2009b, Waltert et al. 2009, Craigie et al. 2010), this is a result that has significant implications for protected area management. The consistent unnatural selection of forage areas by ungulates due to poaching

impact could have negative impacts on forage resources (Ruggiero 1992), ecosystem services (Wright and Duber 2001, Brodie et al. 2009) and biodiversity through cascading effects (Ripple and Beschta 2007, Eisenberg et al. 2013). This effect could be worse in small- to medium-sized protected areas.

4.7 CONCLUSION

In conservation areas, where managers attempt to simulate the natural processes and heterogeneity of ecosystems (Grant et al. 2011), patch use dynamics of large herbivores is a critical aspect to consider. In this study, we demonstrated how red hartebeest and zebra actively use particular types of burnt patches with suitable forage, and that their choice of foraging patches was influenced by direct and secondary poaching effects. This illustrates that both fire management and anti-poaching action could potentially impact ecosystems (Ripple and Beschta 2007, Eisenberg et al. 2013). This is especially the case for more intensively managed small- to medium-sized conservation areas like Mkambati Nature Reserve.

**Chapter 5: *Intrinsic and extrinsic factors
influencing large African herbivore movements***

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Rob Slotow*

ABSTRACT

Understanding environmental as well as anthropogenic factors that influence large herbivore ecological patterns and processes should underpin their conservation and management. We assessed the influence of intrinsic (feeding niche, digestive strategy), extrinsic environmental (seasonality, landscape heterogeneity) and extrinsic anthropogenic (fencing) factors on movement behaviour of eight African large herbivore species. We were particularly interested in scaling effects in response to complexity using movement metrics as response indicators. Four frequency distributions were used to model the distribution of individual animal step length data. A cumulative odds ordinal logistic regression with proportional odds was used to determine the effect of season, feeding niche, number of vegetation types, home range size, and fences on the number of exponential distributions observed. The dominant movement behaviour was Brownian motion, with one to four exponential distributions. In other words, large herbivores used multi-scale small area restricted searches, mixed with possible multi-scale large movements in the process of finding suitable forage resources. When animals faced the trade-off between forage quality and quantity during the dry season, they moved further between forage areas and water sources in order to get to better forage, which added to the number of movement scales observed. Elephants (*Loxodonta africana*) had a lower number of movement scales, compared to all the other feeding types, which could be attributed to them being able to switch between browse and graze, thereby avoiding interspecific competition at lower feeding heights during the dry seasons. However, no difference in the number of movement scales could be detected among ruminant grazers, ruminant mixed feeders and non-ruminant grazers, which may need more frequent data-points to discriminate. The number of movement scales increased in more heterogeneous areas. Animals with larger home ranges, which are also larger species, and animals more restricted by fences, had fewer movement scales. In order for managers to effectively manage protected areas and associated biodiversity they need take cognisance of the different scales animals operate under, and the different factors that may be important for different species.

5.1 INTRODUCTION

Environmental heterogeneity, such as in water or forage availability, species traits, and anthropogenic influences have a substantial effect on the ecological patterns and processes that shape the distribution of large herbivores (Boone and Hobbs 2004, Loarie et al. 2009, Vanak et al. 2010, Cornélis et al. 2011, Duffy et al. 2011). Understanding how these factors influence the movement behaviour of large herbivores is important for protected area managers, as these could influence individual species' ability to persist, and have a negative effect on other species in an ecosystem (Fortin et al. 2005, Ripple and Beschta 2007). Environmental heterogeneity occurs at different spatial and temporal scales, which makes it difficult to predict at what scales resource selection by large herbivores occurs (Senft et al. 1987a, Bailey et al. 1996), and poor understanding may result in mismatch in the scale at which interventions are made relative to the underlying biological system (Delsink et al. 2013).

Large herbivores select resources at different scales: plant part, plant species, vegetation types and landscape regional scale (Jarman 1974, Senft et al. 1987b, Bailey et al. 1996, Prins and Van Langevelde 2008a, Owen-Smith et al. 2010). In most cases, there is a proportional relationship between the time a large herbivore spends in an area, and the available quality and quantity of forage (Bailey et al. 1996, Owen-Smith et al. 2010). This relationship between herbivores and their environment can be detected in distinct movement scales (Frair et al. 2005), which takes place at several scale levels: from steps between foraging stations, to daily movement in home ranges, to seasonal migratory movements (Viswanathan et al. 1999, Bartumeus et al. 2005, Searle et al. 2007, Prins and Van Langevelde 2008a).

There is considerable interspecific variability in herbivore morphological traits (van Soest 1996), and animals react to their environment in different ways, related to these traits (Jarman 1974, McNaughton and Georgiadis 1986, Bailey et al. 1996, Prins and Van Langevelde 2008a). African ecosystems are well known for their exceptional diversity of large mammalian herbivores, with the majority consisting of bovids, which are ruminants, co-existing with a few equids, which are non-ruminants (Prins and Olf 1998b, Gagnon and Chew 2000, Grange et al. 2004). Early studies have

identified a variety of feeding patterns or feeding niche categories among large herbivores (Lamprey 1964, Hofmann and Stewart 1972, Gagnon and Chew 2000). These feeding niches are normally driven by morphological traits such as body size, feeding type, digestive strategy and muzzle width (Jarman 1974, van Soest 1996, Shipley 1999). Broader feeding types categorise large herbivores into grazers, mixed feeders and browsers (Grunow 1980, McNaughton and Georgiadis 1986).

The digestive strategy of a ruminant relies on efficient extraction and use of protein at the cost of increasing intake rate and processing capability (Bell 1971, Hofmann 1989, Shipley 1999). The non-ruminant is much more tolerant of poor quality forage but must maintain a high rate of intake to be able to survive on this type of food (Bell 1971, Illius and Gordon 1992, Shipley 1999). Their selectivity is, therefore, much less intense compared to ruminants (Bell 1971). A large number of studies have focussed on the topic of animal movement versus environmental heterogeneity (extrinsic factors) (Gross et al. 1995, Frair et al. 2005, de Knegt et al. 2007, Humphries et al. 2010, de Jager et al. 2011), but only a few have investigated the role of morphological traits (intrinsic factors) in animal movement behaviour (Searle et al. 2007, Prins and Van Langevelde 2008a).

Abiotic factors, such as surface water supplies, are one of the primary determinants of large-scale distribution patterns of large herbivores, and act as constraints within which they have to interact with biotic features such as forage resources (Bailey et al. 1996, Redfern et al. 2003, Smit et al. 2007). In many cases, large herbivores select different habitats, and move differently, during times of low versus high resource availability (Ager et al. 2003, Venter and Watson 2008, Cornélis et al. 2011, Birkett et al. 2012). This is because they become nutritionally stressed during the dry season when both forage quality and quantity are reduced (Prins 1996). Surface water sources can dry up, which influences the trade-off foragers face between nutritional requirements and surface-water constraints when forage quantity is reduced (Redfern et al. 2003).

Forage quality and quantity are most affected near water sources, because animals tend to congregate in these areas due to water dependency (Redfern et al. 2003). The reduced forage

quantities during dry years force large herbivores to travel further from water sources to meet their nutritional requirements (Redfern et al. 2003, Venter and Watson 2008). The trade-off between nutritional requirements and surface-water constraints that species face varies according to the species' water dependence, size, feeding type and digestive system (Redfern et al. 2003, Smit et al. 2007). For example, in Kruger National Park, grazers are more dependent on artificial water sources, compared to browsers, and mixed-feeders are more dependent on rivers (Smit et al. 2007).

The amount of space animals' use can be defined by their home range size (Funston et al. 1994, Leggett 2006). Larger species tend to have larger home range sizes (Lindstedt et al. 1986), and feed at coarser grain scales, which could potentially influence the number of spatial scales at which animals move, or are responsive to (Prins and Van Langevelde 2008a). The available space for animals to use, and the influence of reserve fences (Boone and Hobbs 2004, Loarie et al. 2009, Naidoo et al. 2012), could also influence animal movement by limiting larger migratory movements (Boone and Hobbs 2004, Loarie et al. 2009, Naidoo et al. 2012).

Animal movements consists of a discrete series of displacements (steps, varying in length) separated by successive re-orientation events (turning angles)(Bartumeus et al. 2005). Animal forage and search behaviour has been generally described using two different types of random movement behaviours, namely: random walks (Brownian motion) and Lévy walks (Viswanathan et al. 1996, Viswanathan et al. 1999, Bartumeus et al. 2005, Edwards et al. 2007). Random walks are essentially similar steps (on the same spatial scale) separated by orientation and changing turn angles (Viswanathan et al. 1999). Lévy walks reflect clusters of shorter steps that are connected by rare large steps (Edwards et al. 2012). Lévy walkers can outperform Brownian random walkers in forage searching efficiency as they revisit patches far less often, and because the larger steps potentially increase the probability of finding new patches in a shorter time (Viswanathan et al. 1999, Raposo et al. 2009, Viswanathan 2010).

More recently the composite Brownian motion emerged as a strong alternative model to the Lévy walks (Benhamou 2007, de Jager et al. 2011, Schultheiss and Cheng 2011, Jansen et al. 2012, Reynolds 2013), where animals switch between two or more Brownian walks (i.e. switch spatial scale), each characterised by an exponential step-length distribution representing a movement scale (Jansen et al. 2012, Reynolds 2013). Brownian walks at two or more different scales (composite Brownian motions), e.g., a small-scale area-restricted search (within patches) mixed with a set of large scale movements (between patches), can be an optimal approach to find suitable forage (Benhamou 2007).

We tested whether eight African large herbivore species, with a variety of morphological traits (feeding types and digestive strategies), coming from landscapes of varying vegetation heterogeneity, showed a difference in step length distributions and movement scale complexity (i.e. number of movement scales). Our data was ideal for this purpose as it covered various species from a number of different habitat types. In addition, we also tested a number of hypotheses related to factors that could affect movement scale complexity: a) we expected that large herbivores would show more movement scales during the dry season because reduction in forage resources forces them to move larger distances to meet their dietary requirements; b) we predicted that animals with different intrinsic traits, specifically feeding type and digestive strategy, would differ in their number of movement scales because these influences how they interact with habitats and forage resources; c) we expected more movement scales in areas with higher heterogeneity because forage resources would be more variable in what they offer under different conditions; d) we expected species with larger home ranges, which are normally larger bodied species (which we confirm with our data), to have fewer movement scales because they feed at a courser grain scale; and e) we expected species that are more constrained by fences to have fewer movement scales due to large migratory movements and their “natural” ranging behaviour being restricted.

5.2 STUDY AREA

The species data originated from eight different reserves in South Africa representing various levels of seasonal variability, heterogeneity, area size, and large herbivore assemblages (Table 5.1). The

species studied were impala (*Aepyceros melampus*), red hartebeest (*Alcelaphus buselaphus*), blue wildebeest (*Connochaetes taurinus*), eland (*Tragelaphus oryx*), African buffalo (*Syncerus caffer*), Cape mountain zebra (*Equus zebra*), plains zebra (*Equus burchelli*) and African elephant (*Loxodonta africana*) (Table 5.1). Data from GPS-UHF and GPS-GSM collars that were produced as part of our own (Mkambati and Baviaanskloof) and a number of other published studies (Jachowski et al. 2012, Shrestha et al. 2012, Delsink et al. 2013), and unpublished studies were used.

All field work that took place on Mkambati and Baviaanskloof were conducted by, or under the supervision of the first author, a staff member of the Eastern Cape Parks and Tourism Agency, as part of the operational activities of the appointed management authority of Mkambati (Eastern Cape Parks and Tourism Agency Act no. 2 of 2010, Eastern Cape Province, South Africa). Field work on the other reserves was ethically and legally approved, and was conducted by the various relevant institutions (Jachowski et al. 2012, Shrestha et al. 2012, Delsink et al. 2013) including the management authority of Welgevonden Private Game Reserve.

5.3 METHODS

The collars were set to take a coordinate reading every 30 min, 1 hour or 2 hours which was dependent on the study area. Data downloaded from the collars were converted to GIS format, and any parts of the data sets with missing values were removed. Data were converted to the same time frequency (2 hour intervals) by removing data points in-between, as the majority of the data were collected at this time interval.

Step lengths (distance between each locality point recorded by the GPS-UHF and GPS-GSM collars) were calculated for each animal's data set using Geospatial Modelling Environment (Beyer 2012) and ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). All step lengths < 6 m were excluded during the analysis in order to remove non-movements and false movements due to GPS-error.

Table 5.1: The species and reserves investigated during this study. Biomes were classified according to (Rutherford et al. 2006b)

Study area and biome	Species studied with number of data subsets	Geographical location	Size (ha)
Mkambati Nature Reserve – Grassland	Eland (<i>Tragelaphus oryx</i>) (n = 5) Plains zebra (<i>Equus burchelli</i>) (n = 5) Red hartebeest (<i>Alcelaphus buselaphus</i>) (n = 9)	31°13'– 31°20' S and 29°55'– 30°04' E	7720
Baviaanskloof Nature Reserve - Fynbos	Cape mountain zebra (<i>Equus zebra</i>) (n = 6) African buffalo (<i>Syncerus caffer</i>) (n = 4)	33°26'–33°53' S and 23° 35'–24° 59' E	211476
Kruger National Park - Savanna	African elephant (<i>Loxodonta africana</i>) (n = 17)	22°20'–25°32' S and 30°53'–32°02' E	2300000
Pilanesberg National Park - Savanna	African elephant (<i>Loxodonta africana</i>) (n = 4)	25°8'–25°22' S and 26°57'–27°13' E	55000
Mkhuze Game Reserve - Savanna	African elephant (<i>Loxodonta africana</i>) (n = 1)	27°33'–27°48' S and 32°08' - 32°25' E	45291
Mapungubwe National Park - Savanna	Impala (<i>Aepyceros melampus</i>) (n = 5) Eland (<i>Tragelaphus oryx</i>) (n = 5) Blue wildebeest (<i>Connochaetes taurinus</i>) (n = 9)	22°10'– 22°17' S and 29°08'– 29°32' E	28168
Welgevonden Private Game Reserve -Savanna	Plains zebra (<i>Equus burchelli</i>) (n = 14) Blue wildebeest (<i>Connochaetes taurinus</i>) (n = 13)	24°10'– 24°25' S and 27°45'– 27°56' E	33000
Asante Sana Private Game Reserve - Nama-Karoo	Impala (<i>Aepyceros melampus</i>) (n = 3) Eland (<i>Tragelaphus oryx</i>) (n = 6) Blue wildebeest (<i>Connochaetes taurinus</i>) (n = 8)	32°15'– 32°21' S and 24°52'– 25°04' E	10700

Two subsets of data were extracted from each animal's data set representing two dry season months (July/August) and two wet season months (January/February). For the reserve in the winter rainfall area, i.e. Baviaanskloof Nature Reserve, we used July/August as the wet season and January/February as the dry season. In order to test our hypotheses we identified a number of explanatory variables, i.e. season, feeding niche, number of vegetation types, home range size and level of space use. Feeding niche represented a combination of the feeding niche and digestive system of each species and was grouped into ruminant grazers (red hartebeest, blue wildebeest, African buffalo), non-ruminant grazers (plains zebra and Cape mountain zebra), ruminant mixed feeders (impala and eland) and non-ruminant mixed feeders (African elephant). Number of vegetation types represented the number of categories, as classified by (Mucina and Rutherford 2006), that were visited by the animals over that period determined by the location (GPS) points. Vegetation types visited were grouped into three categories: ≤ 2 vegetation types, 3 vegetation types and ≥ 4 vegetation types.

We were not able to use body size as an explanatory variable in the analysis because, with it included, the assumption of proportional odds was not met, as assessed by a full likelihood ratio test comparing the residual of the fitted location model to a model with varying location parameters ($X^2 = 26.377, p = 0.091$). Larger bodied species however, normally have larger home ranges (Lindstedt et al. 1986), so we regressed the natural logarithm of species body mass against the natural logarithm of home range size, which indicated a significant positive correlation ($r(100) = 0.920, p < 0.001$) when outliers were removed (identified using box-plots) (Figure 5.1). We were, therefore, able to use home range size as a proxy for body size because it was intrinsically connected. Home range size (H) was calculated as the minimum convex polygon in hectares using the 'bounding containers' tool in ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) and divided into quartiles using IBM-SPSS Statistics 21 (SPSS Inc., Chicago IL). The resultant four home range groupings was ≤ 954 ha (small); 955-2524 ha (medium); 2525-6348 ha (medium-to-large); and ≥ 6349 ha (large).

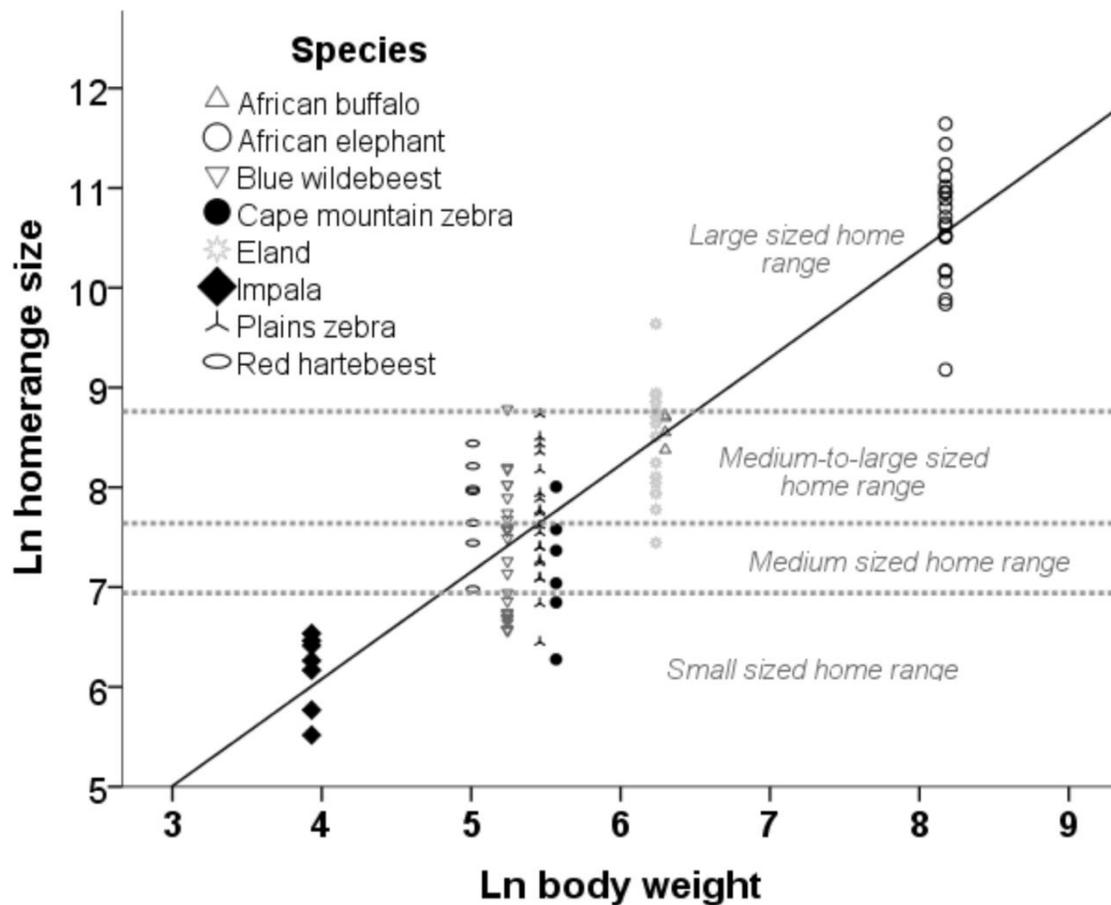


Figure 5.1: The regression line indicates a linear relationship between the natural logarithm of species body weight (kg) plotted against home range size (ha) for the species studied ($R^2 = 0.827$; $y = 1.79 + 1.07 * x$). The reference lines separate the different home range size groupings used in our analysis.

The level of space use, or space use index (SUI), independent variable was calculated as:

$$\text{SUI} = H/s$$

where s is nature reserve size in hectares. The space use index gives a relative value of how much of the space available to an individual animal was used (i.e how much the animal is contained/bounded by the boundaries/fences of the reserve relative to their home range). The closer to 1 this index was the more the animal used all the available space within the reserve.

The level of space use variable was divided into quartiles using IBM-SPSS Statistics 21 (Armonk, NY: IBM Corp.). The resultant four space use groupings was ≤ 0.028 (low); 0.029-0.060 (medium); 0.061-0.181 (medium-to-high); and ≥ 0.182 (high).

5.4 DATA ANALYSIS

Regarding step length, four frequency distributions were used to express this distribution for the data subsets: (a) exponential (Brownian motion); (b) power law (Lévy walk); c) truncated power law distributions (truncated Lévy walk); and (d) hyper exponential functions (composite Brownian walk) that are mixtures of two, three or four exponential distributions following the methodology of (Jansen et al. 2012) (Table 5.2). The lower truncation value was set to 6 m (see above). A model selection procedure based on the Akaike Information Criterion (AIC) was applied to compare the step length distributions (Jansen et al. 2012) (Figure 5.2 and Table 5.2). While one model may indeed be favoured over another, it might not be a suitable model (Edwards et al. 2012), so we used Kolmogorov-Smirnov (KS) goodness-of-fit tests and R^2 values to test if the models were consistent with the data. The statistical tests were conducted using R (R-Development-Core-Team 2011). R-codes for step length analysis are available from <http://mathbio.bl.rhul.ac.uk/People/alla/r-code>.

A cumulative odds ordinal logistic regression with proportional odds was used to determine the effect of season, feeding niche, number of vegetation types, home range size, and fences on the number of movement scales (number of different exponential distributions within the same dataset) using IBM-SPSS Statistics 21 (Armonk, NY: IBM Corp.).

Table 5.2: Probability density function, inverse cumulative, Maximum Likelihood Estimate (MLE) and log-likelihood functions for exponential, power law, truncated power law and hyper-exponential (mix of exponentials) distributions (Jansen et al. 2012) used to model the movement data.

Models	Probability density function	Inverse cumulative	MLE or log-likelihood
Exponential (Brownian motion)	$P(x) = \lambda e^{-\lambda(x-x_{\min})}$	$P(X \geq x) = e^{-\lambda(x-x_{\min})}$	$\lambda_{best} = \frac{1}{\frac{1}{n} \sum_{i=1}^n x_i - x_{\min}}$
Power law (Lévy walk)	$P(x) = \frac{\mu - 1}{x_{\min}^{1-\mu}} x^{-\mu}$	$P(X \geq x) = \left(\frac{x}{x_{\min}}\right)^{1-\mu}$	$\mu_{best} = 1 + \frac{1}{\frac{1}{n} \sum_{i=1}^n \log x_i - \log x_{\min}}$
Truncated power law (Lévy walk)	$P(x) = \frac{\mu - 1}{x_{\min}^{1-\mu} - x_{\max}^{1-\mu}} x^{-\mu}$	$P(X \geq x) = 1 - \frac{x_{\min}^{1-\mu} - x^{1-\mu}}{x_{\min}^{1-\mu} - x_{\max}^{1-\mu}}$	$L = n(\log(\mu - 1) - \log(x_{\min}^{1-\mu} - x_{\max}^{1-\mu})) - \mu \sum_{i=1}^n \log x_i$
Mix of exponentials (Composite Brownian walk)	$P(x) = \sum_{j=1}^k p_j \lambda_j e^{-\lambda_j(x-x_{\min})}$ with $\sum_{j=1}^k p_j = 1$	$P(X \geq x) = \sum_{j=1}^k p_j e^{-\lambda_j(x-x_{\min})}$	$L = \sum_{j=1}^k \log P(x_j)$

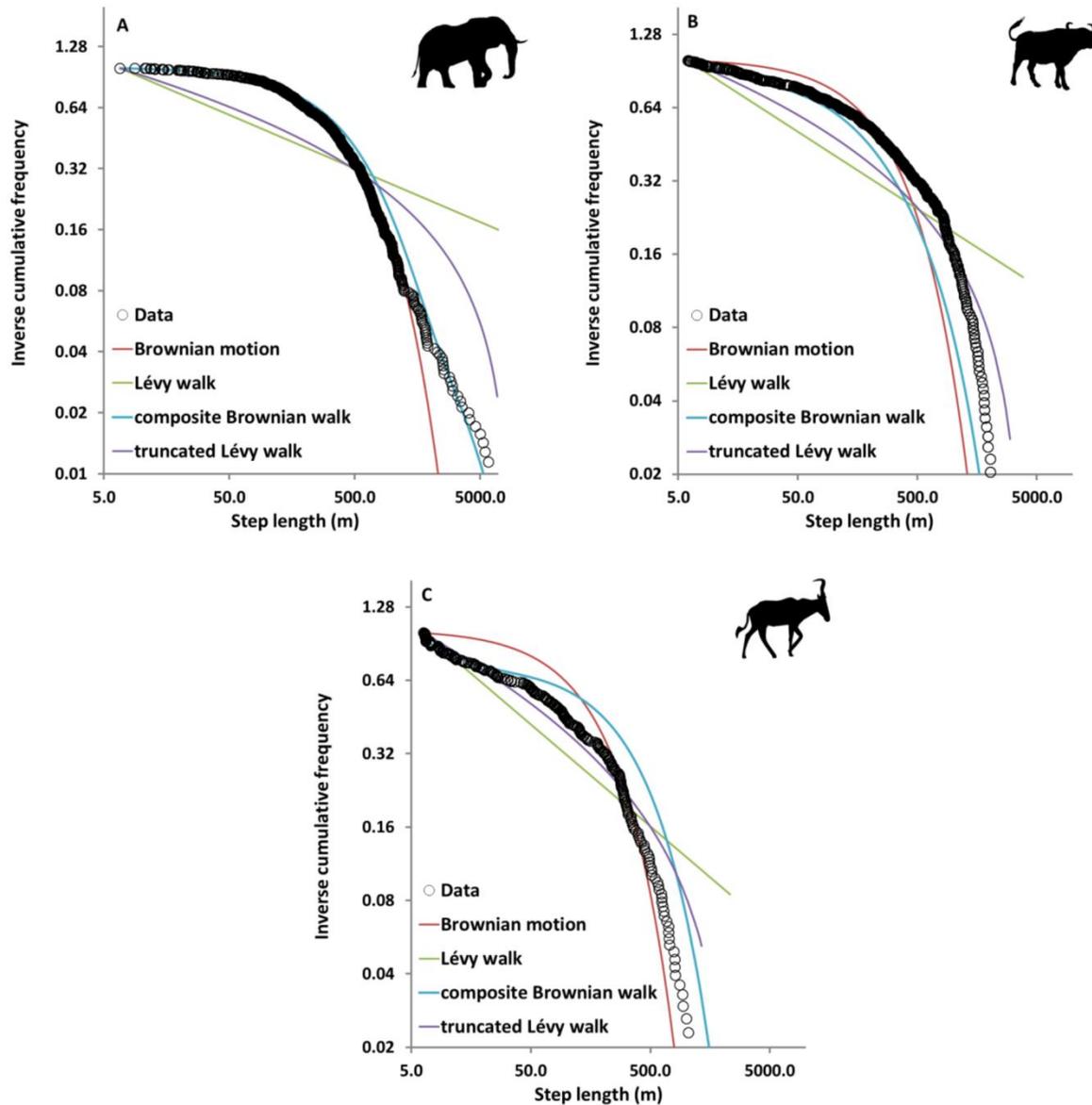


Figure 5.2: Examples indicating the step length distributions with the four frequency distributions used to model step length distribution. The circles represent the inverse cumulative frequency of step length data. The curves represent Brownian motion, Lévy walk, a truncated Lévy walk, and a composite Brownian walk consisting of a mixture of two, three or four exponentials depending on which model was favoured. Models favoured in these examples are (A) Brownian walk with 2 exponential distributions ($p_1 = 0.917$, $\lambda_1 = 0.002$, $\lambda_2 = 0.0004$); (B) Brownian walk with 3 exponential distributions ($p_1 = 0.137$, $p_2 = 0.325$, $p_3 = 0.538$, $\lambda_1 = 0.123$, $\lambda_2 = 0.007$, $\lambda_3 = 0.002$); (C) Brownian walk with 4 exponential distributions ($p_1 = 0.678$, $p_2 = 0.179$, $p_3 = 0.086$, $p_4 = 0.057$, $\lambda_1 = 0.008$, $\lambda_2 = 0.061$, $\lambda_3 = 0.297$, $\lambda_4 = 0.002$). An individual result of an elephant, buffalo and red hartebeest are displayed in these examples.

For the movement scales, the ordinal dependent variable was number of exponential step-length distributions, i.e. movement scales (grouped as 1 and 2 movement scales; 3 movement scales and 4 movement scales) derived from the step length distribution model which produced the best fit according to the Akaike weights and Kolmogorov-Smirnov goodness-of-fit tests (Addendum A). Individual datasets with one and two movement scales were combined due to the low number of movements with only one scale ($n=6$ from $N=114$).

5.5 RESULTS

We tested a total of 114 animal data subsets from eight species in eight reserves (Appendix B). For all the individual animals tested, the resulting Akaike weights mainly supported the composite Brownian motion step length distributions with one, two, three or four movement scales (Figure 5.3). For impala, red hartebeest, blue wildebeest and Cape mountain zebra, the resulting Akaike weights most supported the composite Brownian motion step length distributions with three or four movement scales (Figure 5.3). For eland, the resulting Akaike weights mainly supported the composite Brownian motion step length distributions with three or four movement scales in the dry season, but two and three movement scales in the wet season (Figure 5.3). For African buffalo, the Akaike weights mainly supported the composite Brownian motion step length distributions with three movement scales (Figure 5.3). For plains zebra, the resulting Akaike weights mainly supported the composite Brownian motion step length distributions with three or four movement scales in the wet season but two and three movement scales in the dry season (Figure 5.3). For African elephant, the Akaike weights mainly supported the composite Brownian motion step length distributions with three movement scales in the dry season and two in the wet season (Figure 5.3).

The cumulative odds ordinal logistic regression with proportional odds test had the following results. Separate binomial logistic regressions indicated that there were proportional odds ($X^2 = 15.904$, $p = 0.196$), which meant that each independent variable had an identical effect at each cumulative division of the ordinal dependent variable, once body weight was removed (see methods). There was also no multicollinearity detected amongst the independent variables.

