Conservation ecology and social behaviour of southern white rhinoceros (*Ceratotherium simum simum*)

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PhD 2020

Conservation ecology and social behaviour of southern white rhinoceros (*Ceratotherium simum simum*)

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A thesis submitted in partial fulfilment of the requirements of Manchester Metropolitan University for the degree of Doctor of Philosophy

Department of Natural Sciences
Manchester Metropolitan University
in collaboration with Knowsley Safari Park

2020

Abstract

Southern white rhinoceros, *Ceratotherium simum simum*, have extremely low reproductive output in captivity, and there is substantial variation in reproductive success between certain wild populations. To investigate whether social and ecological factors influence female reproduction, this study used data collected from four white rhinoceros populations in Kenya, alongside demographic studbook data from the European captive population.

Using population viability analysis, I show that the European captive population is projected to decline 2% annually under current demographic parameters. The proportion of females calving annually (10%) is the main factor limiting population growth, which must increase to 17% to prevent further population decline. Additionally, high infant mortality rates and severe reproductive skew are also of concern. Mean group age, group size and the presence of another breeding female were key factors mediating female breeding behaviour and reproductive success, and thus inadequate social conditions may contribute towards low female reproductive output in captivity.

Using social network analysis, I demonstrate that wild white rhinoceros display age-specific association patterns and a strong tendency to form cliques. Individuals often formed long-lasting associations, persisting for at least seven months, and social connectivity related to female reproductive success. Grouping patterns varied between populations, most likely due to differences in population density and habitat. Vegetation assessments conveyed that high grass cover, both shorter grass and trees, and low elevation were key features of white rhinoceros habitat across populations. Differences in habitat quality and grazing pressure between populations had little impact on breeding performance, but did influence individual core range size, which increased as population density decreased.

The results from this work provide important new insights on white rhinoceros social behaviour and ecology that can be used to inform their conservation management, such as translocations and estimates of ecological carrying capacity in the wild, and group compositions likely to improve female reproductive output in captivity.

Acknowledgements

The work in this thesis would not have been possible without the help and support from a number of people.

Firstly, I would like to thank my supervisory team: Caroline Bettridge, Selvino de Kort and Bradley Cain. This work would not have been initiated without your vision, and I am extremely grateful for the opportunity to carry out this research. Thank you for your support and guidance throughout the last three and a half years.

Thank you to Manchester Metropolitan University, Knowsley Safari Park and the International Rhino Foundation for funding, without which this research could not have taken place.

Thank you to the staff at Knowsley Safari Park that provided valuable guidance with this work. In particular, I would like to thank Bridget Johnson for providing invaluable knowledge on several aspects of this PhD. I am extremely grateful to Lars Versteege for sharing the European white rhinoceros studbook with me, without which two chapters of this thesis would not have been possible. I would also like to thank BIAZA for providing support on the questionnaire survey, and to all of the institutions that completed the questionnaire and contributed valuable information to this project.

I would like to thank the Kenya Wildlife Service for allowing me to carry out this research in Kenya. In particular, I am deeply grateful to Fred Omengo, who facilitated my work across the study sites, provided me with extensive knowledge and guidance on this work, and was always very welcoming during my visits to Kenya.

I am extremely grateful to all of the people that assisted with fieldwork in Kenya. At Ol Pejeta Conservancy, I would like to thank Samuel Mutisya for providing valuable input on this project, and the rhino monitoring team for their assistance during data collection. Thanks especially go to Isaac Kipkoech for his invaluable help in the field.

At Meru National Park, I would like to thank Geoffrey Bundotich for facilitating this work, and the scientists that assisted with fieldwork. In particular, thanks go to Meshek for help with plant identification, and Peter Gitonga for assistance during long days of data collection. I am grateful to the entire rhino monitoring team for their help tracking rhinos, and for always welcoming me into camp for chai. I am especially grateful to Bernard Munuka and Ndereba Manyara for their assistance during fieldwork, and for providing great company in the field.

At Lake Nakuru National Park, I would like to thank Catherine Wambani for facilitating this work, Alice Bett for valuable guidance on this project, and all of the scientists that helped with fieldwork. In particular, I would like to thank Eveline, Anita and Evans, for their assistance with plant identifications, and for their help carrying out countless vegetation plots. I am very grateful to the entire rhino monitoring team for helping me to locate rhinos on a daily basis. Special thanks go to Joey and Hillary Kemboi for their assistance during fieldwork, and for keeping us safe in the field.

At Lewa Wildlife Conservancy, I would like to thank David Kimitti for facilitating this work, and for providing invaluable data that contributed towards this research. I am extremely grateful to everyone in the Lewa research office that provided help with this project. Special thanks go to Edwin Kisio for his assistance with plant ID's, and to Ian Lemaiyan for his valuable knowledge on Lewa's rhinos, and for giving me a bird's-eye view of my study subjects. I am thankful to all of the rhino monitoring team at Lewa for their help tracking rhinos. In particular, I would like to thank Dickson for his valuable assistance and continued enthusiasm during fieldwork.

Thanks also go to the students that assisted with data collection and provided many laughs in the field: Ashley Ray, Nik Long, Jack Surgey, George Porter and Courtney Yau. I am also forever grateful to Brandon Hays, not only for letting me stay with you when funding was getting tight, but also for providing great company in Nanyuki during breaks from the field.

I am extremely grateful for the support from all of my friends over the last three and a half years, especially those in the E401 and E402 offices. In particular, Maria Loroño, Giada Porcedda, Jaqueline Morrison, Ollie Metcalf and Saule Akhmetkaliyeva. Most importantly, a massive thanks go to Harry Marshall; I could not have done this without your support.

Lastly, I am eternally grateful to my Mum and Dad for their continuous love and support, which has allowed me to get to where I am today. Thank you for always encouraging me to follow my dreams.

Dedication

This thesis is dedicated to my Grandmother, Molly Bissett, who inspired my curiosity and love of the natural world.

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1 INTRODUCTION

1.1 BACKGROUND

1.1.1 Species conservation management

1.1.1.1 The importance of species conservation

Thousands of species worldwide are threatened with extinction due to increasing anthropogenic pressures, such as changes in land and sea use for agriculture and human settlements, pollution and climate change, the introduction of invasive species, and exploitation for food, the pet trade or traditional medicines (United Nations, 2020). The International Union for Conservation of Nature (IUCN) has classified over 31,000 species to be at risk of extinction, including 41% of amphibians, 25% of mammals and 14% of birds (IUCN, 2020). These figures reinforce the urgency to conserve remaining species, and globally reduce anthropogenic pressures to more sustainable levels.

1.1.1.2 In situ conservation

In situ conservation involves the preservation of ecosystems and the protection and management of viable species within their natural habitats (Ajayi, 2019). Whilst the designation of protected areas encompassing a particular habitat or population has become the basis of most in situ conservation strategies, it does not always ensure the viability of a population or ecosystem (Western et al., 2020). Protected species may be vulnerable to population fragmentation, either through human encroachment and habitat loss, or due to fencing or geographical boundaries inhibiting their movement (Newmark, 2008). In such cases, isolated populations can be managed as one connected meta-population (McCullough, 1994), and human-mediated translocations can allow gene flow between populations (Açakaya et al., 2007; IUCN, 2013). When a population is subject to harmful conditions within its natural habitat, it may be necessary to translocate individuals to more secure areas, or establish new populations through reintroduction (IUCN, 2013).

In situ conservation actions do not always ensure the preservation of threatened taxa. For example, creating protected areas or employing reintroduction programmes may be ineffective for species suffering widespread mortalities due to illegal poaching or disease (Zhang et al., 2015; Lorch et al., 2016). In such cases, it may be beneficial to invest resources in ex situ conservation (i.e. captive populations) whilst the threats in the wild persist (Zhang et al., 2017; Berthinussen et al., 2019).

1.1.1.3 Ex situ conservation

Ex situ conservation, or the preservation of species outside of their natural habitat, has become increasingly important. Captive breeding programmes have played a pivotal role in the recovery of several species, including the black-footed ferret, *Mustela nigripes,* (Jachowski and Lockhart, 2009)*,* Californian condor, *Gymnogyps californianu,* (Toone and Wallace, 1994), Guam rail, *Rallus owstoni,* (Ballou et al., 2010) and greater stick-nest rat, *Leporillus conditor,* (Ballou et al., 2010). Captive populations can function as a genetic and demographic reservoir, maintaining a reproductively viable population that is protected from any threats in the wild (Lacy, 1997; Ballou et al., 2010), and can be used as a source for possible reintroduction efforts in the future (Earnhardt, 2010; Zimmermann, 2010). Zoological institutions also provide a platform for scientific research that may not be feasible in the wild, allowing the acquisition of important biological samples for genetic analysis (Frankham et al., 2010; Ogden et al., 2018), or artificial insemination techniques to promote the propagation of critically endangered species (Tunstall et al., 2018).

1.1.1.4 Ex situ population management

For captive breeding to be successful, ex situ populations must be carefully managed, both scientifically and cooperatively, at either a regional or a global level (Foose and Wiese, 2006; Leus et al., 2011). Efforts should be made to maintain both the genetic diversity and natural characteristics of wild populations, ensuring captive-born individuals remain reproductively and behaviourally viable for future reintroduction efforts (Foose and Wiese, 2006). Moreover, captive populations should be self-sustaining, requiring no further supplementation from their wild counterparts after the founder population has been established (WAZA, 2005). Coordinated captive breeding programmes, such as the European Endangered Species Programme (EEP) (WAZA, 2019), scientifically manage individuals from different zoological institutions as a meta-population. Their main aim is to increase population size as quickly as possible to avoid extinction, whilst also retaining founder genetic diversity and an age and sex structure that allows for reliable reproduction, and possible surplus reproduction for reintroduction efforts (Ballou et al. 2010). Many captive breeding programmes now also aim to follow the ‘One Plan Approach to Conservation’, whereby conservation strategies encompass both in situ and ex situ populations to improve the global conservation of a species (Gusset and Dick, 2013).

Ongoing monitoring of population growth and reproductive output is vital to ensure captive populations are performing well. Modelling species extinction risk and identifying factors limiting population growth can help to guide appropriate management actions to improve population sustainability (Edwards et al., 2015). Population viability analysis (PVA) is a useful tool in captive management (Leimgruber et al., 2008; Zeoli et al., 2008; Edwards et al., 2015), which uses quantitative methods and demographic parameters to predict future growth rates and extinction risk (Keedwell, 2004). PVA provides a framework to evaluate population performance under current, or alternative, management practices (Suter et al., 2014; Edwards et al., 2015; Kumar et al., 2016), and can be used to identify the factors limiting a populations growth (Mortensen and Reed, 2016), allowing targeted management strategies to be developed.

1.1.1.5 Reproduction and conservation management

To develop conservation strategies and predict future population trends, it is often necessary to gain an understanding of the target species' reproduction, and the factors that drive reproductive success. Whilst an individual's reproduction is mediated by intrinsic factors, such as genetics or age, extrinsic factors, such as weather patterns, predation pressure, food availability, and the social environment, can also influence individual reproductive success (Wolff, 1997).

In mammals, food availability is arguably the most important mediator of female reproductive success (White, 1983; McNamara and Houston, 1994), due to the energetic costs associated with lactation and pregnancy (Bronson, 1989). Extrinsic factors that limit resource availability thus have a large impact on females living in harsh or unstable environments in situ. For example, inter-specific competition and rainfall drive forage availability for grazing mammals (McNaughton, 1984), and female reproduction is largely mediated by both grazing pressure and spatio-temporal variation in rainfall patterns (Derry and Boone, 2010). Understanding the ecological factors that mediate reproduction in threatened species is important to ensure management strategies are effective, and that designated conservation areas are capable of supporting viable populations. If a population is larger than an area can support, growth may start to decline through density-dependent regulation (Bonenfant et al., 2009). For example, body condition and reproduction decline in populations of North American elk, *Cervus elaphu*, maintained at high densities (Stewart et al., 2005).

The concept of “ecological carrying capacity” refers to the maximum number of animals a given area can support based on the available resources (McCullough, 1992). Ecological carrying capacity can differ considerably between both populations and seasons due to several factors. For example, variation in rainfall patterns, habitat availability and dynamics, invasive species, the frequency and impact of fires, and the abundance of competing species influence forage abundance for grazing mammals (Sinclair and Norton-Griffiths, 1984). The ongoing monitoring of population demographics and reproductive performance, as well as vegetation and habitat assessments, is thus crucial to ensure in situ populations are managed below their ecological carrying capacity.

Social relationships serve important functions in many species, including predator avoidance (Hasenjager and Dugatkin, 2017), territory defence (Siracusa et al., 2019) and resource exploitation (Mueller et al., 2013). An understanding of a species’ social behaviour is also often necessary to develop effective in situ conservation management strategies, as specific social structures or inter-individual relationships may be crucial for individual survival and population persistence (Silk, 2007; Goldenberg et al., 2019). For example, social relationships can provide individuals with information on the location of high quality feeding sites (Valone and Templeton, 2002; Tóth et al., 2017). Management strategies that disrupt natural social behaviours or ranging patterns could therefore influence individual body condition and reproductive success (Testa and Adams, 1998; Milenkaya et al., 2015), and this may have a greater impact on juvenile animals with limited knowledge and experience finding food (Mueller et al., 2013; Sheppard et al., 2018).

Reproduction in captivity is less likely to be driven by factors that limit resource availability, as captive animals are usually maintained in a controlled environment and provided with supplementary food. On the other hand, creating natural conditions in captivity is difficult (Rose and Croft, 2015), and aspects of the captive environment can impact individual welfare and reproductive success. Failure to breed in captivity has been linked to a range of different factors, including inappropriate diet (Setchell et al., 1987), space availability (Carlstead et al., 1999; Peng et al., 2007; Maisch, 2010), enclosure substrate (Blay and Côté, 2001; Little et al., 2016), the impact of inbreeding depression (Merola, 1994), and social conditions (Abello and Colell, 2006).

In particular, captive management may prevent the formation of important social bonds or group structures (Rose and Croft, 2015), and this can have a negative impact on an individual's fitness and wellbeing (Price and Stoinski, 2007). Low breeding success in captivity has frequently been linked to stress caused by pro-longed confinement in sub-optimal captive environments (Peng et al., 2007; Descovich et al., 2012; Marshall et al., 2016), and limited opportunity to interact with con-specifics (Mallapur et al., 2009; Swaisgood and Shulte, 2010). For example, pig-tailed macaques (*Macaca nemestrina*) housed in high density conditions have a higher incidence of foetus abortions than those housed in smaller groups (Ha et al., 1999). Identifying the factors that inhibit reproduction in captivity can be extremely difficult, and for many endangered taxa, effective management techniques are still to be developed (Snyder et al., 1996).

Understanding the factors that regulate a species' reproduction, and the way in which these factors influence animals differently in the wild versus captivity, is thus important for the global conservation management of threatened species.

1.1.2 The southern white rhinoceros (Ceratotherium simum simum)

1.1.2.1 Historical distribution

There are two subspecies of white rhinoceros: the northern, *Ceratotherium simum cottoni*, and the southern*, Ceratotherium simum simum.* Historically, the southern subspecies was widespread throughout southern Africa, ranging from Zululand in South Africa, through to Botswana, Zimbabwe, Namibia and Eswatini (Emslie, 2020). It was geographically separated by over 2000km from the northern subspecies, which inhabited areas of the Democratic Republic of Congo, Uganda, Chad, South Sudan and Central African Republic (Emslie, 2020).

Over-hunting during the 1800's lead to the rapid extirpation of the southern white rhinoceros, and it was thought to be extinct by the late 19th century (Owen-Smith, 1975). However, in 1895, a population of less than 50 individuals was discovered in Kwazulu-Natal, South Africa (Emslie, 2020), and after over a century of careful protection and management, the wild population has steadily increased to around 18,000 individuals (Emslie et al., 2019). South Africa remains the stronghold for southern white rhinoceros, conserving over 93% of the wild population (Knight et al., 2015). Smaller populations also exist in Namibia, Botswana, Eswatini, Uganda and Zimbabwe after successful reintroductions and in Kenya and Zambia after introductions to areas outside of their natural range.

As recently as 1960, there were more than 2000 northern white rhinoceros remaining in the wild (Emslie and Brooks, 1999). However, an upsurge in poaching and civil unrest in its range countries lead to the rapid decline of the northern subspecies, and there have been no confirmed sightings of northern white rhinoceros in the wild since 2006 (Emslie, 2020). Whilst several individuals were taken into captivity in an effort to save the subspecies, failure to breed successfully in the captive environment has left the northern white rhinoceros on the brink of extinction; now only two females remain in a private wildlife conservancy in Kenya (Tunstall et al., 2018).

1.1.2.2 Current conservation status and poaching threat

Demand for rhino horn escalated from 2007, and illegal poaching now threatens rhinoceros species worldwide (Di Minin et al., 2015). Whilst white rhinoceros numbers increased rapidly between 1992 and 2010, population growth slowed as the rate of poaching increased (Emslie et al., 2019), and between 2012 and 2017, the African population declined by 15% (International Rhino Foundation, 2019). Although annual white rhinoceros poaching rates have declined year on year since 2012 (Emslie et al., 2019), the continental population is still in decline, and thus poaching remains an imminent threat. Estimates of wild white rhinoceros are now between 17,212 and 18,915 individuals (Emslie et al., 2019), and their continued protection and conservation management remains vital to prevent their extinction in the wild.

1.1.2.3 The southern white rhinoceros in Kenya

The southern white rhinoceros was introduced to Kenya in the 1960’s and 70’s, in an effort to expand its range and protection, and improve tourism and education due to its high visibility (Okita-Ouma et al., 2007). Whilst the southern subspecies is not native to Kenya, fossil evidence and cave paintings suggest that another subspecies of white rhinoceros was likely to have existed in East Africa previously (Emslie, 2020). Poaching rates in Kenya have been substantially lower than in other white rhinoceros range countries (Emslie et al., 2019), and this is largely due to the strict protection of rhinoceros within small, fenced sanctuaries. The Kenyan population has grown rapidly, and now there are over 500 southern white rhinoceros distributed across the country's private wildlife conservancies and national parks (Emslie et al., 2019). Consequently, Kenya now holds the third largest number of white rhinoceros in Africa (Emslie et al., 2019), and Kenyan populations play an important role in their conservation.

1.1.2.4 White rhinoceros social behaviour

White rhinoceros are the most social of the rhinoceros species; females and sub-adults form groups of up to six individuals in the wild (Owen-Smith, 1975), and larger aggregations of up to 18 individuals have been observed (du Toit et al., 2006). Associations between individuals may be temporary, lasting less than one month, but can persist for extended periods of time (Owen-Smith, 1975). Adult females are almost always accompanied by a calf or several sub-adults, whereas adult males tend to be solitary (Owen-Smith, 1975). Sub-adults form persistent associations with one another, or with an adult female without a young calf (Owen-Smith, 1975). However, associations with adult females dissolve upon the birth of a new calf, when females no longer tolerate sub-adult companions (Shrader and Owen-Smith, 2002).

Olfactory and vocal signals primarily mediate communication between individuals, as white rhinoceros have relatively poor eyesight (Owen-Smith, 1975; Marneweck et al., 2017). Both males and females of all ages defecate in communal midden heaps, which adult males also use to mark their territory (Owen-Smith, 1975; Rachlow et al., 1999). Research suggests midden heaps act as information centres, signalling the sex, age, territorial and oestrus state of the defecator (Marneweck et al., 2017). Vocal communication also plays an important role in white rhinoceros social interactions (Von Muggenthaler et al., 2003; Policht et al., 2008; Cinková and Policht, 2014), and research has shown that individuals use 'pant calls' to carry information on a caller's sex, age-class and social context (Cinková and Policht, 2014, 2016). Due to their well-developed communication system, inter-individual relationships are likely to serve an important function to white rhinoceros, yet little research has focussed on the factors driving their grouping patterns (exceptions include: Shrader and Owen-Smith, 2002; Shrader et al., 2013), or the potential fitness benefits associated with sociality.

1.1.3 White rhinoceros reproduction and population management

1.1.3.1 Reproduction and population management in situ

Most of our understanding of wild white rhinoceros reproductive behaviour comes from research conducted in South Africa in the 1970's (Owen-Smith, 1973, 1975). Females undergo their first oestrus at around five years of age, remaining within their social group until the birth of their first calf (Owen-Smith, 1975). White rhinoceros are slow-breeders, with a gestation period of 16-18 months. Females usually come into oestrus again once the calf has reached at least six months of age, and inter-calving intervals average 2.5 years long (Owen-Smith, 1975). The calf usually remains with its mother, often as part of a group with other sub-adults, until the female drives it away upon the birth of a new calf (Shrader and Owen-Smith, 2002). Adult females, along with their dependent calf and any sub-adult companions, adopt relatively large home ranges (15-59km^2 (Owen-Smith, 1975; Pienaar et al., 1993; White et al., 2007; Thompson et al., 2016)), which overlap with those of several other individuals and groups (Owen-Smith, 1975; Shrader and Owen-Smith, 2002).

Adult males do not reach sexual maturity until around 8-10 years of age, when they begin to compete for their own territory and adopt an alpha male status (Owen-Smith, 1975). However, around one third of adult males will assume a sub-dominant status, occupying small areas of habitat within alpha males' territories (Owen-Smith, 1975). Usually, only alpha males gain access to females, as sub-dominant males rarely attempt to mate (Owen-Smith, 1975). Territorial males occupy clearly demarcated territories (10-50km^2 (Pienaar et al., 1993; Rachlow et al., 1999; White et al., 2007; Thompson et al., 2016), which are typically smaller than the home ranges of adult females and sub-adult groups (Rachlow et al., 1999; White et al., 2007). Alpha males fiercely defend their territory from other males, and breeding success is often related to both territory grassland cover, and the amount of time an adult female spends within their territory, suggesting males that occupy better quality habitat are favoured by females (White et al., 2007).

Maximising the reproductive output of populations to offset the effects of poaching is a key priority in the management of white rhinoceros (du Toit et al., 2006; Knight et al., 2015). Females generally breed well in the wild, evidenced by an average annual growth rate of 7.1% across the African population between 1992 and 2010, before poaching levels started to escalate (Emslie et al., 2016). However, population growth rate has not been equal across populations, not only due to differences in poaching pressure (Emslie et al., 2019), but also due to variation in birth rates (Owen-Smith, 1975; Rachlow and Berger, 1998; Ververs et al., 2017; Ferreira et al., 2019). The reasons for reproductive disparity between populations remain unclear, but may be linked to differences in population density (Rachlow and Berger, 1998), seasonal and annual variation in resource availability (Ferreira et al., 2019), or population sex and age structure (Ferreira et al., 2015; Emslie, 2020). As the southern white rhinoceros has increased at a rapid rate after emerging from a severe population bottleneck, genetic diversity is likely to be low within certain populations (Braude and Templeton, 2009), and this may also contribute towards reduced fertility (Ruiz-López et al., 2012).

Whilst the designation of protected areas has played a major role in the protection of rhinoceros in Africa (Emslie and Brooks, 1999; Knight et al., 2015), confinement within small sanctuaries or game reserves limits natural dispersal and genetic mixing between populations. Most white rhinoceros populations are managed either nationally or regionally as a meta-population (du Toit et al., 2006), and individuals are exchanged between populations through translocation (Emslie and Brooks, 1999). The on-going monitoring of demographic and reproductive parameters is necessary to ensure populations are managed to maximise productivity. Performance parameters, such as those established by the Southern African Development Community Rhino Management Group (du Toit et al., 2006), are used as benchmarks to assess population performance. Most rhinoceros management strategies aim to achieve an annual meta-population growth rate above 5% (du Toit et al., 2006; Knight et al., 2015; Amin et al., 2017), and measures such as female inter-calving interval length and infant mortality rate, are used to identify whether a population is underperforming (du Toit et al., 2006).

1.1.3.2 Reproduction and population management ex situ

Due to the challenges associated with protecting rhinoceros in the wild, captive populations can serve as important genetic and demographic reservoirs to supplement or re-establish populations. Regional Captive Propagation Programmes, such as the European Endangered Species Programme (EEP) (EAZA, 2020), have been established to coordinate breeding between institutions, with the aim of maintaining a self-sustaining, genetically diverse meta-population.

In 2018, there were 654 white rhinoceros registered in captive institutions across the world (Versteege, 2018). However, captive breeding programmes for white rhinoceros have been failing due to extremely low birth rates (Swaisgood et al., 2006; Reid et al., 2012), and now the number of individuals exported from the wild exceeds the number that still reside in captivity (Swaisgood et al., 2006). Reproduction has been particularly poor in captive-born females, the F1 generation, with as few as 8% of females reproducing in some populations (Schwarzenberger et al., 1998). Furthermore, within the European captive population, just 26% of individuals imported from the wild since the 1950's have ever reproduced (Versteege, 2018).

The factors driving the poor reproductive success of captive female white rhinoceros remain unclear, and most research to date has focussed on the intrinsic factors that limit female reproduction. Studies have shown there is no evidence of reproductive seasonality in females held in captivity (Patton et al., 1999; Brown et al., 2001), but irregular oestrus cycles and acyclicity have frequently been identified as factors limiting female reproduction (Brown et al., 2001; Hermes et al., 2006). For example, in the European and North American Species Survival Program, over 50% of females have absent or erratic oestrous cycle activity (Schwarzenberger et al., 1998; Patton et al., 1999). In addition, captive rhinoceros may develop reproductive organ pathologies. Endometrial and ovarian cysts, uterine leiomyoma, adenoma and adenocarcinoma, are frequently reported in female Sumatran rhinoceros (Schaffer et al., 1994), Indian rhinoceros (Hermes et al., 2014), and white rhinoceros (Radcliffe et al., 1997; Hermes et al., 2006; Hermes and Hildebrandt, 2011), and have been linked to a reduced reproductive lifespan (Hermes et al., 2014).

Reproductive-tract pathologies are likely an age-related consequence of long non-reproductive periods (Hermes et al., 2006), as they are significantly more common in nulliparous than parous females (Hermes et al., 2005, 2006). It has therefore been suggested that pathologies associated with the ageing of female genital organs can be prevented with the achievement of at least one pregnancy (Hermes et al., 2006). However, as irregular oestrus cycles and reproductive-organ pathologies are no more common in captive-born than wild-born females, they do not explain why reproductive output is substantially lower in F1 females (Radcliffe et al., 1997; Schwarzenberger et al., 1998; Patton et al., 1999; Brown et al., 2001; Hermes et al., 2006). Diet has been linked to a loss of fertility in captive female white rhinoceros (Tubbs et al., 2012, 2016), and recent studies suggest that reproduction may be driven by the gut microbiota's transformation of dietary phytoestrogens (Tubbs et al., 2016; Williams et al., 2019).

Studies have also shown there are no differences between the socio-sexual behaviours or reproductive cycles of wild-caught and captive-born females, and males show no preference between the two (Schwarzenberger et al., 1998; Patton et al., 1999; Swaisgood et al., 2006). Reproductive suppression, whereby the reproduction of subordinate individuals is supressed by dominants, has been proposed as a cause of poor reproduction in captive female white rhinoceros (Carlstead and Brown, 2005). Consequently, most zoos aim to transfer females out of their natal group before reaching sexual maturity, as it is possible that females hormonally suppress reproduction in their daughters (Versteege, 2018). There is conflicting evidence for the existence of reproductive suppression in white rhinoceros (Carlstead and Brown, 2005; Swaisgood et al., 2006; Metrione and Harder, 2011), as research has shown that F1 females may be more likely to breed when housed with F0 females, than when not (Swaisgood et al., 2006). This suggests social facilitation of reproduction may exist in white rhinoceros.

1.1.4 Potential drivers of white rhinoceros reproduction

1.1.4.1 Social conditions ex situ

Captive females are often housed in small groups with fewer social partners than they would experience in the wild (Metrione and Eyres, 2014). Across captive populations, group sizes vary considerably, ranging between two and eleven individuals in the European population, with most institutions housing less than five individuals (Versteege, 2017). Inadequate social conditions in the captive environment may cause excessive stress in female white rhinoceros, which could contribute towards their poor reproductive output.

Female white rhinoceros housed in smaller enclosures, and with more individuals, exhibit space maintenance vocalisations more frequently than those housed with just one calf and more space to roam (Metrione et al., 2007). Furthermore, large groups of rhinoceros confined within small captive environments may form dominance hierarchies, which are enforced during competition for food or shade, a behaviour never recorded in wild populations (Metrione et al., 2007). This suggests that female white rhinoceros can become socially stressed within the captive environment. Hormonal evidence may further support this, as females housed alongside another female from adolescence have lower faecal corticosterone levels, the main hormone released during stress, than those introduced at a later stage in life (Metrione and Harder, 2011). Whether social mechanisms mediate reproduction in female white rhinoceros is not yet understood, and requires further investigation.

1.1.4.2 Resource availability and population density in situ

White rhinoceros are *megaherbivores* that exists solely on a diet of grass (Owen-Smith, 1988). Extrinsic factors, such as rainfall, therefore largely influence their food availability, and this can also affect their reproduction and survival. For example, the survival of white rhinoceros calves is related to the level of rainfall experienced during the two preceding years, and population growth rate is positively correlated with rainfall (Ferreira et al., 2015). Furthermore, populations in areas prone to severe droughts are likely to suffer higher mortality rates and lower birth rates due to reduced grass biomass (Ferreira et al., 2019). Variation in resource availability and habitat quality is thus likely to contribute towards the differences in reproductive output between populations.

Biotic factors, such as inter-specific competition and grazing pressure, may also influence white rhinoceros reproduction. Whilst resource partitioning may reduce niche overlap between species with different feeding preferences or digestive strategies (Jarman and Sinclair, 1984), during the dry season when resources are more scarce, inter-specific competition may become more apparent (Hempson et al., 2015). As increased herbivore mortalities during a drought are primarily linked to a reduction in food availability, rather than a lack of drinking water (Knight, 1995; Dudley et al., 2001), the provision of artificial water resources may further exacerbate this (Knight, 1995).

It has also been suggested that white rhinoceros birth rates are likely to be subject to density-dependent regulation (Ferreira et al., 2015). It is therefore important to closely monitor demographic performance parameters and inter-specific associations in populations, and to employ active management strategies, such as translocations or alterations to reserve design, in order to buffer the potential impacts of resource availability on population persistence.

To maximise breeding performance, and minimise death rates due to limited food availability, rhinoceros populations should be managed below ecological carrying capacity (du Toit et al., 2006). It has been suggested that 75% of ecological carrying capacity is the highest density in which black rhinoceros, *Diceros bicornis*, can thrive without facing density-dependent feedback in relation to breeding performance and mortality (Adcock, 2001). Breeding performance parameters, such as population growth rate and inter-calving interval length, can thus be used as indicators that a population may be reaching its ecological carrying capacity (Hitchins and Anderson, 1983; Owen-Smith, 1988, 1990; Adcock, 2001).

Whilst variation in resource availability may drive differences in white rhinoceros reproductive success between populations, it is less likely to drive reproductive disparity within populations, particularly in populations enclosed within small reserves, where resources are relatively evenly distributed. Due to the social nature of white rhinoceros, differences in association frequency and social connectivity could also influence female breeding success (Silk et al., 2009; Cheney et al., 2016). Group formation may function as a form of defence from predators or territorial males (Jarman, 1974; Caro et al., 2004), or to transmit information on the location of feeding sites (Mueller et al., 2013; Sheppard et al., 2018). However, as adult female white rhinoceros with young calves are no less vigilant in larger sized groups (Shrader et al., 2013), the potential benefits of group formation in relation to increased defence may only apply to sub-adults. It remains unclear why adult females tolerate sub-adult companions, and further research on the potential fitness consequences associated with female grouping patterns is required to develop a better understanding of the factors driving their social behaviour.

1.1.5 Social network analysis as a tool for white rhinoceros conservation management

1.1.5.1 What is social network analysis?

Social network analysis (SNA) can be used to understand the causes and consequences of complex social and ecological interactions within populations. SNA creates an analytical representation of the observed pattern of associations or interactions between individuals in a population, which can be used to identify social structures and quantify the intensity of associations (Farine and Whitehead, 2015; Silk et al., 2017). This can not only be used to describe the social structure of a population, but can also be used to investigate the relationship between social connectivity and aspects of individual fitness or survival (Silk et al., 2003; Stanton and Mann, 2012; Cheney et al., 2016).

1.1.5.2 *The application of social network analysis to in situ white rhinoceros conservation*

SNA provides an excellent tool in the field of in situ species conservation (Snijders et al., 2017). Animal social networks may be adapted to current environmental conditions, making them vulnerable to rapid environmental change (Snijders et al., 2017). Human-induced spatiotemporal fluctuations in the environment can have a detrimental impact on the social dynamics of a population, by increasing disease transmission and host susceptibility (Harvell et al., 2002), or disrupting important social behaviours, such as mate selection, territoriality and reproduction (Verdade, 1996).

Social networks can act as behavioural indicators, providing early warning of population fragmentation or population crashes (Snijders et al., 2017). Poaching may have serious impacts on white rhinoceros social structure and population viability, through the removal of key individuals with distinct social roles (Snijders et al., 2017). For example, killer whales, *Orcinus orca*, can cope with the removal of random individuals, but not the targeted removal of juvenile females (Williams and Lusseau, 2006). Confinement within small sanctuaries is also likely to increase white rhinoceros encounter rates, as individuals are forced to come together to access clumped resources (Banks et al., 2007). Changes in the rate of social interaction may influence mate choice options and intraspecific competition, both of which can impact individual fitness (Brent, 2015). An increase in aggressive interactions may result in reduced fitness through elevated stress levels, higher injury rates, or the facilitation of disease transmission (Hamede et al., 2009; Snijders et al., 2017). Knowledge of white rhinoceros association patterns can thus guide management interventions, such as the targeted translocation of individuals out of high-density areas.

Whilst reintroduction and translocation programmes often consider population demographics (Sarrazin and Legendre, 2000), or the genetic background of individuals (Haig et al., 1990), they rarely consider existing social bonds (Goldenberg et al., 2019). SNA can be used to identify pre-existing social structures in white rhinoceros populations, and guide the selection of groups for translocation, which may facilitate their long-term social stability post-release (Snijders et al., 2017). For example, black-tailed prairie dogs, *Cynomys* *ludovicianus*, translocated in family units are more likely to survive and reproduce than those translocated without family members (Shier, 2006).

1.1.5.3 The application of social network analysis to ex situ white rhinoceros conservation

SNA also has the potential to improve the management of species in captivity. Social bonds serve as important mediators of individual health, welfare, long-term fitness and reproductive output (Silk et al., 2003, 2010; Silk, 2007; Rose and Croft, 2015). Knowledge of natural social group structures and their impact on individual fitness can be useful for captive breeding programmes, to minimise social stress and enhance the chances of successful reproduction. For example, SNA has shown that manipulating group composition and matriline configuration in groups of captive rhesus macaques, *Macaca mulatta*, can promote social cohesion and reduce aggression and mortality (McCowan et al., 2008).

The stability of social groups in captivity can also have important consequences for individual welfare and breeding success (Rose and Croft, 2015). For example, calves, *Bos taurus*, become distressed when placed with unfamiliar conspecifics (Færevik et al., 2006), and those that are subjected to social instability are less socially confident and more aggressive (Bøe and Færevik, 2003). As captive white rhinoceros are regularly moved between institutions for breeding management (Versteege, 2018), the structure of groups is often transient. In particular, as sub-adult females are often separated from their natal group before reaching sexual maturity (Versteege, 2018), this may have detrimental impacts on individual well-being, as important social bonds are broken and existing group dynamics are altered. Familiarity with conspecifics can be an important mediator of breeding success (Beletsky and Orians, 1989; Grabowska-Zhang et al., 2012). It is thus possible that the low reproductive success of female white rhinoceros is related to inadequate or unstable social conditions in captivity.

Wild white rhinoceros provide an excellent model to examine social networks and reproduction under natural conditions. Due to the long-term monitoring of populations for conservation purposes, extensive demographic records are available to assess female breeding performance. Furthermore, individuals can easily be located and identified by park rangers on a daily basis. Knowledge of the structure of rhinoceros social groups in the wild, and the importance of particular social relationships to individual fitness and reproduction, could therefore be used to inform the selection of groups in captivity. Recreating natural social conditions in the captive environment may then help to reduce social stress (Caro, 1993), and this could stimulate breeding in female white rhinoceros.

1.2 THESIS AIMS

The main aim of this thesis is to identify the social and ecological factors that influence reproduction in female white rhinoceros, to inform the conservation management of in situ and ex situ populations. This can be divided into four main objectives;

1. To determine the viability and reproductive performance of captive rhinoceros, and identify the key factors mediating population growth.
2. To identify aspects of husbandry and social conditions that are related to female white rhinoceros breeding success in captivity.
3. To use social network analysis to describe and analyse the social structure of in situ white rhinoceros populations, and determine whether social connectivity influences female reproduction.
4. To identify important features of white rhinoceros habitat, and determine whether differences in ecology and population density influence population performance.

1.3 THESIS STRUCTURE

To address the objectives of this study, this thesis has the following structure:

Chapter 2

This chapter uses studbook data to investigate the reproductive performance and sustainability of the European captive white rhinoceros population. Demographic performance parameters are used to compare the European population with in situ white rhinoceros populations, and previously established benchmarks. Population viability analysis is used to evaluate the long-term viability of the European population, and sensitivity analyses are used to identify key factors mediating population growth. Areas where the population is underperforming are identified, and improvements required to achieve a self-sustaining population are discussed.

Chapter 3

This chapter uses a multi-institutional comparative approach to assess the impact of varied social conditions and husbandry measures on the breeding success of captive female white rhinoceros. The European white rhinoceros studbook is used to identify aspects of captive management related to institution breeding success, and female calving success, across the entire European population. A questionnaire survey on a sample of European institutions that maintain white rhinoceros is used to identify factors that affect female socio-sexual behaviours, copulation and pregnancy success. Group compositions likely to improve female breeding success are discussed to provide guidance for breeding management.

Chapter 4

This chapter introduces the four in situ study populations in Kenya from which data were collected for chapters 5 and 6, namely: Ol Pejeta Conservancy, Meru National Park, Lake Nakuru National Park and Lewa Wildlife Conservancy. An overview of the climate, habitat and species in each reserve is provided.

Chapter 5

This chapter uses data on group compositions from the four study populations to describe white rhinoceros social network structure and association patterns. Social networks are compared between populations to determine the defining features of white rhinoceros social structure, and identify how population size and density affect grouping patterns. The influence of sex and age-class on social connectivity are investigated, to provide insights on age-sex class social requirements. The temporal stability of pairwise associations is examined, to assess whether familiarity is likely to be important to white rhinoceros. The relationship between female inter-calving interval length and social connectivity is determined, and the potential influence of social conditions on female breeding success is discussed.

Chapter 6

This chapter investigates the habitat use of the four white rhinoceros study populations, and examines how differences in resource availability and population density relate to reproduction and ecological carrying capacity. The ecological variables associated with white rhinoceros habitat are used to identify resources or features likely to be important for reproduction and survival. The differences in ecology and habitat use between populations and seasons are examined, and variables that are likely to cause variation in reproductive output are identified. Variation in resource availability and competition between the study populations are related to differences in ranging behaviour and population performance, and used to provide insights on ecological carrying capacity.

Chapter 7

This chapter summarises the results from chapters 2,3,5 and 6, evaluating the key factors that are likely driving female breeding success in both ex situ and in situ white rhinoceros populations. New insights on white rhinoceros social structure derived from this thesis are highlighted, and the application of this information to white rhinoceros conservation management is discussed. Recommendations to improve breeding success in captivity and increase the conservation potential of wild populations are provided, and directions for future research are discussed.

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2 THE REPRODUCTIVE PERFORMANCE AND FUTURE VIABILITY OF EUROPEAN CAPTIVE SOUTHERN WHITE RHINOCEROS (*CERATOTHERIUM SIMUM SIMUM*)

Abstract

Captive populations play an important role in the conservation of threatened species, as an insurance against extinction in the wild, and as a source for future reintroduction efforts. Due to the threat from poaching, captive breeding programmes have the potential to improve the conservation of the southern white rhinoceros, *Ceratotherium simum simum*. However, establishing self-sustaining captive populations of white rhinoceros has proven extremely difficult due to low female reproductive output, and it is unknown whether current captive populations are viable. This study investigated the recent reproductive performance and sustainability of the European captive white rhinoceros population. Demographic performance parameters were compared with those of in situ populations, and previously established benchmarks, to identify areas where the captive population is underperforming. Population viability analysis was used to assess the long-term viability of the population, and sensitivity analyses were used to identify the demographic parameters limiting population growth. The results suggest the captive population is performing below its potential in comparison to in situ reference populations, and is projected to decline at a rate of approximately 2% per year. The low proportion of females calving each year (10%) is the key factor limiting population growth, though high infant mortality rates further exacerbate this. Furthermore, few individuals have contributed to the captive gene pool, causing a severe reproductive skew in the population. These results suggests that the European captive white rhinoceros population is not sustainable, and is threatened from low genetic diversity and inbreeding. If the population is to act as a safeguard against extinction in the wild, the proportion of females calving annually must increase to a minimum of 17%, and a greater number of individuals must contribute towards the captive gene pool.

2.1 INTRODUCTION

Captive breeding programmes have become increasingly important to the conservation of species that have undergone severe population declines in the wild, due to factors such as habitat loss or extirpation from over-harvesting (Ochoa et al., 2016). Captive populations can act as an insurance against extinction, allowing species to recover in the absence of threats experienced in the wild (Zimmermann, 2010), and providing a source for population supplementation in the future. For captive breeding programmes to succeed, ex situ populations should be self-sustaining, whereby reproduction at least equals mortality, without need for further supplementation from wild populations. Moreover, captive populations must be carefully managed, to maintain both the genetic diversity and natural characteristics of wild populations, allowing them to remain reproductively and behaviourally viable for any future reintroduction efforts (Foose and Wiese, 2006).

Captive breeding programmes have the potential to play an important role in the conservation of the southern white rhinoceros, *Ceratotherium simum simum.* This subspecies has recovered from near extinction in the late 1800's, to a population of around 18,000 individuals (International Rhino Foundation, 2019). However, due to the rise in demand for rhino horn from 2007, illegal poaching has caused the rapid decline of rhinoceros species worldwide (Di Minin et al., 2015). The northern white rhinoceros, *Ceratotherium simum cottoni*, has already been driven to extinction in the wild due to extensive poaching and civil war in its range countries, and there are now only two individuals of this subspecies left, both of which are female (Tunstall et al., 2018). Poaching also threatens the future survival of the southern white rhinoceros, as birth rates are no longer exceeding death rates in many populations (International Rhino Foundation, 2019). This subspecies could therefore be subject to another population crash if the rate of poaching continues to escalate. Maintaining captive populations of southern white rhinoceros is thus crucial, not only to provide a safeguard for this subspecies until the threat from poaching is reduced, but also to retain genetically viable populations for any future reintroduction attempts.

Efforts to maintain a self-sustaining population of southern white rhinoceros in captivity have been hindered by low population growth, and this has been attributed to the low reproductive success of females (Swaisgood et al., 2006). White rhinoceros have inherently low reproductive rates due to an 18-month long gestation period, and consequently, inter-calving intervals less than three years long are considered to indicate good breeding performance (du Toit et al., 2006). Any variation in female breeding success is therefore likely to have a large impact on population persistence and extinction risk.

Reproductive output has been particularly low in females born in captivity, with as few as 8% reproducing in certain ex situ populations (Schwarzenberger et al., 1998). This is extremely low in comparison to wild white rhinoceros, where over 30% of females calve annually in well-performing populations (du Toit et al., 2006). Irregular oestrus cycles and reproductive-organ pathologies are often reported in captive females (Radcliffe et al., 1997; Schwarzenberger et al., 1998; Patton et al., 1999; Brown et al., 2001; Hermes et al., 2006, 2007; Hermes and Hildebrandt, 2011), and have been linked to a reduced reproductive lifespan (Hermes et al., 2014). Research suggests that these irregularities may be caused by pro-longed periods of reproductive inactivity (Hermes et al., 2005, 2006). The reasons why so few females attempt to mate are unclear, and thus breeding white rhinoceros in captivity remains challenging.

The European Endangered Species Programme (EEP) for white rhinoceros is a captive breeding programme that manages white rhinoceros from different zoological institutions across Europe as a single meta-population. The primary goal of captive breeding programmes is to increase population size as quickly as possible to avoid extinction, whilst also retaining founder genetic diversity, and a stable age-sex structure that ensures the population is viable for continued growth and possible reintroduction efforts (Lacy, 1997; Ballou et al., 2010). Captive breeding programmes use studbook databases to maintain a record of population pedigree, and aim to minimise inbreeding by selecting unrelated individuals for potential breeding efforts (Ochoa et al., 2016). However, captive populations can function like small isolated populations in the wild, as with only a limited number of individuals in the breeding pool, some degree of inbreeding and genetic drift is often inevitable (Willoughby et al., 2015). Maintaining genetic diversity in captive populations can be more difficult in species with low reproductive rates (Marker and O'Brien, 1989) or polygynous mating systems, where some individuals do not contribute to the captive gene pool (Renan et al., 2015). The poor breeding success of captive-born female white rhinoceros further exacerbates this, as if only a small proportion of females are contributing to the captive gene pool, reproductive skew and unequal founder representation could further limit the genetic viability of the population (Edwards et al., 2015).

Due to limited population growth, the European captive population has had to rely heavily on importing wild-caught rhinoceros from South Africa to offset low reproductive rates (Versteege, 2007, 2014). The continual addition of wild-caught individuals to the population may have balanced the effects of genetic drift (Ochoa et al., 2016), and maintained some level of genetic diversity in the population. However, there have been few imports from the wild since 2012 (Versteege, 2017), and it is unclear whether the population is now self-sustaining. An assessment of the reproductive performance and viability of the EEP population is urgently required to determine whether it is demographically and genetically viable to support itself.

Population viability analysis (PVA) is a conservation management tool that uses quantitative methods to evaluate the threats faced by a population, their risk of extinction, and their likely future growth rates (Keedwell, 2004). It provides a framework that can be used to evaluate the effectiveness of current management practices (Edwards et al., 2015), and the likely impacts of alternative management strategies on population persistence (Suter et al., 2014; Kumar et al., 2016). PVA uses stochastic simulations to project the fate of a population based on specified demographic and life history parameters, including birth and death rates of particular age-classes, population age structure, and sex ratio. Genetic stochasticity and inbreeding variability can be incorporated into PVA models, and used to assess the long-term genetic viability of a population. Sensitivity analyses can then be used to identify which factors are limiting population growth, such as female fecundity (Edwards et al., 2015), infant mortality (Mortensen and Reed, 2016), or anthropogenic threats (Lacy et al., 2017; Valle et al., 2018). PVA models require extensive data on a species' life-history parameters, which can often be difficult to obtain. However, in captive populations, studbooks provide the detailed demographic information required to determine accurate model parameters. PVA thus provides an excellent tool to improve our understanding of whether captive populations are sustainable over the long-term, under current management practices and demographic parameters.

Whilst PVA models allow the factors limiting population growth to be identified, they cannot assess whether current parameter values are satisfactory. Such questions require a benchmark, to determine whether improvements are required, or are even likely to be possible (Akcakaya and Sjogren-Gulve, 2000). For captive populations, the performance parameters of in situ counterparts provide a good target (Edwards et al., 2015), and can be used to assess the potential for improvement ex situ. Targeted management strategies can then be developed to improve current population performance to a specified level.

This chapter used long-term demographic data and PVA to investigate the reproductive performance and sustainability of the European captive white rhinoceros population. The aim of this chapter was to determine whether the population is demographically and genetically viable, and to identify the key factors mediating population growth. The first objective was to assess current population performance, by comparing demographic performance measures with in situ populations and established benchmarks. The second objective was to evaluate the long-term viability of the population, based on projections of future growth rate and extinction risk under current demographic parameters. The final objective was to identify the demographic factors limiting population growth, and areas where potential improvements could be made.

2.2 METHODS

2.2.1 Population performance

2.2.1.1 Ex situ study population

Demographic data were obtained from the European Association of Zoos and Aquariums (EAZA) studbook for the southern white rhinoceros, using the Single Population Analysis and Records-Keeping System (SPARKS; (ISIS, 2011), and the population management programme PMx (Lacy et al., 2012). A window of the 1st of January 1997 to the 31st December 2016 was used to determine population performance parameters. To account for any recent improvements in reproductive performance, and to provide comparison with available data on in situ reference populations (see following section), population performance was also assessed using a sub-set of the data, from 1st January 2007 to 31st December 2016.

Annual population size was determined from the number of individuals alive in the population at the end of each year. Any individuals that died during the same year they were born were not included in annual population size counts, but were included in annual birth counts. Additionally, the number of white rhinoceros imported and exported from the EEP annually were totalled, to determine the degree to which wild-caught individuals support the population. Demographic data from the EEP studbook were used to determine several aspects of male and female reproductive performance, as well as overall population performance (Table 2.1). For all measures, adult females were defined as being >8 years of age, and adult males as being >13 years of age, on the 1st of July, for each year between 1997 and 2016. These sex-specific age-limits were chosen as female white rhinoceros usually give birth for the first time between 6.5 and 7.5 years old (Owen-Smith, 1973; Metrione and Eyres, 2014; Ververs et al., 2017), whereas males do not reach sexual maturity until around 10-12 years of age (Metrione and Eyres, 2014). Therefore, it would be expected that individuals older than this have had enough time to start breeding. To assess the viability of the current population, the age-sex structure and proportion of (i) breeding individuals (ii) potential breeders and (iii) post-reproductive age females (defined as >34 years old; Versteege, 2017) in the population on the 31st December 2016, were also determined.

2.2.1.2 In situ reference populations

To assesses the reproductive performance of the EEP population, a set of performance indicators established by the Southern African Development Community (SADC) rhino management group (Table 2.1), for both black rhinoceros, *Diceros bicornis,* and white rhinoceros populations in South Africa, were used to provide a benchmark for each demographic parameter (du Toit et al., 2006). Additionally, demographic data from two white rhinoceros populations in Kenya, Lewa Wildlife Conservancy and Meru National Park, were used to provide a measure of recent white rhinoceros population performance in situ. A window from the 1st of January 2007 – 31st December 2018 was used to determine the reproductive performance of the in situ reference populations, as earlier records were either unavailable or incomplete. Reproductive performance parameters were based on 96 individuals from Meru National Park, and 140 individuals from Lewa Wildlife Conservancy, that existed during the aforementioned timeframe.

Table 2.1 The demographic parameters and established benchmarks used to assess the reproductive performance of the European captive white rhinoceros population. Adult females were defined as >8 years of age, and adult males as >13 years of age. Established benchmarks are based on those established by the SADC rhino management group (du Toit et al., 2006)**.**

Demographic parameter	**Established benchmark**	**Description**
Overall population performance		
Growth rate	>5% indicates moderate to good performance.	The mean percentage increase in population size from one year to the next.
Mortality rate	Mortality rates <4% are considered the benchmark.	The mean percentage of the population that died each year.
Birth rate	There is currently no established benchmark for birth rate. To achieve a growth rate >5%, birth rate would need to be >5% higher than mortality rate.	The mean percentage increase in population size due to births each year.
Infant mortality rate	<10% is the ideal benchmark in the wild. However, with no predation pressure in captivity, it may be even lower.	The mean annual percentage of calves that were stillborn, or died before reaching one year of age.
Female reproductive performance		
Female fecundity	>30% of females calving each year indicates moderate fecundity in wild populations, and >40% indicates excellent fecundity. The benchmark was set at >30%, as captive females may have more limited breeding opportunities.	The mean percentage of adult females calving each year. This provides a measure of how many females calve each year, and therefore variation will affect population growth.
Female breeding success	There is no established benchmark for the proportion of females with breeding success across a population. However, achieving close to 100% of females breeding would maximise the genetic diversity of the population.	The percentage of adult females that existed in the population and calved. This provides a measure of how many females have contributed to the EEP population gene pool, and therefore variation will affect the EEP population's genetic diversity.
Inter-calving interval length	<3 years indicates moderate to good fecundity.	The mean length of time, in years, between births for females that have calved more than once.
Female age at first reproduction	>7.5 years old indicates poor population performance. Therefore, <7.5 years was set as the benchmark.	The mean age, in years, of a female when they first calved. This could only be calculated for captive-born females, as the birth dates of most wild-born females are unknown or based on an estimate.
Captive- and wild-born female breeding success	No established benchmark in captivity. Ideally, breeding success would be equal across captive and wild-born females.	The percentage of females that have reproduced and were (i) born in the wild, and (ii) born in captivity.
Male reproductive performance		
Male breeding success	No current benchmark established. As dominant males have greater access to females, some degree of reproductive skew would be expected under natural conditions. In captivity, excess males are kept in bachelor groups (Metrione and Eyres, 2014). This may limit breeding opportunities, which could result in a reproductive skew in the population.	The percentage of adult males that existed in the population and successfully sired offspring.
Male age at first reproduction	There is currently no benchmark for male age at first reproduction. As males reach sexual maturity around the ages of 10-12 (Metrione and Eyres, 2014), an age at first reproduction <15 may be considered good.	The mean age of a male, in years, at the birth of the first calf they sired. This was only calculated for captive-born males, as most birth dates for wild-born males are only an estimate.
Captive- and wild-born male breeding success	No established benchmark in captivity. Ideally, breeding success would be equal across captive and wild-born males.	The percentage of males that reproduced and were (i) born in the wild, and (ii) born in captivity.

2.2.2 Long-term population viability

Population viability analysis (PVA) was conducted using Vortex v10.2.5 (Lacy and Pollak, 2017), to evaluate the demographic sustainability of the European captive white rhinoceros population. Vortex was selected as it is the most suitable PVA software for species with long generations and low levels of fecundity (Lacy, 1993; Lacy et al., 2017). A 100-year timeframe for the model was chosen as shorter timescales can falsely indicate population perpetuity (Suter et al., 2014). Average age-sex-specific mortality rates were obtained from SPARKS data files for the EEP population. Sex-specific mortality rates for each year of age, up until mean sex-specific age of first reproduction, were input into Vortex (Table 2.2). Thereafter, mortality rates were divided into age-sex classes based on reproductive life history and mortality patterns evident in the EEP population (males: 14-23, 24-34 and >34; females: 9-22, 23-34, 35-44 and >44; Table 2.2).

Vortex uses a default inbreeding value of 6.29 lethal equivalents (alleles that are lethal when homozygous) per diploid individual. This is based on the mean number of lethal equivalents estimated from 40 different species of mammals in captivity (O'Grady et al., 2006). However, the southern white rhinoceros population increased at a rapid rate after emerging from a severe population bottleneck at the end of the 19th century, increasing from less than 50 individuals to around 18,000 (Emslie and Brooks, 1999). Small isolated populations are more susceptible to deleterious mutations and genetic drift (Hedrick and Kalinowski, 2000), and thus white rhinoceros are likely to have a much higher genetic load, and an increased susceptibility to inbreeding depression (Keller and Waller, 2002). Whilst there are currently no estimates of genetic load in white rhinoceros, black rhinoceros have also experienced drastic population declines, and estimates suggest they have 16.00 lethal equivalents in relation to offspring production (Cain et al., 2013). Therefore, this was set as the baseline in the PVA model, as it was considered a more accurate representation of genetic load in rhinoceros.

An Inbreeding Coefficient (F) value of F=0.0079 was used to represent the genetic diversity of the starting population in the baseline model. This was based on Wright's Coefficient of Relationship, r (Wright, 1922), which was estimated at r=0.0158, for the entire European white rhinoceros population between 2008 and 2012 (Reid et al., 2012). The Inbreeding Coefficient was obtained by halving the average Coefficient of Relationship (Wright, 1922), i.e. 0.0158/2=0.0079. The breeding sub-population of European white rhinoceros has been estimated to have an average Coefficient of Relationship of r=0.688 (Reid et al., 2012). Therefore, an additional model, using an Inbreeding Coefficient value of F=0.344, was also included. For the baseline model, breeding was limited to pairs of individuals with F<0.25. However, for the additional model, using F=0.344, no limit was included as inbreeding was already extremely high.

Table 2.2. The baseline parameters applied in Vortex for the European captive white rhinoceros population.

Baseline parameter	Description
Mating system	Polygynous, with new selection of mates each year
Female breeding age	From age 8 to age 34
Male breeding age	From age 13 to age 41
Maximum age of survival	52
Litter size	1
Sex ratio at birth	1:1 (male : female)
Offspring dependence	2 years
Mate monopolisation [a]	53%
Female fecundity [b]	10%
Environmental variation in female fecundity [c]	3.4%
Initial population size	301
Infant mortality (0-1 year) [d]	Males 22% and Females 23%
Sub-adult mortality [d]	Males: 1-2 = 5% 2-3 = 6% 3-4 = 1% 4-5 = 2% 5-6 = 2% 6-12 = 1% 12-13 = 2% Females: 1-2 = 4% 2-3 = 5% 3-4 = 2% 4-5 = 2% 5-6 = 2% 6-7 = 1% 7-8 = 2%
Adult mortality [d]	Males: ≥14 and ≤23 = 2% ≥24 and ≤34 = 3% >34 = 12% Females: ≥9 and ≤22 = 2% ≥23 and ≤34 = 3% ≥35 and ≤44 = 8% >44 = 20%

[a] *Based on the percentage of adult males in the EEP population in 2016 that had successfully sired offspring.*

[b] *Based on the mean percentage of females calving each year over the last 10 years, to account for any recent improvements in breeding success.*

[c] *The standard deviation for the percentage of females calving each year over the last 10 years.*

[d] *Based on age- and sex-specific mortality rates acquired using PMx and the EEP white rhinoceros studbook.*

All other baseline scenario parameters (Table 2.2) were determined using the EEP white rhinoceros demographic data, and each model was run with 1000 iterations. The population was considered to be a single, closed population, as breeding between institutions is managed through the EEP studbook, and individuals are only rarely exchanged with institutions outside of Europe (Versteege, 2017). Population carrying capacity was set at 1000, over three times the current population size, to ensure none of the simulations exceeded capacity. Neither harvesting nor supplementation were included in the models, as one purpose of this study was to identify whether population growth could be increased without need for further imports from the wild.

2.2.3 Sensitivity analyses

Sensitivity analysis can be used to explore the dynamics of PVA models, by quantifying how changes in parameter estimates impact model outcomes (Cross and Beissinger, 2008). Sensitivity analyses most commonly model the impact of parameter estimates on extinction probability, or minimum viable population size. However, when applied to long-lived, slow-breeding species, like the white rhinoceros, extinction risk may appear negligible, even though the species may be facing severe population declines and a loss of genetic diversity (de Silva and Leimgruber, 2019). For such species, understanding how vital rates influence population growth rate can provide a better understanding of population viability, and in particular, can determine the proximity of a population to its demographic tipping point, i.e. when growth rate switches from positive to negative (de Silva and Leimgruber, 2019).

Two types of sensitivity analysis were used to determine how the growth rate of the EEP population was impacted by the following vital parameters: female fecundity, standard deviation for female fecundity, infant mortality rate, sub-adult mortality rate, adult mortality rate, inbreeding coefficient and number of lethal equivalents (Table 2.3). A relative sensitivity analysis was used to assess the impact of small changes in vital rates to population growth rate (Cooper et al., 2002; Mortensen and Reed, 2016). A logistic regression analysis was used to determine which of the specified parameters under investigation explained the most variability in whether the population had a positive or negative growth rate after 100 simulated years (McCarthy et al., 1995; Cross and Beissinger, 2008; Mortensen and Reed, 2016), i.e. whether it was self-sustaining. The latter acts as a global sensitivity analysis, as it allows several parameters to be varied simultaneously, and thus more evenly samples the parameter space.

2.2.3.1 Relative sensitivity analysis

For the relative sensitivity analysis, each vital parameter was sequentially varied ±10% of its baseline value (Table 2.2), to determine the impact of small changes in each parameter on mean population growth rate, λ. Each scenario was projected over 100 years with 1000 iterations. The relative sensitivity of the model to changes in each parameter was calculated using the following equation $(\lambda+—\lambda-)/(0.2*\lambda0)$, where $\lambda+$ and $\lambda-$ are the output from adjusted parameter values, $\lambda0$ is the output of the baseline model, and 0.2 is the total perturbation of the parameter values (±10%) (Cooper et al., 2002; Mortensen and Reed, 2016). Parameters with sensitivities >1 or <-1 have a disproportionate influence on population growth rate.

2.2.3.2 Global sensitivity analysis

For the global sensitivity analysis, Latin Hypercube Sampling in Vortex was used to create 1000 parameter sets with input values selected from a range of realistic parameter values (Table 2.3). Each parameter set had 10 iterations, resulting in a dataset of 10,000 populations, each with a mean population growth rate, λ, after 100 years. To investigate how variation in each parameter contributed towards whether the population was self-sustaining, growth rate was transformed to a binary response variable, based on whether each simulation resulted in a mean positive or negative growth rate. All scenarios were run under the specified baseline conditions (Table 2.2), with the exception of the parameters under investigation. As the main purpose of the sensitivity analyses was to identify how population growth could be maximised, population carrying capacity was increased to 10,000, to allow for unrestricted population growth.

Vortex simulation results were analysed using a logistic regression in R version 3.4.1 (R Core Team, 2016). The importance of each parameter was determined by comparing their standardised regression coefficients, i.e. the regression coefficient divided by its standard error (McCarthy et al., 1995). As Variable Inflation Factors (VIF's) indicated severe multi-collinearity between model parameters, two models were employed, including only variables with VIF's <2 within the same model (Zuur et al., 2010). To check all other assumptions of logistic regression were met, independent variables were plotted against the logit of the probability of a positive population growth rate, and visual inspection of plots revealed no non-linearity. Standardised residuals were used to check there were no influential outliers with a Cook's distance >3.

Table 2.3. The baseline values and range tested for each parameter in the global sensitivity analysis.

Parameter	Baseline	Range tested	Justification
Female fecundity	10.0	5.0 – 25.0	The minimum percentage of females breeding in the EEP annually was 5%, whilst the maximum was 15%. In the wild, up to 40% of females can calf annually (du Toit et al., 2006). However, to account for limited breeding opportunity in captivity, the upper limit was set at 25%.
Environmental variation in female fecundity	3.4	0.0 – 7.0	Environmental variation is less likely to affect captive populations. Therefore, the lower limit was set to zero, and the upper limit to just over double the baseline value.
Infant mortality	22.5	12.5 – 32.5	Infant mortality ranged from 8-31% between 1996 and 2007. Therefore, a 10% increase or decrease was within realistic levels.
Sub-adult mortality	Baseline (see Table 2.1)	0.5 x baseline – 2 x baseline	Sub-adult mortality was relatively low across each year of age. Therefore, mortality was varied from half to double its baseline level.
Adult mortality	Baseline (see Table 2.1)	0.5 x baseline – 2 x baseline	Adult mortality was relatively low until the oldest age-sex classes. Therefore, mortality was also varied from half to double its baseline level.
Inbreeding coefficient (*F*)	0.0079	0.0040 – 0.3440	The inbreeding coefficient was halved for the minimum level. The upper level was set at 0.344, potentially the maximum level for the EEP breeding sub-population (Reid et al., 2012).
Lethal equivalents	16.0	6.29 – 18.0	Lethal equivalents was set at 6.29 for the minimum level, based on the mean for captive mammals (O'Grady et al., 2006), and increased by just two for the maximum level, as the baseline value was already based on a very high estimate.