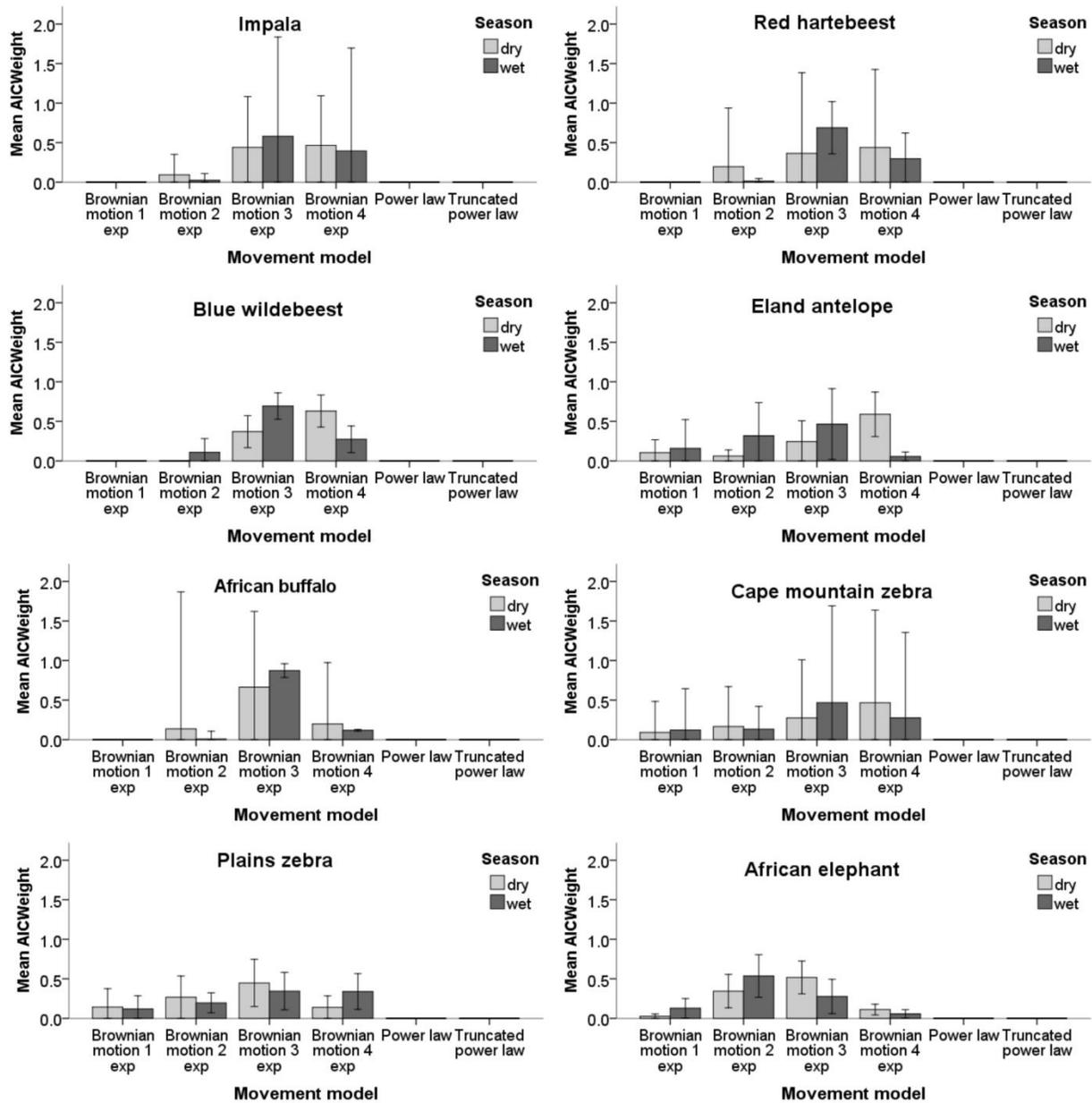


Figure 5.3: The step length distributions best describing movement patterns of the different species. The mean Akaike (AIC) weights of the frequency step length distributions of data subsets indicate which models Brownian motion; Lévy walk; truncated Lévy walk; or composite Brownian walks were favoured in different seasons (see Table 5.1 for sample sizes).

The deviance goodness-of-fit test indicated that the model was a good fit to the observed data, ($X^2(118) = 122.482, p = 0.370$), but a number of cells were sparse, with zero frequencies in 58.1% of cells. However, the final model significantly predicted the dependent variable over and above the intercept-only model ($X^2(12) = 53.728, p < 0.001$). Overall, there was a lower number of movement scales for wet versus dry season (Table 5.3 and Figure 5.4). In general, the feeding type (Wald $X^2(3) = 14.875, p = 0.002$) had a significant effect on the number of movement scales, but there was no significant effect on the number of vegetation types (Wald $X^2(2) = 5.682, p = 0.058$), home range size (Wald $X^2(3) = 6.572, p = 0.087$), or space use index (Wald $X^2(3) = 5.108, p = 0.164$) on the number of movement scales (Figure 5.4). For pairwise contrasts, we detected significantly more movement scales for non-ruminant grazers, ruminant grazers, and ruminant mixed feeders versus non-ruminant mixed feeders (Table 5.3). There were fewer movement scales detected for ≤ 2 vegetation types versus ≥ 4 vegetation types (Table 5.3). A lower number of movement scales for medium-to-large home ranges versus the medium sized home range were also observed (Table 5.3 and Figure 5.1). There were more movement scales for medium-to-high space use indices versus the high space use indices (Table 5.3).

As non-ruminant mixed feeders were driving the odds ratios in the above analysis, we ran an additional ordinal regression analysis where these feeders were excluded from the model. This model also significantly predicted the dependent variable over and above the intercept-only model ($X^2(11) = 30.086, p = 0.002$). In this case there was also a lower number of movement scales detected for wet versus dry season ($X^2(1) = 4.682, p = 0.030$), but neither the feeding type (Wald $X^2(2) = 1.674, p = 0.433$), the number of vegetation types (Wald $X^2(2) = 3.228, p = 0.199$), home range size (Wald $X^2(3) = 6.292, p = 0.098$), nor space use index (Wald $X^2(3) = 7.002, p = 0.072$) had any significant effect on the prediction of the scale of movement.

Table 5.3: The result of the cumulative odds ordinal logistic regression with pairwise comparisons indicating the effect of season, feeding type, home range size, and level of space use on the number of movement scales (p – values in bold indicate significant effects).

Pairwise comparison	B	Std. Error	Wald	df	p-value	Lower Bound	Upper Bound	Exp B	Lower	Upper
Wet season versus Dry season	-1.121	0.409	7.501	1	0.006	-1.924	-0.319	0.326	0.146	0.727
Non-ruminant grazer versus Non-ruminant mixed feeder	4.008	1.274	9.895	1	0.002	1.511	6.505	55.016	4.529	668.266
Non-ruminant grazer versus Ruminant mixed feeder	-0.237	0.656	0.13	1	0.718	-1.522	1.049	0.789	0.218	2.856
Nonruminant grazer versus Ruminant grazer	-0.7	0.544	1.656	1	0.198	-1.766	0.366	0.497	0.171	1.442
Ruminant grazer versus Non-ruminant mixed feeder	4.708	1.26	13.951	1	<0.001	2.237	7.178	110.776	9.368	1309.959
Ruminant grazer versus Ruminant mixed feeder	0.463	0.568	0.666	1	0.414	-0.649	1.576	1.589	0.522	4.835
Ruminant mixed feeder versus Non-ruminant mixed feeder	4.244	1.179	12.969	1	<0.001	1.934	6.554	69.698	6.919	702.055
≤2 Vegetation types versus ≥4 Vegetation types	-1.346	0.676	3.962	1	0.047	-2.672	-0.021	0.26	0.069	0.98
3 Vegetation types versus ≤2 Vegetation types	0.911	0.496	3.379	1	0.066	-0.06	1.883	2.488	0.941	6.573
3 Vegetation types versus ≥4 Vegetation types	-0.435	0.712	0.374	1	0.541	-1.83	0.96	0.647	0.16	2.611
Medium sized home range versus Large sized home range	-0.561	1.082	0.268	1	0.604	-2.682	1.56	0.571	0.068	4.761
Medium sized home range versus Small sized home range	0.113	0.624	0.033	1	0.857	-1.111	1.336	1.119	0.329	3.805

Table 5.3 continued

Pairwise comparison	B	Std. Error	Wald	df	p-value	Lower Bound	Upper Bound	Exp B	Lower	Upper
Medium-to-large sized home range versus Large sized home range	-1.776	1.022	3.022	1	0.082	-3.778	0.226	0.169	0.023	1.254
Medium-to-large sized home range versus Medium sized home range	-1.215	0.599	4.109	1	0.043	-2.39	-0.04	0.297	0.092	0.961
Medium-to-large sized home range versus Small sized home range	-1.102	0.63	3.057	1	0.08	-2.338	0.133	0.332	0.097	1.143
Small sized home range versus Large sized home range	-0.674	1.104	0.372	1	0.542	-2.837	1.49	0.51	0.059	4.438
Low level of space use versus High level of space use	1.272	0.685	3.442	1	0.064	-0.072	2.615	3.566	0.931	13.663
Medium level of space use versus High level of space use	1.191	0.677	3.097	1	0.078	-0.135	2.517	3.29	0.873	12.397
Medium level of space use versus Low level of space use	-0.081	0.573	0.02	1	0.888	-1.203	1.042	0.923	0.3	2.836
Medium-to-high level of space use versus High level of space use	1.37	0.649	4.454	1	0.035	0.098	2.642	3.934	1.103	14.038
Medium-to-high level of space use versus Low level of space use	0.098	0.6	0.027	1	0.87	-1.078	1.274	1.103	0.34	3.577
Medium-to-high level of space use versus Medium level of space use	0.179	0.594	0.09	1	0.764	-0.986	1.344	1.196	0.373	3.833

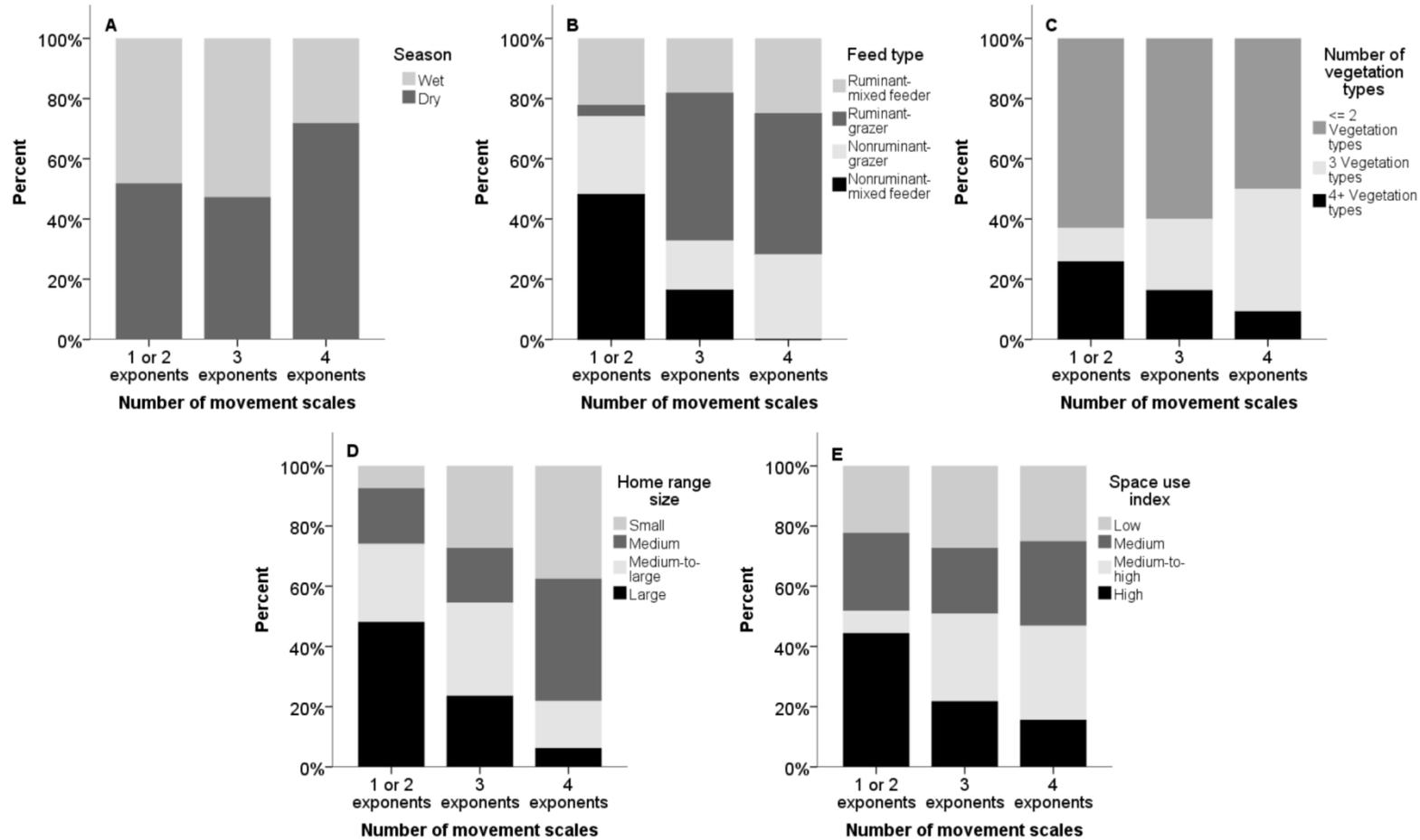


Figure 5.4: The effect of (A) season; (B) feeding type; (C) number of vegetation types; (D) home range size; and (E) level of space use on the number of movement scales indicated by the percentage of data subsets which produced 1 and 2, 3 or 4 movement scales.

5.6 DISCUSSION

A number of studies claim that Lévy walks are often encountered in animal movement (Viswanathan et al. 1996, Viswanathan et al. 1999, Ramos-Fernandez et al. 2003, de Knegt et al. 2007). However, several studies generated controversy because the accuracy of statistical methods that have been used to identify Lévy movement behaviour are questionable (Sims et al. 2007, Humphries et al. 2010, Edwards et al. 2012, Jansen et al. 2012). Our study showed that the dominant movement behaviour of the animals was Brownian motions, with one, or mixtures of a few, movement scales. This confirms more recent evidence that when rigorous statistical procedures are adhered to, the Lévy type movements in the animal world becomes an exception rather than the rule (Benhamou 2007, Edwards et al. 2007, Edwards et al. 2012, Jansen et al. 2012). It also supports the simulations in other studies (Benhamou 2007) that, showed that, in heterogeneous landscapes, Brownian walks at two- or more different movement scales, i.e. small-scale area-restricted searches (within suitable forage areas) combined with large movements (between forage areas), could be used as an optimal strategy to search for habitat patches. However, our study indicated that the complexity in movement scales, were even larger, with multi-scale small area restricted searches (indicating forage item patchiness), mixed with multi-scale large movements (indicating levels of forage suitability in lower quality habitats when moving between high quality habitat patches and movements to water resources).

Regarding the hypothesis that the animals would show more movement scales during the dry season versus the wet season, the results indicated that seasonality was an important factor driving the number of movement scales for the large herbivores tested during this study. Spatial variation in the African landscape results in a heterogeneous distribution of resources that are influenced by rainfall and temperature along seasonal cycles (Funston et al. 1994, Cornélis et al. 2011, Birkett et al. 2012). In many cases, large herbivores select different habitats and show different movement patterns during times of low versus high resource availability (Ager et al. 2003, Venter and Watson 2008, Cornélis et al. 2011, Birkett et al. 2012). This is because they become nutritionally stressed during the dry season when both forage quality and quantity are reduced (Prins 1996). In addition, surface water sources can dry up, which influences the trade-off foragers face between nutritional requirements and surface-water constraints when forage quantity is reduced (Redfern et al. 2003).

Forage quality and quantity are most affected near water sources because animals tend to congregate in these areas due to water dependency (Redfern et al. 2003). The reduced forage quantities during dry years forces large herbivores to travel further from water sources to meet their nutritional requirements (Redfern et al. 2003, Venter and Watson 2008). The fact that, in general there were fewer movement scales detected in the wet season versus the dry season suggest that when animals were forced to trade-off forage quality and quantity during the dry season (Redfern et al. 2006), when they moved further between forage areas and water sources in order to satisfy their forage requirements (Venter and Watson 2008). This could have resulted in the decrease in the number of movement scales that was observed. The effect of water availability on movement scale should, however, be further investigated using finer-scale movement data.

Regarding the hypothesis that animals with different morphological traits (feeding type and digestive system) would have different number of movement scales, the study found that non-ruminant mixed feeders (elephant) generally had a lower number of movement scales, compared to all the other feeding types. Elephants concentrate their foraging within areas of high forage availability that are sufficiently close to water and large enough to optimize the efficiency of foraging (De Knecht et al. 2011). Surface-water is a strong determinant of elephant space use, and may take precedence over the role that landscape heterogeneity plays in their movement (de Beer and van Aarde 2008, De Knecht et al. 2011). Elephants are also able to change their diet from graze to browse in times with low resource availability (de Boer et al. 2000, Codron et al. 2006, Shannon et al. 2013), which enabled them to stay closer to water resources compared to grazers, hence the observed difference found in this study. This poses the question as to why there was such a difference between elephants and the ruminant mixed feeders, i.e. eland and impala, as the diet switching has been observed for both species elsewhere (Watson and Owen-Smith 2000, Codron et al. 2006). It is possible that the difference between elephant versus eland and impala could be related to interspecific competition and availability of browse for browsers at specific heights. There is considerable interspecific competition amongst smaller browsers for forage that gives the taller browsers (elephants) the advantage of feeding at heights where there is less interspecific competition (Cameron and du Toit 2007), and thus lower levels of depletion effects, except in cases where there is heavy intraspecific competition (Chamaille-Jammes et al. 2007, Chamaille-Jammes et al. 2008). It is thus possible that

eland and impala could, therefore, show similar movement scales to the grazers (more movement scales) due to the effect of higher interspecific competition, leading to forage quantity depletion at lower levels in the browse layer, which are similar to a depletion effect in the grass layer. This study does not provide clear evidence for this type of interspecific competition effect, but rather highlights it as a possible hypothesis for future research.

The weak results from testing for differences between the feeding types other than elephant could have been affected by the time interval of our telemetry data. This problem has been identified in other studies (Ager et al. 2003). The smaller ungulates might be exhibiting a finer scale of movement behaviour which the two hour interval frequency of the current data was not able to detect. A higher interval frequency of sampling might be required to detect all movement scales in order to efficiently compare differences amongst the smaller ungulates (ruminant grazers, ruminant mixed feeders and non-ruminant grazers), and testing this hypothesis probably requires a higher temporal resolution of the data.

Regarding the hypothesis that animals will have fewer movement scales in areas with lower vegetation heterogeneity, the results confirmed a lower number of movement scales were there were fewer vegetation types. Large herbivores exhibit distinct scales in movement that are in many cases related to habitat heterogeneity (Redfern et al. 2003, Frair et al. 2005). More movement scales would be expected as herbivores move through a mosaic of vegetation patches of variable suitability (more heterogeneous) compared to more homogeneous vegetation. In this study while vegetation heterogeneity would appear to have had an effect on number of movement scales, the relationship was not strong. We used broad landscape scale vegetation types (Mucina and Rutherford 2006) as there was a lack of a finer scale standardized habitat maps for all the reserves. A stronger relationship might be detected if a finer scale habitat map and higher interval frequency movement data were used.

The hypothesis that species with larger home ranges, which we confirmed are also larger species (Lindstedt et al. 1986, du Toit 1990), will have fewer movement scales was partially supported by this study. Because larger herbivores feed at a coarser grain scale (Prins and Van Langevelde 2008a), we expected them to have fewer movement scales because they interact with their habitat in a less complex manner. However, the results did not convincingly support our hypothesis, because animals with large home ranges were equal in movement scale to those animals with smaller home range sizes. The number of movement scales difference between animals with medium-to-large home ranges versus animals with medium sized home ranges seemed to be driven by the larger species, such as eland and African buffalo, generally having two or three movement scales, which occurred mainly in the medium-to-large home range size grouping. Other species, such as blue wildebeest, red hartebeest, plains zebra and Cape mountain zebra which are considered medium sized grazers, grouped in both the medium-to-large and the medium sized home ranges, and generally moved with a wider (2, 3 and 4) number of movement scales.

The hypothesis that species which are more restricted by fences would have fewer movement scales was confirmed by this study. Because large migratory movements are limited by fences (Boone and Hobbs 2004, Loarie et al. 2009, Naidoo et al. 2012) we expected species to have fewer movement scales because of this restriction. This result has significant implications for protected area management, as it shows that an important part of these species natural ecological processes, i.e. the migratory process and extensive ranging behaviour, is prevented from functioning as it should (Shannon et al. 2006). The implication is that large herbivores that were able to migrate and/or range further, as seasonal forage changes took place, in order to make use of the suitable forage resources in the broader landscape, are now not able to do this. This in turn increases pressure on local forage resources that could result in unnatural overgrazing (Shannon et al. 2006, de Beer and van Aarde 2008).

Identifying movement scale determinants of large herbivores can benefit their management and conservation, as it allows an understanding of herbivore species spatial dynamics, impacts, and associated ecological processes. Scales are defined by rates of foraging and ecosystem processes,

while boundaries between units, at each scale, are defined by animal behaviour (Senft et al. 1987a). The movement data used in the analysis were over relatively short time periods, and did not include year to year changes or major changes over a lifetime. Regardless of this, the results indicate that large herbivore movement behaviour is complex in scale which has important implications for conservation management in protected areas (Coe et al. 1976, Cumming et al. 2010, Delsink et al. 2013). In order for managers to effectively manage protected areas and associated biodiversity they need take cognisance of the different scales animals operate under. This should be followed by implementation of management action at appropriate scales to prevent scale mismatch (Cumming et al. 2010, Delsink et al. 2013).

5.7 CONCLUSION

Our results suggest that intrinsic factors such as large herbivore traits, and extrinsic factors such as, surface water, vegetation heterogeneity, interspecific competition and fences potentially influence the scales at which animals move. Large herbivores deal with limitations in nutritional requirements during low resource times by adapting their movement behaviour, thereby incurring an increased cost of traveling to-and-from water sources in order to satisfy their nutritional requirements (Prins 1996). Anthropogenic influences caused by management actions, for example construction of artificial water holes and fences, have an effect on animal movement that could have significant impacts on ecosystems in protected areas (Redfern et al. 2003, de Beer and van Aarde 2008). Protected area managers should thus be aware of scale complexity in animal movement in order to initiate appropriate conservation management action.

**Chapter 6: *Large grazing herbivores do not use
visual cues to find forage patches at a habitat
patch scale***

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ABSTRACT

Understanding the ecology of large herbivores is conceptually complex, but important for their conservation and management. Finding suitable forage patches in a heterogeneous landscape, where patches change dynamically both spatially and temporally, could be challenging to large herbivores, especially if they have no *a priori* knowledge of the location of the patches. We tested whether three large grazing herbivores with a variety of different traits, improve their efficiency when foraging at a heterogeneous habitat patch scale, by using visual cues to gain *a priori* knowledge about potential higher value foraging patches. For each species (zebra (*Equus burchelli*), red hartebeest (*Alcelaphus buselaphus* subspecies *camaa*) and eland (*Tragelaphus oryx*)), we used Brownian motions, Lévy walks, truncated Lévy walks and composite Brownian walks to model step length distribution for three “visibility of patch” classes. The visibility classes were moving within the same patch, to a different, visible patch, and to a patch not visible from the current patch. All three species favoured Brownian motion models with two or more exponential distributions (composite Brownian movement behaviour) for all three visibility classes, and only a small proportion of their movements were directional regardless of the visibility class. Step lengths were significantly longer for all species when moving to non-visible patches. These large grazing herbivores did not use visual cues when foraging at a habitat patch scale, but rather adapted their movement behaviour to the heterogeneity of the specific landscape. In addition, as composite Brownian movement behaviour best explained movement strategies, complexity in scale of large herbivore movement have the potential to explain movement behaviour in relation to species’ intrinsic traits such as body size, feeding type, digestive strategy and muzzle width.

6.1 INTRODUCTION

Large herbivores may use a range of behaviours to enhance their foraging efficiency (Beekman and Prins 1989, Bailey et al. 1996). However, finding a forage patch in a heterogeneous landscape where patches differ in suitability poses a challenge, especially if individuals have no *a priori* knowledge of the location of the most suitable patches (Senft et al. 1987a, Bailey et al. 1996, Prins 1996). Large herbivores may gain *a priori* knowledge using memory (from a previous visit to the patch) (Edwards et al. 1996, Dumont and Petit 1998, Fortin 2003, Brooks and Harris 2008) or through visual cues (Edwards et al. 1997, Howery et al. 2000, Renken et al. 2008). If the forage resource is complex (e.g., when forage patches are not well defined), or the distribution of the forage patches are likely to change continuously (e.g., when a patch is grazed or the grass sward becomes unpalatable due to ageing), then recalling the location of forage patches may be of limited value (Edwards et al. 1997). In such situations, heterogeneous in both space and time, the ability to recognise and assess different forage patches at a distance through visual cues, would promote foraging success (Edwards et al. 1997). A number of studies have linked movement patterns to the use of memory (Dumont and Petit 1998, Ramos-Fernandez et al. 2003, Brooks and Harris 2008), or use of visual cues at a finer scale (e.g. bite, feeding station and food patch scale) (Laca 1998, Howery et al. 2000, Hewitson et al. 2005) by large herbivores to locate or revisit suitable forage patches. However, no one has tested if large herbivores use visual cues to find forage patches at a broader habitat patch scale.

Animal movements consist of a discrete series of displacements (i.e. step lengths) separated by successive re-orientation events (i.e., turning angles) (Bartumeus et al. 2005). Forage and search behaviour have been described using two different types of random movement behaviours, namely: random walks (Brownian motion) and Lévy walks (Viswanathan et al. 1996, Viswanathan et al. 1999, Bartumeus et al. 2005, Edwards et al. 2007). Random walks reflect essentially similar steps (on the same spatial scale) separated by orientation and changing turn angles (Viswanathan et al. 1999). Lévy walks reflect clusters of shorter steps that are connected by rare large steps (Edwards et al. 2012). Lévy walkers can outperform (i.e., search efficiency) Brownian random walkers as they revisit patches far less often, and because the larger steps potentially increase the probability of finding new patches (Viswanathan et al. 1999, Raposo et al. 2009, Viswanathan 2010).

More recently, the composite Brownian motion emerged as a strong alternative model to the Lévy walks (Benhamou 2007, de Jager et al. 2011, Schultheiss and Cheng 2011, Jansen et al. 2012, Reynolds 2013), whereby animals switch between two or more Brownian walks, each characterised by an exponential step-length distribution (Jansen et al. 2012, Reynolds 2013). In heterogeneous environments, Brownian walks at two different scales (composite Brownian motions), for example a small-scale area-restricted search (within patches) mixed with a set of large movements (between patches), can be close to optimal foraging movement behaviour (Benhamou 2007). The composite Brownian walk closely resembles a Lévy motion, and could be considered as more efficient than ordinary Brownian motions (Schultheiss and Cheng 2011, Reynolds 2013).

We tested whether three grazing herbivore species, with a variety of traits (body size, feeding type, digestive strategy and muzzle width) use visual cues when foraging at the habitat patch scale. By habitat patch scale, we mean a daily range at a 10 hour temporal scale while feeding, walking, drinking, resting with movement within and between habitats as adapted from Owen-Smith (2010) and Bailey et al., (1996). We did this by developing and testing predictions based on movement path shape, directionality and step length under three patch visibility classes (Table 6.1). In particular, we expected directional movement to visible patches, random (Brownian) movement within the same patch and Lévy motion when moving to non-visible patches. Demonstrating a difference between movement behaviour in response to visible versus invisible habitat patches, would enable an understanding of the importance of visual cues to large herbivores when moving between patches at a habitat patch scale.

Table 6.1: Predictions and observations in assessing whether visual cues are used in habitat scale movement/search strategies of zebra, red hartebeest and eland across three different patch visibility classes.

Visibility class	Movement path shape		Directionality		Step length	
	Predicted	Observed	Predicted	Observed	Predicted	Observed
Movement within a visible patch	Brownian motion	Composite Brownian motion	Random	Random	Short, variable length	Short, variable length
Movement to visible patch	Straight line	Composite Brownian motion	Very directional	Random	Long, constant length	Short, variable length
Movement to a patch not visible	Lévy motion	Composite Brownian motion	Very non-directional	Random	Variable length	Long, variable length

6.2 STUDY AREA

Mkambati Nature Reserve is a 77 km² provincial nature reserve situated on the east coast of the Eastern Cape Province, South Africa (31°13'-31°20'S and 29°55'-30°04'E). The climate is mild subtropical with a relatively high humidity (de Villiers and Costello 2013). The coastal location, adjacent to the warm Agulhas Current, causes minimal variation in mean daily temperatures (18 °C winter and 22 °C summer) (de Villiers and Costello 2013). The average rainfall is 1 200 mm, with most precipitation in spring and summer (September - February) (Shackleton 1990). The high rainfall, mild temperatures, and presence of abundant streams and wetlands, results in a landscape that is not water limited in any season. Forests occur in small patches (mostly in fire refuge areas), and wetland habitats are abundant. More than 80% of Mkambati consists of Pondoland–Natal Sandstone Coastal Sourveld grassland (Mucina et al. 2006d). Mkambati contains a range of large herbivore species, but no large predators (Venter et al. 2014b).

The grassland is considered to be nutrient poor (Shackleton et al. 1991, Shackleton and Mentis 1992). Grassland fire stimulates temporary regrowth high in crude protein (8.6% compared to 4.6%, in older grassland), phosphorus concentrations (0.1% compared to 0.05%, in older grassland) and dry matter digestibility (38.6% compared to 27.1%, in older grassland) (Shackleton 1989). Nutrient concentrations remain elevated for up to 6 months post-burn, after which they are comparable to surrounding, unburnt grassland (Shackleton and Mentis 1992). Frequent fires cause a landscape mosaic of nutrient-rich burnt patches within a matrix of older, moribund grassland. This landscape is thus continuously changing due to new fires that are set and the maturing process of the grassland. Recalling the location of grazing forage patches (using memory) would in this case be of limited value which enabled us to test predictions of movement behaviour relative to visibility of forage patches.

6.3 METHODS

Five plains zebra (*Equus burchelli*), six red hartebeest (*Alcelaphus buselaphus* subspecies *camaa*) and five eland (*Tragelaphus oryx*) were fitted with GPS-UHF collars (Africa Wildlife Tracking CC., Pretoria, RSA) between September 2008 and July 2012. All animals were darted by an experienced wildlife veterinarian from a Robinson 44 helicopter. The work was approved by, and conducted in

strict accordance with the recommendations in the approved standard protocols of, the Animal Ethics Sub-committee of the University of KwaZulu-Natal. All field work was conducted by, or under the supervision of the first author, a staff member of the Eastern Cape Parks and Tourism Agency, as part of the operational activities of the appointed management authority of Mkambati (Eastern Cape Parks and Tourism Agency Act no. 2 of 2010, Eastern Cape Province, South Africa). The zebra and red hartebeest were in separate harems or herds when they were collared, but some eland were in the same herd. The collars were set to take a GPS reading every 30 min, and data were downloaded via UHF radio signal. The collars remained functional between 4 and 16 months depending on various factors, including loss of animals to poaching, natural mortality, or malfunctioning. Data downloaded from the collars were converted to geographical information system (GIS) format and sections of the data sets with missing values were removed and not used in the analysis.

Step lengths were calculated for each walk using the Hawth's Analysis Tools extension (Beyer 2007) to ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). "Walks" were extracted per species (Eland $n = 312$; Red hartebeest $n = 309$; Plains zebra $n = 279$). A "walk" consisted of 20 consecutive steps which constituted 10 hours of movement behaviour during daylight hours (6:00AM to 6:00PM)(Figure 6.1). Ten hours of movement represented movement between patches at a habitat patch scale as adapted from (Bailey et al. 1996) and (Owen-Smith et al. 2010). To confirm whether ten hours of movement were indeed within a realistic distance range for the habitat patch scale in our situation, we calculated and compared the mean distance between patches as well as mean animal "walk" distances per species. Starting points were randomly selected, with the visibility from the starting point of each walk being determined using the "viewshed analysis tool" in the Spatial Analyst extension of ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). This resulted in a grid map (raster) layer that indicated all areas that were visible and not visible to the animal from that specific point at its shoulder height (female shoulder height: eland $\bar{x} = 1500$ mm (Posselt 1963); red hartebeest $\bar{x} = 1250$ mm (Stuart and Stuart 2007); plains zebra $\bar{x} = 1338$ mm (Skinner and Chimimba 2005))(Figure 6.1). The end point was classified as the patch where the animal spent the majority ($\geq 50\%$) of the final 3 h (6 locations) of the "walk" (Figure 6.1).