2.3 RESULTS

2.3.1 Population performance

2.3.1.1 Overall population performance

Between January 1st 1997 and December 31st 2016, 467 individuals existed in the European captive white rhinoceros population, consisting of 268 females and 199 males (Figure 2.1a). Two hundred calves were born (104 male, 88 female, and 8 un-recorded sex), and 206 individuals died (95 males and 111 females) during this period. Seven individuals were exported to institutions outside of the EEP population, four individuals were imported from

North American institutions, and four individuals were imported from captive institutions in South Africa. The EEP population was supplemented with 106 individuals imported from the wild between 1997 and 2016, 80 of which were female (75.47%). On average, 4.95 individuals were imported from the wild per year (range: 0-18 individuals). Consequently, 49.22% of individuals that existed in the population between 1997 and 2016 were wild derived (Figure 2.1b).

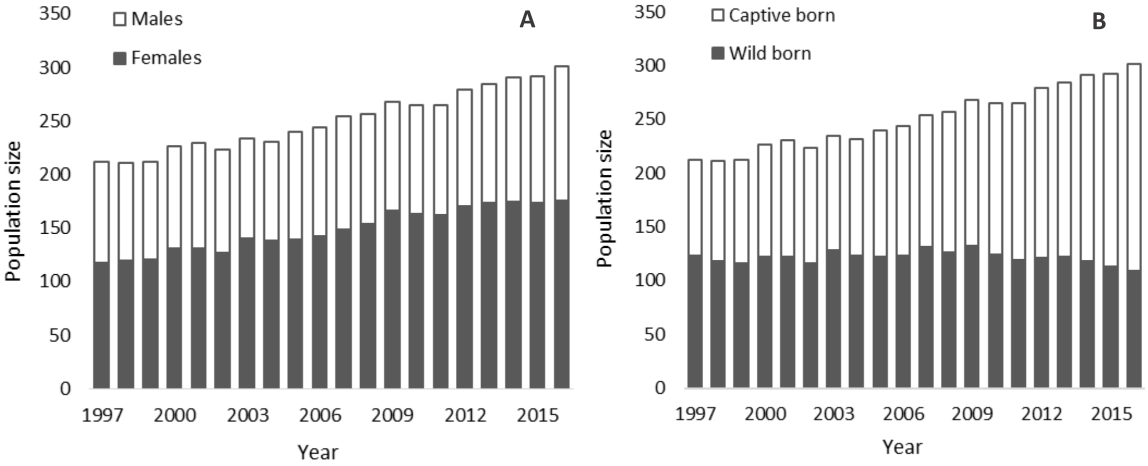

Figure 2.1 The sex structure (a) and birth origin (b) of the European captive white rhinoceros population during the period 1st January 1997 to 31st December 2016.

Despite numerous imports, the mean annual growth rate of the EEP population was only 1.80% per year between 1997 and 2016 (Figure 2.1a). Whilst mean annual growth rate has marginally improved to 2.06% over the last 10 years of this study (2007-2016), it is still well below the 5% established benchmark for white rhinoceros populations, which was more than exceeded by the in situ reference populations, at 8% (Table 2.4). This is largely attributed to the low annual birth rate of the EEP population, which was just 3.87% from 1997-2016, and 4.70% from 2007-2016. These values are very low in comparison with the in situ reference populations, which had an average birth rate of 10.10%.

Although mean annual mortality rate was lower in the in situ reference populations compared to the EEP population during both timeframes (Table 2.4), the EEP population did meet the benchmark of <4% annual mortality. However, mean infant mortality rate was much higher in the EEP population compared to the in situ reference populations for both timeframes, at 22.47% and 18.04% for the 1997-2016 and 2007-2016 periods respectively, in comparison to just 8.44% for the in situ populations. Consequently, the EEP population failed to make the benchmark of <10% infant mortality established for white rhinoceros.

Table 2.4. The mean demographic parameters calculated for the EEP population for the periods 1997-2016 and 2007-2016, and for the in situ reference populations in Kenya from 2007-2018. Previously established benchmarks for each demographic parameter were used as targets (du Toit, 2006). Values in red indicate below-target performance and values in green indicate above-target performance. There are no established benchmarks for white rhinoceros annual birth rate or male age at first reproduction

Demographic parameter	Target	EEP 1997-2016		EEP 2007-2016		In situ reference	
		Mean	SD	Mean	SD	Mean	SD
Annual population growth rate	>5%	1.80	2.39	2.06	1.99	8.00	2.20
Annual birth rate	-	3.87	1.57	4.70	1.66	10.10	2.26
Annual mortality rate	<4%	3.93	1.20	3.96	1.24	2.87	2.58
Infant mortality rate (0-1y)	<10%	22.47	12.49	18.04	10.08	8.44	8.51
Adult females calving per year	>30%	8.61	3.35	10.49	3.37	39.72	8.00
Female age at first reproduction	<7.5y	9.86	5.64	13.49	6.58	7.25	1.65
Female inter-calving interval length	<3y	3.05	1.79	2.82	1.45	2.79	0.62
Male age at first reproduction	-	14.51	6.05	13.73	6.36	13.41	2.98

2.3.1.2 *Female reproductive success*

A total of 222 adult females (defined as >8 years old before 31/12/16) existed in the EEP population between 1997 and 2016. Only 38.29% of adult females contributed offspring to the EEP population, in comparison to 97.83% of adult females across the in situ reference populations (n=48/49). This has created a reproductive skew in the EEP population, as just 12 females (5.41%) constitute 33.00% of all births between 1997 and 2016. Of those females that did reproduce, only 37.65% were born in captivity.

On average, only 8.61% of adult females calved each year (range: 4.50-14.89%) in the EEP population, though this increased to 10.49% during the last 10 years of the study timeframe (2007-2016). However, this is still well below the established benchmark for white rhinoceros populations (>30%), which the in situ reference populations exceeded, at almost 40%. The mean age captive-born females gave birth to their first calf was 9.86 years old for the period 1997-2016 (Figure 2.2a), and 13.49 years old for the period 2007-2016. These values also fail to meet the established benchmark for white rhinoceros (<7.5 years old), which the in situ reference populations were able to meet, at 7.25 years old.

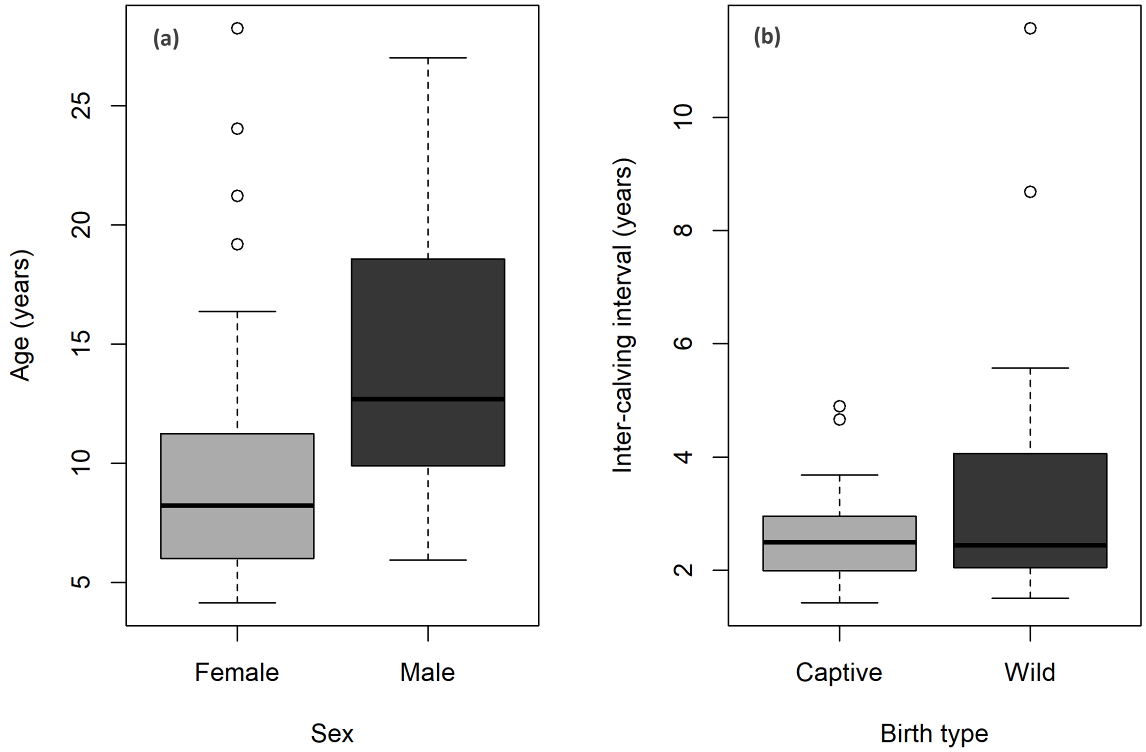

Figure 2.2 The (a) age at first reproduction for captive-born females (n=36) and captive-born males (n=31), and (b) mean inter-calving interval for captive-born females (n=24) and wild-born females (n=28), in the EEP population between 1997 and 2016. The shaded box represents the interquartile range; the line through the box represents the median value; lower and upper whiskers represent the minimum and maximum values; hollow circles represent outliers.

The EEP population also failed to meet the mean inter-calving interval benchmark (<3 years old) during the period 1997-2016, though only marginally, at 3.05 years old. Between 2007 and 2016, mean inter-calving interval length was below the 3-year benchmark, and similar to those of in situ white rhinoceros populations, at 2.82 and 2.79 years long respectively. Notably, captive-born females had shorter mean inter-calving intervals (mean=2.65, SD=0.90) than wild-born females (mean=3.35, SD=2.25). However, this difference was not statistically significant (Mann-Whitney U test: U=306, p=0.591, n = 24 captive and 28 wild), largely due to greater inter-calving interval variance in wild-born females (Figure 2.2b).

2.3.1.3 Male reproductive success

A total of 118 adult males (defined as >13 years old) existed in the EEP population from 1997-2016. A reproductive skew also exists within the male population, as only 37.29% of males successfully sired offspring, and 31.98% of all births between 1997 and 2016 were from females bred with one of just five different males. Based on mating observation records, approximately 51.51% of adult males from the Lewa Wildlife Conservancy population successfully sired offspring during the study timeframe (n=17/33). Of those males that did reproduce in the EEP population, 66.66% were captive-born. The mean age of captive-born males at the birth of the first calf they sired was 14.51 years old from 1997-2016 (Figure 2.2a), and 13.73 years old from 2007-2016, which was very similar to males from the in situ reference populations (13.41 years).

2.3.1.4 Current population performance in the living population

The EEP population contained 176 females and 125 males (n=301) across 77 institutions on the 31st December 2016. The proportion of wild-born individuals in the population has decreased gradually over time (Figure 2.1b). A reproductive skew still exists in the living population, as only 51.77% of reproductive-age females, and 52.73% of reproductive-age males have reproduced. Of those that have reproduced, 38.67% of females and 67.50% of males were born in captivity. The population is aging, as 82.23% of females, and 66.14% of males, are now adults (Figure 2.3), and 14.18% of adult females are of post-reproductive age (>34 years old; Versteege, 2017), and thus are unlikely to reproduce in the future.

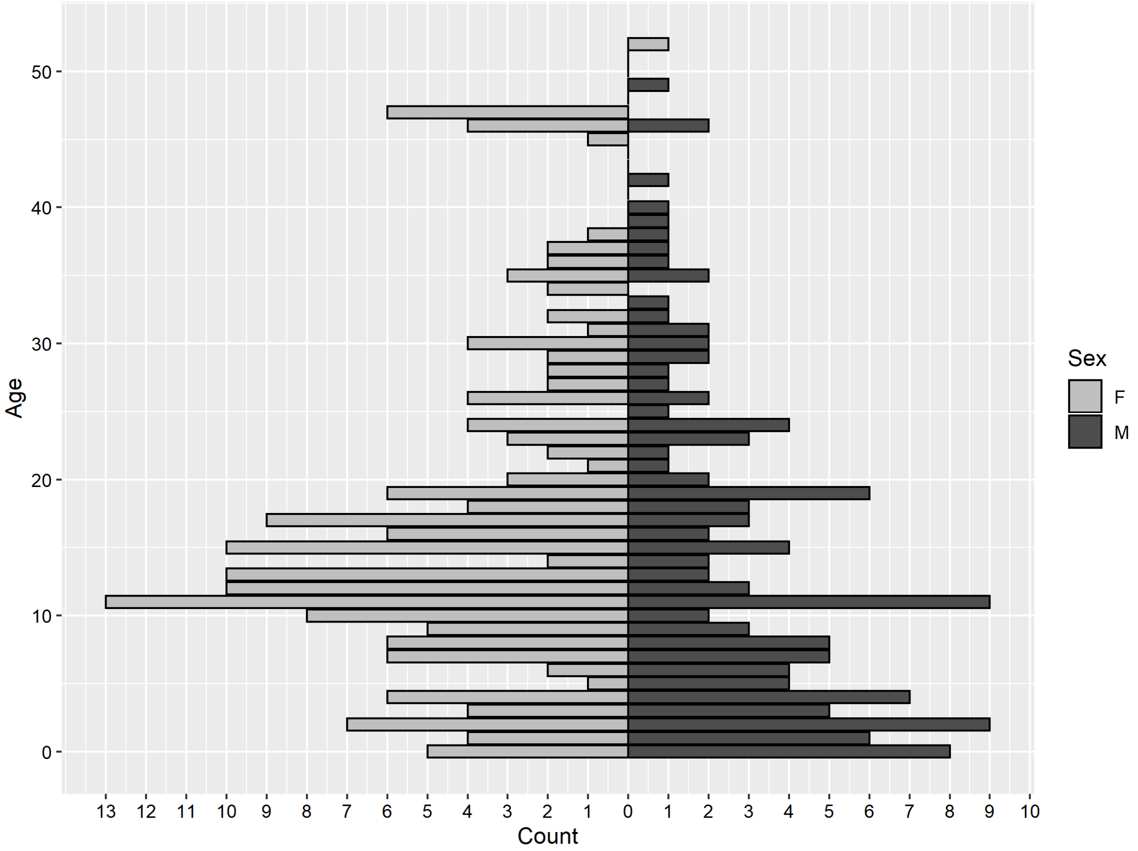

Figure 2.3 Sex and age pyramid of the EEP white rhinoceros population on the 31st December 2016 (n = 301; females = 176, males =125). A growing population should take on the shape of a pyramid, with a wide base and narrow top.

2.3.2 Long-term population viability

Under the baseline scenario, population viability analysis predicts the European captive white rhinoceros population has a 0% probability of extinction within the next 100 years (approximately 7 generations). However, the population is in decline, with a mean exponential rate of increase of -0.0198 (Table 2.5). This represents a mean projected population decline of 1.98% per annum. The mean population size after 100 years across 1000 iterations was just 44.93 individuals, 85.07% smaller than the current population size (n=301 individuals). The baseline scenario predicts the population can maintain 95.58% of its current genetic diversity after 100 years. However, if the starting inbreeding coefficient (*F*) is increased to *F*=0.344, i.e. the potential genetic relatedness of the reproductive-age sub-population, the predicted genetic diversity after 100 years was just 63.20%.

Table 2.5. The mean population growth rate, final population size and remaining genetic diversity, for the EEP white rhinoceros population after 100 simulated years in Vortex. Results from the baseline scenario (10% females calving annually, inbreeding coefficient, *F*=0.0079), an increased inbreeding scenario (*F*=0.344), and two increased female calving scenarios (16% and 17% of females calving annually) are provided. SD represents the standard deviation for that parameter.

Scenario	Growth rate (λ)		Population size (N)		Genetic diversity (GD)	
	λ	SD	N	SD	GD	SD
Baseline	-0.0198	0.0284	44.93	16.78	0.9558	0.0102
Baseline + *F* = 0.344	-0.0198	0.0283	44.97	17.31	0.6320	0.0064
Baseline + 16% female fecundity	0.0020	0.0171	380.35	84.94	0.9796	0.0011
Baseline + 17% female fecundity	0.0051	0.0163	514.94	106.59	0.9807	0.0008

2.3.3 The demographic factors mediating population growth

2.3.3.1 Relative sensitivity analysis

The relative sensitivity analysis indicated that female fecundity (the mean percentage of females calving each year) was the only parameter that had a disproportionate effect on population growth rate (λ; Table 2.6). Infant mortality had the second greatest effect on population growth rate, followed by adult mortality and sub-adult mortality. Environmental variation in female fecundity, number of lethal equivalents (alleles that are lethal when homozygous) and the inbreeding coefficient (*F*; a measure of average genetic relatedness) caused low variation in population growth rate.

2.3.3.2 Global sensitivity analysis

Standardised regression coefficients demonstrated that female fecundity accounted for the most variation in whether the population grew or declined after 100 simulated years, and again was followed by infant mortality (Model 1, Table 2.6). In the second model, both sub-adult and adult mortality had the greatest effect on whether the population was self-sustaining after 100 simulated years, though effect sizes were substantially smaller than in the first model. Environmental variation in female fecundity, number of lethal equivalents and the inbreeding coefficient (*F*) were responsible for little variation in whether the population grew or declined, in both logistic regression models.

Table 2.6. Sensitivity of population growth to changes in EEP white rhinoceros parameter estimates. Sensitivity ranks on absolute values are shown parenthetically. Negative values indicate a negative relationship between the parameter and response. Due to multi-collinearity, adult mortality and sub-adult mortality were omitted from Model 1, and female fecundity was omitted from Model 2.

Parameter	**Sensitivity to λ[a]**	**Sensitivity to probability of +λ[b]**	
		Model 1	**Model 2**
Female fecundity	2.197 (1)	9.468 (1)	-
Infant mortality	-0.631 (2)	-2.376 (2)	-0.425 (3)
Adult mortality	-0.556 (3)	-	-0.600 (2)
Sub-adult mortality	-0.404 (4)	-	-0.624 (1)
Environmental variation in female fecundity	0.102 (5)	-0.148 (4)	-0.090 (4)
Lethal equivalents	-0.025 (6)	-0.272 (3)	-0.056 (6)
Inbreeding coefficient (*F*)	-0.000 (7)	-0.022 (5)	0.086 (5)

[a] *Relative sensitivity to mean exponential rate of increase was determined by varying each parameter ±10% of its baseline value.*

[b] *Sensitivity to probability of a positive population growth rate, +λ, was assessed using logistic regression models and standardised coefficients.*

2.3.3.3 Post-hoc exploratory analysis on female fecundity

As female fecundity was the parameter with the greatest influence on population growth, the baseline scenario model was re-run, sequentially increasing female fecundity by 1%, to determine the minimum level it must reach to obtain a positive mean growth rate. This was achieved under a scenario where 16% of females calve annually, resulting in a mean growth rate of 0.2% per year (Table 2.5). However, the projected population growth trajectory under this scenario levelled off at around 50 years, and then began to decline slowly (Figure 2.4). Increasing female fecundity to 17% increased mean population growth rate to 0.51% per annum, and maintained a positive population trajectory for 100 years.

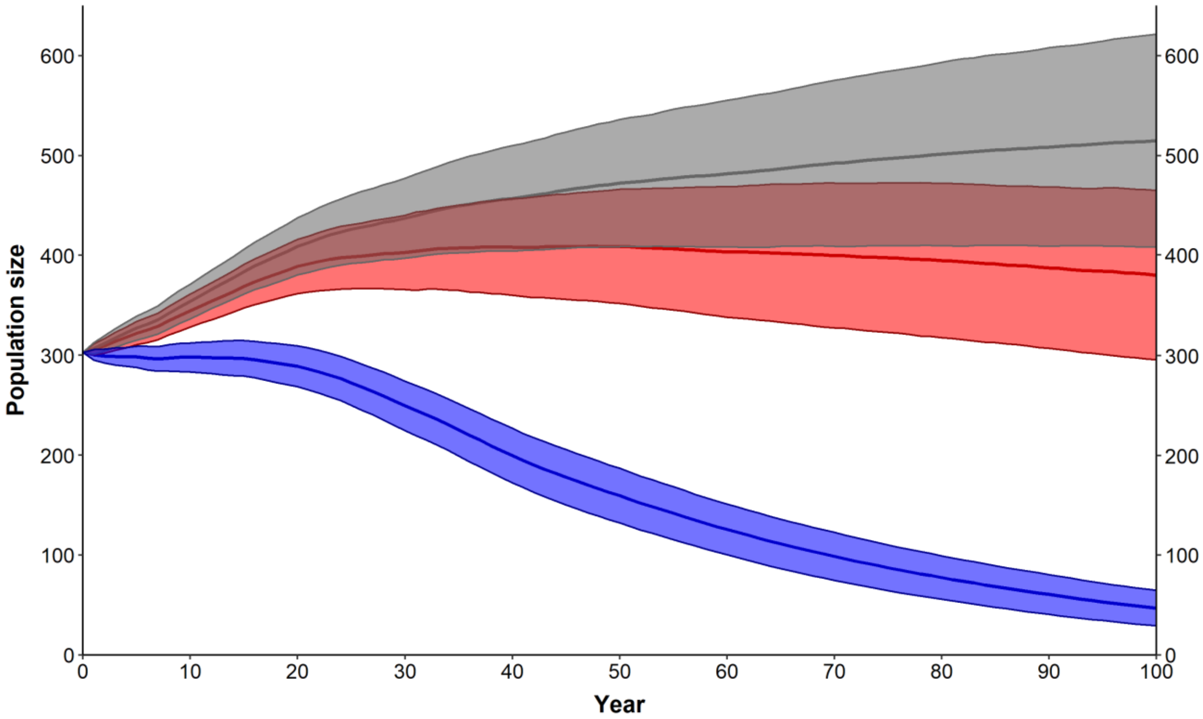

Figure 2.4 Average Vortex population trajectories, with standard error, over the next 100 years for the EEP white rhinoceros population. Projections show the baseline scenario with current female fecundity (10%; blue), the baseline scenario plus 16% female fecundity (red), and the baseline scenario plus 17% female fecundity (grey).

2.4 DISCUSSION

The European captive white rhinoceros population now contains more captive-born than wild-caught individuals, indicating a positive step towards population sustainability. However, when compared to in situ reference populations, it is evident that the population is performing below its potential. Despite numerous imports from the wild, average population growth rate was less than 2% per annum between 1997 and 2016, and if imports are discontinued, the population is projected to decline at a rate of almost 2% per annum. Sensitivity analyses show that the low proportion of females calving each year is the key factor limiting population growth, though high infant mortality rates are also of concern. Furthermore, a large proportion of individuals, particularly captive-born females, are failing to contribute towards the reproductive output of the population. The sub-optimal reproductive performance of females, coupled with high reproductive skew and infant mortality, threatens the demographic and genetic viability of the population.

The low reproductive rate of females is extremely concerning. On average, only 10% of females calved annually in the EEP population, yet almost 40% of females calved annually in the wild reference populations, indicating that the EEP population is severely underperforming. PVA conveys that the proportion of females calving each year must increase to a minimum of 17% for the population to become self-sustaining over the long-term. Mean inter-calving interval between 1997 and 2016 was slightly above the 3-year benchmark indicative of good to moderate fecundity (du Toit et al., 2006). However, between 2007 and 2016, mean inter-calving interval was similar to that of the in situ reference populations, and below the target benchmark. This suggests that individual breeding success has improved over time, and the low reproductive rate of females is not driven by long calving intervals, as those females already reproducing are performing to a satisfactory standard.

The poor reproductive rate of captive females may instead be attributed to other factors. Mean age of first reproduction in captive-born females was high, at 9.86 years and 13.49 years old, for the 1997-2016 and 2007-2016 time-periods respectively. Whilst mean age at first reproduction has been recorded as high as 10.1 years old in females from high density wild populations (Rachlow and Berger, 1998), it is usually between 6.5 and 7.5 years old (Owen-Smith, 1973; Rachlow and Berger, 1998; Ververs et al., 2017). Subsequently, a mean age at first reproduction greater than 7.5 years old is considered to indicate poor population performance (du Toit et al., 2006). Whilst there are no established benchmarks for male white rhinoceros reproductive success, the mean age of males in the EEP population when they first sired a calf was very similar to that of males from the wild reference populations, at 13.73 and 13.41 years old respectively. This would suggest that the reproductive performance of captive-born males is much more adequate than that of captive-born females.

Breeding management constraints in the captive environment are likely to contribute to some extent towards aspects of poor reproductive performance in females. Several institutions house males and females separately when females are not in oestrus, or have young calves (Metrione and Eyres, 2014). Females therefore have less frequent access to males, and less choice of mating partners, than their wild counterparts. Additionally, young females are not always introduced to a breeding bull as soon as they reach sexual maturity, if they are still in their natal herd, or there are no un-related bulls available. Females often form strong social bonds in captivity, and are usually aggressive towards males following their introduction (Metrione and Eyres, 2014). This can also interfere with breeding if a female’s social partner continues to drive a bull away (Boomsma and Sijde, 2010). Consequently, these factors may contribute towards an older age at first reproduction in captive females compared to those in situ.

The main factor driving the poor reproductive rate of the EEP population is the low proportion of females that have ever reproduced (38%). As also found in previous studies, this was more evident in captive-born females (Schwarzenberger et al., 1998; Emslie and Brooks, 1999; Swaisgood et al., 2006; Reid et al., 2012). As 33% of all births came from just 12 females, there is a high reproductive skew within the population. Consequently, the age structure of the current population is similar to that of an ageing population, with a low proportion of calves and sub-adults compared to adults (Ballou et al., 2010). Furthermore, 14% of adult females are of post-reproductive age (>34 years old), making them unlikely to breed again (Versteege, 2017). This may further limit the number of individuals contributing offspring to the population in the future, as when current breeders age, they may be replaced with a smaller number of new breeders (Ballou et al., 2010). Whilst the proportion of males contributing offspring to the population was also low (37%), reproductive skew is common in males in the wild (Guerier et al., 2012), with territorial bulls monopolising breeding over non-territorial bulls (Owen-Smith, 1977). High reproductive skew in wild female white rhinoceros is much more unusual, as evidenced by the wild reference populations, where almost 100% of adult females had successfully reproduced. This suggests that reproductive skew in EEP females may be attributed to living in captivity, which was also identified as a key factor limiting the reproductive output of the EEP black rhinoceros population (Edwards et al., 2015).

The low proportion of individuals contributing to the genetic pool of the EEP population is highly concerning. The maintenance of genetic diversity is crucial for adaptive evolution, and its loss reduces the probability of population persistence (Frankham, 2005). Whilst PVA predicts the entire EEP population can maintain approximately 96% of its current genetic diversity over the next 100 years, when considering only those individuals in the reproducing sub-population, just 63% of current genetic diversity can be retained. Furthermore, the genetic relatedness of the current population is likely to be even higher than previous estimates, which assume that EEP founders are unrelated (i.e. assigning F=0 to founders; Reid et al., 2012). This is a fundamental flaw of captive breeding programmes, but is a particularly erroneous assumption for the southern white rhinoceros. This subspecies went through a severe bottleneck at the end of the 19th century, reducing the global population to less than 50 individuals (Emslie, 2020). Therefore, all living white rhinoceros, both in the wild and in captivity, are descendants of this small population. Consequently, wild populations are typically characterised by very low levels of genetic diversity (Seror et al., 2002; Florescu et al., 2003; Coutts and Rachlow, 2009; Guerier et al., 2012), and therefore wild-caught founders must also have low genetic diversity.

Captive breeding programmes aim to prevent changes to the genetic constitution of captive populations by maintaining a minimum of 90% founder genetic diversity (Foose and Wiese, 2006). This helps to ensure captive animals can maintain the natural characteristics of their wild counterparts, and do not become adapted to living in captivity (Mcphee and Carlstead, 2010). If individuals are to be reintroduced to the wild to supplement depleting populations in situ, they must have the potential to adapt to an ever-changing environment (Ballou *et al.*, 2010). Whilst the exact genetic relatedness of the EEP population is unknown, due to severe reproductive skew and high genetic relatedness among wild-caught founders, the population is likely to be severely inbred. Furthermore, what little genetic diversity that now remains will decrease further if more individuals do not start breeding in the near future. However, inbreeding avoidance could explain why many captive-born females are failing to breed, and thus genetic studies on the EEP population are urgently required to provide a more accurate estimation of founder relatedness.

In addition to deficiencies in reproductive performance and genetic diversity, the high infant mortality rates of the EEP population are also of concern. These were 22% and 23%, for males and females respectively, over double the <10% benchmark. Consequently, infant mortality was identified as the second most important predictor of population growth rate in the sensitivity analyses. The in situ reference populations had a mean infant mortality rate of just 8.5%, similar to those estimated in previous studies on wild rhinoceros; 8.3% in white rhinoceros (Owen-Smith, 1988), 11-23% in Indian rhinoceros, *Rhinoceros unicornis*, (Dinerstein and Price, 1991; Subedi et al., 2017), 8-14% in black rhinoceros (du Toit et al., 2006). However, establishing infant mortality rates in the wild is often difficult due to the number of stillbirths and neonatal deaths that go unrecorded. Consequently, higher infant mortality rates in captivity have also been documented in other rhinoceros species; 23% for the European captive black rhinoceros population (Edwards et al., 2015), and 20% for the international captive Indian rhinoceros population (Zschokke and Baur, 2002). Infant mortality rate in the European black rhinoceros population has decreased substantially in recent years, to just 5.8% between 2001 and 2010, most likely due to improvements in husbandry over time (Edwards et al., 2015). Whilst infant mortality rate in the EEP white rhinoceros population has also fallen in recent years (18% between 2007 and 2016), it has not reduced to the same extent. Therefore, despite improvements in captive white rhinoceros husbandry over time, infant mortality rates are still unusually high.

One possible explanation for high infant mortality rates in captivity may be inbreeding effects, owing to the low genetic diversity and reproductive skew present in the EEP population. When populations pass through a bottleneck, previously rare alleles may increase in frequency, and breeding between closely related individuals can increase the likelihood that deleterious recessive alleles are expressed (Ballou et al., 2010). The reduced fitness of inbred individuals, known as inbreeding depression, can be detrimental for small populations (Frankel and Soulé, 1981). Inbreeding depression has been documented in several species in captivity, including blindness in wolves, *Canis lupus* (Laikre et al., 1993), reduced litter size in bears, *Ursus sp*. (Laikre et al., 1996), increased infant mortality in cheetahs, *Acinonyx jubatus* (O'Brien et al., 1985), and reduced infant growth in Indian rhinoceros (Zschokke and Baur, 2002). It is therefore possible that high levels of inbreeding within the EEP white rhinoceros population have contributed towards high infant mortality rates. Moreover, as environmental stress can be more detrimental for inbred individuals (Bijlsma et al., 2000), females or neonatal calves that are highly inbred may find the captive environment more stressful than less inbred individuals, which may further increase infant mortality rate.

The results of this study suggest that the reproductive performance of the European white rhinoceros population is of great concern. The primary goal of captive breeding programmes is to maintain genetic diversity and demographic stability, to ensure the long-term conservation of a species (Ballou et al., 2010). The EEP white rhinoceros population is not only demographically unsustainable, but its viability is also threatened from low genetic diversity and inbreeding. The number of females calving each year must increase to a minimum of 17%, and a greater proportion of individuals must contribute to the captive gene pool, to improve the future viability of the population. The reasons for the poor reproductive performance of captive female white rhinoceros remain unclear. It is vital that we uncover the root causes of reproductive failure in the captive environment soon, as importing further individuals from the wild is not sustainable. Chapter three therefore uses studbook and questionnaire data to determine whether aspects of the captive environment, and in particular social conditions, may be linked to female reproductive failure. Research on the factors that cause variation in female reproduction in the wild may also provide valuable information to guide breeding management strategies in captivity. Chapters five and six therefore investigate how social and ecological factors influence female reproductive success in wild populations of white rhinoceros.