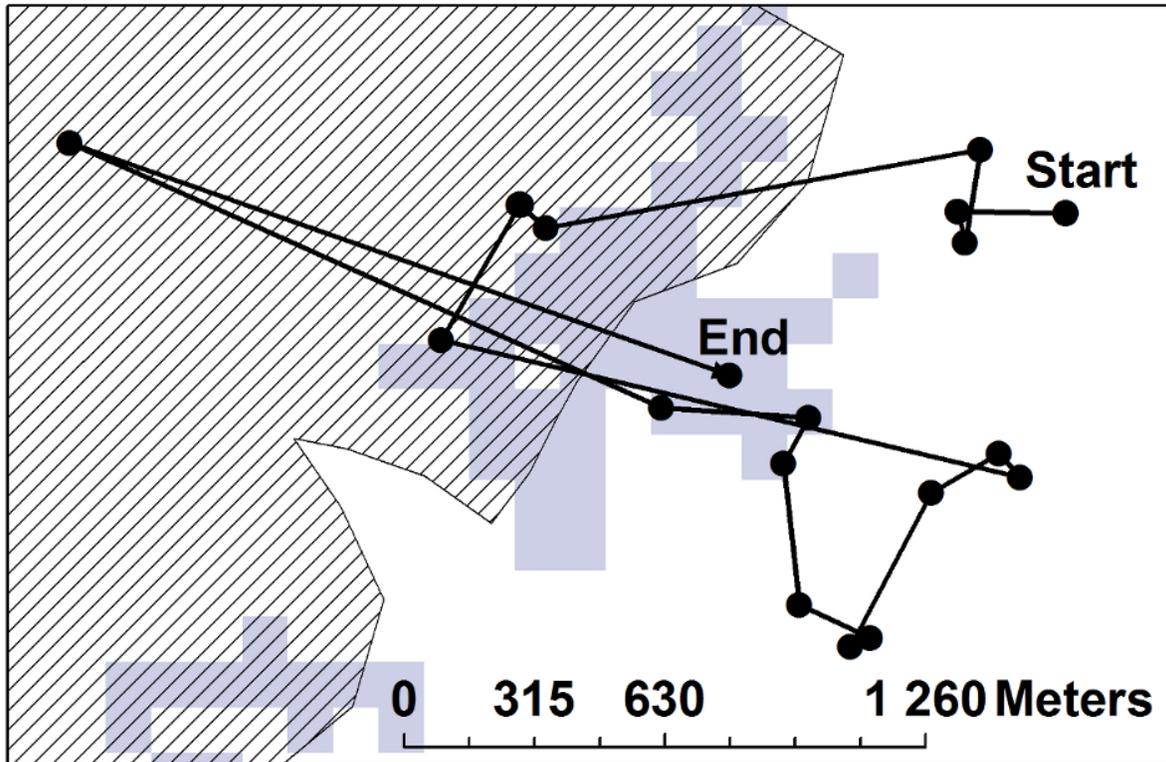


Figure 6.1: An example of a 10 hour “walk” extracted from the data from the departure point (indicated by “Start”) to where the animal ended (indicated by “End”). Here the animal spent the majority of the last three hours of its “walk” in an area which was not visible from the starting point (indicated by grey). The striped area indicates a recent fire patch.

All patches in the landscape were allocated a unique number, and classified as either burnt grassland (fire patches) or unburnt grassland (unburnt patches) (Figure 6.1). The location of the fire patches were recorded by field rangers between January 2007 and July 2012, and later digitally defined on maps using ArcGIS. Each GPS locality along a “walk” was linked to a patch classification using the Spatial Analyst extension of ArcGIS (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) (see Figure 2.2). All unburnt areas (areas that were never noted as burnt between January 2007 and July 2012) were considered as one unburnt patch, and was given the same unique identification number. The “walks” were then classified into three different classes according to the patch visibility, a movement: (a) to within the same patch where the departure point is located; (b) to a new patch that was visible from the departure point; and (c) to a new patch not visible from the departure point. All step lengths < 6 m were excluded during analysis in order to remove non-movements, as well as false movements due to GPS-error.

6.4 DATA ANALYSIS

We tested whether there was excessive variability amongst individual animal step lengths, which could potentially influence the step length models, by comparing mean walk distance for different species and visibility classes using separate ANOVA's.

Four frequency distributions were used to model step length distribution for the three different visibility outcome classes of each species: (a) exponential (Brownian motion); (b) power law (Lévy walk); (c) truncated power law distributions (truncated Lévy walk); and (d) hyper exponential functions (composite Brownian walk) which is a combination of two, three or four exponential distributions following the methodology of Jansen et al. (2012) (Table 5.2). The lower truncation value of the models were specified as the smallest value in the data sets (which was set to 6 m, see above). The unique likelihood functions of the respective probability distributions were used to find the maximum likelihood estimates for the parameters, which were used to plot the distributions and compute Akaike Information Criterion (AIC) weights to compare models (Jansen et al. 2012) (Table 5.2). Although one model may indeed be favoured over another, it may not be a suitable model (Edwards et al. 2012), and the Kolmogorov-Smirnov (KS) goodness-of-fit tests and R^2 values were therefore used to

test if the models were consistent with the data. The statistical tests were conducted using R (R-Development-Core-Team 2011), with R-codes for step length analysis being available from <http://mathbio.bl.rhul.ac.uk/People/alla/r-code>.

Besides the shape of the walk, we further contrasted directionality (concentration of turning angles) and step lengths between the three visibility classes. We used the Rayleigh test of circular uniformity from CircStats package in R (R-Development-Core-Team 2011) to calculate the mean resultant length r for each individual “walk”. This parameter r provided a measure of concentration of turning angles that falls in the interval $[0, 1]$ (Duffy et al. 2011). When r is close to 1, data are highly concentrated in one direction, and when it is close to 0 data are widely dispersed (Duffy et al. 2011). Rayleigh test provides p -values associated with r to test whether it was reasonable to reject angle uniformity. When $r \geq 0.5$ and the p value indicated significance ($p < 0.05$), walks were considered to be concentrated in one direction (directional). We compared mean step lengths for the different visibility class for each species with ANOVA and post-hoc Tukey tests using R (R-Development-Core-Team 2011).

6.5 RESULTS

A visual comparison of an error bar plot confirmed that the mean distance between patches $\bar{x} = 5276 \pm 2846$ as well as mean animal “walk” distances for the different species (Eland $\bar{x} = 3529 \pm 1711$; Red hartebeest $\bar{x} = 2664 \pm 2242$; Zebra $\bar{x} = 5020 \pm 3866$) was within a realistic distance range, reflecting movements at a habitat patch scale, as adapted from Bailey et al. (1996) and Owen-Smith et al. (2010) (Figure 6.2). There was little variability in mean walk lengths amongst individuals and visibility classes for the different species (Table 6.1). We were thus confident that individual step length variability would not have a significant influence on the step length models.

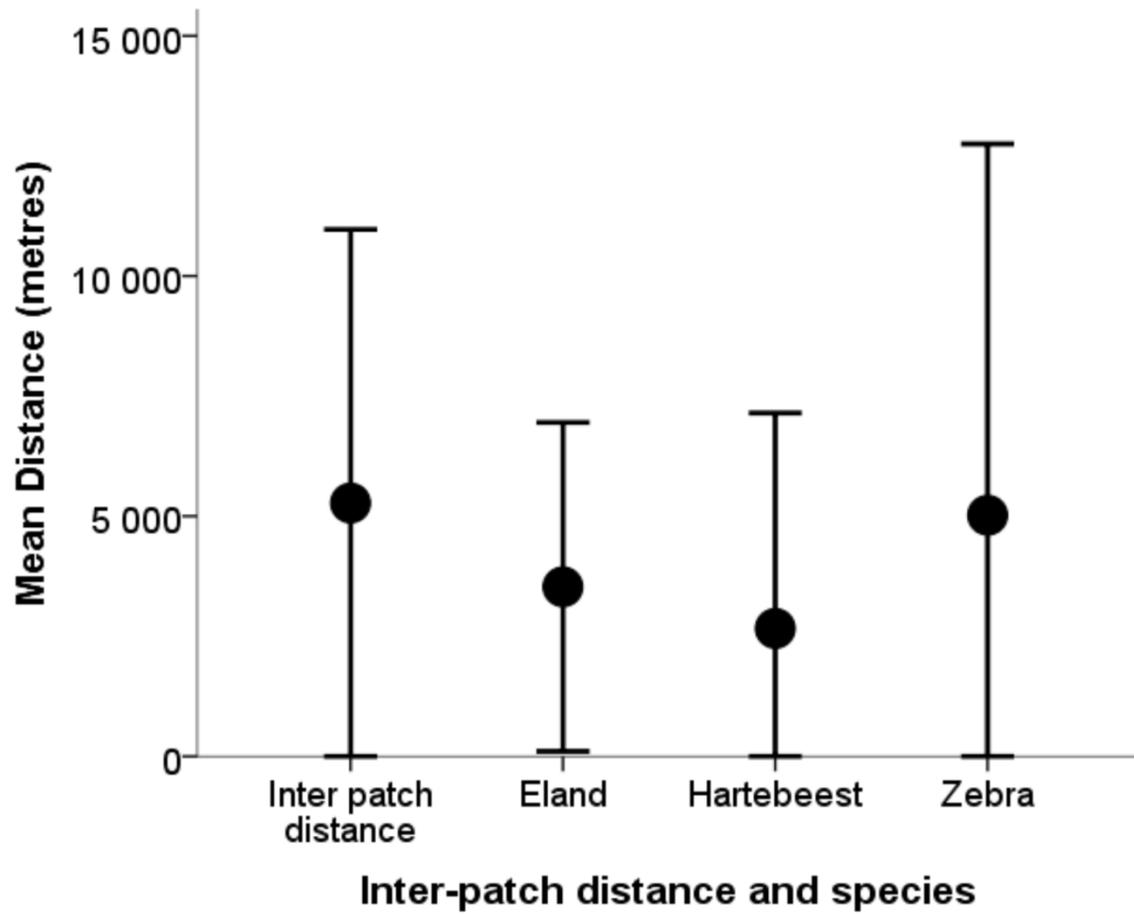


Figure 6.2: The mean distance between patches as well as mean animal “walk” distances per species indicating that ten hours of movement were within a realistic distance range. Horizontal bars indicate \pm SD.

Table 6.2: Individual ANOVA test results indicate limited variability of mean walk length of individuals of different species in the different visibility classes. The only significant results is that of red hartebeest in the 'within visible' class and zebra in the 'to not visible' class.

Visibility class	df	F-value	P-value
<i>Eland</i>			
to not visible	4;156	0.612	0.654
to visible	4; 28	0.213	0.929
within visible	4;110	2.221	0.071
<i>Red hartebeest</i>			
to not visible	5;128	1.928	0.094
to visible	4;23	1.897	0.145
within visible	5;121	3.189	0.010
<i>Zebra</i>			
to not visible	4;136	3.402	0.011
to visible	3; 13	2.516	0.104
within visible	4;114	1.763	0.141

A composite Brownian motion was the best description of movement for all three species for each of the three visibility classes (Table 6.1 and Figure 6.3). For eland, the resulting AIC weights most supported the composite Brownian motion with three exponential distributions for movement to patches not visible to them, and the composite Brownian motion with two exponential distributions for movements by eland to visible, and within visible patches. Red hartebeest movement to patches not visible to them, as well as movement within visible patches, were most supported by the composite Brownian motion with four exponential distributions. Movements by the hartebeest to visible patches were most supported by the composite Brownian motion with three exponential distributions.

For zebra, movement to patches not visible to them was best described by the composite Brownian motion with four exponential distributions. Movements by zebra to, and within, visible patches were most supported by the composite Brownian motion with three exponential distributions. In each case the fit of the preferred model to the data was confirmed by Kolmogorov-Smirnov goodness-of-fit tests (Figure 6.4 and Table 6.4). For eland and zebra, movements were more complex (happened at more spatial scales) to patches not visible compared to those that were visible (Table 6.3).

For all visibility classes, eland movements happened at fewer spatial scales compared to hartebeest and zebra (Table 6.3). In the absence of the composite Brownian motion models, the truncated Lévy walk models best described all three visibility classes for hartebeest, as well as for movement to not visible patches and within the same patch class for zebra (Table D1 in online supplementary information). However, the truncated Lévy walk models were not supported by the goodness-of-fit tests, with a $P < 0.001$ in all these cases except for the hartebeest to visible patches class, where there was still a much stronger support for a composite Brownian motion model (Table 6.4).

A low proportion of walks for eland (7% to not visible; 0% to visible; and 5% within visible) and hartebeest (6% to not visible; 3% to visible; and 8% within visible) in each visibility class were directional ($P < 0.05$) (Figure 6.4). Zebra had a higher proportion of directional walks (12% to not visible; 17% to visible; and 17% within visible) compared to eland and hartebeest (Figure 6.4). For

mean step lengths, the effect of visibility class was highly significant both for pooled species data ($F_{2,875} = 42.4; P < 0.001$), for separate species ($F_{2,875} = 36.3; P < 0.001$), and for the interaction between visibility class and species ($F_{4,875} = 3.3; P = 0.012$) (Figure 6.5).

For all three species, step lengths in the “within visible” and “to visible” classes were of similar length (Tukey test: $P = 0.936$), but the step lengths for both these categories were significantly shorter than step lengths to “not visible” classes ($P < 0.001$). Zebra had significantly longer step lengths compared to the two antelope species ($P < 0.001$), and the difference between eland and hartebeest were smaller ($P = 0.0115$) (Figure 6.5). The longer step lengths for the movement to the non-visible class held for all the species when they were tested independently (Zebra: to visible vs not visible $P = 0.007$; within visible vs not visible $P < 0.001$; Eland: to visible vs not visible $P < 0.001$; within visible vs not visible $P < 0.001$; and Hartebeest: to visible vs not visible $P = 0.022$; within visible vs not visible $P < 0.001$) (Figure 6.5).

Differences among species within visibility classes were not uniform. Zebra had significantly longer step lengths than hartebeest in all visibility classes (to not visible $P < 0.001$; to visible $P = 0.038$; within visible $P < 0.001$), but zebra only had significantly longer step lengths than eland in the “not visible” class ($P < 0.001$) (Figure 6.5). Hartebeest had significantly shorter step lengths than eland in the “within visible” class ($P = 0.026$) and almost significantly shorter in than eland the “to visible” class ($P = 0.081$) (Figure 6.5).

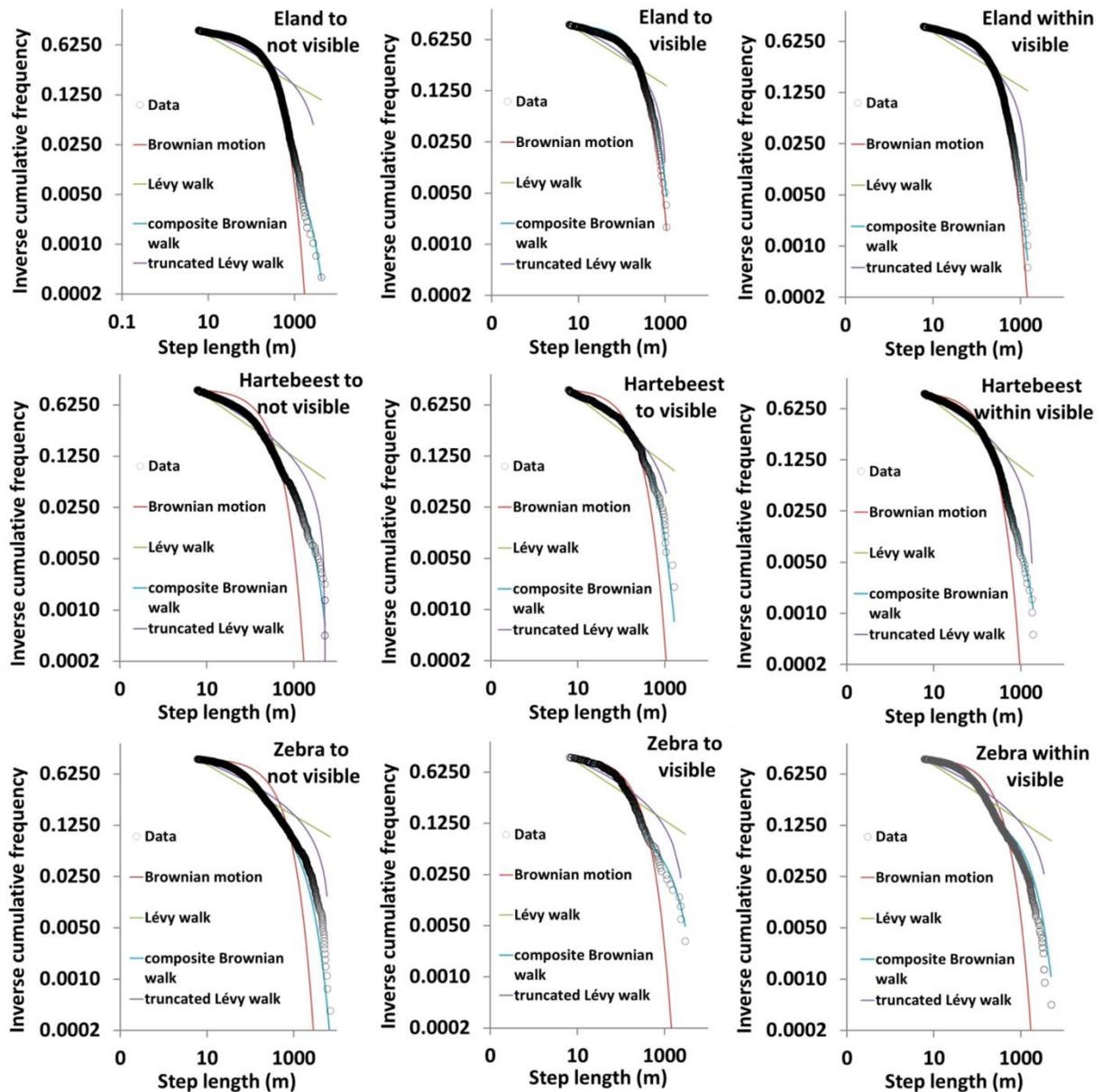


Figure 6.3: The actual step length distribution for eland, hartebeest and zebra movement with four frequency distributions to model step length distribution for the three different visibility outcome classes of each species. The circles represent the inverse cumulative frequency of step length data. The curves represent Brownian motion, Lévy walk, a truncated Lévy walk, and a composite Brownian walk consisting of a mixture of two, three or four exponentials depending on which model best-fit the data.

Table 6.3: The number of spatial scales at which movement took place for eland, red hartebeest and zebra, derived from the composite Brownian walks indicating complexity in spatial scales (see also Table 6.4 for statistical results).

Species	Movement class		
	Movement within visible patch	Movement to a visible patch	Movement to a patch not visible
Eland	2 spatial scales	2 spatial scales	3 spatial scales
Red hartebeest	4 spatial scales	3 spatial scales	4 spatial scales
Zebra	3 spatial scales	3 spatial scales	4 spatial scales

Table 6.4: The best-fit parameters, maximum log-likelihood, Akaike weights, Kolmogorov-Smirnov goodness-of-fit and r^2 values for fitting exponential, power law, truncated power law and mixtures of exponentials to the step length distribution for eland, red hartebeest and zebra from Mkambati Nature Reserve.

Species and movement	n	Models	Parameters	MLL	AIC	AIC Weight	KS- test		r^2
							D-statistic	P-value	
Eland - to not visible	2901	Exponential (Brownian walk)	$\lambda = 0.005$	-18493.36	36988.73	0.0000	0.0807	<0.0001	0.9962
		Power law (Lévy walk)	$\mu = 1.342$	-19708.08	39418.16	0.0000	0.2585	<0.0001	0.8340
		Truncated power law (Lévy walk)	$\mu = 1.100$	-19095.68	38193.37	0.0000	0.1699	<0.0001	0.9325
		Mix of two exponentials (composite Brownian motion)	$p = 0.088; \lambda_1 = 0.225; \lambda_2 = 0.004$	-18330.21	36666.42	0.0000	0.0283	0.1968	0.9991
		Mix of three exponentials (composite Brownian motion)	$p_1 = 0.083; p_2 = 0.022; \lambda_1 = 0.248; \lambda_2 = 0.001; \lambda_3 = 0.005$	-18313.46	36636.92	0.8800	0.0217	0.5008	0.9991
		Mix of four exponentials (composite Brownian motion)	$p_1 = 0.084; p_2 = 3.6 \times 10^{-9}; p_3 = 0.746; \lambda_1 = 0.020; \lambda_2 = 0.237; \lambda_3 = 0.005; \lambda_4 = 0.002$	-18313.45	36640.90	0.1200	0.0217	0.5008	0.9992
Eland - to visible	585	Exponential (Brownian walk)	$\lambda = 0.006$	-3575.82	7153.64	0.0000	0.1060	0.0028	0.9934
		Power law (Lévy walk)	$\mu = 1.370$	-3799.68	7601.37	0.0000	0.2359	<0.0001	0.8578
		Truncated power law (Lévy walk)	$\mu = 1.100$	-3609.01	7220.02	0.0000	0.1726	<0.0001	0.9478
		Mix of two exponentials (composite Brownian motion)	$p = 0.137; \lambda_1 = 0.128; \lambda_2 = 0.005$	-3539.25	7084.49	0.8668	0.0325	0.9172	0.9989
		Mix of three exponentials (composite Brownian motion)	$p_1 = 0.137; p_2 = 0.082; \lambda_1 = 0.128; \lambda_2 = 0.005; \lambda_3 = 0.005$	-3539.25	7088.49	0.1173	0.0325	0.9172	0.9989
		Mix of four exponentials (composite Brownian motion)	$p_1 = 0.136; p_2 = 0.082; p_3 = 0.183; \lambda_1 = 0.128; \lambda_2 = 0.005; \lambda_3 = 0.005; \lambda_4 = 0.005$	-3539.25	7092.49	0.0159	0.0325	0.9172	0.9989

Table 6.4 continued.....

Species and movement	<i>n</i>	Models	Parameters	MLL	AIC	AIC Weight	KS- test		<i>r</i> ²
							D-statistic	P-value	
Eland - within visible	1978	Exponential (Brownian walk)	$\lambda = 0.006$	-12108.87	24219.75	0.0000	0.0935	<0.0001	0.9956
		Power law (Lévy walk)	$\mu = 1.368$	-12875.41	25752.81	0.0000	0.2452	<0.0001	0.8579
		Truncated power law (Lévy walk)	$\mu = 1.100$	-12307.24	24616.48	0.0000	0.1562	<0.0001	0.9502
		Mix of two exponentials (composite Brownian motion)	$p = 0.120; \lambda_1 = 0.136; \lambda_2 = 0.005$	-12004.46	24014.91	0.8592	0.0142	0.9889	0.9997
		Mix of three exponentials (composite Brownian motion)	$p_1 = 0.119; p_2 = 0.096; \lambda_1 = 0.138; \lambda_2 = 0.004; \lambda_3 = 0.005$	-12004.43	24018.87	0.1190	0.0137	0.9928	0.9998
		Mix of four exponentials (composite Brownian motion)	$p_1 = 0.103; p_2 = 0.034; p_3 = 0.304; \lambda_1 = 0.158; \lambda_2 = 1.030; \lambda_3 = 0.005; \lambda_4 = 0.005$	-12004.13	24022.26	0.0218	0.0131	0.9956	0.9998
Hartebeest - to not visible	2213	Exponential (Brownian walk)	$\lambda = 0.005$	-13935.15	27872.29	0.0000	0.2291	<0.0001	0.9425
		Power law (Lévy walk)	$\mu = 1.411$	-13545.73	27093.47	0.0000	0.1645	<0.0001	0.9349
		Truncated power law (Lévy walk)	$\mu = 1.262$	-13328.17	26658.33	0.0000	0.0944	<0.0001	0.9709
		Mix of two exponentials (composite Brownian motion)	$p = 0.710; \lambda_1 = 0.017; \lambda_2 = 0.002$	-13316.05	26638.10	0.0000	0.1012	<0.0001	0.9887
		Mix of three exponentials (composite Brownian motion)	$p_1 = 0.220; p_2 = 0.664; \lambda_1 = 0.132; \lambda_2 = 0.008; \lambda_3 = 0.001$	-13122.11	26254.22	0.2051	0.0230	0.5993	0.9997
		Mix of four exponentials (composite Brownian motion)	$p_1 = 0.209; p_2 = 0.097; p_3 = 0.574; \lambda_1 = 0.139; \lambda_2 = 0.016; \lambda_3 = 0.007; \lambda_4 = 0.001$	-13120.77	26251.54	0.7949	0.0226	0.6245	0.9997

Table 6.4 continued.....

Species and movement	n	Models	Parameters	MLL	AIC	AIC Weight	KS- test		r ²
							D-statistic	P-value	
Hartebeest - to visible	493	Exponential (Brownian walk)	$\lambda = 0.008$	-2900.50	5803.00	0.0000	0.2170	<0.0001	0.9558
		Power law (Lévy walk)	$\mu = 1.452$	-2860.38	5722.76	0.0000	0.1521	<0.0001	0.9425
		Truncated power law (Lévy walk)	$\mu = 1.232$	-2792.53	5587.05	0.0000	0.0669	0.2193	0.9851
		Mix of two exponentials (composite Brownian motion)	$p = 0.362; \lambda_1 = 0.089; \lambda_2 = 0.005$	-2783.51	5573.02	0.0000	0.0467	0.6567	0.9953
		Mix of three exponentials (composite Brownian motion)	$p_1 = 0.151; p_2 = 0.485; \lambda_1 = 0.383; \lambda_2 = 0.004; \lambda_3 = 0.026$	-2769.86	5549.73	0.8808	0.0264	0.9955	0.9987
		Mix of four exponentials (composite Brownian motion)	$p_1 = 0.150; p_2 = 5.3 \times 10^{-5}; p_3 = 0.486; \lambda_1 = 0.384; \lambda_2 = 0.383; \lambda_3 = 0.004; \lambda_4 = 0.026$	-2769.86	5553.73	0.1192	0.0640	0.9955	0.9987
Hartebeest within visible	1949	Exponential (Brownian walk)	$\lambda = 0.009$	-11171.18	22344.35	0.0000	0.1591	<0.0001	0.9776
		Power law (Lévy walk)	$\mu = 1.450$	-11339.83	22681.67	0.0000	0.1724	<0.0001	0.9282
		Truncated power law (Lévy walk)	$\mu = 1.246$	-11092.93	22187.86	0.0000	0.0965	<0.0001	0.9739
		Mix of two exponentials (composite Brownian motion)	$p = 0.289; \lambda_1 = 0.087; \lambda_2 = 0.006$	-10921.14	21848.28	0.0000	0.0369	0.1399	0.9979
		Mix of three exponentials (composite Brownian motion)	$p_1 = 0.209; p_2 = 0.147; \lambda_1 = 0.134; \lambda_2 = 0.003; \lambda_3 = 0.010$	-10888.65	21787.29	0.3021	0.0210	0.7816	0.9996
		Mix of four exponentials (composite Brownian motion)	$p_1 = 0.170; p_2 = 0.055; p_3 = 0.485; \lambda_1 = 0.173; \lambda_2 = 0.002; \lambda_3 = 0.007; \lambda_4 = 0.017$	-10885.81	21785.62	0.6979	0.0185	0.8937	0.9997

Table 6.4 continued.....

Species and movement	n	Models	Parameters	MLL	AIC	AIC Weight	KS- test		r ²
							D-statistic	P-value	
Zebra - to not visible	2713	Exponential (Brownian walk)	$\lambda = 0.003$	-18383.14	36768.27	0.0000	0.2610	<0.0001	0.9047
		Power law (Lévy walk)	$\mu = 1.346$	-18302.17	36606.33	0.0000	0.2385	<0.0001	0.9174
		Truncated power law (Lévy walk)	$\mu = 1.157$	-17876.40	35754.80	0.0000	0.1485	<0.0001	0.9650
		Mix of two exponentials (composite Brownian motion)	$p = 0.766; \lambda_1 = 0.010; \lambda_2 = 0.001$	-17458.78	34923.56	0.0000	0.0240	0.4175	0.9994
		Mix of three exponentials (composite Brownian motion)	$p_1 = 0.221; p_2 = 0.587; \lambda_1 = 0.022; \lambda_2 = 0.007; \lambda_3 = 0.001$	-17443.33	34896.66	0.0452	0.0136	0.9625	0.9998
		Mix of four exponentials (composite Brownian motion)	$p_1 = 0.035; p_2 = 0.302; p_3 = 0.506; \lambda_1 = 0.004; \lambda_2 = 0.004; \lambda_3 = 0.015; \lambda_4 = 0.001$	-17438.28	34890.76	0.9548	0.0133	0.9707	0.9998
Zebra - to visible	326	Exponential (Brownian walk)	$\lambda = 0.006$	-1999.62	4001.23	0.0000	0.1350	0.0053	0.9814
		Power law (Lévy walk)	$\mu = 1.395$	-2066.90	4135.79	0.0000	0.2607	<0.0001	0.8797
		Truncated power law (Lévy walk)	$\mu = 1.172$	-2013.86	4029.72	0.0000	0.1626	0.0003	0.9439
		Mix of two exponentials (composite Brownian motion)	$p = 0.890; \lambda_1 = 0.010; \lambda_2 = 0.001$	-1952.03	3910.06	0.1698	0.0491	0.8272	0.9982
		Mix of three exponentials (composite Brownian motion)	$p_1 = 0.054; p_2 = 0.095; \lambda_1 = 0.186; \lambda_2 = 0.001; \lambda_3 = 0.009$	-1948.57	3907.14	0.7313	0.0368	0.9800	0.9990
		Mix of four exponentials (composite Brownian motion)	$p_1 = 0.054; p_2 = 0.095; p_3 = 0.253; \lambda_1 = 0.186; \lambda_2 = 0.001; \lambda_3 = 0.009; \lambda_4 = 0.009$	-1948.57	3911.14	0.0990	0.0368	0.9800	0.9990

Table 6.4 continued.....