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3 GROUP COMPOSITION INFLUENCES SOCIO-SEXUAL BEHAVIOURS AND BREEDING SUCCESS IN CAPTIVE FEMALE SOUTHERN WHITE RHINOCEROS (*CERATOTHERIUM SIMUM SIMUM*)

Abstract

Southern white rhinoceros, *Ceratotherium simum simum*, birth rates in captivity have been extremely low, and there is substantial variation in breeding success between institutions. To gain an understanding of the factors driving variation in breeding success, this study incorporated a multi-institutional comparative approach. Questionnaire and long-term demographic data on European captive white rhinoceros were used to evaluate the impact of different management practices and social conditions on female reproductive success. Studbook data were used to investigate which variables best predicted both institution and individual female breeding success, and a questionnaire survey was used to determine how variation in husbandry influenced female reproductive behaviour, copulation and pregnancy success. Overall, across the entire European population, institutions housing larger groups had greater breeding success, and females housed alongside another breeding female were more likely to calve. The results also demonstrate that females were more receptive to a breeding bull if they were kept in groups with a lower mean age, and more likely to copulate if they were kept in larger sized groups, or alongside a successfully breeding female. Furthermore, females were more likely to exhibit reproductive behaviour, copulate and become pregnant if they were younger and born in the wild. These results suggest that variation in female reproductive success is related to differences in the social environment between captive institutions, and contradict previous suggestions that low reproductive output is driven mainly by post-copulatory complications, or reproductive suppression. Modifying group compositions accordingly may improve the breeding success and conservation management of captive southern white rhinoceros.

3.1 INTRODUCTION

Captive breeding programmes are becoming increasingly important to the conservation of species that have undergone severe population declines in the wild (Ochoa et al., 2016). According to the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species, captive breeding in zoos and aquariums has played a pivotal role in the recovery of one quarter of the 64 vertebrate species that have had their extinction threat status reduced (Barongi et al., 2015). For mammals in particular, conservation breeding and reintroduction to the wild have proven more successful at promoting species recovery than any other conservation action (Barongi et al., 2015). Consequently, ex situ breeding is now recommended as a key method to reduce species extinction risk (IUCN CPSG, 2019). Captive populations act as safeguard against extinction in the wild, and can help species to recover in the absence of the threats experienced by their wild counter-parts (Zimmermann, 2010). Ex situ animals provide a source for potential reintroduction efforts in the future, and therefore may assist with population recovery in the wild (Earnhardt, 2010). However, establishing self-sustaining captive populations of endangered species is often difficult due to problems associated with reproduction and survivorship in the captive environment (Snyder et al., 1996).

Several aspects of husbandry and enclosure design have been linked to welfare and reproductive success in captivity, including diet (cheetahs, *Acinonyx jubatus,* Setchell et al., 1987), feeding enrichment (African elephants, *Loxodonta africana*, and Asian elephants, *Elephas maximus,* Meehan et al., 2016), space availability (black rhinoceros, *Diceros bicornis,* Carlstead et al. 1999; giant pandas, *Ailuropoda melanoleuca,* Peng et al. 2007; dholes, *Cuon alpinus,* Maisch 2010), enclosure substrate (Scimitar-horned Oryx, *Oryx dammah,* Little et al., 2016; Humboldt penguins, *Spheniscus humboldti,* Blay and Côté, 2001), number of inter-zoo transfers (Asian elephants, Clubb et al., 2008) and public exposure (black rhinoceros, Carlstead et al., 1999). Understanding the factors limiting a species' reproduction in captivity can help to inform management strategies that aim to maximise breeding performance and population persistence.

Captive populations play a crucial role in the conservation management of the southern white rhinoceros, *Ceratotherium simum simum*, as they provide a refuge from the threat of poaching in the wild. However, breeding white rhinoceros in captivity has proven extremely difficult due to the low reproductive rate of females, particularly of those born in the captive environment (Swaisgood et al., 2006). A recent assessment of the captive white rhinoceros population in Europe revealed that it is likely to decline at a rate of approximately 2% per year, if the proportion of females breeding annually does not drastically increase (see Chapter 2). Rampant poaching and failure to breed in captivity have already led to the near extinction of the critically endangered northern white rhinoceros, *Ceratotherium simum cottoni*, with just two females of this subspecies now remaining in captivity (Tunstall et al., 2018). It is therefore vital that the factors limiting breeding success in female southern white rhinoceros are identified, to inform appropriate management strategies and prevent this subspecies from meeting the same fate as its northern counterpart.

The reasons behind the poor breeding success of captive white rhinoceros remain unclear. Several studies have reported irregularities in female oestrus cycles (Radcliffe et al., 1997; Schwarzenberger et al., 1998; Patton et al., 1999; Brown et al., 2001; Hermes et al., 2006, 2007), and reproductive-organ pathologies, such as endometrial and ovarian cysts (Hermes and Hildebrandt, 2011), which have been linked to a reduced reproductive lifespan (Hermes et al., 2014). Reproductive-tract pathologies are significantly more common in nulliparous than parous females (Hermes et al., 2005, 2006), and research suggests they can be prevented with the achievement of at least one pregnancy (Hermes et al., 2006). Whilst these factors may contribute towards reproductive failure post-copulation, they do not explain why so many females fail to engage in mating when they first reach sexual maturity, or why females with no reproductive-tract pathologies do not attempt to breed.

One factor that may influence female breeding success is their captive management. Diet has been linked to a loss of fertility in captive female white rhinoceros (Tubbs et al., 2012, 2016), and recent studies suggest this may be caused by the gut microbiota's transformation of dietary phytoestrogens (Williams et al., 2019). However, the same relationship was not apparent in females born in the wild (Tubbs et al., 2016), and this still does not explain why so many females fail to engage in mating events to begin with. Both small enclosure size and inadequate social environments have been linked to reduced reproductive success in black rhinoceros (Carlstead et al., 1999), and therefore social conditions may too play a role in the breeding success of captive white rhinoceros.

White rhinoceros have the most developed social system of all the rhinoceros species, and olfactory and vocal signals play an important role in their communication (Owen-Smith, 1973; Cinková and Policht, 2015, 2016; Marneweck et al., 2017). In the wild, adult females form groups of up to 18 individuals, with their dependent calves, and both male and female sub-adults (Owen-Smith, 1973; du Toit et al., 2006). In captivity, there is a large amount of variation in group size; ranging from just two individuals at some institutions, to large groups of up to 11 individuals at institutions with greater space availability (Versteege, 2017). The maintenance of social bonds between females may be important for individual wellbeing. For example, females housed together from adolescence have lower faecal corticosterone levels than those introduced later in life (Metrione and Harder, 2011), suggesting familiarity with conspecifics may reduce stress levels.

Failure to breed in captivity has repeatedly been linked to stress resulting from both prolonged confinement in sub-optimal conditions (Peng et al., 2007; Descovich et al., 2012; Marshall et al., 2016), and limited opportunity for social interaction (Mallapur et al., 2009; Swaisgood and Shulte, 2010), in a range of different species. For example, mating group compositions (red pandas, *Ailurus fulgens,* Wei et al. 2005; striped skunks, *Mephitis mephitis,* Larivière et al. 2005), group social structure (great apes, *Hominidae,* Abello & Colell 2006), group size (pig-tailed macaques, *Macaca nemestrina*, Ha et al. 1999; felids, *felidae*, Mellen 1991; penguins, *Spheniscidae*, Blay & Côté 2001; Barbosa et al. 1997) and group age (Scimitar-horned oryx, *Oryx dammah*, Little et al., 2016), have all been linked to reproductive success in captivity. Furthermore, research carried out across 16 North American institutions housing white rhinoceros suggests that institutions housing more than two individuals have greater reproductive output (Metrione, 2010). It is therefore possible that variation in social conditions between institutions may influence female white rhinoceros breeding success, but further research across a larger number of institutions is required to confirm this.

Most studies on the impacts of captive management on animal welfare and breeding success employ simple pairwise approaches, making them vulnerable to single-site and observer bias (Marshall et al., 2016). Research on the factors driving female white rhinoceros breeding success mainly comes from disparate studies on animals in North American institutions (Patton et al., 1999; Brown et al., 2001; Carlstead and Brown, 2005;

Swaisgood et al., 2006; Metrione and Harder, 2011; Tubbs et al., 2016; Williams et al., 2019), and there have been no studies on an entire meta-population. Examining zoo husbandry and social group composition across a meta-population will provide a more thorough assessment of the potential factors driving variation in institution breeding success. However, analysing breeding success at the institution level alone does not incorporate factors that are independent between females, such as female age and birth origin. Previous studies suggest wild-born females have greater breeding success than captive-born females (Swaisgood et al., 2006; Versteege, 2007), and that fertility may decline with age (Metrione and Eyres, 2014; Versteege, 2017). Furthermore, it is unclear whether failed breeding attempts or failure to exhibit reproductive behaviour and copulate cause poor breeding success in females. Examining reproductive behaviour and calving success at the level of the individual female is therefore also necessary to fully investigate the potential factors limiting female reproductive output in captivity.

This chapter used a two-way comparative approach and a questionnaire survey to assess the impact of varied social conditions and husbandry measures on the breeding success of captive female white rhinoceros. The main aim of this chapter was to identify whether aspects of captive management are linked to female breeding success, to inform management strategies aimed at maximising female reproductive output. The first objective of this chapter was to use studbook data to identify potential factors related to both institution breeding success and female calving success, across the entire European population. To determine whether pre-copulatory problems influence female breeding success, the second objective of this chapter was to identify potential husbandry factors related to the occurrence of female socio-sexual behaviours, copulation and pregnancy, across a sample of the European population.

3.2 METHODS

3.2.1 Studbook dataset

All reproductive-age female white rhinoceros and calving events between the years 2012 and 2016 were extracted from the European Endangered species Programme (EEP) studbook for white rhinoceros. This timeframe was chosen as it encompassed current breeding performance and management conditions, and was long enough to capture at least one calving event from currently breeding females, as average inter-calving intervals in white rhinoceros are approximately 2.5 years long (Owen-Smith, 1975; Ververs et al., 2017). Female white rhinoceros usually calve for the first time between the ages of 6.5 and 7.5 years old (Owen-Smith, 1975; Rachlow and Berger, 1998; Ververs et al., 2017), and studbook reports suggests that females in captivity are unlikely to calve after the age of 34 (Versteege, 2017). Therefore, reproductive-age females were defined as females that were >8 years old and <34 years old on 31/12/2016; or that had calved during the study timeframe.

To provide a thorough assessment of the potential factors limiting female reproductive output, breeding success in the EEP was assessed at both the institution level, and at the level of the individual female. To assess institution breeding success, calving data from the studbook were used to determine the proportion of reproductive-age females that calved at each EEP institution (n=57 institutions), between the years 2012 and 2016. Institutions that did not house reproductive-age females, or only housed single-sex or family groups (i.e. mother and offspring), during the study timeframe were omitted from the analyses. To investigate individual female breeding success, calving data from the studbook were used to determine whether or not each reproductive-age female (n=134) calved during the study timeframe. The studbook was used to extract variables that may have limited female breeding success, both at the institution level (mean age of group, mean group size and mean number of adult females in the group), and at the level of the individual female (number of previous transfers between institutions, age, birth origin and presence of a successfully breeding female), during the study timeframe (see Table 3.1 for definitions). Institution level variables were used to assess institution breeding success, and all variables were used to assess female breeding success.

3.2.2 Questionnaire dataset

In November 2017, an online questionnaire on the husbandry and reproductive behaviour of captive white rhinoceros between 01/01/2012 and 31/12/2016 was sent to all EEP institutions housing both male and female white rhinoceros (n=57). This time-period was chosen to provide comparison with the full studbook analysis, and because it was recent

Table 3.1. Summary of all the variables included in the analyses. Reproductive-age females were those >8 and <34 years old on 31/12/16, or females that calved during the study period (01/01/12 - 31/12/16).

Variable	Description	Rationale
Institution breeding success	The proportion of reproductive-age females that calved at an institution during the study period, accounting for the duration of time each female spent at the institution.	To investigate which factors influence institution breeding success across the entire EEP.
Female calving success	Whether or not a reproductive-age female calved during the study period.	To investigate which factors influence female breeding success across the entire EEP.
Reproductive behaviour	Whether or not a female was observed to remain still for >5 seconds whilst a bull attempted to chin-rest or mount[1] (1 = yes, 0 = no).	To investigate which factors influence whether females exhibit socio-sexual behaviours indicating receptiveness when paired with a breeding bull[1].
Copulation	Whether or not females copulated with the breeding bull they were paired with (1 = yes, 0 = no).	To investigate which factors influence whether females copulate with a breeding bull.
Pregnancy	Whether or not a female became pregnant after being paired with a breeding bull (1 = yes, 0 = no).	To investigate which factors influence whether a female became pregnant after being paired with a breeding bull.
Mean group age	The mean age of adult rhinoceros in the group (years).	Average group age can influence breeding success in species such as the scimitar-horned oryx[2].
Mean group size	The mean number of individuals at an institution during the study period, accounting for the duration of time an individual was at each institution.	Group size influences reproductive success in penguins[3], felids[4] and macaques[5]. Research suggests white rhinoceros breed better in groups of >2 individuals[6].
N adult females	The mean number of adult females at an institution during the study period, accounting for the duration of time a female was at an institution.	Female white rhinoceros are more gregarious than males[7]. Therefore, larger adult female groups may improve welfare and stimulate breeding.
Male access	The breeding management strategy used (1 = females sometimes given access to males at night; 0 = females never given access to males at night)	Males and females are usually separated at night. However, constant access to males during oestrus may increase the chances of females mating and becoming pregnant.
Female night access	Whether or not females are housed with other females at night >50% of the time (1 = yes, 0 = no).	Frequent access to other females may reduce social stress[8].
Enclosure size	Total area of outside space available to individuals in m^2, including the hardstand and the paddock.	Enclosure size can influence zoo animal welfare[,9,10,11], and has been linked to calving success in white rhinoceros[6].
Drive through	Whether or not members of the public can drive through the rhino exhibit.	Drive through enclosures often increase public exposure, which has been identified as a stressor in captive black rhinoceros[9].
Latitude	The latitude coordinates of each institution.	White rhinoceros live in temperate regions, but are often housed in cooler climates. Latitude addresses variation in climactic factors such as temperature and rainfall.
Transfers	The number of previous transfers between institutions (0/1 transfer = 0, 2/3 transfers = 1).	Transfers may be a source of stress, as they have been shown to negatively affect captive elephants[12].
Origin	Birth origin (1 = wild, 0 = captivity).	Previous studies suggest captive-born females have lower reproductive output[1,13].
Age	The age of the female in years mid-way through the study period (01/07/2014).	Peak breeding in female white rhinoceros usually occurs between the ages of 5 and 18[14].
Breeding female presence	Whether or not, during the study timeframe, a female was at an institution with another female that successfully mated and calved.	Other breeding females can stimulate ovulation and reproductive behaviour in species such as the squirrel monkey[15].

1. Swaisgood et al. 2006 2. Little et al. 2016 3. Blay & Côté 2001 4. Mellen 1991 5. Ha et al. 1999 6. Metrione, 2010 *7.* Owen-Smith, 1973 *8.Metrione & Harder 2011 9. Carlstead et al. 1999 10. Peng et al. 2007 11. Maisch 2010 12. Clubb et al. 2008 13. Schwarzenberger et al. 1998 14. Versteege 2017 15.* Schiml et al., 1996

enough to allow respondents to remember an individual's behaviour and husbandry conditions. Questionnaires were directed to members of staff that were familiar with the institution's rhinoceros group, such as zookeepers, curators, veterinarians or collection managers. The questionnaire was granted support from the British and Irish Association for

Zoos and Aquariums (BIAZA). Of the 57 institutions, 24 completed the questionnaire (42%), from which 20 (35%) were used in the study, following exclusion of institutions now only housing single-sex or family groups.

The questionnaire (Appendix 1) consisted of 12 questions that addressed aspects of housing management, reproductive behaviours and breeding management. Questionnaire responses were collated and used to provide additional predictor variables that may limit female reproductive behaviour and breeding success (Table 3.1). The questionnaire data was used to create the binary response variables; whether or not a cycling female (i) was observed exhibiting reproductive behaviour when paired with a bull, (ii) was observed copulating with a breeding bull, and (iii) became pregnant after mating with a bull, during the study timeframe. To ensure statistical models would be viable, predictor variables with very low variation or missing responses were not included in any analysis, with the exception of the variable 'enclosure size', which had just two missing responses. Instead, missing values were assigned the mean enclosure size given by respondents (Dodeen, 2003; Little et al., 2016), to reduce the number of variables omitted from the analysis. The variables (i) female oestrus cycle length, and (ii) length of time a female was paired with a breeding bull, were excluded from the analyses due to several missing values.

Due to a modest sample size, the categorical variables (i) how often were females provided with access to other females at night, and (ii) how often were females provided with access to males at night, were condensed to binary responses. These were: (i) whether or not females had access to other females at night >50% of the time, and (ii) whether or not females were ever given access to males at night (i.e. response was not 'Never'). The latter definition was chosen because several institutions (n=4) mentioned that females were only given uninterrupted access to males when they were in oestrus, and whilst this may be a small proportion of the time, it may be an important predictor of female reproductive success. Number of transfers was also condensed to a binary response due to low variation in both the questionnaire and studbook datasets (85% of females in the EEP had been transferred either once or twice).

All analyses on the questionnaire dataset were carried out at the level of the individual female (n=48 reproductive age females). All predictor variables obtained from both the questionnaire and the EEP studbook were included to fully investigate the potential aspects of husbandry or individual life history that best predicted whether females exhibited reproductive behaviour, copulated or became pregnant, when paired with a breeding bull.

3.2.3 Statistical analyses

To check for correlations between predictor variables, *Pearson correlation tests* were used to compare continuous variables, and *Chi-square (χ^2) tests* were used to compare binary variables. Pairs of variables with a correlation coefficient (*r*) >0.7, or a statistically significant χ^2 result ($p<0.05$), were not included in the same model. Instead, alternative models were run, to ensure all potentially important variables were analysed (Zuur et al., 2010). Additionally, *Variance Inflation Factors (VIFs*) were used to check for multi-collinearity between predictor variables. Variables with *VIFs* greater than 2 were considered to indicate moderate multicollinearity (Zuur et al., 2010), and therefore were not included in the same models.

Binomial logistic regression models were used to determine the influence of predictor variables on the proportion of reproductive-age females that calved at each institution in the EEP studbook. To account for over-dispersion in the response variable, caused by a disproportionate number of zeros (i.e. no females calved at an institution; n=27), a quasi-binomial distribution was used. Binomial generalised linear mixed effects models (*GLMMs*), with institution included as a random effect, were used to investigate which factors best predicted: (i) reproductive-age female calving success across the full EEP studbook, (ii) whether or not reproductive-age females from the questionnaire data set (a) exhibited reproductive behaviours, (b) copulated, or (c) became pregnant, following pairing with a breeding bull. To ensure all logistic regression assumptions were met, linearity of independent variables with log odds, and the presence of any influential outliers (*Cook's D* >3.0), were checked for. Visual inspection of scatterplots between predictors and the logit values revealed no non-linear trends, and all standardised residuals were below three. Transformations, including Log_{10}, square root (√) and cube root ($_3$√), were used to adjust variables with uneven variances or skew, and to improve their linear relationship with log odds.

Information theoretic approaches, such as the *Akaike Information Criterion* (*AIC*), account for model selection uncertainty by using measures of predictive power to rank models and obtain robust parameter estimates (Burnham and Anderson, 2002; Grueber et al., 2011).

Model selection and model averaging based on *AIC* values were thus used to determine the relative importance and averaged estimates for the variables in each model set. The *AICc* (*Second-Order AIC*) correction for small sample size was used (Hurvich and Tsai, 1989), as this is recommended when sample size is small in relation to the number of estimated parameters (Burnham and Anderson, 2002). The *AICc* applies a penalty term for the number of parameters in the model, and this prevents the selection of models with too many parameters, thus addressing potential overfitting (Burnham and Anderson, 2002). Following Burnham and Anderson's (2002) rule of thumb, candidate models within 2 *ΔAIC* of the top model have considerable support and should be considered competitive to the top model (Burnham and Anderson, 2002; Harrison et al., 2018). Therefore, *2 ΔAIC* was set as the threshold for model averaging for the binomial *GLMM* models. All statistical analyses were carried out in R version 3.4.1 (R Core Team, 2016). The package *lme4* (Bates et al., 2015) was used to generate global models and the package *MuMIn* (Barton, 2019) was used for model selection and model averaging. Quasi-models in R do not report *AICc* values and therefore model averaging could not be carried out for the institution-level models. Instead, regular likelihood models were used to extract *AICc* values for the Quasi-binomial *GLM* models (Bolker, 2017), and full models were reduced to minimum adequate models based on lowest *AICc*. Lastly, pseudo R-squared values for the Quasi-binomial models were calculated using the *MuMIn* package. This provides a measure of how well each model fits the data, and determines the amount of variation explained by institution alone.

3.3 RESULTS

3.3.1 Factors affecting reproductive success across the entire EEP

Between 2012 and 2016, 54 out of the 134 (40.30%) reproductive-age female white rhinoceros in the EEP population successfully calved at least once, and a total of 76 calves were born. However, 17 (22.37%) calves were either stillborn or died after just 3 days. All other calves were alive at the end of the study timeframe (n=59). Of the 57 institutions from the EEP included in the analyses, just 30 (52.63%) produced any calves. See Appendix 2 for the mean and range of all values included in the analyses.

3.3.1.1 Factors affecting institution breeding success

Model selection based on *AICc* indicated that mean group size was the best predictor of institution breeding success (Table 3.2); a greater proportion of females calved as mean group size increased (Figure 3.1). Mean group age was also identified as predictor of institution breeding success (Table 3.2); the proportion of females that calved at an institution increased as mean group age decreased. However, mean group size only explained 21% of the variation in breeding success between institutions, whilst group age explained less than 5% of the variation (Table 3.2).

Table 3.2. The quasi-binomial GLM predictors and top model output used to explain variation in the proportion of females that calved at each EEP institution between 2012 and 2016. For all models Group Size was Log_{10} transformed, Group Age was √ transformed, and Number of Adult Females was $\sqrt[3]{}$ transformed. R^2 denotes the pseudo-R^2 value. *AICc* values were obtained from models without the quasi-binomial distribution.

	FULL MODEL	TOP MODEL OUTPUT					
Model	**Variables**	**Variable**	**Coefficient**	**SE**	***p-value***	**Model *AICc***	**Model R^2**
A	Group size, Group Age, Latitude	Group Size	2.35	0.67	<0.001	66.27	21.25
B	N Adult Females, Group Age, Latitude	Group Age	-0.49	0.30	0.105	78.60	4.52

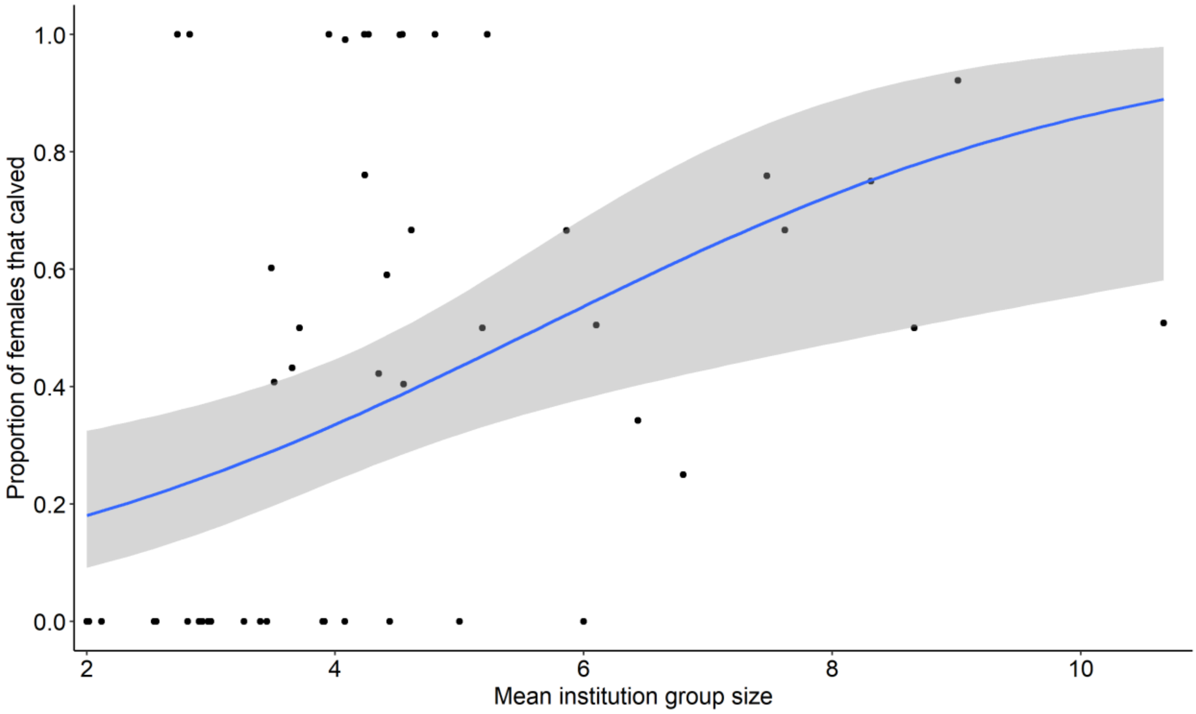

Figure 3.1. The effect of mean group size on the proportion of reproductive-age females that calved at an institution in the EEP studbook. The blue line represents the univariate quasi-binomial logistic regression line and the shaded area represents the 95% confidence intervals around the regression line.

3.3.1.2 Factors affecting female calving success

The model averaged results suggest that female white rhinoceros in the EEP were more likely to calve if they were born in the wild, were of a younger age, were housed alongside a female already successfully breeding, or were housed in a larger sized group (Table 3.3, Figure 3.2). The model with the lowest *AICc* indicated that the presence of a successfully breeding female and birth origin were the best predictors of female calving success (Model D; Table 3.3). The number of adult females in a group was also identified as a predictor of female calving success (Models B and C; Table 3.3). However, as confidence intervals crossed zero in both models, it was not a reliable predictor of calving success. Number of transfers and latitude were also included in averaged models, but had comparatively lower variable importance, and confidence intervals crossing zero (Table 3.3), and thus can be regarded as uninformative parameters, with no discernible effect on female calving success.

Table 3.3 . Averaged model parameters explaining calving success in captive female white rhinoceros in the EEP studbook. For all models, Age and Group Size were Log$_{10}$ transformed, Group Age was $\sqrt{}$ transformed, and Breeding Females was $\sqrt[3]{}$ transformed. Institution was included as a random effect in all models. The mean *AICc* and range, for models with a *ΔAIC* <2, coefficient estimate, standard error, lower and upper confidence intervals, and relative variable importance (*RVI*) for each variable, are provided for each averaged set of models.

FULL MODEL		**AVERAGED MODEL**						
Model	**Predictors**	**Mean *AICc* (range)**	**Predictor**	**Coefficient**	**SE**	**Lower CI**	**Upper CI**	**RVI**
A	Age, Group size, Group age, Latitude	161.63 (160.79 - 162.40)	Age	-1.184	0.481	-2.127	-0.241	1.00
			Group size	1.880	0.556	0.790	2.969	1.00
			Group age	-0.571	0.562	-1.671	0.530	0.31
			Latitude	0.338	0.507	-0.655	1.332	0.21
B	Origin, N Adult females	162.07 (162.07)	Origin	2.439	0.712	1.044	3.833	1.00
			N Adult females	1.359	0.697	-0.007	2.725	1.00
C	Age, Transfers, N Adult females	177.22 (176.60-177.92)	Age	-1.046	0.387	-1.804	-0.287	1.00
			N Adult females	0.561	0.385	-0.193	1.316	0.51
			Transfers	0.364	0.383	-0.386	1.114	0.36
D	Origin, Breeding female	148.73 (148.73)	Origin	1.648	0.443	0.780	2.516	1.00
			Breeding female	1.990	0.435	1.137	2.843	1.00

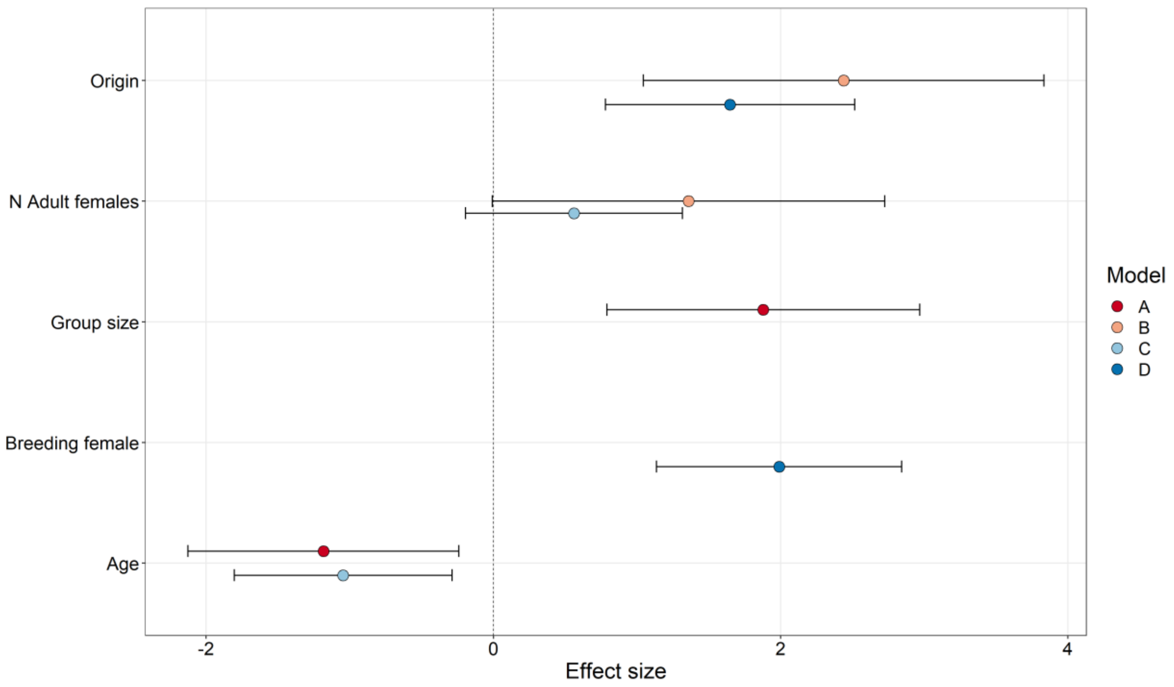

Figure 3.2. Average effect sizes (coefficient averages) and 95% confidence intervals for the averaged model predictors, with an RVI >0.5, used to explain female calving success. All predictors were standardised prior to analysis, meaning effect sizes are comparable. Predictors of the same colour were included in the same models. See Table 3.3 for model parameters.

3.3.2 Factors affecting breeding behaviour and reproduction across a sample of the EEP

There were 48 females of reproductive-age across the 20 institutions that responded to the questionnaire. Calving success across the questionnaire sample was relatively similar to that of the entire EEP reproductive-age female population; of the 48 females included in the questionnaire dataset, 21 (43.75%) successfully calved at least once (40.30% across the entire EEP). A total of 28 calves were born, as five females calved twice, and one female calved three times. Additionally, one female calved recently after translocation to an institution outside of the questionnaire dataset, and therefore this birth was omitted from the analyses. Of the 29 births recorded, five calves were stillborn, and one died at 3 days old. All other calves were alive at the end of the study timeframe (79.31%). Out of the 20 institutions included in the questionnaire dataset, only 10 (50.00%) had breeding success.