Species and movement	<i>n</i>	Models	Parameters	MLL	AIC	AIC Weight	KS- test		<i>r</i> ²
							D-statistic	P-value	
Zebra - within visible	2225	Exponential (Brownian walk)	$\lambda = 0.005$	-13949.55	27901.10	0.0000	0.1892	<0.0001	0.9485
		Power law (Lévy walk)	$\mu = 1.382$	-14216.97	28435.94	0.0000	0.2521	<0.0001	0.8963
		Truncated power law (Lévy walk)	$\mu = 1.203$	-13922.82	27847.65	0.0000	0.1699	<0.0001	0.9476
		Mix of two exponentials (composite Brownian motion)	$p = 0.835; \lambda_1 = 0.011; \lambda_2 = 0.001$	-13447.30	26900.59	0.0003	0.0166	0.9181	0.9999
		Mix of three exponentials (composite Brownian motion)	$p_1 = 0.013; p_2 = 0.162; \lambda_1 = 1.476; \lambda_2 = 0.001; \lambda_3 = 0.011$	-13437.36	26884.72	0.8807	0.0099	0.9999	0.9999
		Mix of four exponentials (composite Brownian motion)	$p_1 = 0.013; p_2 = 9.3 \times 10^{-5}; p_3 = 0.825; \lambda_1 = 1.460; \lambda_2 = 1.46; \lambda_3 = 0.011; \lambda_4 = 0.001$	-13437.36	26888.72	0.1189	0.0103	0.9998	0.9999

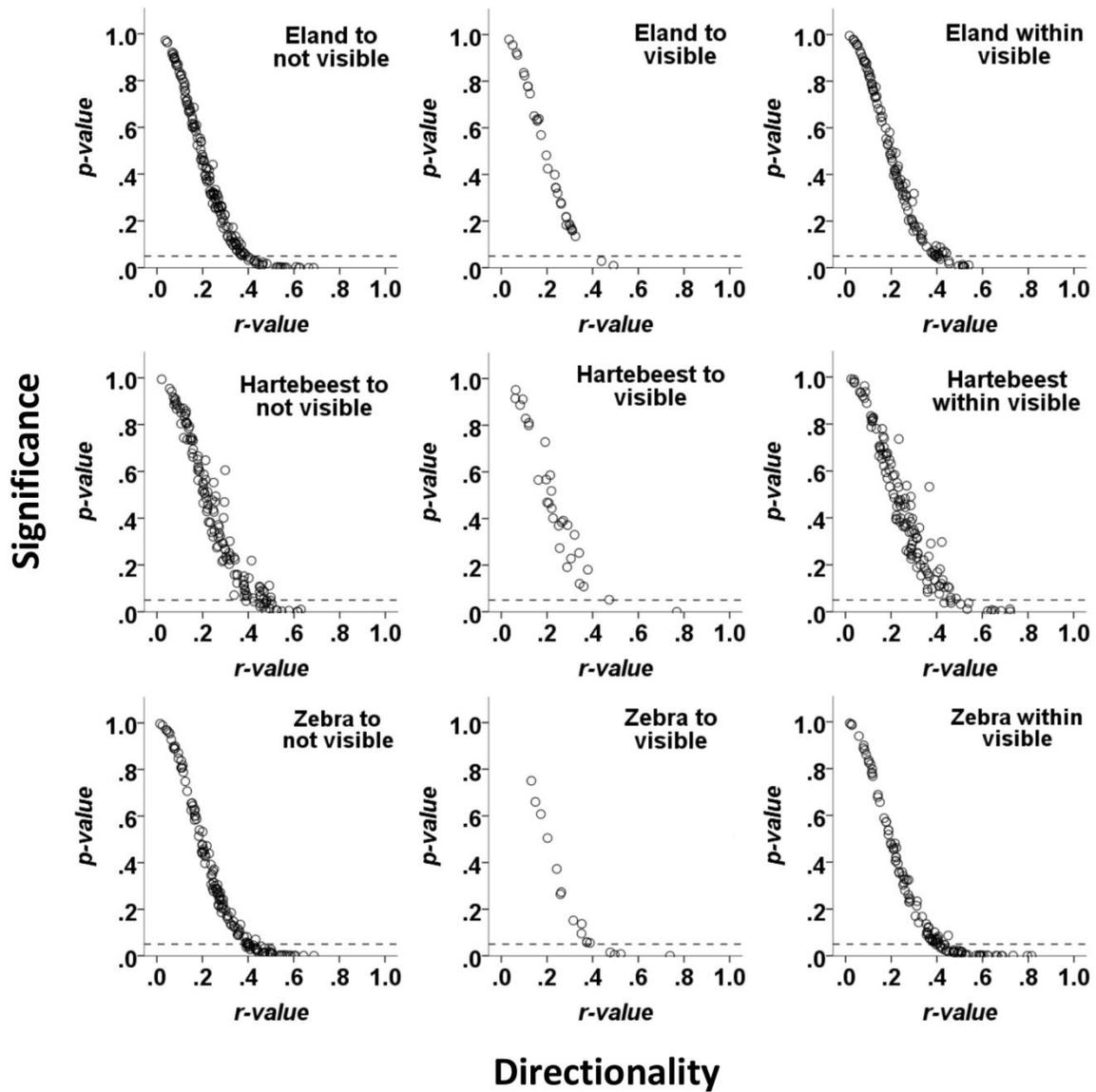


Figure 6.4: The effect of visibility classes on the directionality of “walks” of the zebra, red hartebeest and eland studied in Mkambati Nature Reserve. When $r \geq 0.5$ and the p value indicated significance ($p < 0.05$ as indicated by the reference line), walks were considered as concentrated in one direction (directional) (Duffy et al. 2011).

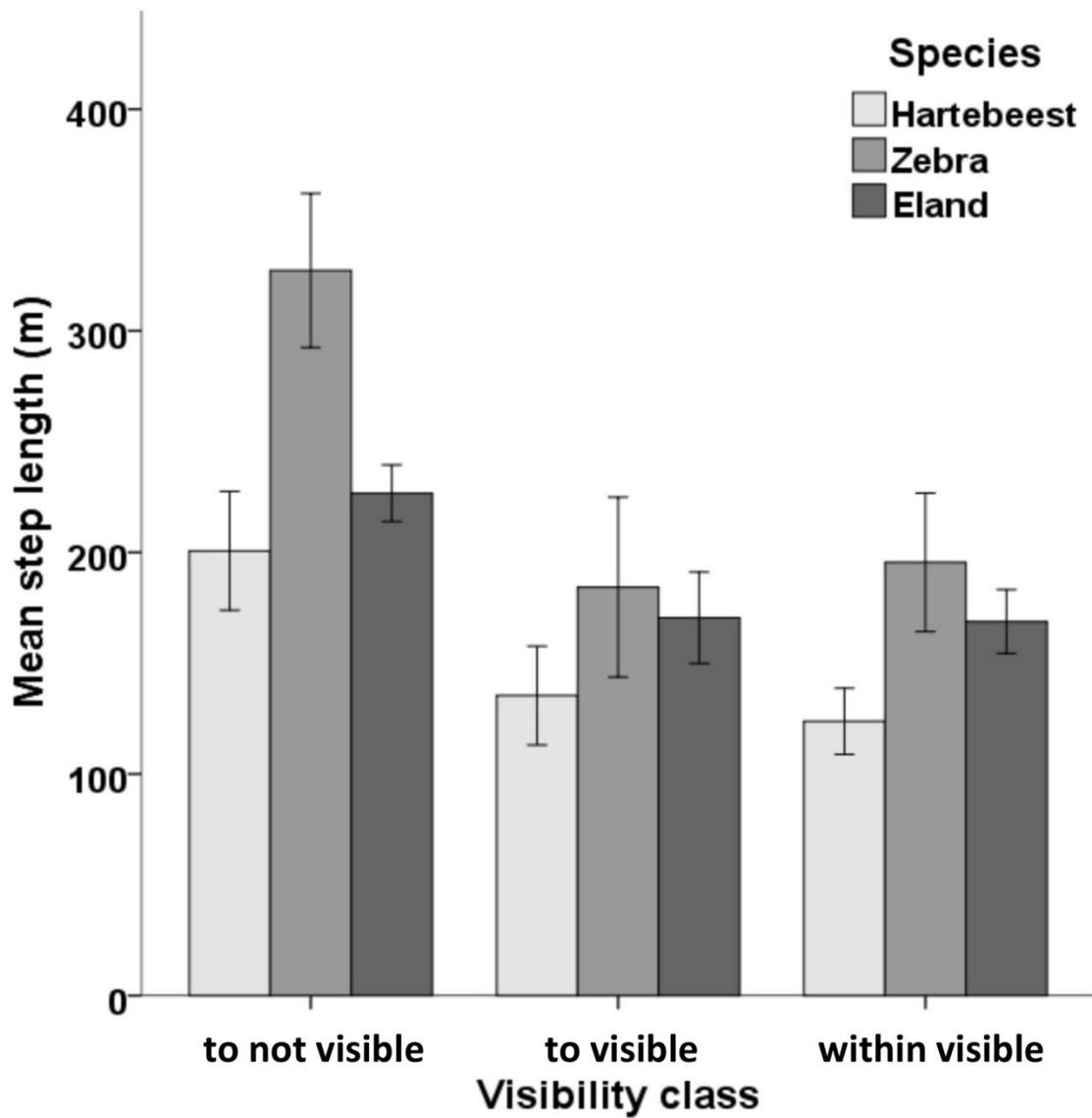


Figure 6.5: The effect of visibility classes on mean step length of zebra, hartebeest and eland studied in Mkambati Nature Reserve. Error bars indicate 95% Confidence Interval

6.6 DISCUSSION

A composite Brownian motion was observed for three study species when they were moving to new habitat patches. Our hypothesis that large herbivores use visual cues when moving to search for patches at a habitat patch scale could thus be rejected. Our results support the simulations by Benhamou (2007) which showed that, in patchy environments Brownian walks at two- or more different scales (composite Brownian motions), combining small-scale area-restricted searches (within patches) and large movements between patches, were used as an optimal strategy to search for habitat patches.

Our study demonstrates scale complexity in grazers' behaviour. One or more small area restricted searches within patches were mixed with one or more large-scale movements between patches. The search pattern found in this study supports a more "adaptive approach" (Benhamou 2007, Reynolds and Rhodes 2009), because when a suitable patch is encountered it triggers switching from several levels of more extensive search modes to several levels of more intensive within-patch search modes. During these fine scale search modes at the bite, feeding station and food patch scale (Owen-Smith et al. 2010) animals would make use of visual and olfactory cues to find suitable forage items (Edwards et al. 1997, Laca 1998). At courser scales (e.g. habitat patch scale), herbivores would randomly move, with an increased intensity (larger step lengths) until they are able to detect more suitable forage (at the finer scale) (Benhamou 2007). The search patterns displayed by our study animals thus indicate an adaption of their movement to the patchiness of the environment rather than a spontaneously generated power-law distribution (Lévy movement) of step lengths, which would be expected if visual cues (or the lack thereof) had played a major role (Benhamou 2007). Adaptations of animal movement behaviour to patchiness at the habitat scale, was observed elsewhere (Viswanathan et al. 1999, de Knegt et al. 2007, Duffy et al. 2011), and is convincingly confirmed by this study.

The main difference detected among the three visibility classes was that longer step lengths were used during movements to non-visible patches versus visible patches. The finding complies with observations made by Laca (1998) who studied searching behaviour of domestic cattle. Cattle

showed a strong tendency to move in the same direction when animals had no memory about food locations, regardless of failures and successes in finding food (Laca 1998). Combining observations by Laca (1998) with our observations we can expect that when animals cannot see patches from a distance, e.g. at a habitat patch scale, (and have no memory about patch distribution), they are more likely to move larger distances in the same direction.

In addition, the zebra used larger step lengths, had more directional walks, and their movements were more complex in scale, compared to eland and hartebeest. These variations could be linked to differences in the species intrinsic traits, such as digestive system, muzzle width and body weight (Senft et al. 1987a, Prins and Van Langevelde 2008b). Non-ruminant zebra, are less efficient at digesting food, and have to maintain a higher intake-rate to maintain their energy requirements (Bell 1971, Demment and Soest 1985, Illius and Gordon 1992). This should cause them to move more frequently from one food patch to another as food patches are depleted due to grazing (Bell 1971). In addition, zebra have a wider muzzle than the two ruminant species which makes them capable of using very short grass swards (which are common in recently burned grass patches). Zebra have been shown to prefer newly burned grassland (Sensenig et al. 2010), but the lower biomass in recently burned patches are depleted much quicker, forcing them to keep moving to new food patches (Venter et al. 2014a). In addition, higher directionality of zebra movement could indicate that they may be more efficient in finding new forage patches. Both these factors would cause higher movement intensity and complexity, as we observed with zebra. Red hartebeest also had complex movement scales, but compared to zebra and eland had the shortest step lengths. Red hartebeest is an example of a concentrate selector; its skull morphology is specially adapted to enable them to be very selective at times when good forage is scarce (Schuette et al. 1998). In areas with much moribund vegetation, grazing ruminants such as the red hartebeest face particular constraints because nearly all vegetation biomass has a low quality, which reduces food intake rates (Drescher et al. 2006a, Drescher et al. 2006b, van Langevelde et al. 2008). By being more selective, hartebeest would probably need to have more spatially complex movement scales. Red hartebeest, being the smaller ruminant (compared to eland), needing less, but better quality, forage to meet their nutritional and energy requirements (Demment and Soest 1985, Illius and Gordon 1992), used a strategy where they foraged using random, smaller step lengths whether they were moving within patches or to

unseen patches. They thus made use of both less suitable patches and more nutritious patches in a similar way.

Eland movements, by contrast, were less complex in scale compared to both zebra and hartebeest, which could be related to their body size and digestive system. Eland are one of the larger African ruminant species and are considered to be selective feeders (which includes browse) that requires a diet of high nutritive value, low fibre and high protein content (Arman and Hopcraft 1975). They also have a relatively small rumen in relation to their body size and retain food in the rumen for a shorter time (comparable to cattle), which allows for a greater appetite (compared to hartebeest) (Arman and Hopcraft 1975). It is, therefore, surprising that they showed less complexity in movement scale compared to zebra and hartebeest. This behaviour could possibly be linked to their diet, as being able to browse, they can overcome the challenge of dealing with a landscape of nutrient poor moribund grassland by eating forbs and trees (when available). Forbs are common, especially in newly burned patches in Mkambati (Shackleton 1989). In the case of trees, which is a resource that does not change as continuously burnt grassland, eland should be able to return to browsing patches by using memory. This could possibly explain the less complex movement behaviour. However one would have expected more directional movements if that were the case.

The results of this study are consistent with the hypothesis that large grazers do not use visual cues when making foraging decisions at a habitat patch scale, but rather adapt their search mode according to habitat or forage heterogeneity and quality. However, the evidence should be seen as circumstantial rather than conclusive. Further research is needed in order to eliminate alternative explanations such as habitat patch distance. In addition, the composite Brownian movement behaviour outcomes showed that complexity in scale of large herbivore movement has the potential to explain movement behaviour in relation to species traits such as body size, feeding type, digestive strategy and muzzle width.

Chapter 7: Conclusion

7.1 INTRODUCTION

This chapter highlights the main research findings and how these addressed the research aim and objectives. I also provide conservation management recommendations and list potential future research focus areas.

The behaviour ecology of large mammalian herbivores reflects the choices they make, expressed in the form of changes in behaviour (Gaillard et al. 2010). Foraging theory concerns specifically activities related to the acquisition of food (Owen-Smith et al. 2010), and in the context of this thesis, I addressed herbivore movement and patch use decisions (Stephens and Krebs 1986, Owen-Smith et al. 2010). The interaction between herbivores and their environment can be detected in their movement behaviour (Frair et al. 2005), which takes place at several scale levels: from steps between foraging stations, to daily movement in home ranges, to seasonal migratory movements (Prins and Van Langevelde 2008a). Advances in GPS tracking (telemetry) technology have made the acquisition of high quality fine scale movement data possible (Hebblewhite and Haydon 2010, Owen-Smith et al. 2010). Fine scale movement tracking data are useful in studies on habitat selection (Creel et al. 2005, Galanti et al. 2006), home range behaviour (Shannon et al. 2006, Massé and Côté 2012), animal migration (Boone et al. 2006, Hebblewhite and Merrill 2011), ecology and conservation of species (Royer et al. 2005, Hays et al. 2006), conservation impacts (Proffitt et al. 2009, Phipps et al. 2013) and projecting impacts of climate change (Durner et al. 2009). Many of these studies are characterized by a focus on the spatial and temporal aspects of the species behaviour, i.e. where and when animals move, predator-prey or herbivore-forage interactions, with many studies researching a single species only (Mårell et al. 2002, Fortin et al. 2005, Rahimi and Owen-Smith 2007, Winnie and Creel 2007, Loarie et al. 2009). There are also a myriad of publications on search efficiency in movement behaviour (Viswanathan et al. 1996, Viswanathan et al. 1999, Bartumeus 2005, Benhamou 2007, Edwards et al. 2007, Bartumeus 2009, Edwards et al. 2012, Jansen et al. 2012).

Intrinsic factors such as body size, muzzle width, digestive system and feeding type, can influence the way large herbivores interact with their environment (Bell 1971, Bailey et al. 1996, Gordon and Illius 1996, Clauss and Hummel 2005, Prins and Van Langevelde 2008b, Hopcraft et al. 2011).

Intrinsic factors also determine the way large herbivores react to extrinsic factors such as seasonal changes of forage resources, competition, predation, poaching, fire, artificial water holes and fences (Prins 1996, Boone and Hobbs 2004, Fischer and Eduard 2007, Creel and Christianson 2008, Valeix et al. 2009a, Waltert et al. 2009, Parrini and Owen-Smith 2010, Sensenig et al. 2010, Vanak et al. 2010, Hassan and Rija 2011).

Many studies have focused on either intrinsic or extrinsic factors (see references above), but only few studies managed to link the two components and applied such understanding to real-time conservation practise and implications for management (Vanak et al. 2010, Delsink et al. 2013, Jachowski et al. 2013). This study use movement behaviour to compare the effect of intrinsic and extrinsic influences on different species, and to define how they respond to these influences. Understanding these interactions are important for the long term conservation of large mammalian herbivore populations because both intrinsic and/or extrinsic factors could influence species persistence as well as ecosystem health (Boyce 1998, Grant et al. 2011). In addition, such understanding can assist in conservation planning and management of herbivore assemblages in protected areas (Gaylard and Ferreira 2011, Grant et al. 2011).

The aim of the study was to determine how African large herbivore species, influenced by various intrinsic factors, respond, through movement behaviour, to extrinsic factors in protected areas. The results of the study indicate that intrinsic factors such as individual species traits (body size, muzzle width, digestive system and feeding type) can influence the way large herbivores interact with their environment, and that these factors in turn determine how large herbivores react to extrinsic factors such as poaching, fire, artificial water holes and fences.

7.2 RESEARCH FINDINGS

In order to answer my research question, I focussed on four separate research objectives:

1. My first objective was to conduct a situation analysis on Mkambati Nature Reserve in order to determine how well grazing herbivores have become established since their introduction,

how this was influenced by facilitation and competition, and what the implications were for ecological restoration. I concluded that the absence of larger grazers in the Mkambati grazer assemblage was creating an ecosystem devoid of facilitatory effects exerted by these species, which in turn leads to an ecosystem that cannot maintain its herbivore assemblage structure. The functioning of grazing ecosystems are driven by various patterns and processes (Bailey et al. 1996), and excluding certain species, weight ranges or guilds could potentially be detrimental to ecosystem functioning (Cromsigt and Olf 2006, Waldram et al. 2008). I propose a biogeographical and biological approach to reconstructing grazer assemblages for protected areas. This approach should take cognisance of all the potential risks facing managers (Spear and Chown 2009), and should be focussed on improving incomplete understanding and reducing the identified risks. This can be achieved by an adaptive management approach underpinned by an efficient monitoring system (Biggs and Rogers 2003). Thresholds of potential concern, designed to detect undesirable changes in biodiversity, could function to guide management and catalyse change in management action when needed (Biggs et al. 2011). I concluded that a protected area restoration strategy, that aims to simulate the natural processes and heterogeneity of a system (Goodman 2003), should make full use of all the tools available to reconstruct past species assemblages. These tools are not limited to historical distribution data (Boshoff and Kerley 2010), but also include biogeographic and biological approaches (Prins and Olf 1998a). This part of the study provided a useful approach to follow in planning of restoration of grazer ecosystems in protected areas. This approach will increase the scientific rigour needed conservation management decision making processes (Biggs et al. 2011), and enhance the effectiveness of protected areas in conserving biodiversity (Goodman 2003).

2. The second objective of this study was to determine what factors influence forage patch use behaviour. In conservation areas, where managers attempt to simulate the natural processes and heterogeneity of ecosystems (Goodman 2003), inter-patch movement behavioural responses of large herbivores are a critical aspect to consider (Gibbs et al. 1999, Carbutt and Goodman 2013). In this study, I demonstrated how red hartebeest (*Alcelaphus buselaphus camaa*) and plains zebra (*Equus burchelli*) actively use particular types of burnt patches with suitable forage, and that their choice of foraging patches was

influenced by poaching risk and fire. The implications of this for protected area managers are that the impact of unregulated poaching and human induced fire regimes have significant effects in the spatial behaviour of large herbivores (Gude et al. 2006, Thaker et al. 2010). Because of this there could be a considerable edge effect on large herbivore habitat use within protected areas (Woodroffe and Ginsberg 1998, Balme et al. 2010). Both fire management and anti-poaching action could thus have an unanticipated impact on ecosystems (Ruggiero 1992, Ripple et al. 2001, Searle et al. 2008, Eisenberg et al. 2013). This is especially the case for more intensively managed small- to medium-sized conservation areas (Kerley et al. 2008). The interesting discovery in this part of the study was that animals select the areas they forage in, based on extrinsic influences such as poaching risk. The implication for conservation management is that direct and indirect poaching effects could cause undesirable ecosystem change. Anti-poaching action is thus not just about protecting target species but also protecting ecosystems and biodiversity in general.

3. The third objective of the study was to determine the factors effecting scale of movement of large herbivores. Identifying determinants of large herbivore movement scale can benefit their management and conservation, as it allows the understanding of herbivore species spatial dynamics and associated ecological processes (Delsink et al. 2013, Jachowski et al. 2013). Scales are defined by rates of foraging and ecosystem processes, and boundaries between units, at each scale, are defined by animal behaviour (Senft et al. 1987a, Bailey et al. 1996). My results suggest that water and landscape heterogeneity, large herbivore traits, interspecific competition and fences influence the scale complexity of large herbivore movement. The results demonstrate that species deal with limitations in nutritional requirements during low resource times by adapting their movement behaviour, thereby incurring an increased cost of traveling to-and-from water sources in order to satisfy their nutritional requirements (Redfern et al. 2003, Smit et al. 2007, de Beer and van Aarde 2008). A novel discovery of this part study was that the influence of intrinsic factors, and their effect on extrinsic factors could be detected in movement scale complexity.

4. My fourth objective was to establish if large herbivores use visual cues when searching for new patches at a habitat patch scale. No studies have been able to demonstrate if large herbivores use visual cues when foraging at a habitat-patch scale. My study suggests that large herbivores indeed don't appear to use visual cues when foraging at a habitat-patch scale, but rather adapt their search mode according to habitat or forage heterogeneity and quality (Benhamou 2007).

7.3 DISCUSSION AND RECOMMENDATIONS

Intrinsic factors such as, body size, muzzle width, digestive system and feeding type, influence the way large herbivores interact with their environment (Bell 1971, Bailey et al. 1996, Gordon and Illius 1996, Clauss and Hummel 2005, Prins and Van Langevelde 2008b, Hopcraft et al. 2011). These intrinsic factors, in turn, determine how large herbivores respond to extrinsic factors such as seasonal changes of forage resources, competition, predation, poaching, fire, artificial water holes and fences (Prins 1996, Boone and Hobbs 2004, Fischer and Eduard 2007, Creel and Christianson 2008, Valeix et al. 2009a, Waltert et al. 2009, Parrini and Owen-Smith 2010, Sensenig et al. 2010, Vanak et al. 2010, Hassan and Rija 2011). Protected areas are facing increasingly complex challenges in understanding and conserving their biodiversity features (Venter et al. 2008). These challenges are mostly driven by anthropogenic influences (Venter et al. 2008, Biggs et al. 2011), which are extrinsic factors directly affecting large herbivore assemblages, as have been demonstrated in my study.

Strategic protected area management planning, which deals with protected area operations, requires a great deal of information and understanding of ecosystem patterns and processes to be effective (Biggs and Rogers 2003, Goodman 2003). This is especially the case when an adaptive management approach is followed (Biggs and Rogers 2003), because, to be able to measure the effect of management action on ecosystems requires a monitoring system that produces a great deal of high quality information (Biggs et al. 2011, Gaylard and Ferreira 2011). A better understanding of the link between intrinsic factors and extrinsic factors and their effect on spatial behaviour is important for the management of large herbivore assemblages and mitigation of anthropogenic influences on ecosystem processes (Jachowski et al. 2013). My study have been able to link intrinsic

factors, i.e. body size, muzzle width, digestive system and feeding type, effects on movement behaviour to what appears to be the effects of extrinsic factors, i.e. seasonal changes of forage resources, competition, predation, poaching, fire, water sources and fences. More importantly, I have demonstrated that different species react to environmental influences in different ways. This is important because it highlights the danger of a “one shoe fits all” kind of protected area management approach. For example, artificial water holes were created in Kruger National Park, between 1902 and 1980, in order to enhance wildlife numbers (Harrington et al. 1999, Venter et al. 2008). The provision of artificial waterholes attracted high numbers of zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) to areas in the park where they were normally present in low densities only, particularly during drought conditions (Harrington et al. 1999). This, in turn, had cascading effects through increased predation on rarer antelope such as roan antelope (*Hippotragus equinus*), due to a build-up in lion (*Panthera leo*) numbers, following the zebra and wildebeest influx, which had a devastating effect on roan antelope (Harrington et al. 1999). Similar cascading effects have been observed in Yellowstone with interactions between wolves (*Canis lupus*), elk (*Cervus elaphus*) and aspen trees (*Populus tremuloides*) (Boyce 1998, Ripple et al. 2001, Ripple and Beschta 2007). Managing a protected area for a single species or single objective, without considering how other species react to the same influence could thus have negative consequences.

Another important extrinsic factor is poaching, which currently has a negative effect on large herbivore populations in Africa (du Toit 1995, Fischer and Eduard 2007, Vie et al. 2009, Waltert et al. 2009, Craigie et al. 2010). Poaching can cause large herbivores to respond in the same way as they do to natural predators by choosing to ignore risk when deciding where to forage (Prins 1996), avoiding risky areas (Creel et al. 2005, Valeix et al. 2009a), or by moving out of harm’s way when poachers are encountered (Fischhoff et al. 2007, Winnie and Creel 2007). My study indicated that species such as plains zebra were more responsive, in their patch selection behaviour, to avoiding poaching risk, than red hartebeest. However both species’ choice of foraging patches was influenced by direct and secondary poaching effects. This means that animals in protected areas exposed to poaching exhibits unnatural resource use patterns which affects forage resources in an unnatural way. This could potentially affect protected areas negatively (Boyce 1998, Ripple et al. 2001).

My study also highlights the importance of scale complexity in large herbivore movement behaviour, especially where extrinsic factors such as seasonality, vegetation heterogeneity, surface water supplies and the effect of fences are concerned. My study furthermore emphasised that the behaviour was driven by intrinsic factors in a prominent way. Resource heterogeneity occurs at different spatial and temporal scales, which make it difficult, but important, to determine at which particular scale resource selection by large herbivores might occur (Senft et al. 1987a, Bailey et al. 1996). Scale mismatches occur when the scale of ecological variation and the scale of protected area management action are aligned in such a way that functions of the socio-ecological system are disrupted and components of the ecosystem are lost as a consequence (Cumming et al. 2010). When scale mismatches occur in protected area management, the risk of failing to achieve set conservation management targets increase (Cumming et al. 2010, Delsink et al. 2013). Delsink et al. (2013) have shown that, even though Kruger National Park has an adaptive management approach (Biggs and Rogers 2003), they have failed to move away from setting numerical targets in their elephant management, due to scale mismatch in elephant movement behaviour and their landscape approach. My study emphasise the importance of scale in the conservation management of large herbivore assemblages.

It is thus important for protected area managers to carefully evaluate possible effects of their intended management actions on large grazer assemblages, by considering effects on all species, or at least functional groups of species (Blondel 2003). When an adaptive management approach is followed (Biggs and Rogers 2003) thresholds of potential concern (TPC's) (Biggs et al. 2011), and associated monitoring programs (McGeoch et al. 2011), should also be set and developed by functional group. This should prevent managers from not anticipating possible effects of management action on non-target species. This approach would improve management effectiveness (Boyce 1998, Goodman 2003).

In many protected areas, the management interventions are intended to restore ecological patterns and processes that have been affected by anthropogenic disruption (Heinen 2002, Suding et al. 2004, Hayward 2009a). A common element of these interventions is to reintroduce 'suitable' species

to, or remove 'undesirable' species from, protected areas (Griffith et al. 1989, Novellie and Knight 1994, Fischer and Lindenmayer 2000, Atkinson 2001, Gusset et al. 2008). The reintroduction of indigenous herbivores to an ecosystem reintroduces natural disturbance and processes that are thought to support or promote the re-establishment of local diversity (Simenstad et al. 2006). Conservation authorities opt to use a precautionary approach when deciding which species to introduce or maintain in protected areas, as non-indigenous species are potentially harmful to habitats in which they did not evolve (Spear and Chown 2009, Spear et al. 2011). A critical aspect of this restoration process is the selection of species that are 'suitable'. In many instances, the past is used to determine which species are suitable, assuming that indigenous species are the most appropriate to achieve restoration objectives (List et al. 2007, Hayward 2009a, Boshoff and Kerley 2010).

My study on the current grazer assemblage in Mkambati Nature Reserve suggests that there was a lack of beneficial facilitation by larger and mega grazers (Owen-Smith 1987, Truett et al. 2001, Waldram et al. 2008) which could have resulted in competitive exclusion and subsequent local extinction of some species.

In addition, I indicated that the assemblage prescribed by the current policy (ECPB 2010), based on historical distribution data only, could result in a depauperate grazer assemblage with an increased likelihood for interspecific competition. In the context of the current policy, I determined that facilitation is unlikely because of: an unusually small grazing species assemblage for a grass dominated ecosystem (Rowe-Rowe 1994, Boshoff and Kerley 2001, Bonyongo and Harris 2007, Klop and Prins 2008), the lack of 'mega' grazers in the assemblage (Bell 1982, Fritz et al. 2002), and a high risk because of competition effects (Chapin et al. 2000, Zavaleta et al. 2001, Lagendijk et al. 2012). The effect of such a depauperate grazer assemblage could be: a higher fire frequency, caused by fuel load build-up when grass biomass is not effectively cropped by grazers (Bond and Keeley 2005, Fuhlendorf et al. 2009, Leonard et al. 2010), and an ecosystem devoid of facilitatory effects which in turn leads to an ecosystem which is unable to maintain its herbivore assemblage

structure (Prins and Olff 1998a). Both these factors carries a high biodiversity risk, and I therefore do not recommended the current policy for implementation in Mkambati.

The 'biogeographic' assemblage that I proposed in this study, has a full, evenly spread, grazer species assemblage, which provides the potential opportunity for a grazing ecosystem that allows for beneficial facilitatory effects. This leads to an ecosystem that should be able to maintain its herbivore assemblage structure better. The advantages of this assemblage are that it should be able to maximize production and utilization in the forage layer which could increase grazer biomass (Prins and Olff 1998a), and it potentially allows for an escape from Mkambati's current 'fire trap' of a very high fire return rate (Waldram et al. 2008). The restoration of mega- and larger grazers to Mkambati could have additional benefits such as decreasing risk of unnatural fire regimes caused by poachers. If the fuel load is decreased in this way, unnatural fire occurrence could be decreased and the potential effect on large herbivores concentrating in certain areas (due to poaching fires) could potentially decrease (a problem identified in chapter 4). The strength of this approach lies in the ability to overcome the problem of depauperate grazer assemblages, which were caused by a lack of historical data for the region, by using biogeography and ecological processes, to assist in effectively predicting grazer assemblages that can actually achieve restoration goals.

The following recommendations are made for the ecological restoration of Mkambati Nature Reserve:

1. To introduce larger grazers first (see Table 3.1) and stop the removal of plains zebra (*Equus burchelli*), as this is where the critical gap is. Here the introduction of African buffalo (*Syncerus caffer*) and white rhino (*Ceratotherium simum*) should be prioritized to fill this critical gap of 'mega' grazers in the assemblage (Bell 1982, Fritz et al. 2002).
2. For white rhino, there is no confirmation from historical data that the species was present in the immediate vicinity of the protected area, but my biological and biogeographical predictions contradict the historical assessment. The reintroduction should thus be approached using a strategic adaptive management approach (Biggs and Rogers 2003).

3. This should take place through an iterative process of setting reintroduction objectives, implementing reintroduction actions and evaluating the implications of their outcomes for future management action (Biggs and Rogers 2003, Gaylard and Ferreira 2011, Roux and Foxcroft 2011). This would involve setting thresholds of potential concern (TPC's)(Biggs et al. 2011), and intensively monitoring the species' effect on the ecosystem and the grazer assemblage (McGeoch et al. 2011).
4. Based on the monitoring results and TPC's, decisions can be made to remove or maintain them, depending on the monitoring outcomes.
5. More introductions should follow after this, following the same process, until the grazer assemblage is fully restored.