Of the 48 females in the questionnaire dataset, 35 (73%) were observed showing reproductive behaviour when paired with a breeding bull, 31 (65%) were observed copulating with a breeding bull, and 23 (48%) successfully became pregnant. Of those that became pregnant, 21 calved during the study timeframe, and two females were still pregnant at the end of the study timeframe.

3.3.2.1 Factors affecting female reproductive behaviour

Females were more likely to exhibit reproductive behaviour if they were born in the wild, were of a younger age, were housed with a female already successfully breeding, and were housed in a group with a younger mean age (Figure 3.3.). The model with the lowest *AICc* indicated that group age was the best predictor of whether or not a female was receptive to a male (Model 1A; Table 3.4). Number of adult females in a group and number of transfers had comparatively lower variable importance, and confidence intervals crossing zero (Table 3.4), and thus do not appear to effect female reproductive behaviour.

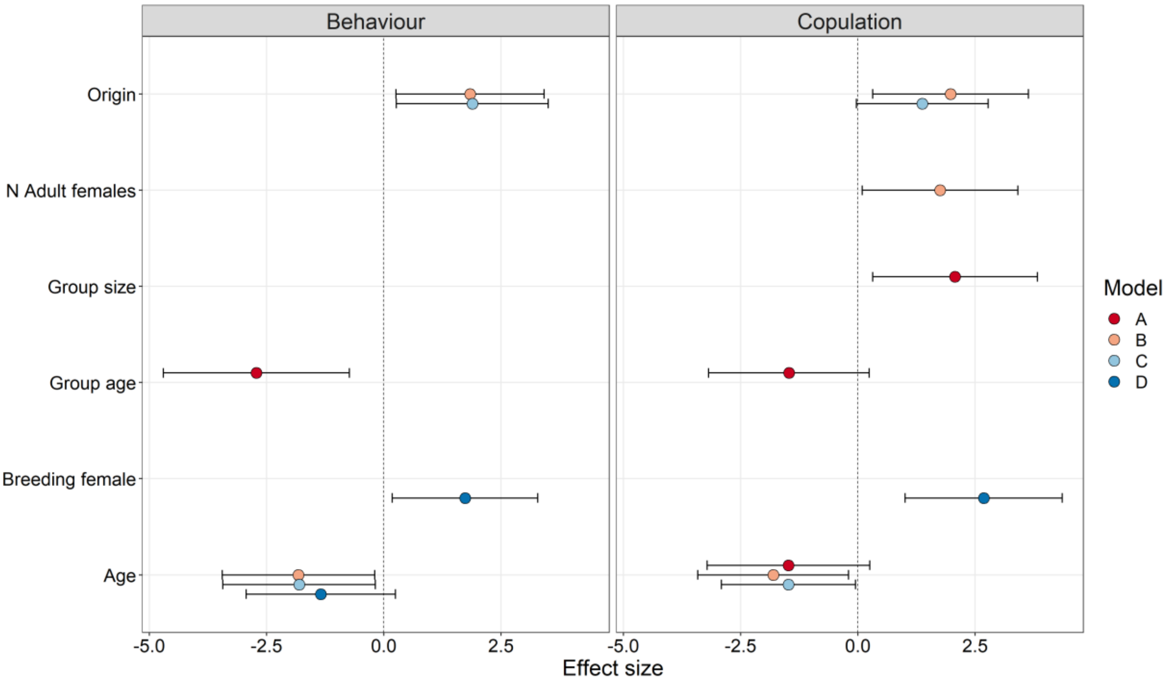

Figure 3.3. Average effect sizes (coefficient averages) and 95% confidence intervals for the averaged model predictors, with an RVI >0.5, used to explain whether reproductive behaviour (left) or copulation (right) were observed from females. All predictors were standardised prior to analysis, meaning effect sizes are comparable. Predictors of the same colour were included in the same models. See Table 3.4 for model parameters.

3.3.2.2 Factors affecting female copulation success

Females were more likely to copulate with a breeding bull if they were born in the wild, were of a younger age, were housed with a successfully breeding female, were housed in a larger sized group, or were housed with a larger number of adult females (Figure 3.3). Based on model *AICc,* the presence of a successfully breeding female was the best predictor of whether or not a female copulated with a breeding bull (Model 2D; Table 3.4). Enclosure size, latitude, and drive through had comparatively lower variable importance, and

Table 3.4 Averaged model parameters explaining reproductive behaviour, copulation and pregnancy success in the female white rhinoceros included in the questionnaire dataset. For all models, Age was Log$_{10}$ transformed, Crash size was √ transformed and Enclosure size was $_3$√ transformed. Institution was included as a random effect in all models. The mean AICc and range, for the models with a ΔAIC <2, coefficient estimate, standard error, lower and upper confidence intervals, and relative variable importance (RVI) for each variable are provided for each averaged set of models.

FULL MODEL		**AVERAGED MODEL**						
Model	**Predictors**	**Mean AICc (range)**	**Predictor**	**Coefficient**	**SE**	**Lower**	**Upper**	**RVI**
1. Reproductive behaviour								
A	Age, Group Size, Group age, Enclosure size, Latitude	50.87 (50.13-51.61)	Group age	-2.720	1.011	-4.702	-0.738	1.00
			Age	-0.750	0.826	-2.369	0.870	0.32
B	Age, Origin, Drive through, N Adult females	54.66 (53.78-55.54)	Origin	1.840	0.805	0.261	3.419	1.00
			Age	-1.820	0.830	-3.447	-0.194	1.00
			N Adult females	0.629	0.766	-0.872	2.129	0.29
C	Age, Origin, Male access, Transfers	54.39 (53.78-55.00)	Origin	1.887	0.827	0.266	3.508	1.00
			Age	-1.807	0.830	-3.433	-0.181	1.00
			Transfers	-0.904	0.843	-2.556	0.748	0.35
D	Age, Breeding female, Female access, Drive through	55.06 (54.66-55.46)	Age	-1.343	0.813	-2.936	0.250	0.60
			Breeding female	1.731	0.791	0.181	3.281	1.00
2. Copulation								
A	Age, Group Size, Group age, Enclosure size, Latitude	59.92 (58.90 - 60.78)	Group size	2.073	0.897	0.315	3.831	1.00
			Age	-1.480	0.885	-3.214	0.254	0.67
			Group age	-1.470	0.875	-3.185	0.245	0.60
			Enclosure size	-0.946	0.880	-2.670	0.778	0.33
			Latitude	-0.589	0.780	-2.118	0.939	0.09
B	Age, Origin, Drive through, N Adult females	60.52 (59.71-61.33)	Origin	1.975	0.847	0.315	3.634	1.00
			N Adult females	1.754	0.848	0.092	3.415	1.00
			Age	-1.807	0.821	-3.417	-0.197	1.00
			Drive through	-0.775	0.806	-2.354	0.805	0.31
C	Age, Origin, Male access, Transfers	63.49 (62.63-64.35)	Age	-1.482	0.729	-2.911	-0.053	1.00
			Origin	1.372	0.717	-0.032	2.777	0.70
D	Age, Breeding female, Female access, Drive through	54.46 (53.98-55.09)	Breeding female	2.683	0.856	1.004	4.362	1.00
			Age	-1.061	0.799	-2.627	0.505	0.45
			Drive through	-1.148	0.926	-2.963	0.668	0.42
3. Pregnancy								
A	Age, Group Size, Group age, Enclosure size, Latitude	60.48 (60.01-60.98)	Group size	2.278	1.005	0.308	4.247	1.00
			Age	-1.636	0.908	-3.415	0.143	0.75
			Group age	-1.655	1.024	-3.662	0.353	0.67
B	Origin, Drive through, N Adult females	54.62 (53.92-55.88)	Origin	2.502	1.030	0.484	4.521	1.00
			N Adult females	0.923	1.085	-1.204	3.050	0.27
C	Age, Origin, Male access, Transfers	66.36 (65.37-67.20)	Age	-1.747	0.936	-3.582	0.087	0.80
			Male access	1.107	1.041	-0.934	3.148	0.29
D	Age, Breeding female, Female access, Drive through	51.91 (51.66-52.16)	Age	-1.421	0.911	-3.208	0.365	0.56
			Breeding female	3.019	0.818	1.415	4.623	1.00

confidence intervals crossing zero (Table 3.4), and therefore were regarded as uninformative parameters.

3.3.2.3 Factors affecting female pregnancy success

Model averaging indicated that females born in the wild, housed in larger sized groups, or housed alongside a successfully breeding female, were more likely to become pregnant after being paired with a breeding bull (Table 3.4), and thus had greater pregnancy success. Group age and female age were also identified as predictors of female pregnancy success. However, both had confidence intervals crossing zero, suggesting they are not reliable predictors of pregnancy success (Figure 3.4). The model with the lowest *AICc* indicated that the presence of a breeding female was the best predictor of whether or not a female became pregnant after they were paired with a breeding bull (Model D; Table 3.4). Male access was also included in the averaged model set, although it had no apparent effect on female pregnancy success, as demonstrated by confidence intervals encompassing zero.

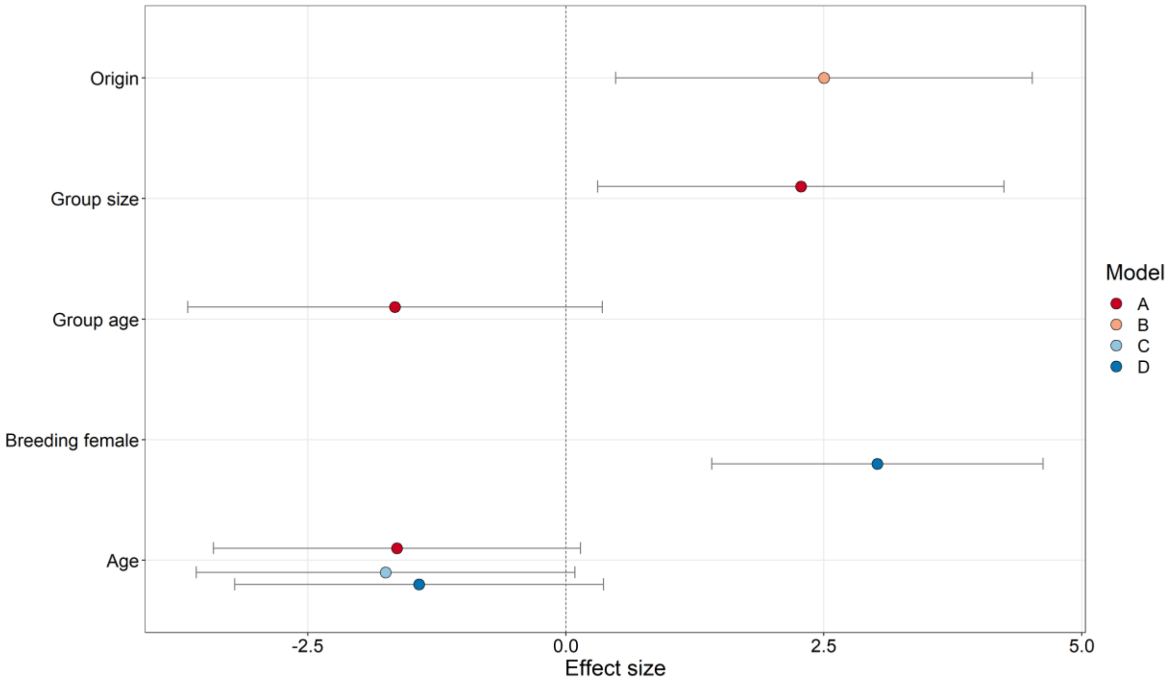

Figure 3.4 Average effect sizes (coefficient averages) and 95% confidence intervals for the averaged model predictors with an RVI >0.5 used to explain whether females became pregnant after being paired with a breeding bull. All predictors were standardised prior to analysis, meaning effect sizes are comparable. Predictors of the same colour were included in the same models. See Table 3.4 for model parameters.

3.4 DISCUSSION

The results of this chapter suggest that variation in social conditions across European institutions may influence female southern white rhinoceros breeding success. In particular, mean group size was identified as the most important predictor of institution breeding success across the entire European meta-population, and was also a key predictor of several essential components of female calving success, including whether or not a female copulated, or became pregnant, when paired with a breeding bull. Mean group age was the most important predictor of female reproductive behaviour, with females in younger groups being more likely to exhibit reproductive behaviour towards a breeding bull. However, overall, the presence of a successfully breeding female was the best predictor of female calving success across the entire EEP, and whether or not females copulated or became pregnant following pairing with a breeding bull. Both female age and birth origin were also linked to female reproductive success, with wild-born and younger females being more likely to exhibit reproductive behaviour, copulate and become pregnant, than captive-born or older females.

Mean group size was identified as the best predictor of institution breeding success across the entire EEP, and results from the questionnaire analyses demonstrated that females were more likely to copulate with a bull, and become pregnant, if they were housed in larger sized groups. This strongly suggests that reproduction in females is socially facilitated, and contradicts previous hypotheses that female white rhinoceros may reproductively suppress one another in the captive environment (Carlstead and Brown, 2005). As institutions prefer to have female biased sex ratios to increase reproductive output (Metrione and Eyres, 2014), group size and number of adult females in the group were highly correlated. Based on model *AICc* values and effect sizes, group size was a better predictor in all models. This suggests that group size is more important to female reproductive success than large, specifically female, groups. However, the presence of experienced breeders may greatly improve female reproductive success.

The presence of a breeding female was identified as the best predictor of female calving success across the entire European captive white rhinoceros population. Furthermore, females included in the questionnaire dataset were more likely to exhibit reproductive behaviour, copulate and become pregnant, if they were housed alongside a breeding female, compared to those that were housed with females that were either no longer breeding, or that were yet to successfully calve. In the wild, female white rhinoceros regularly live in groups with their calf and sub-adults, and have large home ranges that overlap with numerous other groups (Owen-Smith, 1975). Consequently, females frequently come into contact with individuals from other groups, and aggregations of over 10 rhinoceros are not uncommon (du Toit et al., 2006). Social relationships often last for periods of over five months in the wild (Owen-Smith, 1975; Shrader and Owen-Smith, 2002). However, grouping patterns can change periodically, and when females have young calves they tend to become less tolerant of associates (Shrader and Owen-Smith, 2002; Metrione et al., 2007). In captivity, companionships regularly persist for several years, and individuals are kept in close proximity with limited opportunity to change associates, except when a female companion has a new-born calf (Metrione et al., 2007). Consequently, females may develop stronger social bonds in captivity than in the wild.

Social familiarity has been shown to positively influence reproductive success in several other taxa (Grabowska-Zhang et al., 2012; Martin and Shepherdson, 2012), and research on captive female white rhinoceros shows that individuals housed together from adolescence have lower levels of stress related corticosterone than those housed together later in life (Metrione and Harder, 2011). This suggests that familiarity with social partners may reduce stress in female white rhinoceros, and could be linked to reproduction. As white rhinoceros are often transferred between institutions for breeding management purposes (Versteege, 2017), I hypothesised this may break important social bonds, and have potential consequences on individual wellbeing and fitness. However, this chapter found no discernible effect of number of transfers on female breeding success. This may be because males are more frequently transferred than females, and consequently 58% of females in the EEP had only been transferred once, or had never been transferred. Nevertheless, when making management decisions about which females to move between institutions, it may still be important to consider existing social bonds.

Due to the social nature of white rhinoceros, institutions are already recommended to house at least four females and two males to create optimal breeding conditions (Metrione and Eyres, 2014). Yet, between 2012 and 2016, the mean number of white rhinoceros at EEP institutions housing reproductive-age females was just four. Furthermore, as most institutions predominantly house adult males separately when females are not in oestrus, or are accompanied by young calves, the average group size experienced by females was more likely just three individuals. The results of this study highlight the importance of captive social group structures to both the breeding behaviour and reproduction of female white rhinoceros, and stress the need to increase group sizes in those institutions housing less than four individuals to promote breeding success.

The mechanisms that may be driving social facilitation of reproduction in white rhinoceros are unclear. Female white rhinoceros are frequently aggressive towards adult males, both in the wild and in captivity (Owen-Smith, 1973; Cinková and Bičík, 2013). Therefore, females may become stressed by males if they are in sub-optimal group compositions or spatial environments, and are unable to interact with males as they would naturally in the wild. Alternatively, the presence of other breeding females may stimulate ovulation in white rhinoceros. In captive female squirrel monkeys, *Saimbi sciureus*, the presence of social companions has been linked to more regular ovarian cycles and increased conception rates (Schiml et al., 1996). This could also apply to captive female white rhinoceros, as females have been observed to synchronise their oestrus cycles when they are particularly 'bonded' (Brown et al., 2001). Why female white rhinoceros have better reproductive success in larger groups, and in the presence of experienced breeders, evidently requires further investigation.

Poor reproductive output in captive-born female white rhinoceros has repeatedly been identified as a major factor limiting their population growth in captivity (Schwarzenberger et al., 1999; Swaisgood et al., 2006). The results of this study show that females born in the wild were not only more likely to calve than females born in captivity, but they were also more likely to exhibit reproductive behaviour and copulate with a breeding bull. This contradicts previous findings, which suggest that wild-born females are no more likely to display socio-sexual or copulatory behaviours than captive-born females (Swaisgood et al., 2006). This led to the conclusion that post-copulatory complications are most likely the cause of reproductive failure in captive-born females. However, the results of this chapter suggest that deficiencies in socio-sexual behaviours in captive-born females may indeed play a role in their poor breeding success, as 27% of reproductive-aged females failed to exhibit reproductive behaviour when paired with a breeding bull, and 35% did not engage in a mating event. Consequently, pre-copulatory complications in female white rhinoceros should not be overlooked.

The inconsistency between the results of this study and those of Swaisgood et al (2006) may be attributed to methodological differences, as both studies had a similar sample size for questionnaire analysis (this study: n=48; Swaisgood et al: n=55). In this study, the socio-sexual behaviours 'chin-rest' and 'mount' were combined as 'reproductive behaviour', and respondents were asked whether females were receptive to any of these reproductive behaviours when paired with a male. Swaisgood et al (2006) analysed these behaviours separately, and it is unclear what the time-period or management situation parameters were for their questionnaire respondents. Nevertheless, the authors mention that the relationship between copulatory behaviour and birth origin showed a non-significant tendency, with captive-born females being less likely to copulate than wild-born females, as also found in this study. Therefore, compromised or absent socio-sexual behaviour in captive-born females may indeed explain their poor reproductive performance to some extent, and the differences between the socio-sexual behaviour of captive- and wild-born female's warrants further investigation.

Age was also identified as an important predictor of female breeding success. Both younger females, and females that were part of group with a lower mean age, were more likely to exhibit reproductive behaviour than older females, or females that were housed in groups with a greater mean age. Furthermore, younger females were more likely to copulate with a breeding bull, and become pregnant, than older females. There is currently no evidence of reproductive senescence in white rhinoceros, as females can reproduce from the age of around 3 years old until their early 40's (Metrione and Eyres, 2014). However, females rarely successfully reproduce in captivity after the age of 34 (Versteege, 2017), most likely due to health complications associated with old age. Females that were over the age of 34 were not included in the analyses for this study, to reduce any potential influence that complications related to very old age have on reproduction. Yet, there was still an effect of age on both breeding behaviour and reproductive success.

According to data from the North American regional studbook for white rhinoceros, only 3% of females have an age at first reproduction greater than 20, suggesting fertility may indeed decline with age (Metrione and Eyres, 2014). Of the 80 reproductive-age females in the EEP that failed to reproduce during the time period of this study, only 21 had ever reproduced before, and 43 were over the age of 20 and had never reproduced, suggesting they are unlikely to reproduce in the future. Pro-longed periods of reproductive inactivity have been linked to an increase in the incidence of reproductive pathologies and oestrus cycle irregularities in female white rhinoceros (Hermes et al., 2006). This could explain the negative effect of age on reproductive success, as older females that have not bred previously may have had more time to develop reproductive organ pathologies or irregular oestrus cycles than younger females. Research suggests that the ageing process of the female reproductive tract can be prevented with the achievement of at least one successful pregnancy (Hermes et al., 2006). Therefore, because mean group age also appears to be linked to female reproductive success, it may be beneficial to house adolescent females reaching sexual maturity alongside young breeding females, rather than older females that have never bred, to try to stimulate reproduction as early on as possible.

Whilst this study had a relatively modest sample size limiting the number, and complexity, of variables that could be viably analysed in relation to female reproduction, it has demonstrated that variation in social conditions do influence female breeding success. Previous research suggested that reproductive failure in white rhinoceros was largely attributed to post-copulatory complications (Swaisgood et al., 2006). The results from this chapter suggest that pre-copulatory reproductive problems, in particular the absence of socio-sexual behaviours, may also contribute towards poor reproductive output in captive female white rhinoceros. Group size and age structure should be carefully considered when choosing individuals to exchange between institutions for breeding purposes, and where possible, keeping sexually mature females in large groups alongside breeding females may help to stimulate socio-sexual behaviours and reproduction. Further studies should focus on understanding the development of female socio-sexual behaviours in captivity, and how natural grouping patterns in the wild impact female reproduction, to provide further guidance on the breeding management of white rhinoceros in captivity. Chapter five addresses the latter, using social network analysis to investigate the social structure of four populations of white rhinoceros in Kenya, and the impacts of social connectivity on female reproductive success. The results of this chapter are also likely to be relevant to the management of other species with complex social systems and low reproductive success in captivity, and demonstrate the importance of considering an individual's social environment when making captive breeding management decisions.

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3.6 APPENDICES

Appendix 1

Questionnaire survey questions

Institution

1. What is the name of your institution?
2. What is your role at the institution?
3. How long have you worked at this institution?
    - < 1 year
    - 1 – 2 years
    - 2 – 5 years
    - > 5 years

Housing management

4. Do you have a drive through enclosure? (Y/N)
5. How often were your female rhinos provided with access to males at night during (and including) the years 2012 to 2016?
    - Always
    - Over 75% of the time
    - Between 50% and 75% of the time
    - Between 25% and 50% of the time
    - Less than 25% of the time
    - Never
6. How often were your female rhinos provided with access to other females at night during (and including) the years 2012 to 2016?
    - Always
    - Over 75% of the time
    - Between 50% and 75% of the time
    - Between 25% and 50% of the time
    - Less than 25% of the time
    - Never

7. Were all of your rhinos provided with access to one another on a daily basis between (and including) the years 2012 and 2016? (Y/N)

If No is selected, respondent is redirected to question 9. If Yes is selected, respondent goes to question 8.

8. What is the total size of your rhino outside enclosure space (m^2)?

Respondent is then redirected to question 10.

9. Please indicate the different groups individuals were kept in between (and including) 2012 and 2016, and the length of time they were managed this way. Example of online format shown in table below.

	Names of individuals	Start date housed together (no earlier than 01/01/2012)	End date housed together (no later than 31/12/2016)	Total outside enclosure size (m^2)
Group 1				
Group 2				

Male reproductive behaviour

10. Please use the following drop-down menu to indicate how frequently each male has been observed performing the following reproductive behaviours whilst housed with a cycling female. Please include all males that have been present at your institution at some point between (and including) 2012 and 2016. Example of online format shown in table below.

Name	Chin rest (male rests head on female’s hindquarters)	Anogenital investigation (male smells anogential area of female)	Mount	Copulation	Ejaculation
	Never Less than once per month Multiple times per month Multiple times per week Multiple times per day	Same options	Same options	Same options	Same options

Female reproductive behaviour

11. Please use the following drop-down menu to indicate how frequently each female has been observed performing the following reproductive behaviours whilst cycling and housed with an adult male. Please include all females that have been present at your institution at some point between (and including) 2012 and 2016. Example of online format shown in table below.

Name	Hold (female remains still for > 5 seconds whilst male attempts to chin rest or mount)	Copulation	Average cycle length if known (days)
	Never Less than once per month Multiple times per month Multiple times per week Multiple times per day	Same options	Same options

Breeding management

12. Please indicate which male-female pairs you have attempted to breed between (and including) 2012 and 2016. Example of online format shown in table below.

Name of female	Name of male	Length of time they were provided access to each other (weeks)	Were male reproductive behaviours observed?	Were female reproductive behaviours observed?	Was copulation observed?	Was pregnancy achieved?	Is the female currently pregnant?
			Y/N	Y/N	Y/N	Y/N	Y/N

Appendix 2

Table 3.5 Mean and range for all of the variables included in the studbook and questionnaire analyses.

Variable	Studbook mean (min-max)	Questionnaire mean (min-max)
Institution breeding success (Proportion that calved)	0.37 (0.0-1.0)	NA
Female calving success (1= yes; 0 =no)	0.40 (0.0-1.0)	0.46 (0.0-1.0)
Reproductive behaviour (1= yes; 0 =no)	NA	0.73 (0.0-1.0)
Copulation (1= yes; 0 =no)	NA	0.65 (0.0-1.0)
Pregnancy (1= yes; 0 =no)	NA	0.48 (0.0-1.0)
Mean group age (years)	18.73 (6.7-35.4)	18.75 (8.1-31.2)
Mean group size	4.39 (2.0-10.9)	4.40 (2.0-8.4)
N adult females	2.60 (0.9-6.0)	2.70 (1.0-5.0)
Male access (1= occasionally; 0 =never)	NA	0.45 (0.0-1.0)
Female night access (1= >50% of the time; 0 = <50% of the time)	NA	0.55 (0.0-1.0)
Enclosure size (m^2)	NA	49,085 (141- 218,530)
Drive through (1= yes; 0 = no)	NA	0.30 (0.0-1.0)
Latitude (°)	48.89 (24.2-58.7)	48.49 (37.0-55.8)
Number of transfers (0/1 = 0; 2/3 =1)	0.35 (0.0-1.0)	0.42 (0.0-1.0)
Origin (1 = wild, 0 = captivity)	0.57 (0.0-1.0)	0.65 (0.0-1.0)
Age (years)	15.38 (4.5-33.4)	15.25 (4.5-32.9)
Breeding female presence (1 = yes; 0 = no)	0.52 (0.0-1.0)	0.54 (0.0-1.0)

4 STUDY POPULATIONS

4.1 INTRODUCTION

The data presented in chapters five and six were collected from four populations of southern white rhinoceros, *Ceratotherium simum simum*, in Kenya. These included two populations from wildlife conservancies: Ol Pejeta Conservancy and Lewa Wildlife Conservancy, and two from national parks: Meru National Park and Lake Nakuru National Park (Figure 4.1). Whilst Kenyan wildlife conservancies are managed privately for the purpose of conservation, Kenyan national parks are managed by the government through the Kenya Wildlife Service (KWS). The four study populations comprised a total of 201 white rhinoceros, and represented approximately 36% of Kenya's white rhinoceros population at the end of 2017 (n=510 at the end of 2017; (Emslie et al., 2019). All ecological and behavioural data were collected between March 2017 and August 2019 (Table 4.1).

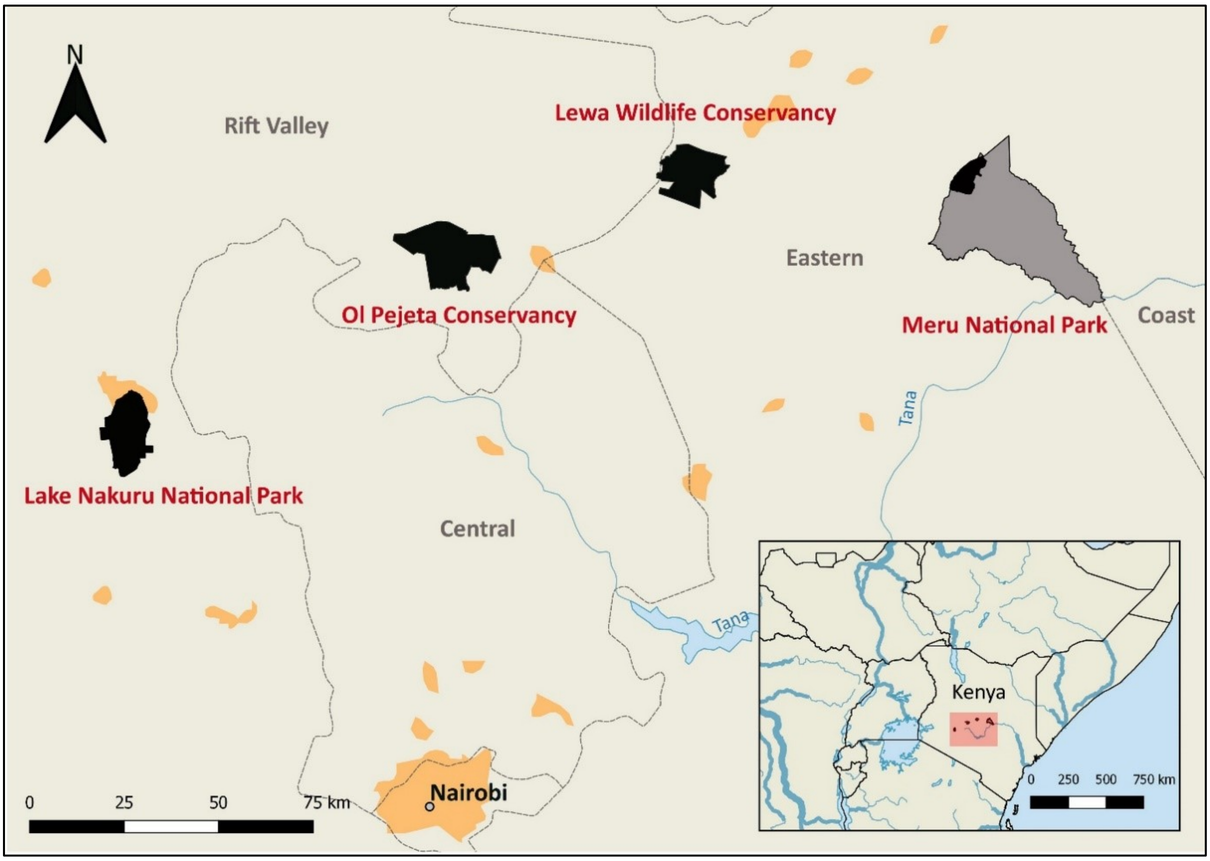

Figure 4.1 The location of the four study sites in Kenya, Eastern Africa. The area of each study site is shaded black. To show the location of the study site within Meru National Park, the rhino sanctuary is shaded black and the full area of the park is shaded grey. Orange shading indicates major urban areas and grey dashed lines show province boundaries.

Dates of birth and sex were available for rhinoceros in all populations, and were used to assign age-sex classes (defined in Chapter 5), and determine the age and sex structure of the study populations during data collection periods (Table 4.1).

Table 4.1 The age-sex structure, population size and area size (km^2) available to rhinoceros, for each study population during data collection periods.

Population	Data collection period	Adult males	Adult females	SA males	SA females	Calves	Total males	Total females	Total pop.	Area size
Ol Pejeta	March 2017	3	5	4	1	4	10	7	**17**	295
	June/July 2017	3	5	5	1	4	10	8	**18**	
	July/Aug 2018	4	5	6	2	4	11	8	**21**	
Meru	July/Aug 2017	12	18	7	10	17	27	37	**64**	51
	Feb/Mar 2018	12	21	8	12	18	32	39	**71**	
Nakuru	June/July 2018	1	6	3	0	3	6	7	**13**	134
Lewa	July/Aug 2019	23	21	17	15	21	49	45	**96**	250

Note that total males and total females do not always sum to total population as sex data for some calves were missing.