A protected area restoration strategy that aims to simulate the natural processes and heterogeneity of a system should thus make full use of all the tools available to reconstruct past species assemblages. These tools are not limited to historical distribution data but include biogeographic and biological approaches. It is however recognized that socio-economic considerations play an increasing role in protected area management. It is thus important that planned restoration actions also take cognisance of these aspects. My works focused on the ecological and biodiversity aspects only.

Acceptable forage or habitat patches might not be discernible from a distance, may change with influence from other herbivores (Arsenault and Owen-Smith 2002, Kohi et al. 2011), and their location may shift continuously as forage quality changes due to abiotic circumstances (e.g., fire, rainfall or flood recession) (Olf et al. 2002, Archibald and Bond 2004, de Knegt et al. 2008, van Beest et al. 2010). Herbivores are therefore faced with a challenge in how to find and choose good quality forage patches in a landscape where the location and quality of such patches are continuously changing (Senft et al. 1987a, Bailey et al. 1996). Large herbivores may use a range of behaviours to enhance their foraging efficiency (Beekman and Prins 1989, Bailey et al. 1996). They may gain *a priori* knowledge using memory (from a previous visit to the patch) (Edwards et al. 1996, Dumont and Petit 1998, Fortin 2003, Brooks and Harris 2008) or find new patches through visual cues (Edwards et al.

1997, Howery et al. 2000, Renken et al. 2008). If the presentation of the forage resource is complex (e.g. when forage patches are not well defined), or the distribution of forage patches are likely to change continuously, then recalling the location of forage patches may be of limited value (Edwards et al. 1997). In such heterogeneous situations, i.e. in both space and time, the capacity to recognise and assess (reward) different forage patches, at a distance through visual cues, would promote foraging success (Edwards et al. 1997).

This last part of my study was more of biological interest rather than of significant conservation management importance. However it addressed a question which remained unanswered up to now. A number of field based studies have linked movement patterns to the use of memory by large herbivores to locate or revisit suitable forage patches (Ramos-Fernandez et al. 2003, Brooks and Harris 2008). Research has also shown that large herbivores use visual cues at a food-patch (finer) scale (Edwards et al. 1997, Howery et al. 2000, Renken et al. 2008). However, no studies have been able to show if large herbivores use visual cues when foraging at a habitat-patch scale. My study provided evidence that large herbivores possibly make limited use visual cues when foraging at a habitat-patch scale. Such understanding of the scale at which herbivores make decisions, will influence their behaviour, and this will indicate the scale of biological relevance to the herbivores (Jachowski et al. 2012, Delsink et al. 2013, Jachowski et al. 2013). It is important to note that this study only focussed on three species in a specific grazing ecosystem and that the results are derived from a limited sample size. It could be that the results are not conclusive enough. It is thus recommended that there needs to be more independent investigations to confirm that these results. It is therefore, important to understand, define and monitor the scale of behaviour to ensure that management interventions are planned at the correct spatial scale (Delsink et al. 2013).

7.4 FUTURE WORK

While this study has answered a number of questions, it has raised additional ones that could benefit from research:

In the conclusion of Chapter 3, I question the conventional approach of only using historical distribution data when planning reintroductions of animals to protected areas for ecological restoration. I also proposed that this approach be strengthened by using biological and biogeographical methods. My proposed approach can, however, still be refined and expanded upon. Specific research questions in this regard are:

1. Is a biogeographic area the relevant spatial feature to use and does it make adequate provision of forage during seasonal cycles? This is especially relevant to the assumed historical migratory movements of a number of African species. Are there other spatial features that would be more relevant to use, for example vulture movements (some bird species migratory and seasonal movement habits are ancient (Salewski and Bruderer 2007), and could provide clues to where large mammal migrations took place in the past) or the modelling of regional seasonal forage quality changes related to rainfall patterns.
2. Do the hypothesised facilitation processes derived from the modelled grazer assemblages actually take place in well packed assemblages?
3. Could the species packing approach be applied to browsers and perhaps even to large predators?
4. What role do other morphological features, for example muzzle width, play in facilitation and competition between large herbivores?
5. What role does sexual dimorphism play in facilitation and competition between large herbivores?
6. How would socio-economic considerations influence restoration objectives under different protected area scenarios?
7. Are there limitations to the number of species a system could cope with?

In addition, the approach used in this research should also be replicated and tested in other ecosystems. Where historical animal records are concerned, there is also a need to explore how this is influenced by old travel routes (Bernard and Parker 2006), what causes gaps in historical distribution data as well as possible pre-colonial anthropogenic effects on wildlife. Currently, many unsubstantiated assumptions (for example, rivers are effective barriers to animal movement and

therefore drive distribution patterns) made from these data sets need to be properly validated (Venter, *personal observation*).

During my investigation into patch use behaviour, I concluded that poaching and fire play a significant role in how animals decide to use these patches. I recommended that patch use behaviour in relation to fire and risk effects should be unpacked at a finer scale. A specific question around this topic is:

8. How is patch use related to daily changes in quality and quantity of the forage resource as well as risk? When reward in relation to energy cost is unravelled, patch use could be linked to optimal foraging theory.

I was able to show that water and heterogeneity, large herbivore traits and interspecific competition influenced the scales at which large herbivores move. The questions that should be highlighted are related to both the temporal and spatial scale:

9. Could differences in movement scales be detected with finer frequency data (10 to 30 min location intervals) between; species with different traits, fine scale vegetation types (heterogeneity), biomes, and different types of water sources (artificial and natural)?
10. What is the effect of time on movement scale complexity, i.e. day, week, month and year?

My study provided evidence that large grazers do not use visual cues when foraging at a habitat patch scale but rather adapt their search mode according to habitat or forage heterogeneity and quality. Two research question remains to be answered adequately:

11. How do visual and/or olfactory cues play a role at finer scales of selection?
12. At what scale do animals make the switch from using visual cues to only using displacement movement?

7.5 CONCLUDING REMARKS

In my study, I demonstrated that individual species' intrinsic traits can influence the way large herbivores interact with their environment. These factors determine, in turn, how large herbivores react to extrinsic factors such as poaching, fire, artificial water holes and fences which are important to consider in the conservation management of protected areas. The study thus had a strong focus on application.

My study's findings also had broader implications. For example I showed that the Hutchinson's weight ratio theory (Hutchinson 1959) can be used in an innovative way to predict species assemblages, as was previously proposed as a testable model by Prins and Olf (1998). The important take-home-message I needed to convey was that current models in predicting assemblages are grossly inadequate, and a new approach was needed. The publication that was published on this topic will hopefully be catalyst for change in the way we think about restoration of protected areas in the future.

Since Viswanathan et al. (1996) produced one of the first publications opening the debate on whether Lévy walks could be used as a movement model for animals, a large number of publications either supported or rejected it as viable (Bartumeus 2005, Bartumeus et al. 2005, Benhamou 2007, Edwards et al. 2007, Edwards 2008, Bartumeus 2009, Auger-Méthé et al. 2011, de Jager et al. 2011, Edwards 2011, Grünbaum 2011, Edwards et al. 2012, Jansen et al. 2012). The whole debate was recently only reasonably resolved by two authors who provided adequate statistical models to show that composite Brownian motions are in fact more suitable in explaining animal movement (Edwards et al. 2012, Jansen et al. 2012). The resultant composite Brownian motions, with the more robust statistical models, opened a new avenue which I explored in my study. I was now able to use scale complexity in composite Brownian motions to test a number of hypotheses. I thus moved away from the now exhausted debate on Lévy walks versus Brownian motions, and used the recently developed models to answer my research questions.

However, in my view, the most important contribution my study made was to effectively link extrinsic and intrinsic factors to animal behaviour, and to protected area management. In my experience as a conservation practitioner I have seen too many times that well intended decisions around large herbivore management, that are not well grounded in strong understanding of animal behaviour, have unintended negative consequences. This problem is also highlighted in several literature sources (Harrington et al. 1999, Craigie et al. 2010, Grant et al. 2011, Delsink et al. 2013, Cromsigt and te Beest 2014). In many cases, conservation management authorities are forced by prevailing circumstances to make these decisions, and little can be done other than to mitigate or manage the consequences. But, in some cases, conservation management decisions can be improved by simply considering a broader range of cause-effect mechanisms, such as extrinsic and intrinsic factors on animal behaviour. Hopefully, my study has broadened knowledge sufficiently in order to contribute to this.

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APPENDIX A: Papers already published of work from this study

A1: VENTER, J.A., PRINS, H.H.T., BALFOUR, D.A., SLOTOW, R., 2014. Reconstructing grazer assemblages for protected area restoration. PLOS ONE 9(3): e90900

Reconstructing Grazer Assemblages for Protected Area Restoration

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Abstract

Protected area management agencies often struggle to reliably reconstruct grazer assemblages due to a lack of historical distribution data for their regions. Wrong predictions of grazing assemblages could potentially affect biodiversity negatively. The objective of the study was to determine how well grazing herbivores have become established since introduction to the Mkambati Nature Reserve, South Africa, how this was influenced by facilitation and competition, and how indigenous grazer assemblages can best be predicted for effective ecological restoration. Population trends of several grazing species were investigated in order to determine how well they have become established since introduction. Five different conceivable grazing assemblages reflecting a range of approaches that are commonly encountered during conservation planning and management decision making were assessed. Species packing was used to predict whether facilitation, competition or co-existence were more likely to occur, and the species packing of the different assemblages were assessed using ANCOVA. Reconstructing a species assemblage using biogeographic and biological information provides the opportunity for a grazer assemblage that allows for facilitatory effects, which in turn leads to an ecosystem that is able to maintain its grazer assemblage structure. The strength of this approach lies in the ability to overcome the problem of depauperate grazer assemblages, resulting from a lack of historical data, by using biogeographical and biological processes, to assist in more effectively reconstructing grazer assemblages. Adaptive management of grazer assemblage restoration through reintroduction, using this approach would further mitigate management risks.

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Introduction

There have been alarming declines in large mammal populations in protected areas in Africa in the last three decades, which are mainly attributed to habitat loss as well as to consumptive use [1,2]. In southern Africa, protected areas have been more successful in maintaining their large mammal populations due to effective conservation management [2,3]. In many of these protected areas, the management interventions are intended to restore ecological patterns and processes that have been affected by anthropogenic disruption [4–6]. A common element of these interventions is to reintroduce 'suitable' species to, or remove 'undesirable' species from, protected areas [7–11].

The reintroduction of indigenous herbivores to an ecosystem, reintroduces natural disturbance and processes that are thought to support or promote the re-establishment of local diversity [12]. A reintroduction is considered to be successful if it results in a self-sustaining population [9]. Reintroductions of large mammals to protected areas have had various levels of success over the last few decades [7–9]. Most of the unsuccessful reintroductions are attributed to unsuitable habitat [13], animals being non-indigenous (outside of their historical distribution range) [7], and to behavioural problems of the reintroduced animals [14,15]. Often, however, these explanations are either tautological, or based on suppositions. Conservation authorities opt to use a precautionary

approach when deciding which species to introduce or maintain in protected areas, as non-indigenous species are potentially harmful to habitats in which they did not evolve [16,17]. A critical aspect of this restoration process is the selection of species that are 'suitable'. In many instances, the past is used to determine which species are suitable, assuming that indigenous species are the most appropriate to achieve restoration objectives [4,18,19]. This piecing together of the past is frequently based on historical mammal distribution data (historical records in diaries, journals and correspondence of early explorers, settlers, hunters, missionaries or naturalists as well as from archaeological records and rock paintings) thus leading to the reconstruction of local historic animal assemblages [5,18–20]. But the process of deciding which species is 'suitable' or 'undesirable' is not an exact science and is open to criticism [19,20].

Resource competition and facilitation could have a significant effect on the structure and species-richness of large mammal assemblages [21–23]. Allometric relationships between body size and metabolic rate, and body size and gut capacity, predict that larger grazers can survive on lower quality forage but require higher bulk intake diets [24,25]. Conversely, smaller grazers require higher quality forage, but can cope with lower quantities of it [25]. This suggests that for species within the same guild, the more similar in size the more similar a niche they would occupy [21,26]. This increases the likelihood of competitive interactions

A2: VENTER, J.A., NABE-NIELSEN, J., PRINS, H.H.T., SLOTOW, R., 2014. Forage patch use by grazing herbivores in a South African grazing ecosystem. *Acta Theriologica* 59:457–466.

Forage patch use by grazing herbivores in a South African grazing ecosystem

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Abstract Understanding how different herbivores make forage patch use choices explains how they maintain an adequate nutritional status, which is important for effective conservation management of grazing ecosystems. Using telemetry data, we investigated nonruminant zebra (*Equus burchelli*) and ruminant red hartebeest (*Alcelaphus buselaphus* subspecies *camax*), use of burnt patches in a landscape mosaic of nutrient-poor, old grassland interspersed with young, recently burnt, nutrient-rich grass patches. The Mkambati Nature Reserve landscape on the east coast of South Africa provided large grazers with a challenge in finding and using appropriate patches in which to forage to meet their nutritional requirements. In Mkambati, grassland fires, mostly ignited by poachers, induce regrowth of young nutrient-rich grass, which subsequently attract grazers. We tested if the study animals

foraged more in burnt patches than in the unburned grassland and whether burnt patch use was related to the distance to the previously visited burnt patch, burnt patch size, burnt patch age, and distance to areas with high poaching risk using MANOVA. In general, zebra moved faster than red hartebeest, and both species moved faster in unburnt grassland than in burnt patches. Red hartebeest and zebra patch selection were influenced by interpatch distance, patch age, patch size, and poaching risk. A limited set of intrinsic traits, i.e., body mass, digestion strategy, and muzzle width, yielded different patch use rules for the two species. Large ungulates patch use behaviour varied among species and across conditions and was influenced by anthropogenic impacts such as poaching and changed fire regimes. This could potentially affect biodiversity negatively and needs to be factored into management of conservation areas.

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Keywords Grazing ecosystem · Large herbivore · Mkambati
Nature Reserve · Poaching · Red hartebeest · Zebra

Introduction

Conservation managers attempt to simulate natural processes and maintain heterogeneity of ecosystems to promote conservation outcomes in protected areas (Grant et al. 2011). For large African ungulates whose populations have declined over the last three decades (Craigie et al. 2010), effective conservation management is crucial (Carbutt and Goodman 2013). Understanding how species in a system vary their behaviour to meet their biological needs and deal with anthropogenic impacts should underpin such conservation management strategies (Gibbs et al. 1999). This paper presents the results of a study that investigated the patch use behaviour of two different grazing ungulate species.

APPENDIX B: The best-fit parameters, maximum log-likelihood, Akaike weights, Kolmogorov-Smirnov goodness-of-fit and r^2 values for fitting exponential, power law, truncated power law and mixtures of exponentials to the step length distribution for impala, blue wildebeest, eland, red hartebeest, African buffalo, plains zebra, Cape mountain zebra and African elephant from a number of wildlife areas in South Africa

Species	ID	Property	Season	Model	MLL	AIC	AIC Weight	KS-D	KS p-value	R ²
African buffalo	AG446	Baviaanskloof Nature Reserve	dry	Brownian motion	-3846.6600	7.6953E+03	0.0000	0.0991	0.0095	0.9940
African buffalo	AG446	Baviaanskloof Nature Reserve	dry	Brownian motion 2exp	-3808.2150	7622.4300	3.0000E-04	0.0532	0.4233	0.9962
African buffalo	AG446	Baviaanskloof Nature Reserve	dry	Brownian motion 3exp	-3798.5300	7607.0610	7.3980E-01	0.0202	0.9999	0.9994
African buffalo	AG446	Baviaanskloof Nature Reserve	dry	Brownian motion 4exp	-3797.5760	7609.1530	2.5990E-01	0.0183	1.0000	0.9996
African buffalo	AG446	Baviaanskloof Nature Reserve	dry	Power law	-4090.7270	8183.4550	0.0000E+00	0.2862	2.20E-16	0.8099
African buffalo	AG446	Baviaanskloof Nature Reserve	dry	Truncated power law	-3939.5900	7881.1800	0.0000E+00	0.2128	0.0000	0.9084
African buffalo	AG446	Baviaanskloof Nature Reserve	wet	Brownian motion	-4487.7190	8.9774E+03	0.0000	0.1575	0.0000	0.9802
African buffalo	AG446	Baviaanskloof Nature Reserve	wet	Brownian motion 2exp	-4394.4350	8794.8700	0.0000E+00	0.0535	0.3062	0.9947
African buffalo	AG446	Baviaanskloof Nature Reserve	wet	Brownian motion 3exp	-4382.3820	8774.7640	8.8080E-01	0.0153	1.0000	0.9997
African buffalo	AG446	Baviaanskloof Nature Reserve	wet	Brownian motion 4exp	-4382.3820	8778.7640	1.1920E-01	0.0153	1.0000	0.9997
African buffalo	AG446	Baviaanskloof Nature Reserve	wet	Power law	-4642.5380	9287.0760	0.0000E+00	0.2385	2.20E-16	0.8708
African buffalo	AG446	Baviaanskloof Nature Reserve	wet	Truncated power law	-4463.4030	8928.8060	0.0000E+00	0.1544	0.0000	0.9555
African buffalo	AG447	Baviaanskloof Nature Reserve	dry	Brownian motion	-4532.0210	9.0660E+03	0.0000	0.1411	0.0000	0.9818
African buffalo	AG447	Baviaanskloof Nature Reserve	dry	Brownian motion 2exp	-4471.8260	8949.6530	2.7290E-01	0.0243	0.9901	0.9992
African buffalo	AG447	Baviaanskloof Nature Reserve	dry	Brownian motion 3exp	-4469.0560	8948.1130	5.8930E-01	0.0137	1.0000	0.9997
African buffalo	AG447	Baviaanskloof Nature Reserve	dry	Brownian motion 4exp	-4468.5090	8951.0180	1.3790E-01	0.0167	1.0000	0.9997
African buffalo	AG447	Baviaanskloof Nature Reserve	dry	Power law	-4767.5370	9537.0750	0.0000E+00	0.2519	2.20E-16	0.8778
African buffalo	AG447	Baviaanskloof Nature Reserve	dry	Truncated power law	-4550.4970	9102.9940	0.0000E+00	0.1851	0.0000	0.9584
African buffalo	AG447	Baviaanskloof Nature Reserve	wet	Brownian motion	-4234.5870	8.4712E+03	0.0000	0.1304	0.0000	0.9890
African buffalo	AG447	Baviaanskloof Nature Reserve	wet	Brownian motion 2exp	-4162.8680	8331.7370	1.5600E-02	0.0509	0.3897	0.9963
African buffalo	AG447	Baviaanskloof Nature Reserve	wet	Brownian motion 3exp	-4156.8520	8327.7040	8.6700E-01	0.0159	1.0000	0.9995
African buffalo	AG447	Baviaanskloof Nature Reserve	wet	Brownian motion 4exp	-4156.8520	8327.7040	1.1730E-01	0.0159	1.0000	0.9995
African buffalo	AG447	Baviaanskloof Nature Reserve	wet	Power law	-4430.7000	8863.4000	0.0000E+00	0.2512	2.20E-16	0.8591

Species	ID	Property	Season	Model	MLL	AIC	AIC Weight	KS-D	KS p-value	R ²
African buffalo	AG447	Baviaanskloof Nature Reserve	wet	Truncated power law	-4229.8070	8461.6150	0.0000E+00	0.1860	0.0000	0.9451
African elephant	A99	Pilanesberg National Park	dry	Brownian motion	-3899.3330	7.8007E+03	0.0000	0.0906	0.0259	0.9902
African elephant	A99	Pilanesberg National Park	dry	Brownian motion 2exp	-3884.1620	7774.3250	1.6280E-01	0.0208	0.9998	0.9996
African elephant	A99	Pilanesberg National Park	dry	Brownian motion 3exp	-3880.6520	7771.3030	7.3760E-01	0.0189	1.0000	0.9996
African elephant	A99	Pilanesberg National Park	dry	Brownian motion 4exp	-3880.6540	7775.3090	9.9600E-02	0.0189	1.0000	0.9996
African elephant	A99	Pilanesberg National Park	dry	Power law	-4241.1690	8484.3390	0.0000E+00	0.3283	2.20E-16	0.8385
African elephant	A99	Pilanesberg National Park	dry	Truncated power law	-4040.0350	8082.0700	0.0000E+00	0.2943	0.0000	0.9251
African elephant	AG015	Kruger National Park	wet	Brownian motion	-5619.5290	1.1241E+04	0.1559	0.0676	0.0833	0.9972
African elephant	AG015	Kruger National Park	wet	Brownian motion 2exp	-5616.0280	11238.0600	6.9930E-01	0.0705	0.0632	0.9972
African elephant	AG015	Kruger National Park	wet	Brownian motion 3exp	-5615.9850	11241.9700	9.8800E-02	0.0705	0.0632	0.9972
African elephant	AG015	Kruger National Park	wet	Brownian motion 4exp	-5614.7470	11243.4900	4.6100E-02	0.0691	0.0727	0.9972
African elephant	AG015	Kruger National Park	wet	Power law	-6394.2010	12790.4000	0.0000E+00	0.4245	2.20E-16	0.7052
African elephant	AG015	Kruger National Park	wet	Truncated power law	-6097.8660	12197.7300	0.0000E+00	0.4662	0.0000	0.8012
African elephant	AG017	Kruger National Park	dry	Brownian motion	-3790.4540	7.5829E+03	0.0000	0.0658	0.2428	0.9960
African elephant	AG017	Kruger National Park	dry	Brownian motion 2exp	-3786.4130	7578.8260	0.0000E+00	0.0658	0.2428	0.9959
African elephant	AG017	Kruger National Park	dry	Brownian motion 3exp	-3757.2060	7524.4130	8.9020E-01	0.0288	0.9877	0.9990
African elephant	AG017	Kruger National Park	dry	Brownian motion 4exp	-3757.2990	7528.5980	1.0980E-01	0.0309	0.9748	0.9989
African elephant	AG017	Kruger National Park	dry	Power law	-4178.1720	8358.3450	0.0000E+00	0.3663	2.20E-16	0.8076
African elephant	AG017	Kruger National Park	dry	Truncated power law	-4030.8340	8063.6690	0.0000E+00	0.3148	0.0000	0.8898
African elephant	AG017	Kruger National Park	wet	Brownian motion	-3527.2280	7.0565E+03	0.0968	0.0668	0.2872	0.9940
African elephant	AG017	Kruger National Park	wet	Brownian motion 2exp	-3523.1380	7052.2760	7.8270E-01	0.0691	0.2509	0.9941
African elephant	AG017	Kruger National Park	wet	Brownian motion 3exp	-3523.1380	7056.2760	1.0590E-01	0.0691	0.2509	0.9941
African elephant	AG017	Kruger National Park	wet	Brownian motion 4exp	-3523.1210	7060.2410	1.4600E-02	0.0691	0.2509	0.9940
African elephant	AG017	Kruger National Park	wet	Power law	-3961.8640	7925.7290	0.0000E+00	0.3963	2.20E-16	0.7302
African elephant	AG017	Kruger National Park	wet	Truncated power law	-3793.5090	7589.0190	0.0000E+00	0.3963	0.0000	0.8254
African elephant	AG319	Kruger National Park	dry	Brownian motion	-4791.1610	9.5843E+03	0.0002	0.0343	0.8045	0.9976
African elephant	AG319	Kruger National Park	dry	Brownian motion 2exp	-4785.2940	9576.5870	1.1900E-02	0.0429	0.5403	0.9977
African elephant	AG319	Kruger National Park	dry	Brownian motion 3exp	-4779.0020	9568.0040	8.7010E-01	0.0458	0.4565	0.9978
African elephant	AG319	Kruger National Park	dry	Brownian motion 4exp	-4779.0020	9572.0040	1.1770E-01	0.0458	0.4565	0.9978
African elephant	AG319	Kruger National Park	dry	Power law	-5327.7260	10657.4510	0.0000E+00	0.3605	2.20E-16	0.7734
African elephant	AG319	Kruger National Park	dry	Truncated power law	-5084.9850	10171.9700	0.0000E+00	0.3176	0.0000	0.8746
African elephant	AG320	Kruger National Park	dry	Brownian motion	-5686.8360	1.1376E+04	0.1162	0.0463	0.4112	0.9968

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African elephant	AG320	Kruger National Park	dry	Brownian motion 2exp	-5682.9350	11371.8700	7.7820E-01	0.0463	0.4112	0.9968
African elephant	AG320	Kruger National Park	dry	Brownian motion 3exp	-5682.9350	11375.8700	1.0530E-01	0.0463	0.4112	0.9968
African elephant	AG320	Kruger National Park	dry	Brownian motion 4exp	-5686.8360	11387.6700	3.0000E-04	0.0463	0.4112	0.9968
African elephant	AG320	Kruger National Park	dry	Power law	-6440.2000	12882.4000	0.0000E+00	0.4054	2.20E-16	0.8150
African elephant	AG320	Kruger National Park	dry	Truncated power law	-6114.5100	12231.0200	0.0000E+00	0.4381	0.0000	0.8906
African elephant	AG322	Kruger National Park	dry	Brownian motion	-5360.9860	1.0724E+04	0.0073	0.0548	0.2358	0.9944
African elephant	AG322	Kruger National Park	dry	Brownian motion 2exp	-5354.4790	10714.9600	6.6310E-01	0.0604	0.1489	0.9943
African elephant	AG322	Kruger National Park	dry	Brownian motion 3exp	-5353.3050	10716.6100	2.9030E-01	0.0618	0.1318	0.9942
African elephant	AG322	Kruger National Park	dry	Brownian motion 4exp	-5353.3050	10720.6100	3.9300E-02	0.0618	0.1318	0.9942
African elephant	AG322	Kruger National Park	dry	Power law	-6028.2570	12058.5100	0.0000E+00	0.3904	2.20E-16	0.6796
African elephant	AG322	Kruger National Park	dry	Truncated power law	-5713.0870	11428.1700	0.0000E+00	0.4213	0.0000	0.7871
African elephant	AG322	Kruger National Park	wet	Brownian motion	-5466.4550	1.0935E+04	0.4659	0.0430	0.5384	0.9986
African elephant	AG322	Kruger National Park	wet	Brownian motion 2exp	-5466.4550	10938.9100	6.3000E-02	0.0430	0.5384	0.9986
African elephant	AG322	Kruger National Park	wet	Brownian motion 3exp	-5462.5710	10935.1400	4.1490E-01	0.0445	0.4957	0.9986
African elephant	AG322	Kruger National Park	wet	Brownian motion 4exp	-5462.5710	10939.1400	5.6200E-02	0.0445	0.4957	0.9987
African elephant	AG322	Kruger National Park	wet	Power law	-6180.3910	12362.7800	0.0000E+00	0.3989	2.20E-16	0.7870
African elephant	AG322	Kruger National Park	wet	Truncated power law	-5876.2910	11754.5800	0.0000E+00	0.4261	0.0000	0.8654
African elephant	AM119	Mkhuze Game Reserve	wet	Brownian motion	-5427.4570	1.0857E+04	0.1434	0.0268	0.9694	0.9992
African elephant	AM119	Mkhuze Game Reserve	wet	Brownian motion 2exp	-5423.8340	10853.6700	7.4090E-01	0.0268	0.9694	0.9992
African elephant	AM119	Mkhuze Game Reserve	wet	Brownian motion 3exp	-5425.1490	10860.3000	2.6900E-02	0.0253	0.9826	0.9991
African elephant	AM119	Mkhuze Game Reserve	wet	Brownian motion 4exp	-5421.9550	10857.9100	8.8800E-02	0.0164	1.0000	0.9997
African elephant	AM119	Mkhuze Game Reserve	wet	Power law	-6002.1190	12006.2400	0.0000E+00	0.3616	2.20E-16	0.7756
African elephant	AM119	Mkhuze Game Reserve	wet	Truncated power law	-5695.5950	11393.1900	0.0000E+00	0.3869	0.0000	0.8703
African elephant	AM13	Pilanesberg National Park	dry	Brownian motion	-3942.4280	7.8869E+03	0.0000	0.0944	0.0162	0.9860
African elephant	AM13	Pilanesberg National Park	dry	Brownian motion 2exp	-3938.8300	7883.6590	0.0000E+00	0.0944	0.0162	0.9859
African elephant	AM13	Pilanesberg National Park	dry	Brownian motion 3exp	-3924.4750	7858.9500	8.8030E-01	0.0315	0.9518	0.9984
African elephant	AM13	Pilanesberg National Park	dry	Brownian motion 4exp	-3924.4710	7862.9410	1.1970E-01	0.0315	0.9518	0.9985
African elephant	AM13	Pilanesberg National Park	dry	Power law	-4300.7710	8603.5410	0.0000E+00	0.3389	2.20E-16	0.8738
African elephant	AM13	Pilanesberg National Park	dry	Truncated power law	-4083.7370	8169.4740	0.0000E+00	0.3167	0.0000	0.9449
African elephant	AM14	Pilanesberg National Park	dry	Brownian motion	-3725.9870	7.4540E+03	0.0000	0.1332	0.0002	0.9700
African elephant	AM14	Pilanesberg National Park	dry	Brownian motion 2exp	-3689.8550	7385.7100	8.6180E-01	0.0469	0.6008	0.9970
African elephant	AM14	Pilanesberg National Park	dry	Brownian motion 3exp	-3689.8550	7389.7100	1.1660E-01	0.0469	0.6008	0.9970

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African elephant	AM14	Pilanesberg National Park	dry	Brownian motion 4exp	-3689.5460	7393.0910	2.1500E-02	0.0469	0.6008	0.9968
African elephant	AM14	Pilanesberg National Park	dry	Power law	-4019.9390	8041.8790	0.0000E+00	0.3396	2.20E-16	0.8327
African elephant	AM14	Pilanesberg National Park	dry	Truncated power law	-3851.6120	7705.2240	0.0000E+00	0.2758	0.0000	0.9227
African elephant	AM6	Pilanesberg National Park	dry	Brownian motion	-3668.4130	7.3388E+03	0.0000	0.0690	0.1669	0.9922
African elephant	AM6	Pilanesberg National Park	dry	Brownian motion 2exp	-3655.4270	7316.8540	2.0590E-01	0.0268	0.9919	0.9996
African elephant	AM6	Pilanesberg National Park	dry	Brownian motion 3exp	-3652.2020	7314.4050	7.0060E-01	0.0268	0.9919	0.9996
African elephant	AM6	Pilanesberg National Park	dry	Brownian motion 4exp	-3652.2170	7318.4340	9.3500E-02	0.0287	0.9824	0.9996
African elephant	AM6	Pilanesberg National Park	dry	Power law	-4014.9210	8031.8420	0.0000E+00	0.3295	2.20E-16	0.8626
African elephant	AM6	Pilanesberg National Park	dry	Truncated power law	-3826.1880	7654.3750	0.0000E+00	0.2893	0.0000	0.9371
African elephant	AM67	Kruger National Park	dry	Brownian motion	-3910.9780	7.8240E+03	0.0000	0.0984	0.0178	0.9898
African elephant	AM67	Kruger National Park	dry	Brownian motion 2exp	-3906.8300	7819.6610	0.0000E+00	0.0984	0.0178	0.9897
African elephant	AM67	Kruger National Park	dry	Brownian motion 3exp	-3829.4970	7668.9950	8.8090E-01	0.0697	0.1870	0.9982
African elephant	AM67	Kruger National Park	dry	Brownian motion 4exp	-3829.4980	7672.9960	1.1910E-01	0.0697	0.1870	0.9982
African elephant	AM67	Kruger National Park	dry	Power law	-4310.9890	8623.9780	0.0000E+00	0.3955	2.20E-16	0.8280
African elephant	AM67	Kruger National Park	dry	Truncated power law	-4176.8540	8355.7080	0.0000E+00	0.3361	0.0000	0.8868
African elephant	AM67	Kruger National Park	wet	Brownian motion	-4472.5960	8.9472E+03	0.0450	0.0551	0.4009	0.9963
African elephant	AM67	Kruger National Park	wet	Brownian motion 2exp	-4467.8510	8941.7030	7.0080E-01	0.0570	0.3592	0.9962
African elephant	AM67	Kruger National Park	wet	Brownian motion 3exp	-4466.9180	8943.8350	2.4130E-01	0.0532	0.4454	0.9957
African elephant	AM67	Kruger National Park	wet	Brownian motion 4exp	-4467.8510	8949.7030	1.2800E-02	0.0570	0.3592	0.9963
African elephant	AM67	Kruger National Park	wet	Power law	-5065.1040	10132.2080	0.0000E+00	0.4297	2.20E-16	0.8247
African elephant	AM67	Kruger National Park	wet	Truncated power law	-4834.1700	9670.3400	0.0000E+00	0.4829	0.0000	0.8841
African elephant	AM67b	Kruger National Park	dry	Brownian motion	-4713.0990	9.4282E+03	0.0000	0.0990	0.0058	0.9908
African elephant	AM67b	Kruger National Park	dry	Brownian motion 2exp	-4708.9430	9423.8860	0.0000E+00	0.0990	0.0058	0.9899
African elephant	AM67b	Kruger National Park	dry	Brownian motion 3exp	-4627.5820	9265.1650	9.0480E-01	0.0386	0.7665	0.9981
African elephant	AM67b	Kruger National Park	dry	Brownian motion 4exp	-4627.8340	9269.6680	9.5200E-02	0.0369	0.8155	0.9981
African elephant	AM67b	Kruger National Park	dry	Power law	-5139.2060	10280.4120	0.0000E+00	0.3792	2.20E-16	0.7431
African elephant	AM67b	Kruger National Park	dry	Truncated power law	-4974.2910	9950.5820	0.0000E+00	0.3238	0.0000	0.8368
African elephant	AM67b	Kruger National Park	wet	Brownian motion	-4675.5410	9.3531E+03	0.0185	0.0651	0.1686	0.9939
African elephant	AM67b	Kruger National Park	wet	Brownian motion 2exp	-4670.1960	9346.3930	5.2390E-01	0.0668	0.1478	0.9939
African elephant	AM67b	Kruger National Park	wet	Brownian motion 3exp	-4668.3980	9346.7970	4.2800E-01	0.0771	0.0624	0.9934
African elephant	AM67b	Kruger National Park	wet	Brownian motion 4exp	-4669.0690	9352.1390	2.9600E-02	0.0753	0.0727	0.9936
African elephant	AM67b	Kruger National Park	wet	Power law	-5208.0850	10418.1690	0.0000E+00	0.3921	2.20E-16	0.7479

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African elephant	AM67b	Kruger National Park	wet	Truncated power law	-4976.4170	9954.8350	0.0000E+00	0.3750	0.0000	0.8474
African elephant	AM67c	Kruger National Park	dry	Brownian motion	-4247.1310	8.4963E+03	0.1259	0.0667	0.1813	0.9935
African elephant	AM67c	Kruger National Park	dry	Brownian motion 2exp	-4243.3580	8492.7160	7.4150E-01	0.0667	0.1813	0.9934
African elephant	AM67c	Kruger National Park	dry	Brownian motion 3exp	-4243.2060	8496.4120	1.1680E-01	0.0667	0.1813	0.9933
African elephant	AM67c	Kruger National Park	dry	Brownian motion 4exp	-4243.2060	8500.4120	1.5800E-02	0.0667	0.1813	0.9933
African elephant	AM67c	Kruger National Park	dry	Power law	-4720.2310	9442.4610	0.0000E+00	0.3852	2.20E-16	0.7227
African elephant	AM67c	Kruger National Park	dry	Truncated power law	-4532.1980	9066.3950	0.0000E+00	0.3667	0.0000	0.8217
African elephant	AM67c	Kruger National Park	wet	Brownian motion	-4306.1040	8.6142E+03	0.1021	0.0565	0.3854	0.9978
African elephant	AM67c	Kruger National Park	wet	Brownian motion 2exp	-4302.0720	8610.1450	7.7840E-01	0.0585	0.3442	0.9978
African elephant	AM67c	Kruger National Park	wet	Brownian motion 3exp	-4302.0720	8614.1450	1.0540E-01	0.0585	0.3442	0.9978
African elephant	AM67c	Kruger National Park	wet	Brownian motion 4exp	-4302.0770	8618.1530	1.4200E-02	0.0585	0.3442	0.9978
African elephant	AM67c	Kruger National Park	wet	Power law	-4822.0040	9646.0080	0.0000E+00	0.4055	2.20E-16	0.7667
African elephant	AM67c	Kruger National Park	wet	Truncated power law	-4611.4240	9224.8480	0.0000E+00	0.4133	0.0000	0.8566
African elephant	AM67d	Kruger National Park	dry	Brownian motion	-4234.0450	8.4701E+03	0.1131	0.0613	0.2487	0.9976
African elephant	AM67d	Kruger National Park	dry	Brownian motion 2exp	-4230.1290	8466.2580	7.6880E-01	0.0613	0.2487	0.9976
African elephant	AM67d	Kruger National Park	dry	Brownian motion 3exp	-4230.1290	8470.2590	1.0400E-01	0.0613	0.2487	0.9976
African elephant	AM67d	Kruger National Park	dry	Brownian motion 4exp	-4230.1290	8474.2580	1.4100E-02	0.0613	0.2487	0.9976
African elephant	AM67d	Kruger National Park	dry	Power law	-4784.5850	9571.1710	0.0000E+00	0.3964	2.20E-16	0.7361
African elephant	AM67d	Kruger National Park	dry	Truncated power law	-4539.6810	9081.3620	0.0000E+00	0.4252	0.0000	0.8339
African elephant	AM90	Kruger National Park	dry	Brownian motion	-4043.1920	8.0884E+03	0.0000	0.0951	0.0156	0.9903
African elephant	AM90	Kruger National Park	dry	Brownian motion 2exp	-4040.9860	8087.9710	0.0000E+00	0.0951	0.0156	0.9901
African elephant	AM90	Kruger National Park	dry	Brownian motion 3exp	-4001.8700	8013.7400	5.6200E-01	0.0448	0.6558	0.9974
African elephant	AM90	Kruger National Park	dry	Brownian motion 4exp	-4000.1190	8014.2380	4.3800E-01	0.0466	0.6044	0.9974
African elephant	AM90	Kruger National Park	dry	Power law	-4458.8690	8919.7390	0.0000E+00	0.3731	2.20E-16	0.7685
African elephant	AM90	Kruger National Park	dry	Truncated power law	-4312.0060	8626.0130	0.0000E+00	0.3116	0.0000	0.8587
African elephant	AM90	Kruger National Park	wet	Brownian motion	-4238.3390	8.4787E+03	0.0000	0.0728	0.1010	0.9947
African elephant	AM90	Kruger National Park	wet	Brownian motion 2exp	-4235.9430	8477.8860	0.0000E+00	0.0728	0.1010	0.9942
African elephant	AM90	Kruger National Park	wet	Brownian motion 3exp	-4204.2430	8418.4860	8.0230E-01	0.0213	0.9995	0.9995
African elephant	AM90	Kruger National Park	wet	Brownian motion 4exp	-4203.6440	8421.2880	1.9770E-01	0.0213	0.9995	0.9995
African elephant	AM90	Kruger National Park	wet	Power law	-4645.5250	9293.0490	0.0000E+00	0.3552	2.20E-16	0.7857
African elephant	AM90	Kruger National Park	wet	Truncated power law	-4462.8990	8927.7970	0.0000E+00	0.3144	0.0000	0.8760
African elephant	AM92	Kruger National Park	dry	Brownian motion	-5170.2210	1.0342E+04	0.0000	0.0882	0.0084	0.9881

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African elephant	AM92	Kruger National Park	dry	Brownian motion 2exp	-5108.2080	10222.4200	6.3190E-01	0.0413	0.5880	0.9990
African elephant	AM92	Kruger National Park	dry	Brownian motion 3exp	-5108.2080	10226.4200	8.5500E-02	0.0413	0.5880	0.9990
African elephant	AM92	Kruger National Park	dry	Brownian motion 4exp	-5105.0120	10224.0200	2.8270E-01	0.0413	0.5880	0.9990
African elephant	AM92	Kruger National Park	dry	Power law	-5640.0640	11282.1300	0.0000E+00	0.3627	2.20E-16	0.8261
African elephant	AM92	Kruger National Park	dry	Truncated power law	-5415.5680	10833.1400	0.0000E+00	0.3129	0.0000	0.9020
Blue wildebeest	AG227	Welgevonden Game Reserve	wet	Brownian motion	-5239.7920	1.0482E+04	0.0000	0.3636	0.0000	0.7956
Blue wildebeest	AG227	Welgevonden Game Reserve	wet	Brownian motion 2exp	-4788.9770	9583.9530	0.0000E+00	0.0955	0.0049	0.9898
Blue wildebeest	AG227	Welgevonden Game Reserve	wet	Brownian motion 3exp	-4749.5070	9509.0140	8.8080E-01	0.0545	0.2799	0.9981
Blue wildebeest	AG227	Welgevonden Game Reserve	wet	Brownian motion 4exp	-4749.5070	9513.0140	1.1920E-01	0.0545	0.2799	0.9981
Blue wildebeest	AG227	Welgevonden Game Reserve	wet	Power law	-4941.7010	9885.4020	0.0000E+00	0.1924	4.87E-11	0.9377
Blue wildebeest	AG227	Welgevonden Game Reserve	wet	Truncated power law	-4808.6390	9619.2780	0.0000E+00	0.1030	0.0018	0.9800
Blue wildebeest	AG228	Welgevonden Game Reserve	dry	Brownian motion	-5657.7710	1.1318E+04	0.0000	0.1969	0.0000	0.9661
Blue wildebeest	AG228	Welgevonden Game Reserve	dry	Brownian motion 2exp	-5541.8490	11089.7000	0.0000E+00	0.0977	0.0024	0.9847
Blue wildebeest	AG228	Welgevonden Game Reserve	dry	Brownian motion 3exp	-5540.1220	11090.2400	0.0000E+00	0.0963	0.0029	0.9852
Blue wildebeest	AG228	Welgevonden Game Reserve	dry	Brownian motion 4exp	-5506.8210	11027.6400	1.0000E+00	0.0496	0.3508	0.9955
Blue wildebeest	AG228	Welgevonden Game Reserve	dry	Power law	-5887.3640	11776.7300	0.0000E+00	0.2762	2.20E-16	0.8577
Blue wildebeest	AG228	Welgevonden Game Reserve	dry	Truncated power law	-5663.7300	11329.4600	0.0000E+00	0.2323	0.0000	0.9323
Blue wildebeest	AG228	Welgevonden Game Reserve	wet	Brownian motion	-5166.5700	1.0335E+04	0.0000	0.3427	0.0000	0.8553
Blue wildebeest	AG228	Welgevonden Game Reserve	wet	Brownian motion 2exp	-4817.4400	9640.8810	0.0000E+00	0.0475	0.4331	0.9956
Blue wildebeest	AG228	Welgevonden Game Reserve	wet	Brownian motion 3exp	-4792.3520	9594.7050	7.1870E-01	0.0415	0.6060	0.9990
Blue wildebeest	AG228	Welgevonden Game Reserve	wet	Brownian motion 4exp	-4791.2910	9596.5810	2.8130E-01	0.0415	0.6060	0.9990
Blue wildebeest	AG228	Welgevonden Game Reserve	wet	Power law	-4980.9010	9963.8020	0.0000E+00	0.2047	1.07E-12	0.9426
Blue wildebeest	AG228	Welgevonden Game Reserve	wet	Truncated power law	-4809.5360	9621.0710	0.0000E+00	0.1172	0.0002	0.9871
Blue wildebeest	AG231	Welgevonden Game Reserve	dry	Brownian motion	-5628.2060	1.1258E+04	0.0000	0.4655	0.0000	0.7359
Blue wildebeest	AG231	Welgevonden Game Reserve	dry	Brownian motion 2exp	-5031.1830	10068.3700	0.0000E+00	0.0842	0.0195	0.9943
Blue wildebeest	AG231	Welgevonden Game Reserve	dry	Brownian motion 3exp	-4998.8200	10007.6400	8.8080E-01	0.0521	0.3389	0.9963
Blue wildebeest	AG231	Welgevonden Game Reserve	dry	Brownian motion 4exp	-4998.8200	10011.6400	1.1920E-01	0.0521	0.3389	0.9963
Blue wildebeest	AG231	Welgevonden Game Reserve	dry	Power law	-5196.2750	10394.5500	0.0000E+00	0.2251	8.55E-15	0.9273
Blue wildebeest	AG231	Welgevonden Game Reserve	dry	Truncated power law	-5037.2530	10076.5100	0.0000E+00	0.1424	0.0000	0.9676
Blue wildebeest	AG231	Welgevonden Game Reserve	wet	Brownian motion	-5759.7290	1.1521E+04	0.0000	0.4591	0.0000	0.7592
Blue wildebeest	AG231	Welgevonden Game Reserve	wet	Brownian motion 2exp	-5160.3340	10326.6700	0.0000E+00	0.0742	0.0526	0.9940
Blue wildebeest	AG231	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5143.4560	10296.9100	1.0000E-04	0.0561	0.2508	0.9968

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Blue wildebeest	AG231	Welgevonden Game Reserve	wet	Brownian motion 4exp	-5132.2180	10278.4400	9.9990E-01	0.0530	0.3114	0.9984
Blue wildebeest	AG231	Welgevonden Game Reserve	wet	Power law	-5336.1850	10674.3700	0.0000E+00	0.2136	1.66E-13	0.9482
Blue wildebeest	AG231	Welgevonden Game Reserve	wet	Truncated power law	-5164.3860	10330.7700	0.0000E+00	0.1409	0.0000	0.9819
Blue wildebeest	AG232	Welgevonden Game Reserve	dry	Brownian motion	-6152.8340	1.2308E+04	0.0000	0.4269	0.0000	0.7835
Blue wildebeest	AG232	Welgevonden Game Reserve	dry	Brownian motion 2exp	-5612.2470	11230.4900	0.0000E+00	0.0665	0.1004	0.9947
Blue wildebeest	AG232	Welgevonden Game Reserve	dry	Brownian motion 3exp	-5598.5150	11207.0300	8.8080E-01	0.0665	0.1004	0.9952
Blue wildebeest	AG232	Welgevonden Game Reserve	dry	Brownian motion 4exp	-5598.5150	11211.0300	1.1920E-01	0.0665	0.1004	0.9952
Blue wildebeest	AG232	Welgevonden Game Reserve	dry	Power law	-5895.2330	11792.4700	0.0000E+00	0.2482	2.20E-16	0.9447
Blue wildebeest	AG232	Welgevonden Game Reserve	dry	Truncated power law	-5671.5910	11345.1800	0.0000E+00	0.2201	0.0000	0.9788
Blue wildebeest	AG232	Welgevonden Game Reserve	wet	Brownian motion	-5406.7780	1.0816E+04	0.0000	0.2644	0.0000	0.9187
Blue wildebeest	AG232	Welgevonden Game Reserve	wet	Brownian motion 2exp	-5189.2510	10384.5000	1.0000E-04	0.0620	0.1477	0.9948
Blue wildebeest	AG232	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5178.2760	10366.5500	4.8580E-01	0.0591	0.1880	0.9967
Blue wildebeest	AG232	Welgevonden Game Reserve	wet	Brownian motion 4exp	-5176.2190	10366.4400	5.1410E-01	0.0591	0.1880	0.9966
Blue wildebeest	AG232	Welgevonden Game Reserve	wet	Power law	-5461.1490	10924.3000	0.0000E+00	0.2201	1.14E-14	0.9135
Blue wildebeest	AG232	Welgevonden Game Reserve	wet	Truncated power law	-5256.6530	10515.3100	0.0000E+00	0.1625	0.0000	0.9741
Blue wildebeest	AG233	Welgevonden Game Reserve	dry	Brownian motion	-6631.0430	1.3264E+04	0.0000	0.2607	0.0000	0.9081
Blue wildebeest	AG233	Welgevonden Game Reserve	dry	Brownian motion 2exp	-6403.4870	12812.9700	0.0000E+00	0.0566	0.1966	0.9952
Blue wildebeest	AG233	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6385.0330	12780.0700	7.4500E-01	0.0510	0.3016	0.9981
Blue wildebeest	AG233	Welgevonden Game Reserve	dry	Brownian motion 4exp	-6384.1050	12782.2100	2.5500E-01	0.0662	0.0833	0.9977
Blue wildebeest	AG233	Welgevonden Game Reserve	dry	Power law	-6832.5560	13667.1100	0.0000E+00	0.2979	2.20E-16	0.8673
Blue wildebeest	AG233	Welgevonden Game Reserve	dry	Truncated power law	-6546.4540	13094.9100	0.0000E+00	0.3200	0.0000	0.9322
Blue wildebeest	AG234	Welgevonden Game Reserve	dry	Brownian motion	-6604.5160	1.3221E+04	0.0000	0.2214	0.0000	0.9292
Blue wildebeest	AG234	Welgevonden Game Reserve	dry	Brownian motion 2exp	-6427.1830	12802.7700	0.0000E+00	0.0649	0.1011	0.9934
Blue wildebeest	AG234	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6396.3830	12804.6100	7.1550E-01	0.0494	0.3534	0.9964
Blue wildebeest	AG234	Welgevonden Game Reserve	dry	Brownian motion 4exp	-6395.3050	12804.6100	2.8450E-01	0.0494	0.3534	0.9963
Blue wildebeest	AG234	Welgevonden Game Reserve	dry	Power law	-6858.1000	13718.2000	0.0000E+00	0.2948	2.20E-16	0.8422
Blue wildebeest	AG234	Welgevonden Game Reserve	dry	Truncated power law	-6563.1530	13128.3100	0.0000E+00	0.3470	0.0000	0.9096
Blue wildebeest	AG235	Welgevonden Game Reserve	dry	Brownian motion	-3998.0190	7.9980E+03	0.0000	0.2117	0.0000	0.9527
Blue wildebeest	AG235	Welgevonden Game Reserve	dry	Brownian motion 2exp	-3808.2930	7622.5860	0.0000E+00	0.0757	0.0714	0.9967
Blue wildebeest	AG235	Welgevonden Game Reserve	dry	Brownian motion 3exp	-3791.5450	7593.0900	0.0000E+00	0.0448	0.6058	0.9964
Blue wildebeest	AG235	Welgevonden Game Reserve	dry	Brownian motion 4exp	-3778.6130	7571.2260	1.0000E+00	0.0396	0.7528	0.9969
Blue wildebeest	AG235	Welgevonden Game Reserve	dry	Power law	-4023.0150	8048.0310	0.0000E+00	0.2582	2.20E-16	0.8626

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Blue wildebeest	AG235	Welgevonden Game Reserve	dry	Truncated power law	-3945.6820	7893.3650	0.0000E+00	0.1721	0.0000	0.9224
Blue wildebeest	AG235	Welgevonden Game Reserve	wet	Brownian motion	-3880.6670	7.7633E+03	0.0078	0.0466	0.4870	0.9959
Blue wildebeest	AG235	Welgevonden Game Reserve	wet	Brownian motion 2exp	-3874.7370	7755.4740	3.9670E-01	0.0481	0.4446	0.9965
Blue wildebeest	AG235	Welgevonden Game Reserve	wet	Brownian motion 3exp	-3872.4580	7754.9150	5.2460E-01	0.0481	0.4446	0.9948
Blue wildebeest	AG235	Welgevonden Game Reserve	wet	Brownian motion 4exp	-3872.4580	7758.9160	7.1000E-02	0.0481	0.4446	0.9947
Blue wildebeest	AG235	Welgevonden Game Reserve	wet	Power law	-4212.4030	8426.8050	0.0000E+00	0.2702	2.20E-16	0.8368
Blue wildebeest	AG235	Welgevonden Game Reserve	wet	Truncated power law	-4010.1480	8022.2960	0.0000E+00	0.1910	0.0000	0.9292
Blue wildebeest	AG236	Welgevonden Game Reserve	dry	Brownian motion	-5218.8280	1.0440E+04	0.0000	0.2618	0.0000	0.9068
Blue wildebeest	AG236	Welgevonden Game Reserve	dry	Brownian motion 2exp	-4922.4450	9850.8900	0.0000E+00	0.0444	0.5185	0.9965
Blue wildebeest	AG236	Welgevonden Game Reserve	dry	Brownian motion 3exp	-4914.6530	9839.3070	0.0000E+00	0.0414	0.6078	0.9965
Blue wildebeest	AG236	Welgevonden Game Reserve	dry	Brownian motion 4exp	-4899.8190	9813.6390	1.0000E+00	0.0473	0.4350	0.9977
Blue wildebeest	AG236	Welgevonden Game Reserve	dry	Power law	-5283.7030	10569.4050	0.0000E+00	0.3166	2.20E-16	0.8049
Blue wildebeest	AG236	Welgevonden Game Reserve	dry	Truncated power law	-5113.7350	10229.4690	0.0000E+00	0.2367	0.0000	0.8901
Blue wildebeest	AG236	Welgevonden Game Reserve	wet	Brownian motion	-4290.9900	8.5840E+03	0.0000	0.0481	0.4456	0.9968
Blue wildebeest	AG236	Welgevonden Game Reserve	wet	Brownian motion 2exp	-4279.6440	8565.2890	8.5000E-03	0.0310	0.0000	0.9980
Blue wildebeest	AG236	Welgevonden Game Reserve	wet	Brownian motion 3exp	-4273.4890	8556.9770	5.4040E-01	0.0434	0.5777	0.9970
Blue wildebeest	AG236	Welgevonden Game Reserve	wet	Brownian motion 4exp	-4271.6690	8557.3380	4.5110E-01	0.0434	0.5777	0.9970
Blue wildebeest	AG236	Welgevonden Game Reserve	wet	Power law	-4683.7220	9369.4440	0.0000E+00	0.3039	2.20E-16	0.7999
Blue wildebeest	AG236	Welgevonden Game Reserve	wet	Truncated power law	-4499.1630	9000.3250	0.0000E+00	0.2233	0.0000	0.8986
Blue wildebeest	WIL16	Asante Sana Game Reserve	dry	Brownian motion	-4084.8750	8.1718E+03	0.0000	0.1108	0.0006	0.9966
Blue wildebeest	WIL16	Asante Sana Game Reserve	dry	Brownian motion 2exp	-3871.6330	7749.2660	0.0000E+00	0.0569	0.2299	0.9981
Blue wildebeest	WIL16	Asante Sana Game Reserve	dry	Brownian motion 3exp	-3830.3080	7670.6170	8.7550E-01	0.0524	0.3183	0.9957
Blue wildebeest	WIL16	Asante Sana Game Reserve	dry	Brownian motion 4exp	-3830.2590	7674.5190	1.2450E-01	0.0524	0.3183	0.9953
Blue wildebeest	WIL16	Asante Sana Game Reserve	dry	Power law	-4239.3740	8480.7480	0.0000E+00	0.256	2.20E-16	0.8270
Blue wildebeest	WIL16	Asante Sana Game Reserve	dry	Truncated power law	-4152.4320	8306.8640	0.0000E+00	0.1707	0.0000	0.8974
Blue wildebeest	WIL17	Asante Sana Game Reserve	dry	Brownian motion	-4018.1030	8.0382E+03	0.0000	0.1021	0.0021	0.9976
Blue wildebeest	WIL17	Asante Sana Game Reserve	dry	Brownian motion 2exp	-3841.8280	7689.6570	0.0000E+00	0.0549	0.2766	0.9985
Blue wildebeest	WIL17	Asante Sana Game Reserve	dry	Brownian motion 3exp	-3801.5350	7613.0710	3.6000E-03	0.0442	0.5431	0.9952
Blue wildebeest	WIL17	Asante Sana Game Reserve	dry	Brownian motion 4exp	-3793.9230	7601.8460	9.9640E-01	0.0412	0.6349	0.9958
Blue wildebeest	WIL17	Asante Sana Game Reserve	dry	Power law	-4190.0360	8382.0730	0.0000E+00	0.253	2.20E-16	0.8250
Blue wildebeest	WIL17	Asante Sana Game Reserve	dry	Truncated power law	-4101.2230	8204.4460	0.0000E+00	0.1662	0.0000	0.8990
Blue wildebeest	WIL17	Asante Sana Game Reserve	wet	Brownian motion	-4419.8990	8.8418E+03	0.0000	0.1043	0.0013	0.9902

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Blue wildebeest	WIL17	Asante Sana Game Reserve	wet	Brownian motion 2exp	-4400.0020	8806.0030	0.0000E+00	0.1058	0.0011	0.9881
Blue wildebeest	WIL17	Asante Sana Game Reserve	wet	Brownian motion 3exp	-4301.7210	8613.4410	8.8080E-01	0.0611	0.1632	0.9959
Blue wildebeest	WIL17	Asante Sana Game Reserve	wet	Brownian motion 4exp	-4301.7210	8617.4410	1.1920E-01	0.0611	0.1632	0.9959
Blue wildebeest	WIL17	Asante Sana Game Reserve	wet	Power law	-4648.8420	9299.6840	0.0000E+00	0.3085	2.20E-16	0.8023
Blue wildebeest	WIL17	Asante Sana Game Reserve	wet	Truncated power law	-4525.1680	9052.3350	0.0000E+00	0.1997	0.0000	0.8936
Blue wildebeest	WIL18	Asante Sana Game Reserve	dry	Brownian motion	-3969.7890	7.9416E+03	0.0000	0.1448	0.0000	0.9932
Blue wildebeest	WIL18	Asante Sana Game Reserve	dry	Brownian motion 2exp	-3812.7940	7631.5880	0.0000E+00	0.0806	0.0258	0.9952
Blue wildebeest	WIL18	Asante Sana Game Reserve	dry	Brownian motion 3exp	-3788.6280	7587.2560	0.0000E+00	0.0806	0.0258	0.9927
Blue wildebeest	WIL18	Asante Sana Game Reserve	dry	Brownian motion 4exp	-3612.8300	7239.6600	1.0000E+00	0.0687	0.0850	0.9917
Blue wildebeest	WIL18	Asante Sana Game Reserve	dry	Power law	-4088.3760	8178.7520	0.0000E+00	0.2388	2.20E-16	0.8404
Blue wildebeest	WIL18	Asante Sana Game Reserve	dry	Truncated power law	-4022.7870	8047.5740	0.0000E+00	0.1701	0.0000	0.8932
Blue wildebeest	WIL18	Asante Sana Game Reserve	wet	Brownian motion	-4160.8350	8.3237E+03	0.0000	0.1035	0.0018	0.9920
Blue wildebeest	WIL18	Asante Sana Game Reserve	wet	Brownian motion 2exp	-4111.6600	8229.3200	1.0000E+00	0.1005	0.0026	0.9912
Blue wildebeest	WIL18	Asante Sana Game Reserve	wet	Brownian motion 3exp	-4000.1600	8010.3210	1.0000E+00	0.0487	0.4169	0.9980
Blue wildebeest	WIL18	Asante Sana Game Reserve	wet	Brownian motion 4exp	-4045.6470	8105.2930	0.0000E+00	0.0365	0.7731	0.9977
Blue wildebeest	WIL18	Asante Sana Game Reserve	wet	Power law	-4340.8230	8683.6460	0.0000E+00	0.2922	2.20E-16	0.8367
Blue wildebeest	WIL18	Asante Sana Game Reserve	wet	Truncated power law	-4251.6430	8505.2870	0.0000E+00	0.2055	0.0000	0.9050
Blue wildebeest	WIL19	Asante Sana Game Reserve	dry	Brownian motion	-4095.7550	8.1935E+03	0.0000	0.0925	0.0064	0.9978
Blue wildebeest	WIL19	Asante Sana Game Reserve	dry	Brownian motion 2exp	-4030.3270	8066.6530	0.0000E+00	0.0478	0.4294	0.9984
Blue wildebeest	WIL19	Asante Sana Game Reserve	dry	Brownian motion 3exp	-3902.5210	7815.0420	2.0040E-01	0.0463	0.4701	0.9974
Blue wildebeest	WIL19	Asante Sana Game Reserve	dry	Brownian motion 4exp	-3899.1370	7812.2740	7.9960E-01	0.0373	0.7394	0.9975
Blue wildebeest	WIL19	Asante Sana Game Reserve	dry	Power law	-4265.5770	8533.1530	0.0000E+00	0.2493	2.20E-16	0.8394
Blue wildebeest	WIL19	Asante Sana Game Reserve	dry	Truncated power law	-4176.5210	8355.0420	0.0000E+00	0.1627	0.0000	0.9101
Blue wildebeest	WIL19	Asante Sana Game Reserve	wet	Brownian motion	-3798.9180	7.5998E+03	0.0000	0.1296	0.0001	0.9817
Blue wildebeest	WIL19	Asante Sana Game Reserve	wet	Brownian motion 2exp	-3732.5120	7471.0240	0.0000E+00	0.1243	0.0003	0.9800
Blue wildebeest	WIL19	Asante Sana Game Reserve	wet	Brownian motion 3exp	-3635.1230	7280.2460	8.8320E-01	0.0560	0.3313	0.9965
Blue wildebeest	WIL19	Asante Sana Game Reserve	wet	Brownian motion 4exp	-3635.1460	7284.2920	1.1680E-01	0.0560	0.3313	0.9965
Blue wildebeest	WIL19	Asante Sana Game Reserve	wet	Power law	-3968.5190	7939.0380	0.0000E+00	0.303	2.20E-16	0.8057
Blue wildebeest	WIL19	Asante Sana Game Reserve	wet	Truncated power law	-3862.9420	7727.8850	0.0000E+00	0.1961	0.0000	0.8974
Blue wildebeest	WIL20	Asante Sana Game Reserve	dry	Brownian motion	-4106.0900	8.2142E+03	0.0000	0.1174	0.0002	0.9965
Blue wildebeest	WIL20	Asante Sana Game Reserve	dry	Brownian motion 2exp	-3859.6630	7725.3270	0.0000E+00	0.0565	0.2336	0.9983
Blue wildebeest	WIL20	Asante Sana Game Reserve	dry	Brownian motion 3exp	-3817.3230	7644.6470	8.8640E-01	0.0550	0.2610	0.9959