4.2 OL PEJETA CONSERVANCY

4.2.1 Overview

Ol Pejeta Conservancy (Ol Pejeta) is a 365km^2 wildlife conservancy located at 0.00˚N, 36.96°E in the Laikipia District of Kenya, approximately 220km north of Nairobi, and 20km west from Nanyuki town. Ol Pejeta integrates cattle with wildlife; approximately 600 cattle graze the plains during the day, and at night they are kept within predator-proof bomas (Ol Pejeta Conservancy, 2019). The wildlife conservation area within the conservancy, in which all rhinoceros reside, is approximately 295km^2 (Figure 4.2). Southern white rhinoceros in Ol Pejeta are divided between a free ranging and a fenced population, within a small endangered species enclosure (2.83km^2). This study focussed solely on the free-ranging population, which was established using animals sourced from nearby private reserves between 2007 and 2013. There were 17 free ranging southern white rhinoceros in the Ol Pejeta population during the first data collection period in March 2017, and 21 during the last data collection period in mid-2018 (Table 4.1) due to four births during the study.

4.2.2 Climate and habitat

Laikipia usually experiences two periods of heavy rainfall annually; between March and May (the long rains), and between October and December (the short rains), and average annual rainfall in the conservancy ranges between 600mm and 800mm. Ol Pejeta is located close to the foot of Mount Kenya, at an altitude of 1,600m above sea level. Temperatures in the conservancy range from 8°C at night to 29°C in the day. Ol Pejeta is composed of a grassland-woodland mosaic, and is characterised by poor-draining 'black-cotton' soil. The Ewaso Ngiro river runs from the south to the north of the conservancy (Figure 4.2), and whilst it is largely impassable to wildlife during periods of heavy rain, most animals can cross the river throughout the rest of the year. Several seasonal streams flow into the river, and dams and boreholes dispersed across the conservancy provide additional water for wildlife and cattle throughout the year.

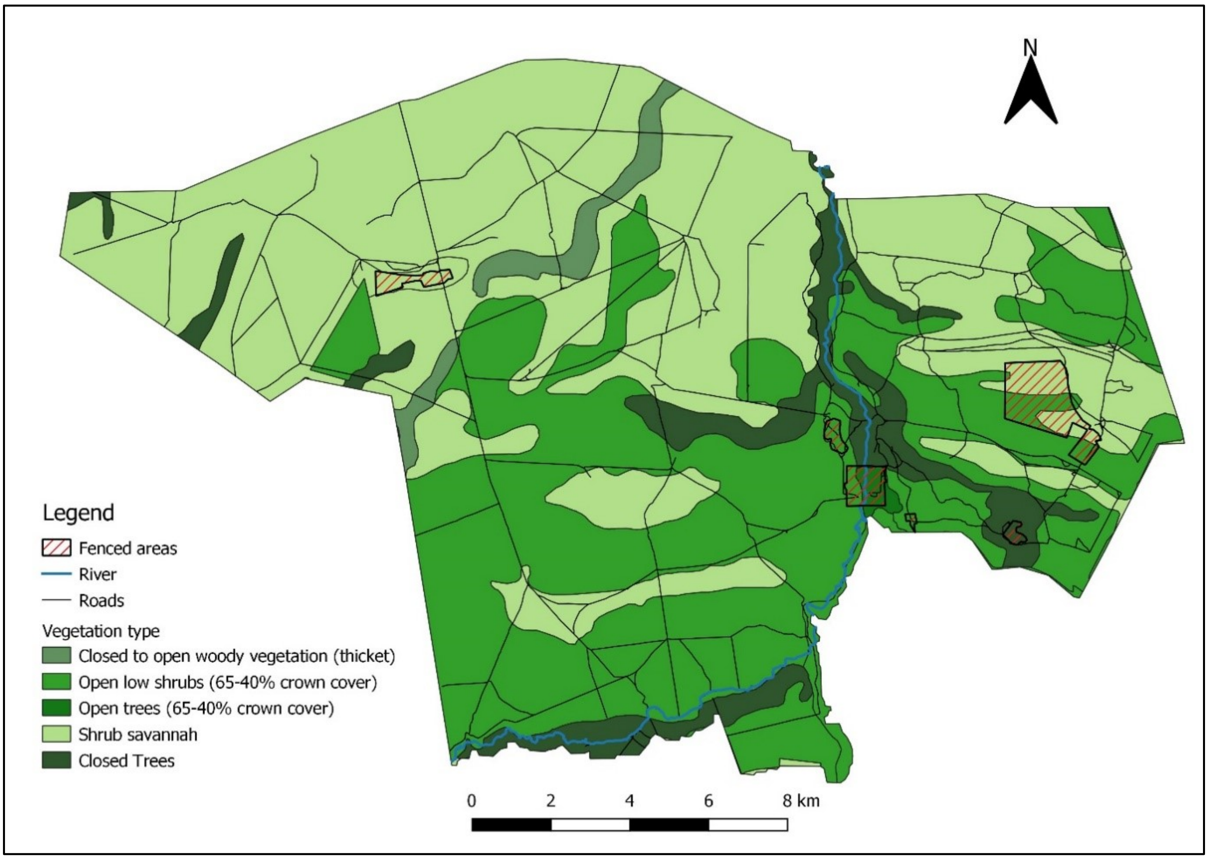

Figure 4.2. Vegetation map of Ol Pejeta Conservancy wildlife conservation area, showing fenced areas that rhinoceros cannot access, and the main road network. Vegetation classification and land cover were obtained from the AFRICOVER project (Di Gregorio and Latham, 2009).

The dominant woody tree species is *Acacia drepanolobium* in areas of higher elevation, whilst *Euclea divinorum* dominates moist areas in the valleys and stream depressions at lower elevations. The grassland plains are dominated by *Themeda triandra,* with patches of *Cynadon dactylon* in areas of less intensive grazing. Large carnivores found on the conservancy include lions, *Panthera leo*, spotted hyena, *Crocus crocata*, and cheetah, *Acinonyx jubatus*. Large herbivores include elephant, *Loxodonta africana*, buffalo, *Syncerus caffer*, giraffe, *Giraffa reticulata*, plains and Grevy's zebra , *Equus burchelli and E. grevyi*, impala, *Aepyceros melampus*, Thomson's and Grant's gazelle, *Gazella thomsonii and G. granti*, and both black and white rhinoceros, *Diceros bicornis and Ceratotherium simum*.

4.3 MERU NATIONAL PARK

4.3.1 Overview

Meru National Park (Meru) is an 870km^2 national park managed by KWS, located in the Eastern Province of Kenya, approximately 350km north-east of Nairobi (0.09°N, 38.19°E). Meru forms part of a greater conservation area, connected to Kora National Park and both Bisanadi and Mwingi National Reserves. Rampant poaching and civil unrest decimated most wildlife populations in Meru in the 1980's and 90's (Ojwang' et al., 2017), and the white rhinoceros population was re-established in the early 2000's using animals sourced mainly from Lake Nakuru National Park. Both black and white rhinoceros in Meru were fenced within a 51km^2 sanctuary during the time of this study (Figure 4.3). There were 64 white rhinoceros in the sanctuary during the first data collection period in June-July 2017, and 71 during the second in February-March 2018 (Table 4.1), due to seven births during the study.

4.3.2 Climate and habitat

Meru National Park has a warmer climate than the other study sites, with temperatures ranging between 10°C at night and 32°C in the day. The park experiences similar rainfall patterns to Ol Pejeta, with long rains occurring from March-April, and short rains occurring from October-December. Annual rainfall ranges between 300-600mm in most areas, and is greatest in areas of higher altitude in the northwest of the park. The sanctuary is located in the north of the park (Figure 4.3), and lies at approximately 750m above sea level.

The habitat in the sanctuary is composed of dense thicket, tropical forest, shrub and tree grasslands and swamp, intersected by streams and three permanent rivers (namely the Bwatherongi, Mutundu and Rojewero). The dominant woody tree species are *Acacia tortilis, Combretum apiculatum and Commiphora spp.* in the grasslands, and *Hyphaene thebaica and Raphia farinifera* (Doum and Raffia palm) in the dense riverine forests. *Sehima nervosum* and *Pennisetum mezianum* dominate the drier areas of grassland, whilst *Panicum maximum* and *Cynadon dactylon* are dominant in wetter areas. Large carnivores in Meru include lions, leopards, *Panthera pardus*, and spotted hyena. Large herbivores include elephant, buffalo, plains and Grevy's zebra, waterbuck, *Kobus ellipsiprymnus*, giraffe, and both black and white rhinoceros. With the exception of rhinoceros, most animals move freely in and out of the sanctuary, including elephants, which routinely break down the fencing.

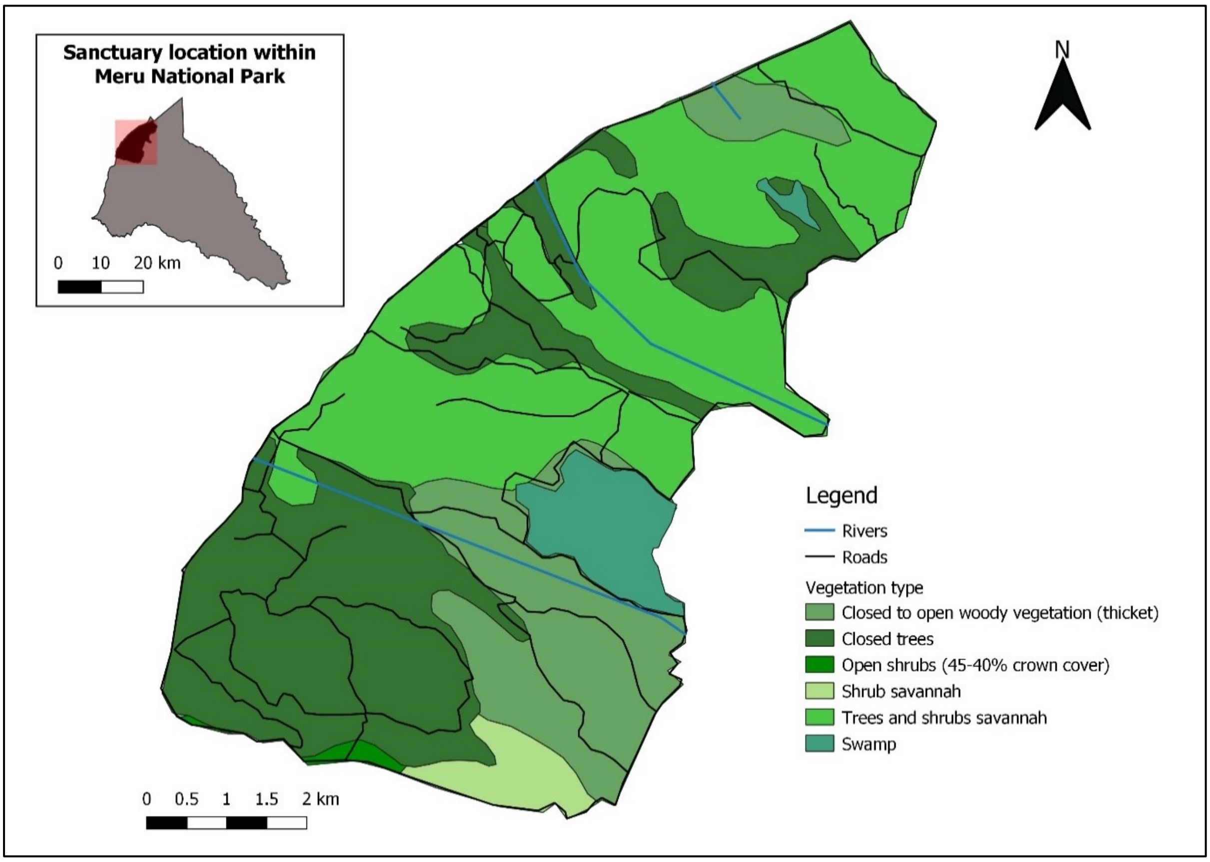

Figure 4.3. Vegetation map of the Meru rhinoceros sanctuary, showing the location of the sanctuary within Meru National Park, and the main road network in the sanctuary. Vegetation classification and land cover were obtained from the AFRICOVER project (Di Gregorio and Latham, 2009).

4.4 LAKE NAKURU NATIONAL PARK

4.4.1 Overview

Lake Nakuru National Park (Nakuru) is a 188km^2 national park surrounding Lake Nakuru (Figure 4.4), also managed by KWS, and located in Kenya's Central Rift Valley, approximately 150km north-west of Nairobi, and just 4km from Nakuru town-centre (0.37°S, 36.08°E). Nakuru was one of the first rhinoceros sanctuaries established in Kenya, opening in 1983, and received most of its founding population of white rhinoceros from South Africa in the 1990's. Whilst Nakuru had the second largest white rhinoceros population in Kenya in 2006 (Okita-Ouma et al., 2007), numbers have decreased dramatically in recent years due to illegal poaching (Save the Rhino, 2014), disease outbreaks (Gachohi et al., 2019), and translocations to other Kenyan populations. At the time of data collection in June-July 2018, the white rhinoceros population consisted of 13 individuals, including only one adult male (Table 4.1).

Figure 4.4. Vegetation map of Lake Nakuru National Park, showing the lake and main road network in the park. Vegetation classification and land cover were obtained from the AFRICOVER project (Di Gregorio and Latham, 2009).

4.4.2 Climate and habitat

Nakuru has a dry sub-humid to semi-arid climate, with average annual rainfall between 800mm and 900mm, and temperatures ranging between 9°C at night and 28°C in the day. The heaviest periods of rainfall are between late March and May, and there are frequent light rain showers from June-December. The lowland areas surrounding the lake lie at an altitude of around 1200m, whilst the surrounding hills and cliffs rise to over 1750m above sea level. The lake has increased substantially in size over recent years, and at the time of this study, covered an area of approximately 54km^2. This has significantly reduced the amount of habitat available for terrestrial animals. Three seasonal rivers (namely the Joro, Enderit and Makalia) flow into the lake from the south and east

The park's habitat consists of a mosaic of grassland, *Acacia* forest, scrub woodland and marsh surrounding the saline lake. The dominant tree species include *Acacia xanthophloea* in the lowland forests around the lake, *Euphorbia candelabrum* in the drier areas of bushland, and *Tarconanthus camphoratus* spp. on the slopes and hilltops. Both *Cynadon nlemfuensis* and *Cynadon dactylon* are the dominant grass species in the park. Large carnivores in Nakuru include lions, leopards and spotted hyena. Large herbivores include buffalo, plains zebra, impala, waterbuck, Grant's and Thomson's gazelle, hippopotamus, *Hippopotamus amphibious*, the endangered Rothschild's giraffe, *Giraffa camelopardalis rothschildi*, and both black and white rhinoceros. There are no elephants in Nakuru.

4.5 LEWA WILDLIFE CONSERVANCY

4.5.1 Overview

Lewa Wildlife Conservancy (Lewa) is a 250 km^2 private conservancy located in the Isiolo District of Kenya (0.23°N, 37.44°E), approximately 20km south of Isiolo town, and 200km north-east of Nairobi. Lewa established a 20km^2 black rhinoceros sanctuary in 1983, and in 1994, extended the sanctuary across the entire ranch (Figure 4.5), and established a white rhinoceros population. The majority of the founding white rhinoceros population came from Solio ranch, located nearby in Laikipia County, and Lewa has since been used to supplement the Ol Pejeta and Meru populations. In 2014, the boundary between Lewa and Borana Conservancy, adjoining Lewa's western boundary, was removed to allow movement of animals between the two, and expand potential habitat space (Lewa Wildlife Conservancy, 2019). However, the majority of white rhinoceros still resided in Lewa during the time of this study (95%), and just two sub-adult males migrated to Borana during the study period. At the time of data collection in July-August 2019, the total white rhinoceros population across Lewa and Borana comprised 96 individuals, with five individuals residing permanently in Borana, which were not included in the study.

4.5.2 Climate and habitat

The climate in Lewa is more arid than in the other study sites, with an average annual rainfall between 300mm and 500mm, and periods of drought are relatively common. The average temperature experienced by Lewa ranges from 11°C at night to 27°C during the day. Patterns of heavy rainfall are similar to that experienced in Ol Pejeta, with two distinct wet seasons each year during March-May and October-December. Lewa is situated 1,500-2,100m above sea level, to the north of the montane forests in Ndare Ngare that give rise to Mount Kenya. The habitat in Lewa is comprised of bushland, riverine forest, and significant patches of open savannah. The terrain in the conservancy is characterised by rolling plains, steep hills and valleys, and rocky outcrops. Lewa is comprised of areas of 'black cotton' soil, with poor drainage, as well as areas of red loam. The dominant woody species include *Acacia drepanolobium* and *Acacia seyal* on the plains, and several *Acacia* species, including *A.tortillis, A.nilotica and A.mellifera,* on the hills. The grasses *Pennisetum stramineum* and *Pennisetum mezianum* dominate the plains. Large carnivores in Lewa include lion, cheetah, leopard and spotted hyena. Large herbivores in the conservancy include elephant, giraffe, buffalo, both plains and Grevy's zebra, eland, *Taurotragus oryx*, waterbuck, and a significant population of both black and white rhinoceros.

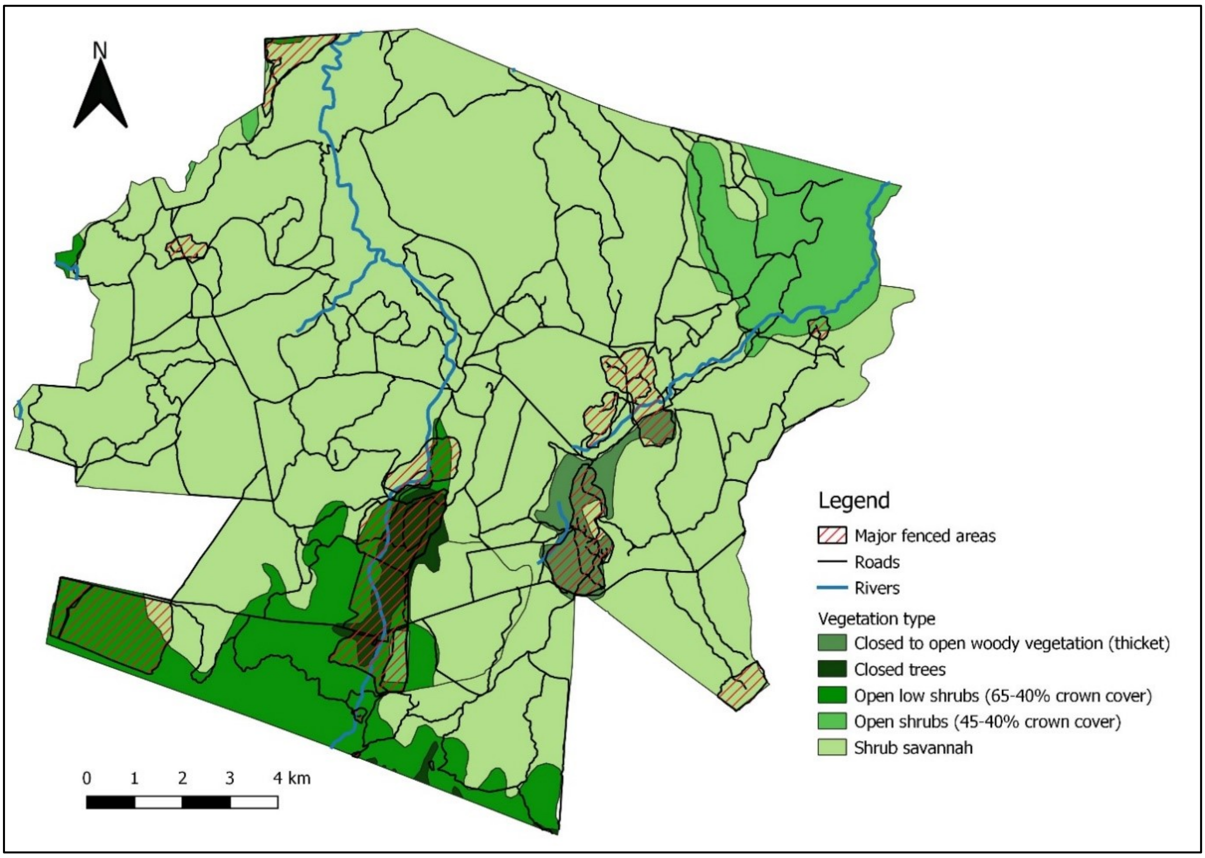

Figure 4.5. Vegetation map of Lewa Wildlife Conservancy, showing the major fenced areas that rhinoceros cannot access, and the main road network in the conservancy. Vegetation classification and land cover were obtained from the AFRICOVER project (Di Gregorio and Latham, 2009).

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5 AGE AND SEX-SPECIFIC ASSOCIATION PATTERNS IN SOUTHERN WHITE RHINOCEROS *(CERATOTHERIUM SIMUM SIMUM)* AND IMPLICATIONS FOR FEMALE REPRODUCTIVE SUCCESS

Abstract

Social relationships and association patterns are often important for individual fitness and population persistence. An understanding of a species' social environment and grouping patterns can therefore be crucial for their conservation management. There is substantial variation in reproductive output between certain populations of southern white rhinoceros, *Ceratotherium simum simum*. As white rhinoceros are a gregarious species, knowledge of their social structure and the impact of social conditions on reproduction could therefore help to inform their conservation management. This chapter used social network analysis to investigate the social structure and grouping patterns of four populations of white rhinoceros in Kenya. Social networks were used to investigate how sex and age influence social connectivity, and whether inter-individual relationships persist over time. Calving data were then used to investigate how female social connectivity influences breeding success. The results from this chapter demonstrate that white rhinoceros have a complex social structure characterised by a tendency to form preferred associations within cliques. Population cohesiveness and individual association rates differed between study populations, suggesting population size, density or ecology may influence their social structure. Age-class also influenced grouping patterns, as sub-adults associated more frequently, and were more likely to form strong associations within cliques, than adults were. Individuals often formed long-lasting associations, persisting for at least seven months, and associations between females were the most temporally stable. Female association frequency, connectedness and tendency to associate in cliques, related to inter-calving interval length, but this varied with ecological context. The results from this chapter provide important new insights on white rhinoceros sociality that can be used to improve their social conditions in captivity, and inform management strategies in the wild, such as the selection of individuals for translocation.

5.1 INTRODUCTION

Social relationships and association patterns serve important functions in many species, including predator avoidance (Hasenjager and Dugatkin, 2017), territory defence (Siracusa et al., 2019) and resource exploitation (Mueller et al., 2013). Specific social relationships (e.g. parent-offspring, mating partners, group members) or social structures (e.g. dominance hierarchies, territories) may be crucial for both individual and population persistence (Silk, 2007; Goldenberg et al., 2019). Therefore, the adaptive fitness benefits associated with the maintenance of social bonds often out-weigh the negative impacts of group living, such as intragroup competition, by improving the survival, fitness or health of individuals that can optimally navigate their social environment (Brent et al., 2013; McFarland et al., 2017).

Despite the importance of social behaviour to the reproduction and survival of many species, its application in the field of conservation management remains relatively underused (Berger-Tal et al., 2016; Brakes et al., 2019). Social network analysis provides a useful set of tools to uncover the subtleties of a species' social organisation (Carter, Brand, et al., 2013), and has potential to inform species conservation management (Snijders et al., 2017). For example, knowledge of a species' social network can facilitate the understanding of how disease, social information or genes may transfer between individuals in a population (Wey et al., 2008). Social network studies have also been used to investigate how the removal of key individuals impacts social organisation and population viability (Williams and Lusseau, 2006), and how ecological conditions influence association patterns and the frequency of agnostic interactions (Leu et al., 2016).

Translocations and reintroductions are frequently used to enable gene flow between fragmented populations, supplement existing populations, or establish new populations of threatened species (IUCN, 2013). However, many efforts have failed because of inadequate planning or insufficient resources (Seddon et al., 2007; Taylor et al., 2017). Whilst most strategies consider demographics (Sarrazin and Legendre, 2000), or genetics (Haig et al., 1990), when selecting candidates for reintroduction or translocation efforts, important aspects of a species' social behaviour are often overlooked (Goldenberg et al., 2019). In species with complex association patterns and social behaviours, this may disrupt existing population dynamics and processes, reducing the future viability of a population.

Social network analysis can identify pre-existing social structures in a population, which can guide the selection of individuals for translocation or reintroduction efforts, and facilitate their long-term social stability post-release. For example, black-tailed prairie dogs, *Cynomys ludovicianus,* translocated in family units (Shier, 2006), and Stephen's kangaroo rats, *Dipodomys stephensi*, translocated with neighbours (Shier and Swaisgood, 2012), are both more likely to survive and reproduce than those not translocated in familiar groups.

Several social network studies have demonstrated the importance of social relationships to reproductive success. For example, research has shown that male Assamese macaques, *Macaca assamensis*, with strong social bonds sire more offspring than those with few strong social bonds (Schülke et al., 2010), and female humpbacked whales, *Megaptera novaeangliae*, with stronger and more stable associations reproduce more successfully (Ramp et al., 2010). Indirect relationships can also influence an individual's reproduction and survival (Snijders et al., 2017; Goldenberg et al., 2019). For example, vampire bats, *Desmodus rotundus*, with more weak associations are less affected by food shortages than those with few weak associations (Carter et al., 2017), and female chacma baboons, *Papio hamadryas ursinus*, with well-connected social partners have higher offspring survival than those with less well-connected social partners (Cheney et al., 2016). Social network analysis can thus identify social structures important to a species' reproduction and survival, which can be used to inform conservation management decisions that aim to improve population performance and viability (Snijders et al., 2017).

Determining how both age and sex influence association patterns is fundamental to understanding a species' baseline social structure. Many species alter their social behaviour as they mature (Linklater and Cameron, 2009; Patriquin et al., 2010; Wey and Blumstein, 2010), and knowledge of the differences in sociality between age-classes will help to inform appropriate management actions for juvenile or adult animals. Furthermore, comparing sociality between the sexes will identify how males and females contribute towards overall network structure, which may uncover their differing priorities in relation to fitness and survival. For example, in mammals, male reproductive success is limited by access to females, whereas female reproductive success is more often limited by access to resources (Trivers, 1972). Therefore, whilst males are more likely to benefit from associates that increase their access to females (Bygott et al., 1979), females may benefit from developing relationships that increase their access to resources. Moreover, as social networks can vary between populations of the same species, due to factors such as population size and density (Farine, 2017), predator abundance (Muller et al., 2019), anthropogenic disturbance (Belton et al., 2018), or environmental conditions (Leu et al., 2016), employing a multi-population approach provides a more rigorous assessment of a species' baseline social structure.

White rhinoceros, *Ceratotherium simum*, are an excellent model species for social network analysis and its application to conservation management. Due to the ongoing threat from illegal poaching, rhinoceros populations require intensive protection and monitoring to remain viable. Subsequently, detailed long-term demographic data are often available, and individuals can be identified and located by park rangers on a regular basis. White rhinoceros are the most social of the rhinoceros species, with females and sub-adults forming aggregations of up to 18 individuals (du Toit et al., 2006), and associations often lasting for several months (Owen-Smith, 1975). Furthermore, they have complex communication systems, using both olfactory and acoustic signals to communicate social information such as sex, age, and oestrus state (Cinková and Policht, 2014, 2015; Marneweck et al., 2017). However, there is little understanding of white rhinoceros social structure in the wild (Owen-Smith, 1975; Shrader and Owen-Smith, 2002; Cinková et al., 2009), the underlying factors driving their association patterns, or the potential fitness consequences associated with sociality.

Captive management of southern white rhinoceros, *Ceratotherium simum simum*, is not sustainable due to low levels of reproduction (see Chapter 2), particularly in captive-born females (Swaisgood et al., 2006), and reproductive disparity also exists between certain populations in the wild (Rachlow and Berger, 1998; Ververs et al., 2017). Female inter-calving interval length has previously been linked to population density, with population growth rate and calf recruitment rate being lower in high-density populations (Rachlow and Berger, 1998). However, substantial variation in inter-calving interval length also exists within populations (Owen-Smith, 1975; Rachlow and Berger, 1998; Ververs et al., 2017), and the mechanisms driving this remain unknown. Due to the social nature of the white rhinoceros, variation in social connectivity may influence female reproductive success.

In both captivity and in the wild, rhinoceros are frequently translocated for breeding management purposes. Such social upheaval may have a detrimental impact on individual welfare, as important social bonds and existing group structures are altered, and this may disrupt natural breeding behaviour and reproductive success (Price and Stoinski, 2007). Identifying current group compositions and considering these during routine management decisions, like translocations, may help to improve their success by minimising disruption to social dynamics. Furthermore, knowledge of white rhinoceros association patterns will help to inform population management strategies, such as estimates of ecological carrying capacity or population viability.

This chapter uses data on group compositions from four populations of southern white rhinoceros in Kenya to describe their social network structure and association patterns. The main aim of this chapter was to identify features of white rhinoceros social structure to inform their conservation and breeding management. The first objective was to compare the social networks of different populations, to determine the defining characteristics of white rhinoceros social structure, and identify how population density and size may influence association patterns. The second objective was to determine how sex and age-class affect social connectivity, to provide insight into age-sex class social requirements. The third objective was to determine whether inter-individual relationships persist over time, to assess whether familiarity with conspecifics is likely to be important to white rhinoceros. The final objective of this chapter was to determine the influence of social connectivity to female reproductive success.

5.2 METHODS

5.2.1 Study populations

Four populations of southern white rhinoceros in Kenya were included in this study, from Ol Pejeta Conservancy, Meru National Park, Lake Nakuru National Park and Lewa Wildlife Conservancy (hereafter referred to as Ol Pejeta, Meru, Nakuru and Lewa). Each reserve varied in both total land area and white rhinoceros population size (Table 5.1), allowing social structure to be compared across different population sizes and densities. All data were collected between March 2017 and August 2019 (Table 5.1), outside peak rainfall periods (see Chapter 4), when all areas of reserves were accessible. See Chapter 4 for a full description of the four study sites.

Table 5.1 Summary of the four white rhinoceros populations included in the study, and the data used for social network analysis. Objective is the research question the data collected during that time-period contributed to. Total area and density were calculated for the wildlife conservation area (295km^2) in Ol Pejeta, rather than the entire conservancy (365km^2), and in Nakuru, estimates excluded the 54km^2 lake. Number of independent groups refers to those used to generate social networks, i.e. only groups including individuals observed on at least five independent days. Mean sighting rate refers to the mean number of days individuals observed on at least five independent days were seen.

Population	**Area** (km^2)	**Objective**	**Time period**	**Population size**	**Population density** (rhino/km^2)	**Number of days**	**Number of groups**	**Mean sighting rate**
Ol Pejeta	295	3	March 17	17	0.06	10	46	7.2
		1,3	June 17	18	0.06	11	74	8.9
		3	July/Aug 18	21	0.07	10	44	8.2
Meru	51	1,2,3,4	June/July 17	65	1.25	28	160	9.4
		3	Feb/Mar 18	71	1.39	31	218	11.7
Nakuru	134	1	June/July 18	13	0.07	16	59	9.7
Lewa	250	1,4	July/Aug 19	96	0.40	31	200	7.6

5.2.2 Group structure data collection

Study sites were divided into two approximately equal sections, which were searched for rhinoceros once a day, in either the morning (between 06:00 and 11:00) or late afternoon (between 15:00 and 19:00), alternating daily. Rhinoceros were not searched for outside of these times as they were most often resting in dense vegetation, making sightings and identification more difficult. As rhinoceros in Lewa were dispersed across a larger area than those in other populations, Lewa was divided into four approximately equal sections, and searches were alternated between sections and time of day, so that each section was searched every two days. Searches were conducted from a vehicle on roads within each section, which were driven in an unstructured order each day. Due to the vegetation density and poor visibility in Meru, off-road routes in areas of dense vegetation were also searched, in an attempt to locate individuals not visible from the roads.

A group of rhinoceros was defined as one individual, or a set of individuals within 20m of each other, or a set of individuals engaged in the same behaviour and within 50m of each other. The first distance threshold was set as previous research suggests white rhinoceros groups are ‘seldom separated by more than 20m’ (Owen-Smith, 1975), which corresponded with the majority of group observations in this study. The second threshold was set because during observation periods in this study, individuals occasionally ranged up to 50m from one another whilst feeding or moving. As group membership can often change within a day, independence of observations was maintained by using only the first group each day in which an individual was observed for social network analysis. The sampling period used for analysis was therefore set at one day, as this was expected to give individuals adequate opportunity to change groups.

When a group of rhinoceros was located, they were followed either on foot or from a vehicle, until all individuals were identified. All individuals were photographed during each sighting, and identified using unique ear notches or other morphological characteristics (horn size and shape, body size and ear tears), with reference to the photograph database. The date, time and identity of each individual, were recorded during each observation. Individuals were assigned age-classes following criteria described in Table 5.2.

Table 5.2 Description of the criteria used to assign age-sex classes to individual white rhinoceros.

Age-class	Description
Calf	Individual that is still with mother, <4 years old, and mother has not calved again.*
Sub-adult female	Female <6 years old, has not yet calved, and mother has calved again.
Sub-adult male	Male <8 years old and mother has calved again, or male >8 years old and frequently found with a companion (i.e. is not yet solitary).
Adult female	Female >6 years old, or that has already calved.
Adult male	Male >8 years old and solitary.

*There were several cases where the individual was <4 years old and the mother had calved again, and that individual was either with another group, or they had re-joined their mother and her current calf (the latter was usually only the case if the current calf was >6 months old). In these cases, they would be classed as a sub-adult.

The GPS location of the observer was also recorded using a hand-held Garmin GPS. The group's direction from the observer was determined using a compass, and their distance from the observer was estimated by eye. As the observer was most often within 50m of the rhinoceros group, distance estimations were thought to be relatively accurate. To minimise the effects of seasonality and food availability on grouping patterns, only data collected during the same time of year (June-August) were used to compare population networks, age-sex specific association patterns, and the impact of social connectivity of female reproductive success (Objectives 1,2 and 4; Table 5.1). Additional data collection periods were used to assess the stability of social relationships within populations over time (Objective 3).

5.2.3 Social structure comparison between populations

Networks were constructed from observed group compositions using the 'gambit-of the group' method, which specifies that all individuals within a group observed at a point in time are associated (Whitehead and Dufault, 1999). Association rates therefore correspond to how frequently two individuals occurred within the same group. The package *asnipe* (Farine, 2013), in R version 3.4.1, was used to generate an association matrix, where the strength of association between pairs of individuals was defined using the Simple Ratio Index (SRI) (Whitehead, 2008). The SRI provides a measure of association strength based on the proportion of times two individuals were observed together, whilst also accounting for both sample size and the number of times each individual was observed. Therefore, an SRI value of zero indicates that two individuals were never observed together, whilst a value of one indicates that they were always seen together.

Only adults and sub-adults observed on at least five independent days during a data collection period were included in the analysis. A minimum of five days was set as the sighting threshold to maximise the sample size for further analyses, whilst also reducing bias in association indices and the potential for false null associations between individuals with low numbers of sightings (Frère et al., 2010). This increases the reliability that strong associations are based on real grouping preferences, as opposed to random aggregations, or the result of missing data (Carter, Brand, et al., 2013). Males that were only ever observed alone were excluded from social networks (n=1 in Meru, n=1 in Lewa and n=1 Nakuru). To describe the general social network structure of each population, five descriptive network metrics were calculated; mean bond strength, density, mean path length, mean weighted path length and global clustering coefficient (Table 5.3).

5.2.4 Statistical significance tests

Because networks are based on non-independent observations of multiple individuals, null models were used to determine whether social preferences drive the observed network structures, rather than chance alone. Null models generate replicate networks based on the observed network, which have the same number of nodes (individuals) and edges (connections), but the aspect of interest is randomised, e.g. which individuals associate with each other (Farine, 2017). Random networks were generated using ‘pre-network data permutations’ in the R package *asnipe* (Farine, 2013), whereby single observations of two individuals occurring in different groups are swapped incrementally in a ‘checker board’ manner (Farine, 2017). This method of data permutation controls for the number of times an individual was observed, and both the number and size of groups.

Table 5.3. The global network metrics used to describe population social structure, and their definitions.

Network metric	Definition
Mean bond strength	The mean Simple Ratio Index (SRI) value for the network, i.e. the mean association strength between pairs of individuals.
Density	The sum of edge weights (SRI values) divided by the total possible number of edges, i.e. the total association strength between all pairs of individuals divided by the number of possible connections in the network.
Mean path length	The average number of steps along the shortest path, for all possible pairs of nodes, i.e. the average number of associations required to connect one individual to another.
Mean weighted path length	The mean path length taking into account edge weights, i.e. how frequently individuals associate with each other.
Global clustering coefficient	The proportion of closed triads in the network in relation to the proportion of triads with just two edges, i.e. the tendency for individuals to form closed social groups or 'cliques'.

Both the sampling period and geographical location of each group were controlled for, to ensure null models were generated based on the real-time distribution of individuals across each reserve. This accounts for the influence of factors that may vary with space and time, such as individual home ranges, habitat quality, or weather, thus ensuring that the only process randomised is the associations (Aplin et al., 2015; Muller et al., 2019). To control for the influence of spatial variation on association patterns, study areas were divided into grid squares, and data swaps in null models were restricted within each grid. This ensured that pairwise associations were only swapped between individuals that were observed in the same location, and on the same day (Aplin et al., 2015; Muller et al., 2019). In Lewa, Nakuru and Ol Pejeta, average 95% kernel density estimate (KDE) range sizes were 17-53km^2 for adult males, and 29-125km^2 for adult females (see Chapter 6). However, as rhinoceros in Meru were at a much higher density than the other populations (Table 5.1), average 95% KDE range size was just 5km^2 in adult males, and 8km^2 in adult females (see Chapter 6). Therefore, 5km^2 was set as the size of grid squares for data swaps in Meru, and 10km^2 was set as the size of grid squares in the other three populations, as individuals with large ranges are unlikely to traverse their entire range in one day. This provided a conservative estimate of the average area likely to be utilised by individuals in a day.

To determine if the structure of networks were based on social preferences, or were simply due to chance, the mean coefficient of variation (CV) and SRI were used to determine whether pairwise associations in the observed networks were significantly different to

1000 random networks. The CV describes the effect size of preferred/avoided relationships in the observed network (Farine and Whitehead, 2015), whilst the SRI measures the proportion of time two individuals spent together (Whitehead, 2008). A *p-value* was obtained by comparing the number of times the CV or SRI value of the observed network were greater or less than 95% of the randomly generated values. To determine how the other global network metrics varied between populations (clustering coefficient, mean path length and density), metric values were simply compared with each other. Null models were not used to test whether their observed values were non-random because the metrics density and bond strength would have remained the same (Belton et al., 2018), whereas SRI and CV values are better suited for permutation tests used to establish whether networks are non-random (Farine and Whitehead, 2015; Muller et al., 2019).

5.2.5 The influence of sex and age on network position

5.2.5.1 Individual network metrics

To determine how sex and age influence social network position, five node-level network metrics based on SRIs were calculated from the networks generated for Meru and Lewa, using the R package *tnet* (Opsahl, 2009); binary degree, strength, weighted betweenness, Eigenvector centrality and weighted clustering coefficient (Table 5.4). Ol Pejeta and Nakuru were not included in this analysis, as the number of individuals in each age- and sex-class was very small (Ol Pejeta: n=5 adult females, 3 adult males, 4 sub-adult males, 1 sub-adult female; Nakuru: n=6 adult females, 1 adult male, 3 sub-adult males, 0 sub-adult females).

5.2.5.2 Statistical significance tests

Linear regression models were used to determine the relationship, if any, between each network metric and both sex and age. Permutation tests, as described under section 5.2.4 (*Statistical significance tests*), were used to compare the effect size (coefficient of variation, CV) in the observed regression model to the mean effect size generated from 1000 random network regression models. Two-tailed significance was determined at $p<0.025$.

Table 5.4. The node-level network metrics used to describe individual network position, and their definitions.

Network metric	Definition
Binary degree	The number of edges connected to a node; i.e. the number of associates each individual has.
Strength	The weighted equivalent of the binary degree, defined as the sum of all edge weights connected to a node; i.e. an individual's expected rate of association per sample.
Weighted betweenness centrality	The number of shortest paths that flow through a node, taking into account the weight of each edge; i.e. the 'path of least resistance' between two nodes in the network. This measures how important an individual is for connecting disparate groups.
Eigenvector centrality	The sum of the centralities of a node's connections; i.e. how well connected an individual's connections are. This captures the potential importance of certain individuals as social hubs or disease/information propagules.
Weighted clustering coefficient	The proportion of closed triads an individual is part of in relation to those they could be part of; i.e. how well an individual's connections are connected to each other. This provides an estimate of how cliquish the network is due to individuals preferentially associating in closed social units. The weighted clustering coefficient takes into account edge weights, and therefore demonstrates how frequently an individual associates in cliques.

5.2.6 The temporal stability of relationships between individuals

To provide a measure of pairwise stability over time, and between data collection periods, lagged association rates (LARs) were used to calculate the probability that two individuals seen together on a particular day would be seen together again at some point in the future. Pairwise associations during two 1-month periods in Meru, and three approximately 10-day-long periods in Ol Pejeta (Table 5.1), were used to compare the stability of pairwise relationships. This allowed the temporal stability of pairwise relationships to be examined over both the short-term (1 month in Meru, and 10 days in Ol Pejeta) and long-term (7 months in Meru, and both 3 months and 1 year in Ol Pejeta). LARs were calculated from the association data using the R package *asnipe* (Farine, 2013), which applies LAR methodology proposed by Whitehead (1995). Only sub-adults and adults observed on at least five independent days during every data collection period were included in the analyses.

The precision of LARs was estimated using the Jackknife method, whereby replicate datasets were created by omitting one day at a time, and then used to calculate standard error values. The lagged association rate was compared against a null association rate to determine whether the probability two individuals would be seen together again was greater than it would be by chance. Null association rate was calculated using the formula proposed by Whitehead (1995): $N=M/P$, whereby M = the mean number of associates of any individual, and P = the potential number of associates.

The temporal stability of pairwise relationships was examined at three levels; (i) associations between all age-sex classes, (ii) female-female associations, and (iii) sub-adult-sub-adult associations. Male-male associations were not examined, as adult males are both solitary and territorial, and only tend to associate with females within their territory (Owen-Smith, 1975). Examination of the data further supported this; there were only three adult male-adult male associations recorded in Meru, and two in Ol Pejeta, across all data collection periods.

5.2.7 *The influence of social relationships on female reproductive success*

5.2.7.1 *Inter-calving interval length*

Mean female inter-calving interval (ICI) length was used to provide a measure of female reproductive success, calculated as the number of days between the birth date of one calf and the birth date of the subsequent calf. ICI's were calculated for all adult females in Lewa and Meru that had calved at least twice, and where calf date of birth data were available. Ol Pejeta and Nakuru were not included in this set of analyses due to a small sample size of breeding females, and incomplete birth records.

There were six ICI's based on calves that died within one week of birth, and five of these were shorter than the minimum ICI based on surviving calves (619 days), across both populations. Post-partum anoestrus is thought to occur in black rhinoceros, *Diceros bicornis*, (Brown et al., 2001), and this data suggests it may also occur in white rhinoceros. Therefore, the five shorter ICI's were excluded from the analyses on the basis that they did not provide a measure of reproductive success (du Toit et al., 2006), but were a result of the female starting to cycle more quickly than if she were still suckling a calf. The final sample size for statistical analysis was 11 adult females in Meru, and 16 in Lewa.

5.2.7.2 *Social relationship measures*

Five node-level network metrics based on SRI's were used to provide a measure of female social network position (Table 5.4). To further investigate the impact of particular social bonds on female reproductive success, the number of individuals a female was connected to in each age-sex class (adult female, adult male, sub-adult female, sub-adult male) and the sum of the weights of each female's connections to individuals in each age-sex class were also calculated (Stanton and Mann, 2012). This provided a measure of age-sex specific degree and strength for each adult female in the analyses.

5.2.7.3 Statistical analysis

Linear regression models were used to assess the influence of predictor variables on female ICI length. Each population was analysed separately, as factors such as network density and size can influence network metrics (Farine, 2017). The ICI length response variable was log-transformed in all models to improve its distribution. As network metrics are often highly correlated with each other (Farine and Whitehead, 2015), all variables were analysed separately. Permutation tests, as described under section 5.2.4 (*Statistical significance tests*), were used to compare the effect size (coefficient of variation) of each predictor variable, to those generated from 1000 random networks.

5.3 RESULTS

5.3.1 Social structure comparison between populations

Mean group size ranged from 1.5 (Ol Pejeta) to 2.0 (Lewa) when excluding dependent calves, from 2.0 (Ol Pejeta) to 2.7 (Meru) when including dependent calves, and from 2.3 (Nakuru) to 3.2 (Meru) when excluding observations of solitary males (Table 5.5).

Table 5.5. Mean group sizes (±SD) across the four study populations.

Population	Mean group size (±SD)[1]	Mean group size incl. dependent calves (±SD)[2]	Mean group size excl. solitary males (±SD)[3]
Meru	1.9 (±1.3)	2.7 (±1.9)	3.2 (±1.9)
Ol Pejeta	1.5 (±0.7)	2.0 (±1.0)	2.4 (±1.0)
Nakuru	1.8 (±1.1)	2.1 (±1.3)	2.3 (±1.3)
Lewa	2.0 (±1.3)	2.6 (±1.5)	3.0 (±1.5)

1. Mean group size based on groups used for social network analysis (this excludes dependent calves).
2. Mean group size including dependent calves.
3. Mean group size including dependent calves and excluding all observations of solitary adult males.

In Meru, Ol Pejeta and Nakuru, all individuals included were either directly or indirectly connected to each other, and each network had only one large component (Figure 5.1). However, in Lewa, the network comprised one large component and four smaller components (Figure 5.1). Table 5.6 summaries the global network metrics for the four

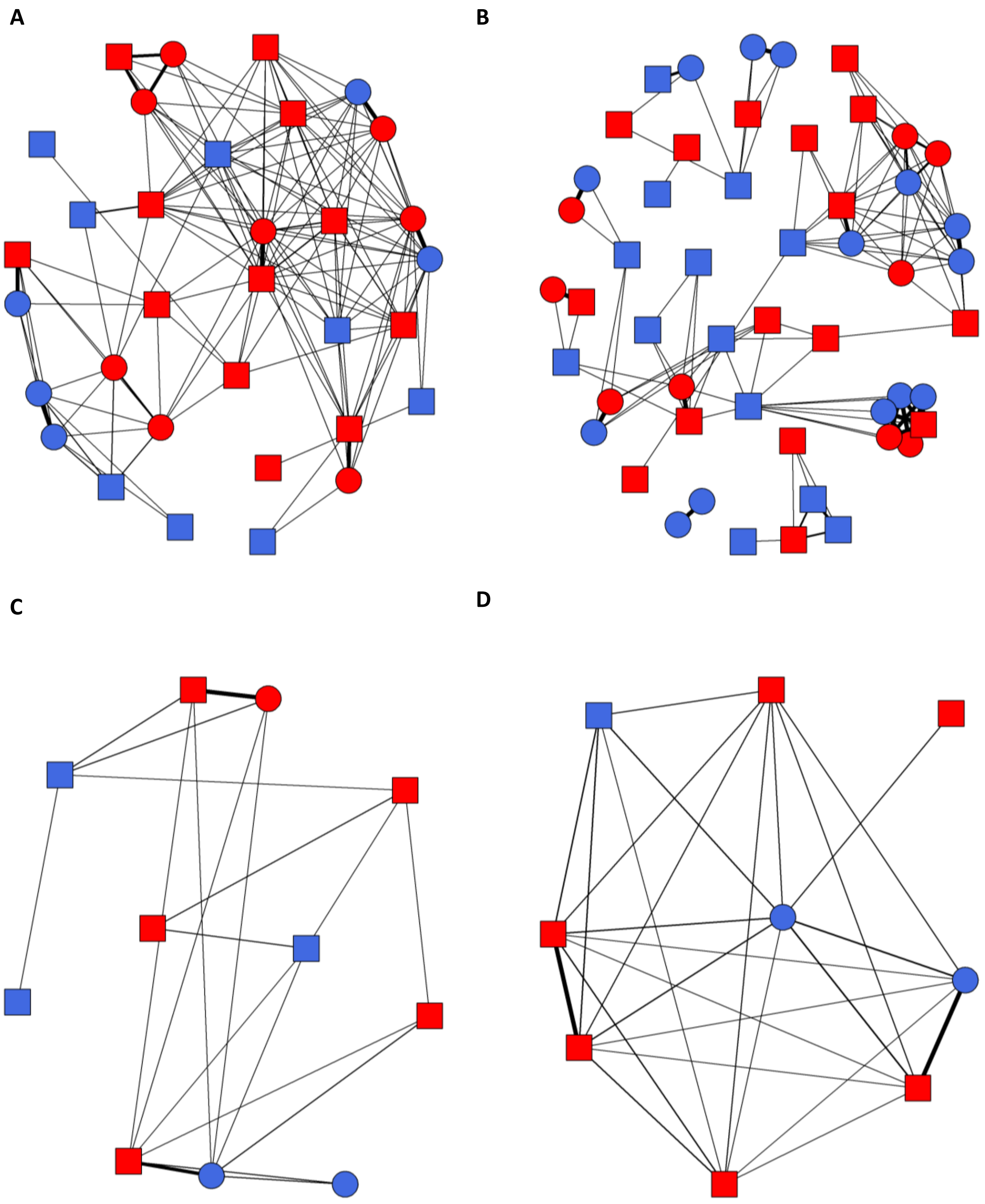

Figure 5.1 The white rhinoceros social networks in (a) Meru (n=33), (b) Lewa (n=52), (c) Ol Pejeta (n=11) and (d) Nakuru (n=9). Nodes are coloured by sex: females = red, males = blue. Node shape represents age class: squares = adults, circles = sub-adults. Edges are undirected and weighted by the Simple Ratio Index; thicker edges represent stronger associations between pairs of individuals. Only individuals observed on at least five independent days are included in social networks.

populations. The proportion of potential pairwise associations observed was directly related to population size; with 75% present in the smallest population (Nakuru), and just 9% present in the largest (Lewa). Network density also corresponded to population size, and was highest in Nakuru (0.132), and lowest in Lewa (0.028). Mean unweighted path length was relatively short across all populations (range: 2.2-3.6), and mean weighted path length was considerably longer in Lewa (11.8). Individuals in Nakuru and Lewa had the highest tendency to form strong connections within cliques, as evidenced by higher global clustering coefficient values.

Table 5.6. Global network metrics for the four study populations. Number and percentage (%) of dyads observed refers to the number of pairwise associations observed and the percentage of potential dyads observed. For the Lewa network, mean path length includes all network components.

Population	Number of dyads observed	% of dyads observed	Mean weighted path length	Mean un-weighted path length	Density	Global clustering coefficient
Meru	278	26.3	3.5	2.2	0.035	0.75
Ol Pejeta	40	36.4	4.3	1.9	0.055	0.77
Nakuru	54	75.0	2.0	1.3	0.132	0.93
Lewa	250	9.4	11.8	3.6	0.028	0.87

Rhinoceros in Meru and Lewa showed clear associations between individuals; the observed CV and mean SRI values were significantly greater than expected by chance (Table 5.7). However, whilst individuals from Ol Pejeta and Nakuru also had preferred associates, they did not spend more time associating with them than would be expected by chance; the observed CV values were significantly greater than those in null models, but the observed SRI values were not (Table 5.7).

Table 5.7. Mean non-zero edge weight (calculated using the Simple Ratio Index, SRI) and coefficient of variation (CV) for the four study populations. *P-values* in bold represent two-tailed significance at p<0.025, using 1000 random network permutations. See Appendix 1 for *p-value* estimation and random model distribution.

Population	Metric	Observed network	Random network	*P-value*
Meru	Mean CV value	349.7	195.4	**<0.001**
	Mean SRI value	0.133	0.102	**0.011**
Ol Pejeta	Mean CV value	325.0	191.2	**<0.001**
	Mean SRI value	0.151	0.138	0.163
Nakuru	Mean CV value	182.7	104.8	**<0.001**
	Mean SRI value	0.176	0.182	0.267
Lewa	Mean CV value	502.1	351.5	**<0.001**
	Mean SRI value	0.295	0.183	**0.001**

5.3.2 *The influence of sex and age on network position*

In Meru, males had a higher tendency to form strong social bonds within cliques than females; weighted clustering coefficient was significantly greater in males compared to females (Table 5.8). On the other hand, in Lewa, females had a higher tendency to form strong social bonds within cliques than males (Table 5.8).

Table 5.8. Average network metrics for males and females observed at least five times in the Meru and Lewa populations. Coefficient of variation (CV) values for the observed network and the mean for 1000 random networks were obtained from linear regression models and represent the observed and expected effect size of sex respectively. *P-values* in bold represent two-tailed significance at p<0.025. See Appendix 2 for sex differences in network metrics, *p-value* estimation and random model ditribution.

	Degree	**Strength**	**Betweenness**	**Clustering coefficient**	**Eigenvector centrality**
Meru					
Males (N=13)	6.31	0.890	20.0	0.77	0.072
Females (N=20)	9.80	1.27	39.7	0.67	0.164
CV observed	-3.492	-0.384	-19.700	0.096	-0.092
CV random (mean)	-3.362	-0.234	-6.819	0.014	-0.059
P-value	0.409	0.031	0.038	**0.021**	0.054
Lewa					
Males (N=27)	4.78	1.42	27.3	0.63	0.046
Females (N=25)	4.84	1.41	46.7	0.80	0.050
CV observed	-0.062	0.016	-19.422	0.171	-0.004
CV random (mean)	-0.270	0.065	17.782	-0.015	0.003
P-value	0.361	0.296	0.042	**<0.001**	0.060

In both populations, sub-adults associated more frequently, and had a higher tendency to form strong social bonds within cliques, than adults did, as evidenced by a significant difference in strength and clustering coefficient between age-classes (Table 5.9). Eigenvector centrality values show that sub-adult's associates were more well-connected than adult's associates were in Meru, but there was no difference between age-classes in Lewa (Table 5.9). Degree measures show that sub-adults had more associates on average than adults in Lewa (Table 5.9). Whilst sub-adults in Meru also had more associates on average than adults, the relationship between degree and age-class was not significant (Table 5.9). Lastly, betweenness measures in Lewa demonstrated that adults were more often situated on the shortest path connecting two individuals in the population than sub-adults were, but there was no difference in betweenness measures for adults and sub-adults in Meru (Table 5.9).

Table 5.9. Average network metrics for sub-adults and adults observed at least five times in Meru National Park and Lewa Wildlife Conservancy. Coefficient of variation (CV) values for the observed network and the mean for 1000 random networks were obtained from linear regression models, and represent the observed and expected effect size of sex respectively. *P-values* in bold represent two-tailed significance at p<0.025. See Appendix 2 for age-class differences in network metrics, *p-value* estimation and random model ditribution.

	Degree	Strength	Betweenness	Clustering coefficient	Eigenvector centrality
			Meru		
Sub-adults (N=13)	9.62	1.60	31.3	0.78	0.178
Adults (N=20)	7.65	0.81	32.4	0.67	0.096
CV observed	1.97	0.782	-1.074	0.115	0.082
CV random (mean)	0.870	0.338	6.002	0.036	0.041
P-value	0.032	**<0.001**	0.091	**0.005**	**<0.001**
			Lewa		
Sub-adults (N=23)	5.61	2.13	24.5	0.82	0.089
Adults (N=29)	4.17	0.85	46.2	0.64	0.016
CV observed	1.436	1.278	-21.646	0.178	0.073
CV random (mean)	2.554	0.795	18.861	-0.014	0.070
P-value	**<0.001**	**0.007**	**0.017**	**<0.001**	0.362

5.3.3 The temporal stability of relationships between individuals

In Meru, pairwise associations between all age-sex classes persisted for over seven months; the lagged association rate remained above the null association rate throughout both data collection periods, and until the penultimate day of data collection (Figure 5.2a), when sighting rate was notably low. In Ol Pejeta, pairwise associations between all age-sex classes were less stable; the lagged association rate declined quickly, and only remained above the null association rate for the first data collection period, and half of the second data collection period (Figure 5.2b).

Female-female associations also persisted throughout both data collection periods in Meru, and were more temporally stable than pairwise associations between all age-sex classes; the difference between the lagged association rate and the null association rate remained greater for female-female associations compared to all age-sex class associations (Figure 5.2c). However, again, the lagged association rate fell below the null association rate on the penultimate day of data collection. In Ol Pejeta, female-female association rate was not temporally stable; the lagged association rate fell below the null association rate during the first data collection period (Figure 5.2d).

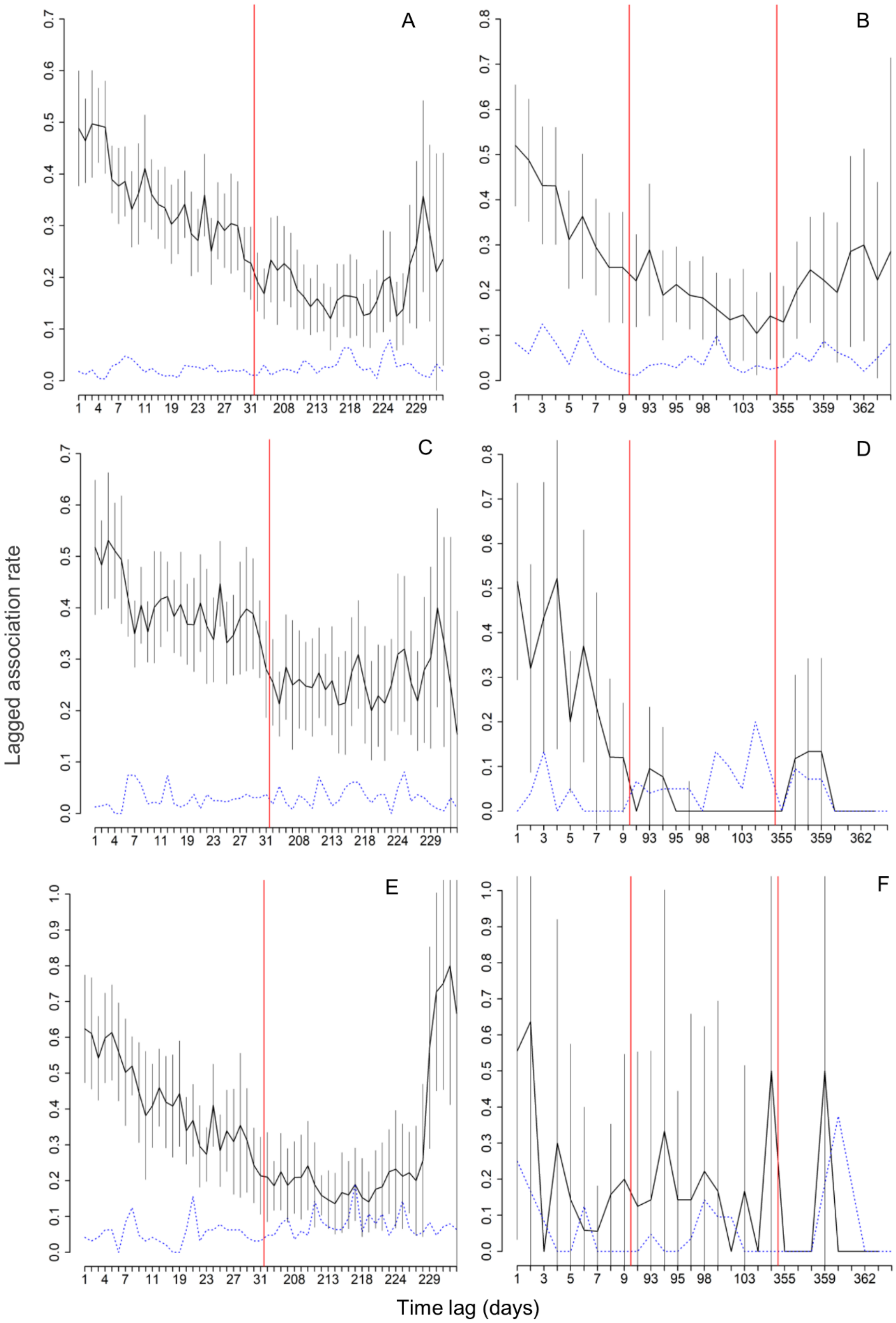

Figure 5.2. Lagged association rates among white rhinoceros in Meru and Ol Pejeta. Associations between all individuals in (a) Meru and (b) Ol Pejeta, female-female associations in (c) Meru and (d) Ol Pejeta, and sub-adult-sub-adult associations in (e) Meru and (f) Ol Pejeta. Standard error bars (vertical lines ±1SE) were estimated using Jackknife methods. The null association rate (blue dashed line) is the lagged association rate expected if individuals randomly associated. Red vertical lines distinguish between data collection periods.

Sub-adult-sub-adult associations persisted throughout the first data collection period in Meru. However, the lagged association rate fell below the null association rate during the second data collection period, before sharply increasing again (Figure 5.2e). In Ol Pejeta, sub-adults did not preferentially associate with other sub-adults; the lagged association rate was no greater than the null association rate during any data collection period (Figure 5.2f).

5.3.4 The influence of social relationships on female reproductive success

Mean inter-calving interval (ICI) length across female white rhinoceros in Meru was 2.72 (±0.50) years (n=11 females), ranging from 2.19 to 3.94 years. Mean ICI length across females in Lewa was 2.74 (±0.39) years (n=16 females), and ranged from 2.18 to 4.72 years. See Appendix 3 for mean ICI length and network metrics for each adult female.

5.3.4.1 Female network position and reproductive success

In Meru, females with a high tendency to form strong connections within cliques had longer calving intervals than females with a low tendency to form strong connections within cliques; ICI showed a significant positive relationship with weighted clustering coefficient (β=0.011, p=0.007). Females in Meru that associated more frequently, or had many well-connected associates, had shorter calving intervals than females that associated less frequently, or had few well-connected associates; ICI showed a significant negative relationship with strength (β=-0.030, p=0.007) and Eigenvector centrality (β=-0.213, p=0.012). On the other hand, in Lewa, females that associated less frequently, or had a high tendency to form strong connections within cliques, had shorter calving intervals than females that associated more frequently, or were less likely to form strong connections within cliques; ICI showed a significant positive relationship with strength (β=0.021, p=0.006), and a significant negative relationship with weighted clustering coefficient (β=-0.126, p<0.001).

5.3.4.2 Female age-sex specific associations and reproductive success

Female ICI was not related to the number of connections to any age-sex class, in either population. In Lewa, females that associated more frequently with other adult females had shorter calving intervals than those that associated less frequently with adult females; ICI showed a significant negative relationship with adult female strength (β=-0.661, p=0.022). Furthermore, females that associated more frequently with adult males, sub-adult males or sub-adult females had longer calving intervals than females that associated less frequently with these age-sex classes; ICI showed a significant positive relationship with adult male strength (β=0.050, $p<0.001$), sub-adult female strength (β=0.054, p=0.001) and sub-adult male strength (β=0.020, p=0.003). Female ICI was not related to any age-sex specific strength in Meru. See Appendix 4 for full permutation test results.