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Blue wildebeest	WIL20	Asante Sana Game Reserve	dry	Brownian motion 4exp	-3817.3780	7648.7560	1.1360E-01	0.0550	0.2610	0.9958
Blue wildebeest	WIL20	Asante Sana Game Reserve	dry	Power law	-4249.1970	8500.3940	0.0000E+00	0.2437	2.20E-16	0.8374
Blue wildebeest	WIL20	Asante Sana Game Reserve	dry	Truncated power law	-4165.8630	8333.7270	0.0000E+00	0.1620	0.0000	0.9037
Blue wildebeest	WIL5	Mapungubwe National Park	dry	Brownian motion	-4937.4440	9.8769E+03	0.0000	0.1431	0.0000	0.9820
Blue wildebeest	WIL5	Mapungubwe National Park	dry	Brownian motion 2exp	-4814.5660	9635.1310	0.0000E+00	0.0912	0.0053	0.9858
Blue wildebeest	WIL5	Mapungubwe National Park	dry	Brownian motion 3exp	-4767.3700	9544.7400	1.5000E-03	0.0449	0.4693	0.9987
Blue wildebeest	WIL5	Mapungubwe National Park	dry	Brownian motion 4exp	-4758.8620	9531.7250	9.9850E-01	0.0351	0.7731	0.9991
Blue wildebeest	WIL5	Mapungubwe National Park	dry	Power law	-5043.3780	10088.7570	0.0000E+00	0.244	2.20E-16	0.8568
Blue wildebeest	WIL5	Mapungubwe National Park	dry	Truncated power law	-4892.7630	9787.5260	0.0000E+00	0.1248	0.0000	0.9543
Blue wildebeest	WIL5	Mapungubwe National Park	wet	Brownian motion	-4728.0110	9.4580E+03	0.0000	0.0877	0.0104	0.9868
Blue wildebeest	WIL5	Mapungubwe National Park	wet	Brownian motion 2exp	-4679.7820	9365.5650	0.0000E+00	0.0848	0.0146	0.9860
Blue wildebeest	WIL5	Mapungubwe National Park	wet	Brownian motion 3exp	-4665.3960	9340.7920	4.8030E-01	0.0468	0.4426	0.9957
Blue wildebeest	WIL5	Mapungubwe National Park	wet	Brownian motion 4exp	-4663.3170	9340.6350	5.1970E-01	0.0512	0.3321	0.9957
Blue wildebeest	WIL5	Mapungubwe National Park	wet	Power law	-5071.0500	10144.1010	0.0000E+00	0.3114	2.20E-16	0.8090
Blue wildebeest	WIL5	Mapungubwe National Park	wet	Truncated power law	-4843.2150	9688.4300	0.0000E+00	0.2442	0.0000	0.9213
Blue wildebeest	WIL6	Mapungubwe National Park	dry	Brownian motion	-4831.1360	9.6643E+03	0.0000	0.1408	0.0000	0.9791
Blue wildebeest	WIL6	Mapungubwe National Park	dry	Brownian motion 2exp	-4747.4780	9500.9560	0.0000E+00	0.1221	0.0001	0.9780
Blue wildebeest	WIL6	Mapungubwe National Park	dry	Brownian motion 3exp	-4700.8150	9411.6310	0.0000E+00	0.0302	0.9093	0.9994
Blue wildebeest	WIL6	Mapungubwe National Park	dry	Brownian motion 4exp	-4659.1050	9332.2100	1.0000E+00	0.0287	0.9361	0.9994
Blue wildebeest	WIL6	Mapungubwe National Park	dry	Power law	-4998.5540	9999.1090	0.0000E+00	0.25	2.20E-16	0.8569
Blue wildebeest	WIL6	Mapungubwe National Park	dry	Truncated power law	-4836.6210	9675.2430	0.0000E+00	0.1351	0.0000	0.9569
Blue wildebeest	WIL7	Mapungubwe National Park	dry	Brownian motion	-4878.9860	9.7600E+03	0.0000	0.1507	0.0000	0.9773
Blue wildebeest	WIL7	Mapungubwe National Park	dry	Brownian motion 2exp	-4734.9260	9475.8520	0.0000E+00	0.1113	0.0003	0.9787
Blue wildebeest	WIL7	Mapungubwe National Park	dry	Brownian motion 3exp	-4688.8710	9387.7430	6.5470E-01	0.0451	0.4665	0.9988
Blue wildebeest	WIL7	Mapungubwe National Park	dry	Brownian motion 4exp	-4687.5110	9389.0230	3.4530E-01	0.0451	0.4665	0.9991
Blue wildebeest	WIL7	Mapungubwe National Park	dry	Power law	-4975.3640	9952.7280	0.0000E+00	0.2211	1.67E-15	0.8762
Blue wildebeest	WIL7	Mapungubwe National Park	dry	Truncated power law	-4808.1950	9618.3910	0.0000E+00	0.1056	0.0007	0.9700
Blue wildebeest	WIL7	Mapungubwe National Park	wet	Brownian motion	-4335.4970	8.6730E+03	0.0000	0.0568	0.2182	0.9957
Blue wildebeest	WIL7	Mapungubwe National Park	wet	Brownian motion 2exp	-4309.6220	8625.2440	2.0000E-04	0.0553	0.2440	0.9953
Blue wildebeest	WIL7	Mapungubwe National Park	wet	Brownian motion 3exp	-4299.3220	8608.6440	8.6500E-01	0.0466	0.4454	0.9976
Blue wildebeest	WIL7	Mapungubwe National Park	wet	Brownian motion 4exp	-4299.1810	8612.3620	1.3480E-01	0.0422	0.5731	0.9977
Blue wildebeest	WIL7	Mapungubwe National Park	wet	Power law	-4636.5110	9275.0230	0.0000E+00	0.2897	2.20E-16	0.8488

Species	ID	Property	Season	Model	MLL	AIC	AIC Weight	KS-D	KS p-value	R ²
Blue wildebeest	WIL7	Mapungubwe National Park	wet	Truncated power law	-4446.7130	8895.4250	0.0000E+00	0.1849	0.0000	0.9451
Blue wildebeest	WIL8	Mapungubwe National Park	dry	Brownian motion	-4760.7390	9.5235E+03	0.0000	0.1695	0.0000	0.9708
Blue wildebeest	WIL8	Mapungubwe National Park	dry	Brownian motion 2exp	-4664.2150	9334.4310	0.0000E+00	0.0678	0.0772	0.9959
Blue wildebeest	WIL8	Mapungubwe National Park	dry	Brownian motion 3exp	-4522.6590	9055.3180	3.7700E-02	0.0523	0.2884	0.9988
Blue wildebeest	WIL8	Mapungubwe National Park	dry	Brownian motion 4exp	-4517.4190	9048.8390	9.6230E-01	0.0367	0.7263	0.9992
Blue wildebeest	WIL8	Mapungubwe National Park	dry	Power law	-4830.1270	9662.2550	0.0000E+00	0.2147	1.34E-14	0.8926
Blue wildebeest	WIL8	Mapungubwe National Park	dry	Truncated power law	-4691.3400	9384.6800	0.0000E+00	0.1017	0.0013	0.9728
Blue wildebeest	WIL8	Mapungubwe National Park	wet	Brownian motion	-4312.5190	8.6270E+03	0.0000	0.0598	0.1724	0.9957
Blue wildebeest	WIL8	Mapungubwe National Park	wet	Brownian motion 2exp	-4251.2410	8508.4830	1.5000E-03	0.0627	0.1350	0.9952
Blue wildebeest	WIL8	Mapungubwe National Park	wet	Brownian motion 3exp	-4242.8470	8495.6930	8.8180E-01	0.0569	0.2175	0.9944
Blue wildebeest	WIL8	Mapungubwe National Park	wet	Brownian motion 4exp	-4242.8690	8499.7380	1.1670E-01	0.0569	0.2175	0.9946
Blue wildebeest	WIL8	Mapungubwe National Park	wet	Power law	-4612.5940	9227.1870	0.0000E+00	0.2843	2.20E-16	0.8169
Blue wildebeest	WIL8	Mapungubwe National Park	wet	Truncated power law	-4438.8660	8879.7330	0.0000E+00	0.1706	0.0000	0.9266
Blue wildebeest	WIL9	Mapungubwe National Park	dry	Brownian motion	-4902.9660	9.8079E+03	0.0000	0.1190	0.0001	0.9848
Blue wildebeest	WIL9	Mapungubwe National Park	dry	Brownian motion 2exp	-4736.9340	9479.8680	0.0000E+00	0.1006	0.0016	0.9842
Blue wildebeest	WIL9	Mapungubwe National Park	dry	Brownian motion 3exp	-4692.0780	9394.1550	4.0500E-01	0.0411	0.5907	0.9974
Blue wildebeest	WIL9	Mapungubwe National Park	dry	Brownian motion 4exp	-4689.6930	9393.3860	5.9500E-01	0.0397	0.6353	0.9976
Blue wildebeest	WIL9	Mapungubwe National Park	dry	Power law	-5058.4250	10118.8510	0.0000E+00	0.2422	2.20E-16	0.8453
Blue wildebeest	WIL9	Mapungubwe National Park	dry	Truncated power law	-4895.9610	9793.9220	0.0000E+00	0.1275	0.0000	0.9480
Blue wildebeest	WIL9	Mapungubwe National Park	wet	Brownian motion	-4698.7190	9.3994E+03	0.0000	0.0781	0.0294	0.9889
Blue wildebeest	WIL9	Mapungubwe National Park	wet	Brownian motion 2exp	-4681.3420	9368.6850	2.0000E-04	0.0753	0.0400	0.9876
Blue wildebeest	WIL9	Mapungubwe National Park	wet	Brownian motion 3exp	-4670.8980	9351.7950	8.8070E-01	0.0593	0.1755	0.9951
Blue wildebeest	WIL9	Mapungubwe National Park	wet	Brownian motion 4exp	-4670.8980	9355.7960	1.1910E-01	0.0593	0.1755	0.9951
Blue wildebeest	WIL9	Mapungubwe National Park	wet	Power law	-5066.3590	10134.7170	0.0000E+00	0.3271	2.20E-16	0.8049
Blue wildebeest	WIL9	Mapungubwe National Park	wet	Truncated power law	-4841.2080	9684.4160	0.0000E+00	0.2504	0.0000	0.9171
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	dry	Brownian motion	-4726.3820	9.4548E+03	0.2740	0.0515	0.3120	0.9965
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	dry	Brownian motion 2exp	-4725.9830	9457.9650	5.5300E-02	0.0515	0.3120	0.9964
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	dry	Brownian motion 3exp	-4722.5640	9455.1280	2.2840E-01	0.0229	0.9931	0.9991
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	dry	Brownian motion 4exp	-4719.9030	9453.8070	4.4230E-01	0.0215	0.9971	0.9991
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	dry	Power law	-5183.0450	10368.0900	0.0000E+00	0.3233	2.20E-16	0.8466
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	dry	Truncated power law	-4922.7930	9847.5870	0.0000E+00	0.2790	0.0000	0.9349

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Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	wet	Brownian motion	-4687.2290	9.3765E+03	0.0000	0.0631	0.1097	0.9936
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	wet	Brownian motion 2exp	-4681.1580	9368.3170	1.0000E-04	0.0631	0.1097	0.9935
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	wet	Brownian motion 3exp	-4669.4730	9348.9470	9.9950E-01	0.0261	0.9655	0.9993
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	wet	Brownian motion 4exp	-4675.1130	9364.2260	5.0000E-04	0.0247	0.9794	0.9993
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	wet	Power law	-5099.6800	10201.3600	0.0000E+00	0.3045	2.20E-16	0.8707
Cape mountain zebra	AG442	Baviaanskloof Nature Reserve	wet	Truncated power law	-4841.3310	9684.6620	0.0000E+00	0.2455	0.0000	0.9508
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	dry	Brownian motion	-4179.1990	8.3604E+03	0.0000	0.0872	0.0214	0.9881
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	dry	Brownian motion 2exp	-4163.2940	8332.5880	4.4100E-02	0.0252	0.9916	0.9989
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	dry	Brownian motion 3exp	-4163.2940	8336.5880	6.0000E-03	0.0252	0.9916	0.9989
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	dry	Brownian motion 4exp	-4156.2240	8326.4490	9.4990E-01	0.0268	0.9827	0.9988
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	dry	Power law	-4548.8570	9099.7140	0.0000E+00	0.3272	2.20E-16	0.8368
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	dry	Truncated power law	-4325.7930	8653.5870	0.0000E+00	0.2903	0.0000	0.9989
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	wet	Brownian motion	-4786.6560	9.5753E+03	0.0000	0.1397	0.0000	0.9706
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	wet	Brownian motion 2exp	-4716.0180	9438.0350	1.9610E-01	0.0260	0.9657	0.9991
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	wet	Brownian motion 3exp	-4716.0180	9442.0350	2.6500E-02	0.0260	0.9657	0.9991
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	wet	Brownian motion 4exp	-4710.6410	9435.2810	7.7730E-01	0.0342	0.7854	0.9992
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	wet	Power law	-5087.7660	10177.5320	0.0000E+00	0.2973	2.20E-16	0.8750
Cape mountain zebra	AG443	Baviaanskloof Nature Reserve	wet	Truncated power law	-4896.8940	9795.7870	0.0000E+00	0.2014	0.0000	0.9492
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	dry	Brownian motion	-4814.3340	9.6307E+03	0.0000	0.0912	0.0045	0.9853
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	dry	Brownian motion 2exp	-4786.9570	9579.9150	4.0110E-01	0.0381	0.6604	0.9987
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	dry	Brownian motion 3exp	4784.5690	9579.1380	5.9150E-01	0.0381	0.6604	0.9986
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	dry	Brownian motion 4exp	-4786.9570	9587.9150	7.3000E-03	0.0381	0.6604	0.9987
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	dry	Power law	-5229.8660	10461.7330	0.0000E+00	0.3211	2.20E-16	0.8812
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	dry	Truncated power law	-4989.1830	9980.3660	0.0000E+00	0.2503	0.0000	0.9499
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	wet	Brownian motion	-4492.7150	8.9874E+03	0.3645	0.0591	0.1773	0.9922
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	wet	Brownian motion 2exp	-4491.2930	8988.5860	2.0460E-01	0.0576	0.1992	0.9919
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	wet	Brownian motion 3exp	-4488.6750	8987.3500	3.7960E-01	0.0519	0.3079	0.9955
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	wet	Brownian motion 4exp	-4488.6750	8991.3500	5.1400E-02	0.0519	0.3079	0.9955
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	wet	Power law	-4911.4410	9824.8810	0.0000E+00	0.3271	2.20E-16	0.8392
Cape mountain zebra	AG444	Baviaanskloof Nature Reserve	wet	Truncated power law	-4461.1470	9324.2950	0.0000E+00	0.2666	0.0000	0.9353

Species	ID	Property	Season	Model	MLL	AIC	AIC Weight	KS-D	KS p-value	R ²
zebra										
Eland	AU073	Mkambati Nature Reserve	dry	Brownian motion	-5278.3190	1.0559E+04	0.0001	0.0515	0.2970	0.9973
Eland	AU073	Mkambati Nature Reserve	dry	Brownian motion 2exp	-5275.6940	10557.3900	1.0000E-04	0.0459	0.4351	0.9970
Eland	AU073	Mkambati Nature Reserve	dry	Brownian motion 3exp	-5264.7970	10539.5900	8.8060E-01	0.0167	1.0000	0.9995
Eland	AU073	Mkambati Nature Reserve	dry	Brownian motion 3exp	-5264.7970	10543.5900	1.1920E-01	0.0167	1.0000	0.9995
Eland	AU073	Mkambati Nature Reserve	dry	Power law	-5819.8780	11641.7600	0.0000E+00	0.3505	2.20E-16	0.7954
Eland	AU073	Mkambati Nature Reserve	dry	Truncated power law	-5549.8300	11101.6600	0.0000E+00	0.3282	0.0000	0.8892
Eland	AU073	Mkambati Nature Reserve	wet	Brownian motion	-4779.0900	9.5602E+03	0.8650	0.0362	0.7556	0.9988
Eland	AU073	Mkambati Nature Reserve	wet	Brownian motion 2exp	-4779.0900	9564.1800	1.1710E-01	0.0362	0.7556	0.9988
Eland	AU073	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4779.0900	9568.1800	1.5800E-02	0.0362	0.7556	0.9988
Eland	AU073	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4779.0900	9572.1800	2.1000E-03	0.0362	0.7556	0.9988
Eland	AU073	Mkambati Nature Reserve	wet	Power law	-5337.4810	10676.9600	0.0000E+00	0.3565	2.20E-16	0.8025
Eland	AU073	Mkambati Nature Reserve	wet	Truncated power law	-5056.5800	10115.1600	0.0000E+00	0.3391	0.0000	0.8924
Eland	EL10	Mapungubwe National Park	dry	Brownian motion	-5013.8870	1.0030E+04	0.0000	0.0847	0.0105	0.9909
Eland	EL10	Mapungubwe National Park	dry	Brownian motion 2exp	-4973.2860	9952.5720	0.0000E+00	0.0820	0.0146	0.9905
Eland	EL10	Mapungubwe National Park	dry	Brownian motion 3exp	-4995.6030	10001.2060	0.0000E+00	0.0178	0.9998	0.9994
Eland	EL10	Mapungubwe National Park	dry	Brownian motion 3exp	-4957.9420	9929.8830	1.0000E+00	0.0246	0.9798	0.9992
Eland	EL10	Mapungubwe National Park	dry	Power law	-5358.9460	10719.8930	0.0000E+00	0.2855	2.20E-16	0.8543
Eland	EL10	Mapungubwe National Park	dry	Truncated power law	-5126.6150	10255.2300	0.0000E+00	0.2063	0.0000	0.9505
Eland	EL11	Mapungubwe National Park	dry	Brownian motion	-4720.6450	9.4433E+03	0.0000	0.0552	0.2447	0.9969
Eland	EL11	Mapungubwe National Park	dry	Brownian motion 2exp	-4717.0070	9440.0150	0.0000E+00	0.0305	0.9057	0.9988
Eland	EL11	Mapungubwe National Park	dry	Brownian motion 3exp	-4717.0070	9444.0150	0.0000E+00	0.0305	0.9057	0.9988
Eland	EL11	Mapungubwe National Park	dry	Brownian motion 3exp	-4688.0690	9390.1370	1.0000E+00	0.0305	0.9057	0.9986
Eland	EL11	Mapungubwe National Park	dry	Power law	-5134.2370	10270.4750	0.0000E+00	0.3096	2.20E-16	0.8455
Eland	EL11	Mapungubwe National Park	dry	Truncated power law	-4915.4160	9832.8320	0.0000E+00	0.2326	0.0000	0.9381
Eland	EL11	Mapungubwe National Park	wet	Brownian motion	-3941.9880	7.8860E+03	0.0000	0.0500	0.4858	0.9973
Eland	EL11	Mapungubwe National Park	wet	Brownian motion 2exp	-3931.0690	7868.1370	0.0000E+00	0.0375	0.8259	0.9989
Eland	EL11	Mapungubwe National Park	wet	Brownian motion 3exp	-3905.5500	7821.0990	8.8290E-01	0.0411	0.7323	0.9989
Eland	EL11	Mapungubwe National Park	wet	Brownian motion 3exp	-3905.5700	7825.1400	1.1710E-01	0.0375	0.8259	0.9989
Eland	EL11	Mapungubwe National Park	wet	Power law	-4274.1620	8550.3240	0.0000E+00	0.3161	2.20E-16	0.8146
Eland	EL11	Mapungubwe National Park	wet	Truncated power law	-4101.9630	8205.9260	0.0000E+00	0.2411	0.0000	0.9146
Eland	EL12	Mapungubwe National Park	dry	Brownian motion	-5136.6120	1.0275E+04	0.0000	0.0564	0.1979	0.9965

Species	ID	Property	Season	Model	MLL	AIC	AIC Weight	KS-D	KS p-value	R ²
Eland	EL12	Mapungubwe National Park	dry	Brownian motion 2exp	-5054.9270	10115.8500	2.8540E-01	0.0495	0.3348	0.9961
Eland	EL12	Mapungubwe National Park	dry	Brownian motion 3exp	-5054.7600	10119.5200	4.5600E-02	0.0481	0.3685	0.9960
Eland	EL12	Mapungubwe National Park	dry	Brownian motion 3exp	-5050.0750	10114.1500	6.6900E-01	0.0206	0.9978	0.9992
Eland	EL12	Mapungubwe National Park	dry	Power law	-5535.8960	11073.7900	0.0000E+00	0.304	2.20E-16	0.8025
Eland	EL12	Mapungubwe National Park	dry	Truncated power law	-5293.0810	10588.1600	0.0000E+00	0.2366	0.0000	0.9161
Eland	EL12	Mapungubwe National Park	wet	Brownian motion	-4812.5730	9.6271E+03	0.0000	0.0433	0.5347	0.9981
Eland	EL12	Mapungubwe National Park	wet	Brownian motion 2exp	-4770.5510	9547.1010	1.4550E-01	0.0404	0.6236	0.9979
Eland	EL12	Mapungubwe National Park	wet	Brownian motion 3exp	-4766.8440	9543.6880	8.0170E-01	0.0202	0.9989	0.9994
Eland	EL12	Mapungubwe National Park	wet	Brownian motion 3exp	-4767.5630	9549.1260	5.2900E-02	0.0216	0.9969	0.9993
Eland	EL12	Mapungubwe National Park	wet	Power law	-5201.3410	10404.6810	0.0000E+00	0.3001	2.20E-16	0.8097
Eland	EL12	Mapungubwe National Park	wet	Truncated power law	-4983.5670	9969.1350	0.0000E+00	0.2237	0.0000	0.9192
Eland	EL22	Asante Sana Game Reserve	dry	Brownian motion	-4700.1860	9.4024E+03	0.0000	0.1427	0.0000	0.9798
Eland	EL22	Asante Sana Game Reserve	dry	Brownian motion 2exp	-4652.9500	9311.8990	0.0000E+00	0.1259	0.0000	0.9777
Eland	EL22	Asante Sana Game Reserve	dry	Brownian motion 3exp	-4508.2610	9026.5230	8.7810E-01	0.0308	0.8875	0.9990
Eland	EL22	Asante Sana Game Reserve	dry	Brownian motion 3exp	-4508.2360	9030.4720	1.2190E-01	0.0308	0.8875	0.9990
Eland	EL22	Asante Sana Game Reserve	dry	Power law	-4832.5250	9667.0500	0.0000E+00	0.2517	2.20E-16	0.8635
Eland	EL22	Asante Sana Game Reserve	dry	Truncated power law	-4722.0520	9446.1040	0.0000E+00	0.1580	0.0000	0.9376
Eland	EL22	Asante Sana Game Reserve	wet	Brownian motion	-3511.1330	7.0243E+03	0.0000	0.0519	0.4849	0.9968
Eland	EL22	Asante Sana Game Reserve	wet	Brownian motion 2exp	-3459.6880	6925.3750	6.0000E-04	0.0519	0.4849	0.9962
Eland	EL22	Asante Sana Game Reserve	wet	Brownian motion 3exp	-3450.3910	6910.7820	8.7290E-01	0.0327	0.9439	0.9990
Eland	EL22	Asante Sana Game Reserve	wet	Brownian motion 3exp	-3450.3230	6914.6460	1.2650E-01	0.0327	0.9439	0.9990
Eland	EL22	Asante Sana Game Reserve	wet	Power law	-3771.5850	7545.1690	0.0000E+00	0.3077	2.20E-16	0.7954
Eland	EL22	Asante Sana Game Reserve	wet	Truncated power law	-3620.6060	7243.2120	0.0000E+00	0.2192	0.0000	0.9114
Eland	EL23	Asante Sana Game Reserve	dry	Brownian motion	-4388.2520	8.7785E+03	0.0000	0.1215	0.0001	0.9829
Eland	EL23	Asante Sana Game Reserve	dry	Brownian motion 2exp	-4268.9460	8543.8920	0.0000E+00	0.1201	0.0001	0.9809
Eland	EL23	Asante Sana Game Reserve	dry	Brownian motion 3exp	-4307.7410	8625.4810	0.0000E+00	0.0367	0.7263	0.9987
Eland	EL23	Asante Sana Game Reserve	dry	Brownian motion 3exp	-4197.4580	8408.9160	1.0000E+00	0.0395	0.6371	0.9989
Eland	EL23	Asante Sana Game Reserve	dry	Power law	-4537.4040	9076.8070	0.0000E+00	0.2444	0.0000	0.8710
Eland	EL23	Asante Sana Game Reserve	dry	Truncated power law	-4454.9270	8911.8530	0.0000E+00	0.1723	0.0000	0.9304
Eland	EL24	Asante Sana Game Reserve	dry	Brownian motion	-4577.0690	9.1561E+03	0.0000	0.2475	0.0000	0.9369
Eland	EL24	Asante Sana Game Reserve	dry	Brownian motion 2exp	-4383.6340	8773.2680	0.0000E+00	0.0811	0.0197	0.9946
Eland	EL24	Asante Sana Game Reserve	dry	Brownian motion 3exp	-4355.8860	8721.7720	0.0000E+00	0.0626	0.1273	0.9977

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Eland	EL24	Asante Sana Game Reserve	dry	Brownian motion 3exp	-4256.0930	8526.1860	1.0000E+00	0.0526	0.2845	0.9973
Eland	EL24	Asante Sana Game Reserve	dry	Power law	-4462.1170	8926.2340	0.0000E+00	0.1679	0.0000	0.9409
Eland	EL24	Asante Sana Game Reserve	dry	Truncated power law	-4391.0700	8784.1410	0.0000E+00	0.0996	0.0019	0.9781
Eland	EL25	Asante Sana Game Reserve	dry	Brownian motion	-4590.4400	9.1829E+03	0.0000	0.1182	0.0001	0.9833
Eland	EL25	Asante Sana Game Reserve	dry	Brownian motion 2exp	-4511.1560	9028.3110	0.0000E+00	0.0348	0.7775	0.9995
Eland	EL25	Asante Sana Game Reserve	dry	Brownian motion 3exp	-4446.0310	8902.0620	5.1280E-01	0.0250	0.9779	0.9992
Eland	EL25	Asante Sana Game Reserve	dry	Brownian motion 3exp	-4444.0830	8902.1650	4.8720E-01	0.0223	0.9942	0.9996
Eland	EL25	Asante Sana Game Reserve	dry	Power law	-4767.7100	9537.4200	0.0000E+00	0.2531	0.0000	0.8731
Eland	EL25	Asante Sana Game Reserve	dry	Truncated power law	-4663.2420	9328.4830	0.0000E+00	0.1613	0.0000	0.9392
Eland	EL25	Asante Sana Game Reserve	wet	Brownian motion	-2039.3640	4.0807E+03	0.0000	0.0446	0.8912	0.9927
Eland	EL25	Asante Sana Game Reserve	wet	Brownian motion 2exp	-2002.8300	4011.6610	8.6260E-01	0.0536	0.7206	0.9922
Eland	EL25	Asante Sana Game Reserve	wet	Brownian motion 3exp	-2002.8310	4015.6620	1.1670E-01	0.0536	0.7206	0.9922
Eland	EL25	Asante Sana Game Reserve	wet	Brownian motion 3exp	-2002.5580	4019.1150	2.0800E-02	0.0625	0.5278	0.9920
Eland	EL25	Asante Sana Game Reserve	wet	Power law	-2197.3750	4396.7490	0.0000E+00	0.2976	0.0000	0.8097
Eland	EL25	Asante Sana Game Reserve	wet	Truncated power law	-2091.8720	4185.7440	0.0000E+00	0.2083	0.0000	0.9226
Eland	SAT64	Mkambati Nature Reserve	dry	Brownian motion	-4037.2530	8.0765E+03	0.6371	0.0322	0.9340	0.9980
Eland	SAT64	Mkambati Nature Reserve	dry	Brownian motion 2exp	-4036.3640	8078.7280	2.0970E-01	0.0340	0.9033	0.9980
Eland	SAT64	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4036.2580	8082.5160	3.1600E-02	0.0376	0.8251	0.9979
Eland	SAT64	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4032.9090	8079.8180	1.2160E-01	0.0376	0.8251	0.9979
Eland	SAT64	Mkambati Nature Reserve	dry	Power law	-4485.7610	8973.5210	0.0000E+00	0.3470	0.0000	0.7929
Eland	SAT64	Mkambati Nature Reserve	dry	Truncated power law	-4256.3280	8514.6560	0.0000E+00	0.3417	0.0000	0.8822
Eland	SAT65	Mkambati Nature Reserve	dry	Brownian motion	-4440.4610	8.8829E+03	0.4082	0.0410	0.6849	0.9981
Eland	SAT65	Mkambati Nature Reserve	dry	Brownian motion 2exp	-4439.6460	8885.2920	1.2480E-01	0.0459	0.5415	0.9980
Eland	SAT65	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4437.9380	8885.8770	9.3200E-02	0.0443	0.5886	0.9981
Eland	SAT65	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4434.5490	8883.0990	3.7380E-01	0.0459	0.5415	0.9981
Eland	SAT65	Mkambati Nature Reserve	dry	Power law	-4963.1540	9928.3070	0.0000E+00	0.3803	0.0000	0.7543
Eland	SAT65	Mkambati Nature Reserve	dry	Truncated power law	-4734.3600	9470.7200	0.0000E+00	0.3541	0.0000	0.8575
Eland	SAT65	Mkambati Nature Reserve	wet	Brownian motion	-4963.3480	9.9287E+03	0.0853	0.0296	0.9149	0.9992
Eland	SAT65	Mkambati Nature Reserve	wet	Brownian motion 2exp	-4959.1200	9924.2400	7.9190E-01	0.0254	0.9763	0.9994
Eland	SAT65	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4959.1200	9928.2400	1.0720E-01	0.0254	0.9763	0.9994
Eland	SAT65	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4959.0470	9932.0930	1.5600E-02	0.0254	0.9763	0.9994
Eland	SAT65	Mkambati Nature Reserve	wet	Power law	-5526.4120	11054.8250	0.0000E+00	0.3526	0.0000	0.7952

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Eland	SAT65	Mkambati Nature Reserve	wet	Truncated power law	-5265.3480	10532.6960	0.0000E+00	0.3202	0.0000	0.8890
Impala	IMP1	Mapungubwe National Park	dry	Brownian motion	-4169.5620	8.3411E+03	0.0000	0.0930	0.0047	0.9899
Impala	IMP1	Mapungubwe National Park	dry	Brownian motion 2exp	-4072.5100	8151.0200	3.0000E-04	0.0701	0.0645	0.9915
Impala	IMP1	Mapungubwe National Park	dry	Brownian motion 3exp	-4062.4850	8134.9700	9.9970E-01	0.0544	0.2529	0.9933
Impala	IMP1	Mapungubwe National Park	dry	Brownian motion 3exp	-4109.9070	8233.8140	0.0000E+00	0.0544	0.2529	0.9934
Impala	IMP1	Mapungubwe National Park	dry	Power law	-4418.9330	8839.8670	0.0000E+00	0.2332	0.0000	0.8588
Impala	IMP1	Mapungubwe National Park	dry	Truncated power law	-4199.6860	8401.3720	0.0000E+00	0.1416	0.0000	0.9560
Impala	IMP1	Mapungubwe National Park	wet	Brownian motion	-3219.9970	6.4420E+03	0.0000	0.0630	0.2658	0.9963
Impala	IMP1	Mapungubwe National Park	wet	Brownian motion 2exp	-3185.4470	6376.8930	6.4000E-02	0.0571	0.3793	0.9959
Impala	IMP1	Mapungubwe National Park	wet	Brownian motion 3exp	-3180.7760	6371.5520	9.2390E-01	0.0276	0.9905	0.9988
Impala	IMP1	Mapungubwe National Park	wet	Brownian motion 3exp	-3183.1110	6380.2210	1.2100E-02	0.0492	0.5699	0.9971
Impala	IMP1	Mapungubwe National Park	wet	Power law	-3429.1300	6860.2590	0.0000E+00	0.2717	0.0000	0.8593
Impala	IMP1	Mapungubwe National Park	wet	Truncated power law	-3286.1950	6574.3910	0.0000E+00	0.1673	0.0000	0.9575
Impala	IMP13	Asante Sana Game Reserve	dry	Brownian motion	-3910.2680	7.8225E+03	0.0000	0.1165	0.0005	0.9930
Impala	IMP13	Asante Sana Game Reserve	dry	Brownian motion 2exp	-3744.8670	7495.7340	0.0000E+00	0.0874	0.0179	0.9944
Impala	IMP13	Asante Sana Game Reserve	dry	Brownian motion 3exp	-3745.3390	7500.6780	0.0000E+00	0.0890	0.0150	0.9948
Impala	IMP13	Asante Sana Game Reserve	dry	Brownian motion 3exp	-3729.6690	7473.3380	1.0000E+00	0.0372	0.7855	0.9988
Impala	IMP13	Asante Sana Game Reserve	dry	Power law	-4073.5010	8149.0020	0.0000E+00	0.2184	0.0000	0.8654
Impala	IMP13	Asante Sana Game Reserve	dry	Truncated power law	-3914.3920	7830.7830	0.0000E+00	0.1133	0.0007	0.9642
Impala	IMP14	Asante Sana Game Reserve	dry	Brownian motion	-4392.3190	8.7866E+03	0.0000	0.1111	0.0004	0.9928
Impala	IMP14	Asante Sana Game Reserve	dry	Brownian motion 2exp	-4162.6400	8331.2800	0.0000E+00	0.0707	0.0626	0.9946
Impala	IMP14	Asante Sana Game Reserve	dry	Brownian motion 3exp	-4163.3800	8336.7590	0.0000E+00	0.0693	0.0720	0.9947
Impala	IMP14	Asante Sana Game Reserve	dry	Brownian motion 3exp	-4147.3150	8308.6310	1.0000E+00	0.0462	0.4509	0.9982
Impala	IMP14	Asante Sana Game Reserve	dry	Power law	-4564.3750	9130.7500	0.0000E+00	0.2280	0.0000	0.8632
Impala	IMP14	Asante Sana Game Reserve	dry	Truncated power law	-4372.2640	8746.5290	0.0000E+00	0.1270	0.0000	0.9637
Impala	IMP14	Asante Sana Game Reserve	wet	Brownian motion	-4379.1410	8.7603E+03	0.0000	0.0649	0.1150	0.9972
Impala	IMP14	Asante Sana Game Reserve	wet	Brownian motion 2exp	-4332.8710	8671.7420	0.0000E+00	0.0442	0.5204	0.9977
Impala	IMP14	Asante Sana Game Reserve	wet	Brownian motion 3exp	-4264.3400	8538.6800	8.1860E-01	0.0265	0.9707	0.9992
Impala	IMP14	Asante Sana Game Reserve	wet	Brownian motion 3exp	-4263.8470	8541.6930	1.8140E-01	0.0265	0.9707	0.9992
Impala	IMP14	Asante Sana Game Reserve	wet	Power law	-4657.7400	9317.4810	0.0000E+00	0.2581	0.0000	0.8341
Impala	IMP14	Asante Sana Game Reserve	wet	Truncated power law	-4414.0780	8830.1570	0.0000E+00	0.1917	0.0000	0.9435
Impala	IMP2	Mapungubwe National Park	dry	Brownian motion	-3416.2330	6.8345E+03	0.0000	0.1153	0.0018	0.9906

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Impala	IMP2	Mapungubwe National Park	dry	Brownian motion 2exp	-3341.6230	6689.2460	0.0000E+00	0.0662	0.1972	0.9941
Impala	IMP2	Mapungubwe National Park	dry	Brownian motion 3exp	-3294.8010	6599.6010	1.0000E+00	0.0321	0.9476	0.9981
Impala	IMP2	Mapungubwe National Park	dry	Brownian motion 3exp	-3332.8740	6679.7490	0.0000E+00	0.0340	0.9194	0.9978
Impala	IMP2	Mapungubwe National Park	dry	Power law	-3572.3240	7146.6480	0.0000E+00	0.2136	0.0000	0.8597
Impala	IMP2	Mapungubwe National Park	dry	Truncated power law	-3424.6870	6851.3740	0.0000E+00	0.1191	0.0011	0.9567
Impala	IMP4	Mapungubwe National Park	dry	Brownian motion	-4574.7480	9.1515E+03	0.0000	0.0774	0.0284	0.9975
Impala	IMP4	Mapungubwe National Park	dry	Brownian motion 2exp	-4505.5530	9017.1070	4.6590E-01	0.0408	0.5952	0.9980
Impala	IMP4	Mapungubwe National Park	dry	Brownian motion 3exp	-4504.3630	9018.7250	2.0740E-01	0.0352	0.7717	0.9984
Impala	IMP4	Mapungubwe National Park	dry	Brownian motion 3exp	-4501.9090	9017.8170	3.2660E-01	0.0267	0.9614	0.9992
Impala	IMP4	Mapungubwe National Park	dry	Power law	-4826.7610	9655.5210	0.0000E+00	0.2447	0.0000	0.8435
Impala	IMP4	Mapungubwe National Park	dry	Truncated power law	-4606.3800	9214.7610	0.0000E+00	0.1519	0.0000	0.9503
Impala	IMP4	Mapungubwe National Park	wet	Brownian motion	-4339.1710	8.6803E+03	0.0000	0.0753	0.0429	0.9963
Impala	IMP4	Mapungubwe National Park	wet	Brownian motion 2exp	-4234.1340	8474.2680	8.8000E-03	0.0487	0.3971	0.9970
Impala	IMP4	Mapungubwe National Park	wet	Brownian motion 3exp	-4271.5680	8553.1350	0.0000E+00	0.0295	0.9292	0.9988
Impala	IMP4	Mapungubwe National Park	wet	Brownian motion 3exp	-4225.4140	8464.8270	9.9120E-01	0.0369	0.7452	0.9981
Impala	IMP4	Mapungubwe National Park	wet	Power law	-4594.2310	9190.4620	0.0000E+00	0.2555	0.0000	0.8414
Impala	IMP4	Mapungubwe National Park	wet	Truncated power law	-4413.5550	8829.1100	0.0000E+00	0.1462	0.0000	0.9495
Plains zebra	AG217	Welgevonden Game Reserve	wet	Brownian motion	-6075.4080	1.2153E+04	0.0000	0.2087	0.0000	0.9161
Plains zebra	AG217	Welgevonden Game Reserve	wet	Brownian motion 2exp	-5908.1610	11822.3200	0.0000E+00	0.1562	0.0000	0.9606
Plains zebra	AG217	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5874.1710	11758.3400	1.7320E-01	0.1486	0.0000	0.9767
Plains zebra	AG217	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5870.6080	11755.2200	8.2680E-01	0.1486	0.0000	0.9766
Plains zebra	AG217	Welgevonden Game Reserve	wet	Power law	-6302.4880	12606.9800	0.0000E+00	0.2808	0.0000	0.8216
Plains zebra	AG217	Welgevonden Game Reserve	wet	Truncated power law	-6005.1450	12012.2900	0.0000E+00	0.3468	0.0000	0.8894
Plains zebra	AG218	Welgevonden Game Reserve	wet	Brownian motion	-6231.8160	1.2466E+04	0.0004	0.0725	0.0495	0.9906
Plains zebra	AG218	Welgevonden Game Reserve	wet	Brownian motion 2exp	-6224.4880	12454.9800	8.1700E-02	0.0725	0.0495	0.9908
Plains zebra	AG218	Welgevonden Game Reserve	wet	Brownian motion 3exp	-6220.1180	12450.2400	8.7400E-01	0.0669	0.0864	0.9919
Plains zebra	AG218	Welgevonden Game Reserve	wet	Brownian motion 3exp	-6221.1110	12456.2200	4.3800E-02	0.0683	0.0755	0.9919
Plains zebra	AG218	Welgevonden Game Reserve	wet	Power law	-6972.1630	13946.3300	0.0000E+00	0.3642	0.0000	0.7315
Plains zebra	AG218	Welgevonden Game Reserve	wet	Truncated power law	-6638.3690	13278.7400	0.0000E+00	0.4580	0.0000	0.8053
Plains zebra	AG219	Welgevonden Game Reserve	dry	Brownian motion	-6259.5380	1.2521E+04	0.0780	0.0549	0.2225	0.9923
Plains zebra	AG219	Welgevonden Game Reserve	dry	Brownian motion 2exp	-6255.3070	12516.6100	7.2550E-01	0.0549	0.2225	0.9923
Plains zebra	AG219	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6254.7400	12519.4800	1.7300E-01	0.0576	0.1778	0.9923

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Plains zebra	AG219	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6254.7380	12523.4800	2.3500E-02	0.0576	0.1778	0.9924
Plains zebra	AG219	Welgevonden Game Reserve	dry	Power law	-6998.2770	13998.5500	0.0000E+00	0.3772	0.0000	0.7343
Plains zebra	AG219	Welgevonden Game Reserve	dry	Truncated power law	-6681.7020	13365.4000	0.0000E+00	0.4170	0.0000	0.8160
Plains zebra	AG219	Welgevonden Game Reserve	wet	Brownian motion	-5724.7960	1.1452E+04	0.0112	0.0383	0.7011	0.9979
Plains zebra	AG219	Welgevonden Game Reserve	wet	Brownian motion 2exp	-5720.1140	11446.2300	1.6320E-01	0.0369	0.7460	0.9980
Plains zebra	AG219	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5716.6080	11443.2200	7.3610E-01	0.0354	0.7893	0.9983
Plains zebra	AG219	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5716.7150	11447.4300	8.9500E-02	0.0369	0.7460	0.9981
Plains zebra	AG219	Welgevonden Game Reserve	wet	Power law	-6406.1690	12814.3400	0.0000E+00	0.3658	0.0000	0.7563
Plains zebra	AG219	Welgevonden Game Reserve	wet	Truncated power law	-6123.3480	12248.7000	0.0000E+00	0.4189	0.0000	0.8303
Plains zebra	AG220	Welgevonden Game Reserve	dry	Brownian motion	-6704.3900	1.3411E+04	0.0000	0.0950	0.0028	0.9910
Plains zebra	AG220	Welgevonden Game Reserve	dry	Brownian motion 2exp	-6700.6550	13407.3100	0.0000E+00	0.0937	0.0034	0.9910
Plains zebra	AG220	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6670.8680	13351.7400	8.6070E-01	0.0358	0.7404	0.9986
Plains zebra	AG220	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6670.6890	13355.3800	1.3930E-01	0.0358	0.7404	0.9986
Plains zebra	AG220	Welgevonden Game Reserve	dry	Power law	-7386.3300	14774.6600	0.0000E+00	0.3664	0.0000	0.7891
Plains zebra	AG220	Welgevonden Game Reserve	dry	Truncated power law	-7052.9680	14107.9400	0.0000E+00	0.4518	0.0000	0.8531
Plains zebra	AG220	Welgevonden Game Reserve	wet	Brownian motion	-5784.0480	1.1570E+04	0.0000	0.0942	0.0053	0.9950
Plains zebra	AG220	Welgevonden Game Reserve	wet	Brownian motion 2exp	-5739.7350	11485.4700	1.8130E-01	0.0478	0.4284	0.9968
Plains zebra	AG220	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5738.0680	11486.1400	1.3000E-01	0.0463	0.4691	0.9969
Plains zebra	AG220	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5734.4000	11482.8000	6.8880E-01	0.0209	0.9986	0.9994
Plains zebra	AG220	Welgevonden Game Reserve	wet	Power law	-6285.7480	12573.5000	0.0000E+00	0.3438	0.0000	0.7512
Plains zebra	AG220	Welgevonden Game Reserve	wet	Truncated power law	-5996.9680	11995.9400	0.0000E+00	0.3976	0.0000	0.8321
Plains zebra	AG221	Welgevonden Game Reserve	dry	Brownian motion	-6168.7750	1.2340E+04	0.0043	0.0587	0.1798	0.9909
Plains zebra	AG221	Welgevonden Game Reserve	dry	Brownian motion 2exp	-6164.2180	12334.4400	5.5000E-02	0.0587	0.1798	0.9910
Plains zebra	AG221	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6159.5060	12329.0100	8.2860E-01	0.0659	0.0965	0.9920
Plains zebra	AG221	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6159.5060	12333.0100	1.1210E-01	0.0659	0.0965	0.9920
Plains zebra	AG221	Welgevonden Game Reserve	dry	Power law	-6879.6740	13761.3500	0.0000E+00	0.3625	0.0000	0.7585
Plains zebra	AG221	Welgevonden Game Reserve	dry	Truncated power law	-6529.1910	13060.3800	0.0000E+00	0.4556	0.0000	0.8294
Plains zebra	AG221	Welgevonden Game Reserve	wet	Brownian motion	-6166.3870	1.2335E+04	0.0000	0.1700	0.0000	0.9739
Plains zebra	AG221	Welgevonden Game Reserve	wet	Brownian motion 2exp	-6032.5260	12071.0500	7.0800E-02	0.0648	0.1081	0.9938
Plains zebra	AG221	Welgevonden Game Reserve	wet	Brownian motion 3exp	-6028.1090	12066.2200	7.9370E-01	0.0663	0.0948	0.9938
Plains zebra	AG221	Welgevonden Game Reserve	wet	Brownian motion 3exp	-6027.8770	12069.7500	1.3550E-01	0.0663	0.0948	0.9939
Plains zebra	AG221	Welgevonden Game Reserve	wet	Power law	-6532.0710	13066.1400	0.0000E+00	0.2839	0.0000	0.8125

Species	ID	Property	Season	Model	MLL	AIC	AIC Weight	KS-D	KS p-value	R ²
Plains zebra	AG221	Welgevonden Game Reserve	wet	Truncated power law	-6239.5960	12481.1900	0.0000E+00	0.3501	0.0000	0.8795
Plains zebra	AG223	Welgevonden Game Reserve	dry	Brownian motion	-5772.0030	1.1546E+04	0.0000	0.0538	0.2581	0.9973
Plains zebra	AG223	Welgevonden Game Reserve	dry	Brownian motion 2exp	-5759.8300	11525.6600	5.0030E-01	0.0354	0.7679	0.9984
Plains zebra	AG223	Welgevonden Game Reserve	dry	Brownian motion 3exp	-5757.9590	11525.9200	4.4010E-01	0.0340	0.8093	0.9988
Plains zebra	AG223	Welgevonden Game Reserve	dry	Brownian motion 3exp	-5757.9590	11529.9200	5.9500E-02	0.0340	0.8093	0.9988
Plains zebra	AG223	Welgevonden Game Reserve	dry	Power law	-6382.3680	12766.7400	0.0000E+00	0.3499	0.0000	0.7589
Plains zebra	AG223	Welgevonden Game Reserve	dry	Truncated power law	-6071.0120	12144.0200	0.0000E+00	0.3994	0.0000	0.8451
Plains zebra	AG223	Welgevonden Game Reserve	wet	Brownian motion	-5745.2960	1.1493E+04	0.0000	0.1164	0.0002	0.9840
Plains zebra	AG223	Welgevonden Game Reserve	wet	Brownian motion 2exp	-5706.2280	11418.4600	1.5340E-01	0.0417	0.5815	0.9985
Plains zebra	AG223	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5702.6700	11415.3400	7.2870E-01	0.0431	0.5375	0.9984
Plains zebra	AG223	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5702.4920	11418.9800	1.1780E-01	0.0417	0.5815	0.9985
Plains zebra	AG223	Welgevonden Game Reserve	wet	Power law	-6239.2550	12480.5100	0.0000E+00	0.3261	0.0000	0.8346
Plains zebra	AG223	Welgevonden Game Reserve	wet	Truncated power law	-5941.3080	11884.6200	0.0000E+00	0.3549	0.0000	0.9086
Plains zebra	AG224	Welgevonden Game Reserve	dry	Brownian motion	-6118.6610	1.2239E+04	0.0000	0.0678	0.0676	0.9934
Plains zebra	AG224	Welgevonden Game Reserve	dry	Brownian motion 2exp	-6111.9290	12229.8600	7.0000E-04	0.0623	0.1137	0.9926
Plains zebra	AG224	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6103.3710	12216.7400	4.5880E-01	0.0285	0.9262	0.9980
Plains zebra	AG224	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6101.2070	12216.4100	5.4060E-01	0.0271	0.9492	0.9980
Plains zebra	AG224	Welgevonden Game Reserve	dry	Power law	-6725.4280	13452.8600	0.0000E+00	0.3537	0.0000	0.7701
Plains zebra	AG224	Welgevonden Game Reserve	dry	Truncated power law	-6436.6760	12875.3500	0.0000E+00	0.3713	0.0000	0.8582
Plains zebra	AG225	Welgevonden Game Reserve	dry	Brownian motion	-6150.6040	1.2303E+04	0.0029	0.0447	0.4518	0.9984
Plains zebra	AG225	Welgevonden Game Reserve	dry	Brownian motion 2exp	-6148.0970	12302.1900	4.9000E-03	0.0203	0.9980	0.9992
Plains zebra	AG225	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6140.9950	12291.9900	7.9760E-01	0.0203	0.9980	0.9992
Plains zebra	AG225	Welgevonden Game Reserve	dry	Brownian motion 3exp	-6140.4060	12294.8100	1.9460E-01	0.0257	0.9673	0.9991
Plains zebra	AG225	Welgevonden Game Reserve	dry	Power law	-6851.8610	13705.7200	0.0000E+00	0.3808	0.0000	0.7609
Plains zebra	AG225	Welgevonden Game Reserve	dry	Truncated power law	-6542.6960	13087.3900	0.0000E+00	0.4146	0.0000	0.8448
Plains zebra	AG225	Welgevonden Game Reserve	wet	Brownian motion	-5680.7770	1.1364E+04	0.0000	0.1007	0.0017	0.9850
Plains zebra	AG225	Welgevonden Game Reserve	wet	Brownian motion 2exp	-5648.4840	11302.9700	3.3900E-01	0.0302	0.9089	0.9985
Plains zebra	AG225	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5647.2720	11304.5400	1.5420E-01	0.0317	0.8771	0.9985
Plains zebra	AG225	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5644.0820	11302.1600	5.0680E-01	0.0360	0.7595	0.9986
Plains zebra	AG225	Welgevonden Game Reserve	wet	Power law	-6190.4890	12382.9800	0.0000E+00	0.3338	0.0000	0.8327
Plains zebra	AG225	Welgevonden Game Reserve	wet	Truncated power law	-5897.6410	11797.2800	0.0000E+00	0.3612	0.0000	0.9053
Plains zebra	AG226	Welgevonden Game Reserve	wet	Brownian motion	-5997.6630	1.1997E+04	0.0000	0.0944	0.0048	0.9875

Species	ID	Property	Season	Model	MLL	AIC	AIC Weight	KS-D	KS p-value	R ²
Plains zebra	AG226	Welgevonden Game Reserve	wet	Brownian motion 2exp	-5967.4080	11940.8200	1.1200E-02	0.0472	0.4369	0.9976
Plains zebra	AG226	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5964.0230	11938.0500	4.4600E-02	0.0472	0.4369	0.9978
Plains zebra	AG226	Welgevonden Game Reserve	wet	Brownian motion 3exp	-5958.9700	11931.9400	9.4430E-01	0.0501	0.3614	0.9981
Plains zebra	AG226	Welgevonden Game Reserve	wet	Power law	-8525.2290	13052.4600	0.0000E+00	0.3407	0.0000	0.7953
Plains zebra	AG226	Welgevonden Game Reserve	wet	Truncated power law	-6229.5730	12461.1500	0.0000E+00	0.3923	0.0000	0.8726
Plains zebra	AU070	Mkambati Nature Reserve	dry	Brownian motion	-5283.3950	1.0569E+04	0.7893	0.0463	0.4112	0.9974
Plains zebra	AU070	Mkambati Nature Reserve	dry	Brownian motion 2exp	-5283.0420	10572.0800	1.5220E-01	0.0490	0.3412	0.9980
Plains zebra	AU070	Mkambati Nature Reserve	dry	Brownian motion 3exp	-5283.1980	10576.4000	1.7600E-02	0.0476	0.3752	0.9978
Plains zebra	AU070	Mkambati Nature Reserve	dry	Brownian motion 3exp	-5280.3560	10574.7100	4.0900E-02	0.0476	0.3752	0.9974
Plains zebra	AU070	Mkambati Nature Reserve	dry	Power law	-5901.7850	11805.5700	0.0000E+00	0.3673	0.0000	0.8587
Plains zebra	AU070	Mkambati Nature Reserve	dry	Truncated power law	-5602.6600	11207.3200	0.0000E+00	0.3469	0.0000	0.9293
Plains zebra	AU074	Mkambati Nature Reserve	dry	Brownian motion	-4995.4190	9.9928E+03	0.2790	0.0619	0.1398	0.9976
Plains zebra	AU074	Mkambati Nature Reserve	dry	Brownian motion 2exp	-4992.4950	9990.9900	7.0290E-01	0.0633	0.1234	0.9976
Plains zebra	AU074	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4995.4190	10000.8380	5.1000E-03	0.0619	0.1398	0.9976
Plains zebra	AU074	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4992.4870	9998.9750	1.3000E-02	0.0633	0.1234	0.9976
Plains zebra	AU074	Mkambati Nature Reserve	dry	Power law	-5583.8250	11169.6490	0.0000E+00	0.3784	0.0000	0.7759
Plains zebra	AU074	Mkambati Nature Reserve	dry	Truncated power law	-5317.4430	10636.8860	0.0000E+00	0.3424	0.0000	0.8782
Plains zebra	AU074	Mkambati Nature Reserve	wet	Brownian motion	-3992.5370	7.9871E+03	0.2483	0.0662	0.1615	0.9911
Plains zebra	AU074	Mkambati Nature Reserve	wet	Brownian motion 2exp	-3989.7790	7985.5570	5.3010E-01	0.0801	0.0501	0.9941
Plains zebra	AU074	Mkambati Nature Reserve	wet	Brownian motion 3exp	-3989.7790	7989.5570	7.1700E-02	0.0801	0.0501	0.9941
Plains zebra	AU074	Mkambati Nature Reserve	wet	Brownian motion 3exp	-3987.0420	7988.0850	1.4980E-01	0.0801	0.0501	0.9941
Plains zebra	AU074	Mkambati Nature Reserve	wet	Power law	-4430.1970	8862.3930	0.0000E+00	0.3693	0.0000	0.8700
Plains zebra	AU074	Mkambati Nature Reserve	wet	Truncated power law	-4217.3170	8436.6340	0.0000E+00	0.3188	0.0000	0.9343
Plains zebra	AU374	Mkambati Nature Reserve	wet	Brownian motion	-4887.4430	9.7769E+03	0.2327	0.0466	0.4253	0.9944
Plains zebra	AU374	Mkambati Nature Reserve	wet	Brownian motion 2exp	-4884.6290	9775.2580	5.2540E-01	0.0551	0.2330	0.9963
Plains zebra	AU374	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4884.6290	9779.2580	7.1100E-02	0.0551	0.2330	0.9963
Plains zebra	AU374	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4881.7530	9777.5060	1.7080E-01	0.0551	0.2330	0.9962
Plains zebra	AU374	Mkambati Nature Reserve	wet	Power law	-5442.8330	10887.6660	0.0000E+00	0.3658	0.0000	0.8666
Plains zebra	AU374	Mkambati Nature Reserve	wet	Truncated power law	-5188.5420	10379.0840	0.0000E+00	0.3234	0.0000	0.9361
Plains zebra	AU375	Mkambati Nature Reserve	wet	Brownian motion	-4840.5140	9.6830E+03	0.8154	0.0709	0.0577	0.9977
Plains zebra	AU375	Mkambati Nature Reserve	wet	Brownian motion 2exp	-4840.5140	9687.0270	1.1030E-01	0.0709	0.0577	0.9977
Plains zebra	AU375	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4840.5140	9691.0270	1.4900E-02	0.0709	0.0577	0.9977

Species	ID	Property	Season	Model	MLL	AIC	AIC Weight	KS-D	KS p-value	R ²
Plains zebra	AU375	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4837.1340	9688.2680	5.9300E-02	0.0738	0.0432	0.9978
Plains zebra	AU375	Mkambati Nature Reserve	wet	Power law	-5469.7070	10941.4150	0.0000E+00	0.3830	0.0000	0.8605
Plains zebra	AU375	Mkambati Nature Reserve	wet	Truncated power law	-5199.8440	10401.6880	0.0000E+00	0.3560	0.0000	0.9288
Red hartebeest	AU063	Mkambati Nature Reserve	wet	Brownian motion	-4184.7020	8.3714E+03	0.0000	0.1317	0.0000	0.9791
Red hartebeest	AU063	Mkambati Nature Reserve	wet	Brownian motion 2exp	-4123.4320	8252.8630	0.0000E+00	0.0423	0.6173	0.9980
Red hartebeest	AU063	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4109.2740	8228.5470	8.8080E-01	0.0157	1.0000	0.9998
Red hartebeest	AU063	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4109.2740	8232.5470	1.1920E-01	0.0157	1.0000	0.9998
Red hartebeest	AU063	Mkambati Nature Reserve	wet	Power law	-4361.1460	8724.2920	0.0000E+00	0.2524	0.0000	0.8667
Red hartebeest	AU063	Mkambati Nature Reserve	wet	Truncated power law	-4217.1900	8436.3800	0.0000E+00	0.1395	0.0000	0.9566
Red hartebeest	AU064	Mkambati Nature Reserve	dry	Brownian motion	-4944.8360	9.8917E+03	0.0000	0.0467	0.4244	0.9986
Red hartebeest	AU064	Mkambati Nature Reserve	dry	Brownian motion 2exp	-4919.4610	9844.9210	4.8700E-02	0.0297	0.9141	0.9987
Red hartebeest	AU064	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4914.6150	9839.2300	8.3790E-01	0.0368	0.7254	0.9984
Red hartebeest	AU064	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4914.6150	9843.2300	1.1340E-01	0.0368	0.7254	0.9984
Red hartebeest	AU064	Mkambati Nature Reserve	dry	Power law	-5415.7640	10833.5280	0.0000E+00	0.3281	0.0000	0.7516
Red hartebeest	AU064	Mkambati Nature Reserve	dry	Truncated power law	-5143.1420	10288.2830	0.0000E+00	0.3112	0.0000	0.8612
Red hartebeest	AU064	Mkambati Nature Reserve	wet	Brownian motion	-4472.8660	8.9477E+03	0.0000	0.0726	0.0571	0.9947
Red hartebeest	AU064	Mkambati Nature Reserve	wet	Brownian motion 2exp	-4453.2110	8912.4210	1.1000E-03	0.0652	0.1136	0.9943
Red hartebeest	AU064	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4444.5440	8899.0870	8.7980E-01	0.0193	0.9996	0.9994
Red hartebeest	AU064	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4444.5440	8903.0870	1.1910E-01	0.0193	0.9996	0.9994
Red hartebeest	AU064	Mkambati Nature Reserve	wet	Power law	-4834.4480	9670.8960	0.0000E+00	0.2889	0.0000	0.8253
Red hartebeest	AU064	Mkambati Nature Reserve	wet	Truncated power law	-4590.7010	9183.4030	0.0000E+00	0.2415	0.0000	0.9286
Red hartebeest	AU065	Mkambati Nature Reserve	wet	Brownian motion	-1902.7850	3.8076E+03	0.0000	0.2426	0.0000	0.9553
Red hartebeest	AU065	Mkambati Nature Reserve	wet	Brownian motion 2exp	-1792.9000	3591.7990	0.0000E+00	0.0754	0.3511	0.9934
Red hartebeest	AU065	Mkambati Nature Reserve	wet	Brownian motion 3exp	-1782.8200	3575.6390	1.1220E-01	0.0426	0.9446	0.9980
Red hartebeest	AU065	Mkambati Nature Reserve	wet	Brownian motion 3exp	-1778.7510	3571.5020	8.8780E-01	0.0361	0.9888	0.9980
Red hartebeest	AU065	Mkambati Nature Reserve	wet	Power law	-1862.7860	3727.5720	0.0000E+00	0.1803	0.0001	0.9212
Red hartebeest	AU065	Mkambati Nature Reserve	wet	Truncated power law	-1816.8000	3635.6010	0.0000E+00	0.0885	0.1831	0.9718
Red hartebeest	AU371	Mkambati Nature Reserve	dry	Brownian motion	-4968.7210	9.9394E+03	0.0000	0.0704	0.0635	0.9953
Red hartebeest	AU371	Mkambati Nature Reserve	dry	Brownian motion 2exp	-4958.8550	9923.7100	0.0000E+00	0.0690	0.0730	0.9945
Red hartebeest	AU371	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4934.6010	9879.2030	1.1860E-01	0.0345	0.8024	0.9982
Red hartebeest	AU371	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4930.5950	9875.1900	8.8140E-01	0.0345	0.8024	0.9983
Red hartebeest	AU371	Mkambati Nature Reserve	dry	Power law	-5393.6000	10789.2000	0.0000E+00	0.3132	0.0000	0.7907

Species	ID	Property	Season	Model	MLL	AIC	AIC Weight	KS-D	KS p-value	R ²
Red hartebeest	AU371	Mkambati Nature Reserve	dry	Truncated power law	-5159.2640	10320.5290	0.0000E+00	0.2658	0.0000	0.8898
Red hartebeest	AU371	Mkambati Nature Reserve	wet	Brownian motion	-4297.9980	8.5980E+03	0.0000	0.0856	0.0165	0.9937
Red hartebeest	AU371	Mkambati Nature Reserve	wet	Brownian motion 2exp	-4270.1420	8546.2840	0.0000E+00	0.0581	0.2196	0.9957
Red hartebeest	AU371	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4256.6490	8523.2980	8.5530E-01	0.0275	0.9654	0.9993
Red hartebeest	AU371	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4256.4260	8526.8520	1.4470E-01	0.0275	0.9654	0.9993
Red hartebeest	AU371	Mkambati Nature Reserve	wet	Power law	-4567.9630	9137.9250	0.0000E+00	0.2661	0.0000	0.8443
Red hartebeest	AU371	Mkambati Nature Reserve	wet	Truncated power law	-4403.6150	8809.2300	0.0000E+00	0.1667	0.0000	0.9372
Red hartebeest	AU372	Mkambati Nature Reserve	wet	Brownian motion	-4389.8270	8.7817E+03	0.0000	0.0694	0.0822	0.9946
Red hartebeest	AU372	Mkambati Nature Reserve	wet	Brownian motion 2exp	-4364.4600	8734.9200	5.1000E-03	0.0211	0.9985	0.9991
Red hartebeest	AU372	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4357.3230	8724.6450	8.7630E-01	0.0211	0.9985	0.9995
Red hartebeest	AU372	Mkambati Nature Reserve	wet	Brownian motion 3exp	-4357.3230	8728.6460	1.1860E-01	0.0211	0.9985	0.9994
Red hartebeest	AU372	Mkambati Nature Reserve	wet	Power law	-4729.1610	9460.3210	0.0000E+00	0.2971	0.0000	0.8263
Red hartebeest	AU372	Mkambati Nature Reserve	wet	Truncated power law	-4521.3810	9044.7610	0.0000E+00	0.2247	0.0000	0.9239
Red hartebeest	AU452	Mkambati Nature Reserve	dry	Brownian motion	-4356.7930	8.7156E+03	0.0000	0.0530	0.3123	0.9974
Red hartebeest	AU452	Mkambati Nature Reserve	dry	Brownian motion 2exp	-4328.3650	8662.7310	5.3970E-01	0.0287	0.9477	0.9988
Red hartebeest	AU452	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4327.7390	8665.4780	1.3660E-01	0.0303	0.9228	0.9989
Red hartebeest	AU452	Mkambati Nature Reserve	dry	Brownian motion 3exp	-4324.8760	8663.7530	3.2370E-01	0.0303	0.9228	0.9988
Red hartebeest	AU452	Mkambati Nature Reserve	dry	Power law	-4737.8990	9477.7980	0.0000E+00	0.3132	0.0000	0.8218
Red hartebeest	AU452	Mkambati Nature Reserve	dry	Truncated power law	-4566.0460	9134.0910	0.0000E+00	0.2209	0.0000	0.9127
Red hartebeest	AU452	Mkambati Nature Reserve	wet	Brownian motion	-4020.0830	8.0422E+03	0.0000	0.1398	0.0000	0.9820
Red hartebeest	AU452	Mkambati Nature Reserve	wet	Brownian motion 2exp	-3959.7750	7925.5500	7.6200E-02	0.0309	0.9309	0.9981
Red hartebeest	AU452	Mkambati Nature Reserve	wet	Brownian motion 3exp	-3955.8390	7921.6790	5.2800E-01	0.0163	1.0000	0.9996
Red hartebeest	AU452	Mkambati Nature Reserve	wet	Brownian motion 3exp	-3954.1270	7922.2550	3.9580E-01	0.0163	1.0000	0.9996
Red hartebeest	AU452	Mkambati Nature Reserve	wet	Power law	-4197.5460	8397.0910	0.0000E+00	0.2228	0.0000	0.8864
Red hartebeest	AU452	Mkambati Nature Reserve	wet	Truncated power law	-4005.4130	8012.8260	0.0000E+00	0.1528	0.0000	0.9682

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