5.4 DISCUSSION

The results of this chapter show that white rhinoceros have a complex social structure characterised by a tendency to form preferred associations within cliques. In addition, population size and density may influence white rhinoceros grouping patterns, as population cohesiveness and individual association rates differed between study populations. These results also suggest that sex has no consistent effect on social connectivity across populations, but age-class does; sub-adults associate more frequently, and are more likely to form strong associations within cliques, than adults are. Furthermore, this study has shown that white rhinoceros often form long-lasting associations, persisting for over seven months, and associations between females are the most temporally stable. Lastly, these results have demonstrated that several aspects of female social connectivity, such as the tendency to form cliques or associate with particular age-sex classes, are related to inter-calving interval length, and therefore association patterns may influence female breeding success.

In the two largest study populations, Meru and Lewa, white rhinoceros social structure was driven by social preference, rather than simply home range overlap or shared resource use (Farine, 2017). However, in the two smaller populations, Ol Pejeta and Nakuru, pairwise association frequency was no greater than would be expected by chance. This may be due to the small size and low density of these populations; individuals come into contact less frequently, and have less opportunity to associate. Additionally, as white rhinoceros associations are most often between sub-adults and adult females (Owen-Smith, 1975), the age-sex structure of the two smaller populations may influence grouping patterns. In particular, the only sub-adults in Nakuru, and three out of the four sub-adults in Ol Pejeta, were males over five years old. Females with young calves are unlikely to tolerate sub-adult males of this age, as they may pose a threat to their calf (Owen-Smith, 1975). This may explain the lower association rates in these populations, as adult females had few potential associates. Nevertheless, in comparison to Rothschild's giraffe, *Giraffa camelopardalis rothschildi*, where mean association strength ranges from just 0.088 to 0.126 (Muller et al., 2019), average pairwise bonds appear to be somewhat stronger in white rhinoceros, ranging from 0.133 to 0.295.

Conversely, white rhinoceros populations tend to be less well-connected than giraffe populations; white rhinoceros network density was just 0.028 and 0.035 in the two largest populations (n=96 in Lewa and n=65 in Meru, respectively), compared to 0.033-0.046 in a large population (n>600) of reticulated giraffes, *Giraffa camelopardalis reticulata* (Carter, Brand, et al., 2013). The lower network density in white rhinoceros can likely be attributed to their territorial behaviour; dominant adult males hold small, clearly demarcated home ranges, whilst adult females occupy larger overlapping home ranges (Owen-Smith, 1975). Consequently, individuals that do not share overlapping ranges are unlikely to associate, thus decreasing overall network density.

A common feature across all four populations was the tendency for individuals to form strong social bonds within cliques; individuals preferentially formed associations with their social partner's associates. Tendency to form cliques was highest in Nakuru and Lewa, and is again a likely consequence of the low population density in these reserves; with less frequent contact between individuals reducing opportunity to change groups (Cheney et al., 2016). Consequently, they may associate more often with the same set of individuals, and develop stronger associations with these individuals. Whilst population density was also low in Ol Pejeta, all rhinoceros were concentrated within one half of the reserve (approximately 186km^2), and therefore had more opportunity to change associates. Nevertheless, all populations demonstrated a relatively high global clustering coefficient, suggesting that cliques may be an important feature of white rhinoceros social structure.

A high clustering coefficient is characteristic of fission-fusion species, such as Rothschild's giraffe (0.77-0.88; Muller et al., 2019), Grevy's zebra, *Equus grevyi* (0.9; Rubenstein et al., 2015), onager, *Equus hemionus*, (0.7; Rubenstein et al., 2015) and African elephants, *Loxodonta africana* (0.88; de Silva and Wittemyer, 2012). Fission-fusion species are those that change group size through the fission and fusion of sub-units in relation to their activity and resource distribution (Kummer, 1971; Aureli et al., 2008). In this respect, white rhinoceros also exhibit the characteristics of a fission-fusion species; females and sub-adults form strong associations within cliques, which often temporarily fuse with other cliques to form larger aggregations. In barbary macaque, *Macaca sylvanus*, affiliation networks, clustering coefficient is highly predictive of individual survival (Lehmann et al., 2016). Therefore, white rhinoceros may gain fitness benefits from forming inter-connected sub-groups, through increased predator detection or feeding efficiency. Familiarity with the same set of social partners may also facilitate cooperation between individuals (Ilany et al., 2015), and create a more stable social environment, whereby social buffering reduces the impact of stressful situations (Wittig et al., 2016).

Mean un-weighted path length increased with population size, but remained short in all populations, ranging from 1.3 to 3.6. Short path lengths are characteristic of species with cohesive societies, such as reticulated giraffe (1.23 and 3.06, Shorrocks and Croft, 2009; 1.7 and 1.8, Carter et al., 2013), Grevy's zebra (1.9, Rubenstein et al., 2015), onager (1.6, Rubenstein et al., 2015) and bottlenose dolphins, *Tursiops spp.* (3.36, Lusseau, 2003). However, when considering how frequently individuals associated, mean path length was much longer in Lewa; individuals were on average 11.8 steps away from each other. This is likely because rhinoceros in Lewa are well-connected within cliques, but not to the population as a whole, as evidenced by a high global clustering coefficient and low network density. Therefore, because individuals rarely associate with conspecifics outside of their clique, mean weighted path length between two random individuals is likely to be very high. Short path lengths are associated with increased information and disease transmission (Reppas et al., 2012), and may be more beneficial in populations under high predation pressure or disturbance, as information on a threat can be quickly transmitted (Muller et al., 2019). The long weighted path length in Lewa could therefore be a consequence of reduced poaching pressure, as at the time of this study, Lewa was the only rhinoceros population in Kenya to have had no poaching incidents since 2013.

Despite apparent differences in the level of sociality between male and female white rhinoceros (Owen-Smith, 1973), this study found no consistent effect of sex on social network position across the study populations. Similarities between the sexes in social network position have also been recorded in reticulated giraffes (Carter, Brand, et al., 2013), Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, (Wiszniewski et al., 2010), and blacktip reef sharks, *Carcharhinus melanopterus* (Mourier et al., 2012). However, the absence of a relationship between sex and social network position in this study may be due to the age-sex structure of individuals included in social networks. In particular, the sample size of males in the Meru network was very small (n=13), which may have made any differences between the sexes difficult to detect. Whilst males that were only observed alone were excluded from the analyses, it is unlikely that this largely influenced the results, as just one adult male was omitted from each population.

Conversely, there was a consistent significant effect of age-class on rhinoceros association patterns; in comparison to adults, sub-adults associated more frequently, and had a higher tendency to associate in cliques. Sub-adults in Meru were also more socially integrated within the population than adults, as evidenced by their greater Eigenvector centrality, and sub-adults in Lewa had more associates on average than adults. Studies in other taxa have shown sub-adults receive fitness benefits from grouping with older, more experienced individuals. For example, in whooping cranes, *Grus americana*, migrations are more efficient if the flock contains a greater number of older, experienced birds (Mueller et al., 2013), and in banded mongoose, *Mungos mungo*, pups' foraging niches are shaped by older foraging escorts (Sheppard et al., 2018). Sub-adult white rhinoceros may be more social than adults because they gain specific benefits from group living, such as increased exposure to new food resources, or protection from predators and territorial males (Shrader and Owen-Smith, 2002).

In the Lewa population, adults had a higher tendency to connect groups together than sub-adults did, as evidenced by their greater betweenness. Individuals with high betweenness can be important for overall network cohesion (Sosa et al., 2020). This suggests adult rhinoceros may play an important role in the maintenance of population social structure or key social processes, such the transmission of disease, or information on resource distribution (Freeman, 1977). In chimpanzees, *Pan troglodytes*, males with high betweenness are more likely to increase in social rank and sire more offspring (Gilby et al., 2013), and this may be a consequence of choosing to develop coalitions that increase their influence over other individuals, and allow them to attain higher dominance and reproductive success (Brent, 2015). The higher betweenness of adult male rhinoceros in comparison to sub-adult males may be a result of them monopolising access to breeding females within their territory (Owen-Smith, 1973), and this may be more evident in low-density populations, like Lewa, where sub-groups come into contact less often.

Sub-adult white rhinoceros often migrate to the periphery of the population, in either pairs or small groups (Owen-Smith, 1981, 1988), to avoid aggression from territorial adult males (Owen-Smith, 1975). Sub-adults are thus likely to associate with fewer groups than adult females, which occupy overlapping ranges with several other individuals (Owen-Smith, 1975; Thompson et al., 2016). Adult females frequently interact with adult males as they move between their territories, either to access favourable resources, or assess mate quality (White et al., 2007), which may also explain why they have higher betweenness than sub-adults. On the other hand, due to the high population density in Meru, adult females are likely to be more constrained in their movements (White et al., 2007), and there is less peripheral habitat available for sub-adults. Consequently, sub-adults are likely to associate with other groups as frequently as adults do, which may explain why there was no difference in betweenness amongst the age-classes in Meru.

White rhinoceros in Meru formed long-term associations that lasted for over seven months, after which data were unavailable. However, the rate of association between pairs of sub-adults was not temporally stable. The sharp increase in sub-adult association rates at the end of the second data collection period suggests that several sub-adults changed preferred associates between data collection periods, which also corresponds to group membership observations. Sub-adults may have changed associates due to a shift in social structure, caused by six births between data collection periods. Adult females drive away their current calf before they are about to calve again (Owen-Smith, 1975), and this introduces new sub-adults to the population. The individuals that these sub-adults choose to group with may be loosely driven by kinship; several sub-adults were always observed with their sibling (n=2 in Meru Period 1; n=4 in Meru Period 2; n=2 in Lewa), or their mother and her current calf (n=4 in Lewa). Kinship drives grouping patterns in several social species, including African elephants (Wittemyer et al., 2009) spotted hyena, *Crocuta crocuta* (Wahaj et al., 2004), and bottlenose dolphins, (C. H. Frère et al., 2010), and thus may explain the change in sub-adult association rates between data collection periods if, for example, an individual changed preferred associates when a closely related sub-adult joined the population.

In Ol Pejeta, there was no evidence of long-term associations between individuals. This may be due to both the small population size, and short duration of data collection periods. Furthermore, there were only four breeding females in the population, all of which calved between data collection periods, causing several shifts in network structure.

In Meru, the rate of association between females remained higher than the rate of association between individuals from all age-sex classes, suggesting females are more likely to develop long-lasting associations with other females than with males. Long-term associations between pairs of females have been recorded in several species, including reticulated giraffes (up to 6 years; Carter et al., 2013), baboons*, Papio cynocephalus ursinus* (up to 14 years; Silk et al., 2006), Bechstein's bats, *Myotis bechsteinii* (up to 5 years; Kerth et al., 2011) and bottlenose dolphins (up to 3 years; Smith et al., 2016). Females may choose to associate with each other to increase protection for their calf against predators, or to gain information on new foraging sites. However, neither of these theories explain why they choose to re-associate with specific females more often than they would by chance. Furthermore, as adult female white rhinoceros do not decrease their vigilance when in larger groups (Shrader et al., 2013), this suggests reduced predation risk is not the main benefit of group formation.

Evidence of long-term associations between pairs of individuals suggests that familiarity is important to female white rhinoceros. Developing strong associations with particular female conspecifics may provide fitness advantages, such as increased reproductive success, longevity or psychological wellbeing (Celine H Frère et al., 2010; Massen et al., 2010). This study found that females in Lewa with a high tendency to form strong social bonds within cliques, or associate frequently with other adult females, had shorter calving intervals than those that did not. This suggests that females that preferentially associate with familiar adult females may obtain fitness benefits through increased reproductive success. However, in Meru, females that developed strong social bonds within cliques had longer inter-caving intervals, and instead, females that associated frequently, or that had well-connected associates, had shorter calving intervals than those that did not.

Other studies demonstrate similar differences in adaptive social organisation between groups of the same, or closely related, species. Early studies suggest that female baboons with stable bonds to many other females have increased longevity (Silk et al., 2010), and enhanced infant survival (Silk et al., 2009), whilst more recent studies suggest that females with well-connected social partners have greater infant survival than those restricted to smaller sub-groups (Cheney et al., 2016). In wild equids, Grevy's zebra are more likely to associate in cliques than onagers are, and it is postulated that this is because onagers live in more arid conditions with sparser forage, making group living more costly (Sundaresan et al., 2007). The different adaptive patterns of social connectivity between the Lewa and Meru white rhinoceros populations may also relate to differences in resource availability. White rhinoceros in Meru were at a much higher density than those in Lewa, and due to the dense vegetation in Meru rhino sanctuary, there are few open areas of grassland available for grazing (see Chapter 6). Therefore, competition is likely much higher in Meru than in Lewa, and consequently, maintaining strong social bonds within a clique may be more costly (VanderWaal et al., 2009; Roberts and Cords, 2013; Silk, 2014). Conversely, when populations are more widely dispersed and individuals come into contact less frequently, as in Lewa, clustering may facilitate cooperation between group members (Ilany et al., 2015; Cheney et al., 2016).

The proximate mechanisms driving the benefits of indirect connections are unclear. However, it has been suggested that having preferred associates, which are themselves preferred associates of many other individuals, may reduce the likelihood of aggressive encounters (Cheney et al., 2016). This is particularly pertinent to the Meru population, where aggressive encounters are likely more frequent due to the high population density. Females in Meru are thus more likely to benefit from having well-connected associates, to reduce the frequency of aggressive encounters, than they are from forming close social bonds within relatively isolated cliques (Cheney et al., 2016). Consequently, this may explain why females in Meru with greater Eigenvector centrality and strength had shorter inter-calving intervals.

Previous research suggests white rhinoceros are relatively solitary, with the exception of calf-cow relationships (Shrader and Owen-Smith, 2002), and adult females show limited group formation due to their low predation risk (Owen-Smith, 1975). This study highlights similarities to species with fission-fusion dynamics, including African elephants, Grevy's zebra, and giraffes, and suggests white rhinoceros may also exhibit fission-fusion association patterns. Due to the temporal variation in their association patterns, white rhinoceros may be further classified as a "higher fission-fusion species"; a species characterised by a high degree of variation in group size and composition (Aureli et al., 2008). Other species that have been described as higher fission-fusion include; giraffes (Carter, Seddon, et al., 2013), chimpanzees, spotted hyena and spider monkeys, *Ateles spp.* (Aureli et al., 2008). Like giraffes, white rhinoceros exhibit structured social patterns, but do not, to our knowledge, display complex cooperative behaviours characteristic of many primates (Carter, Seddon, et al., 2013). Therefore, similar to giraffes, fission-fusion grouping may have evolved from solitary, as opposed to group-living, animals (Aureli et al., 2008; Carter, Seddon, et al., 2013).

It is unlikely that population density is the only factor driving variation in network structure and association patterns between populations. In an attempt to minimise the influence of confounding factors, this study used null models that controlled for spatial-temporal effects, and the same data collection methodology and analytical techniques across populations. Despite this, other factors such as habitat structure and food availability are also likely to be influential, and require further investigation.

Most studies on animal social networks focus solely on one population (Wittemyer et al., 2009; Celine H Frère et al., 2010; Silk et al., 2010; Carter, Brand, et al., 2013; Carter, Seddon, et al., 2013; Best et al., 2014). However, this study highlights that social network structure and association patterns can vary between populations of the same species. Variation in social network structure has also been recorded in other taxa; including adjoining Rothschild's giraffe populations (Muller et al., 2019), and spotted hyena clans (Belton et al., 2018). The results of this study support the use of multiple groups or populations in social network studies, and suggest that interpretations of a species social behaviour generated from a single social network be approached with caution.

In conclusion, the results of this study emphasise the need to centre more attention on white rhinoceros social organisation in relation to their conservation management. White rhinoceros have a complex social structure characterised by a high tendency to form strong associations within cliques, and this is most evident in sub-adults. They often develop long-term associates, and re-association rates are highest between females, which suggests that social relationships and familiarity may serve an important function in females. It is possible that females born in captivity are unable to develop the same types of social relationships as they would in the wild, and this may contribute towards their low reproductive success. In particular, this study found that a female's association frequency, connectedness and tendency to associate in cliques, related to inter-calving interval length, and the adaptive benefits of sociality varied with ecological context. Knowledge of natural association patterns can thus be used to improve white rhinoceros social conditions in captivity, and inform management decisions, such as the selection of individuals for translocation between captive institutions or wild populations.

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5.6 APPENDICES

Appendix 1

Pre-network data permutation tests used to test if networks are non-random

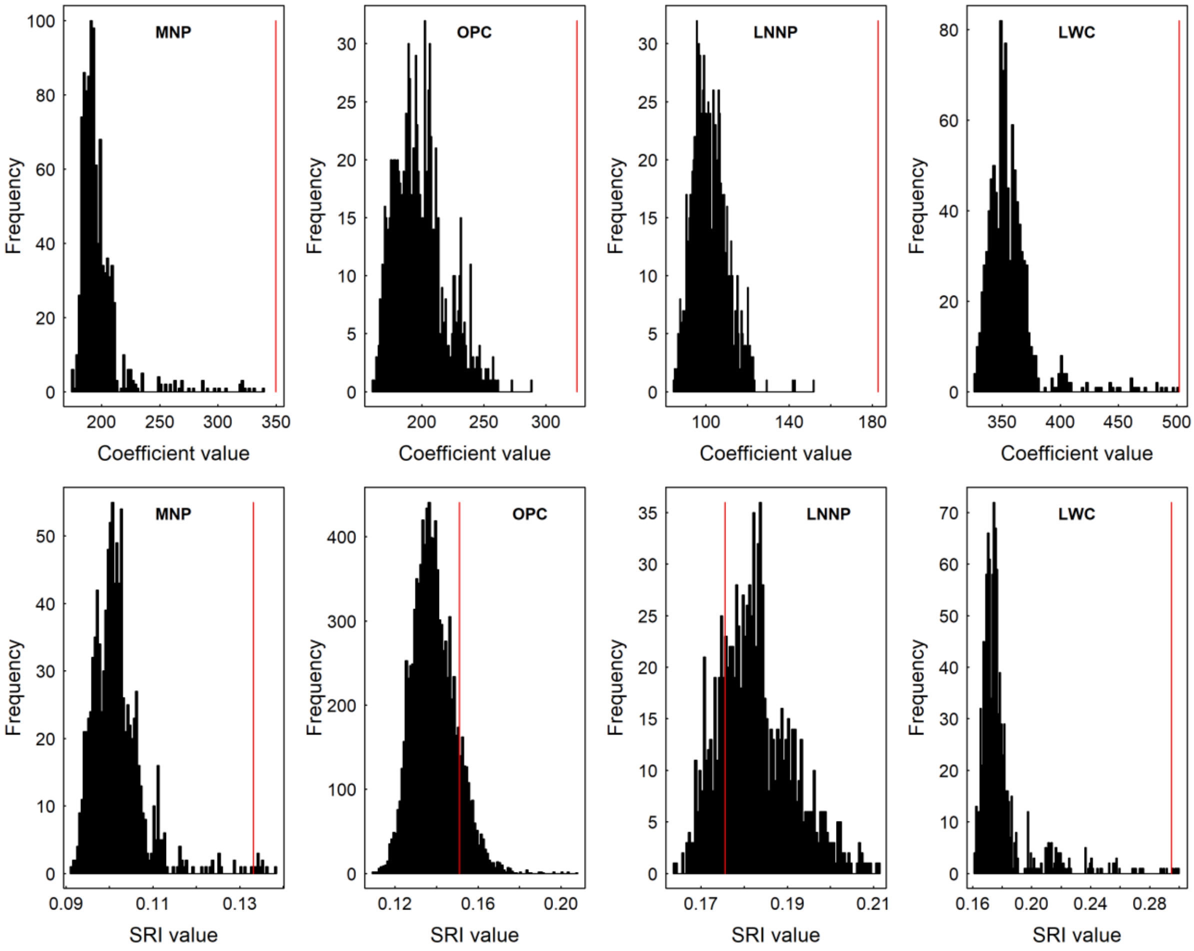

Figure 5.3 Pre-network data permutation tests showing the distribution of coefficient values (above) and Simple Ratio Index (SRI) value (below) from 1000 random networks (black histograms) for the four white rhinoceros populations included in the study; Meru National Park (MNP), Ol Pejeta Conservancy (OPC), Lake Nakuru National Park (LNNP) and Lewa Wildlife Conservancy (LWC). Red vertical lines represent the observed coefficient values from linear regression models. Significance was determined (for $P<0.025$) when fewer than 2.5% of the random values are greater than the observed coefficient or SRI value, or more than 97.5% of the observed coefficient or SRI value.

Appendix 2

Sex differences in network metrics and p-value estimation from null model permutations for Meru National Park and Lewa Wildlife Conservancy

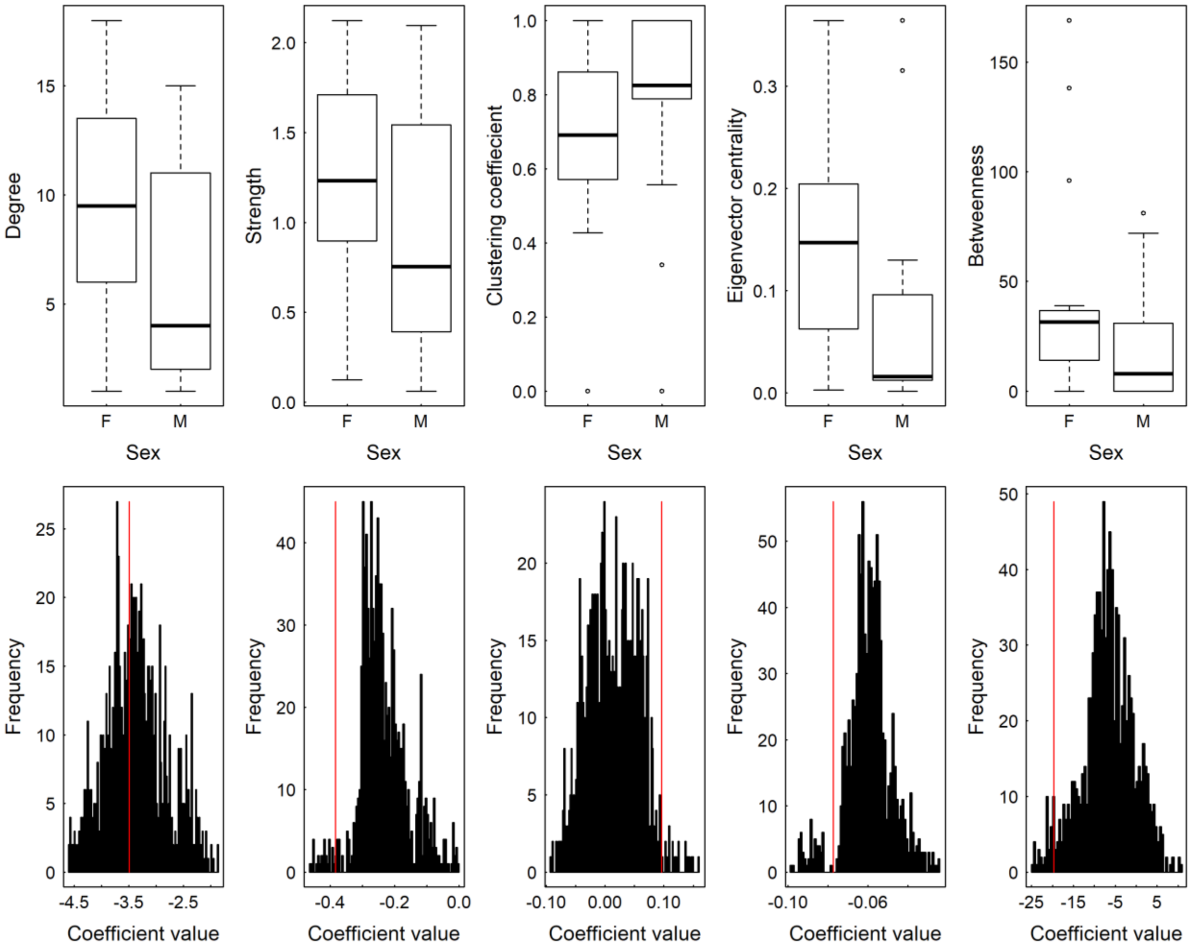

Figure 5.4 The difference between males and females in Meru National Park for the network metrics; degree, strength, clustering coefficient, Eigenvector centrality and betweenness (above), and the distribution of coefficient values from 1000 random networks (black histograms). Red vertical lines represent the observed coefficient values from linear regression models.

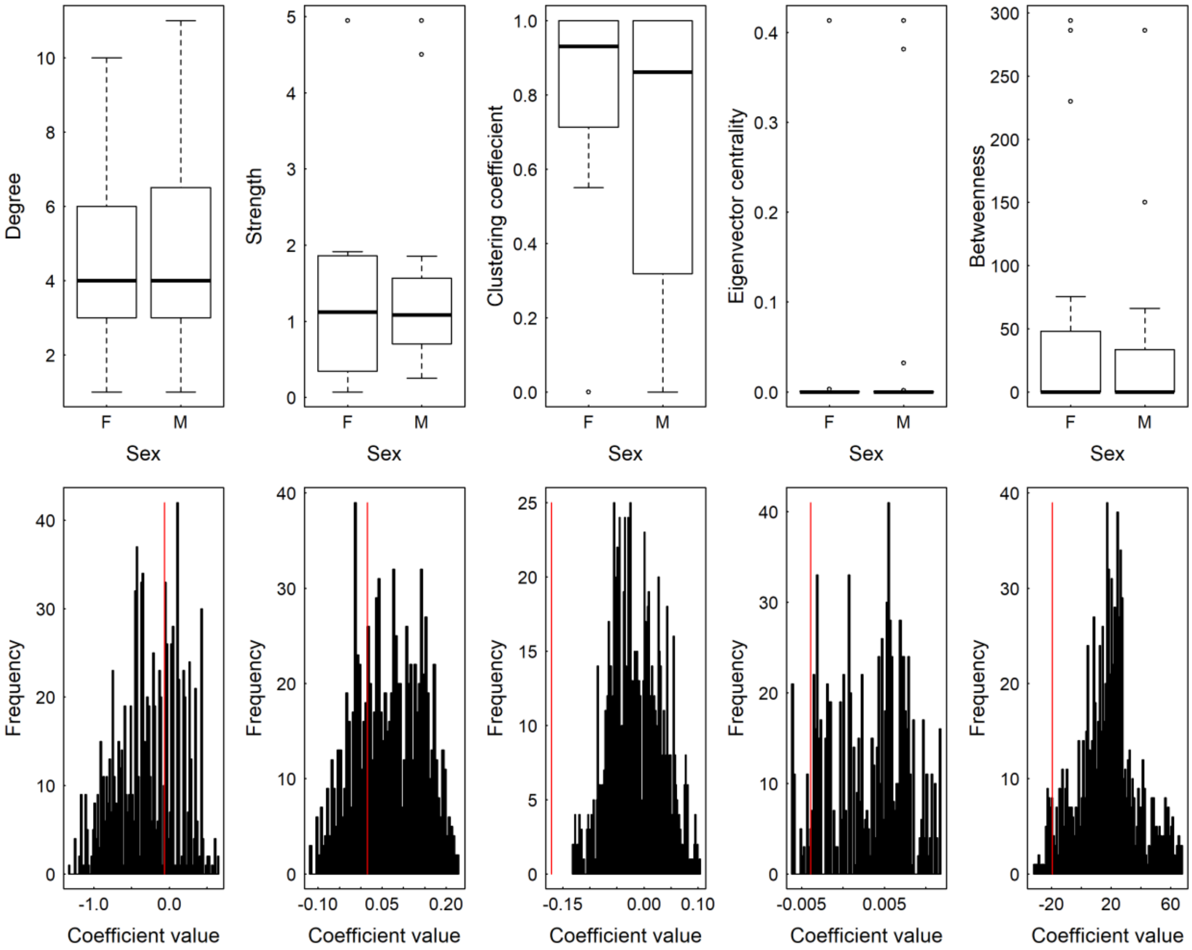

Figure 5.5 The difference between males and females in Lewa Wildlife Conservancy for the network metrics; degree, strength, clustering coefficient, Eigenvector centrality and betweenness (above), and the distribution of coefficient values from 1000 random networks (black histograms). Red vertical lines represent the observed coefficient values from linear regression models.

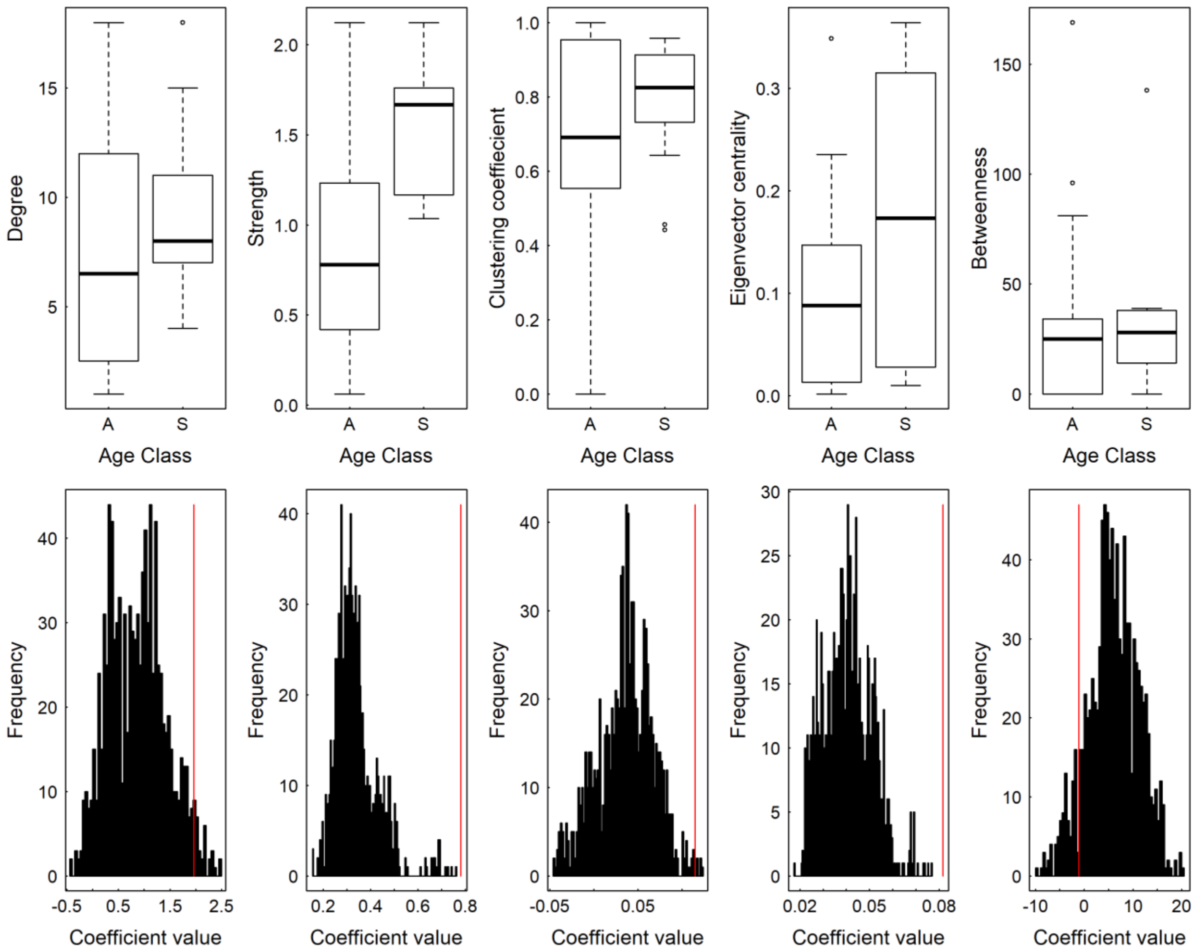

Figure 5.6 The difference between adults (A) and sub-adults (S) in Meru National Park for the network metrics; degree, strength, clustering coefficient, Eigenvector centrality and betweenness (above), and the distribution of coefficient values from 1000 random networks (black histograms). Red vertical lines represent the observed coefficient values from linear regression models.

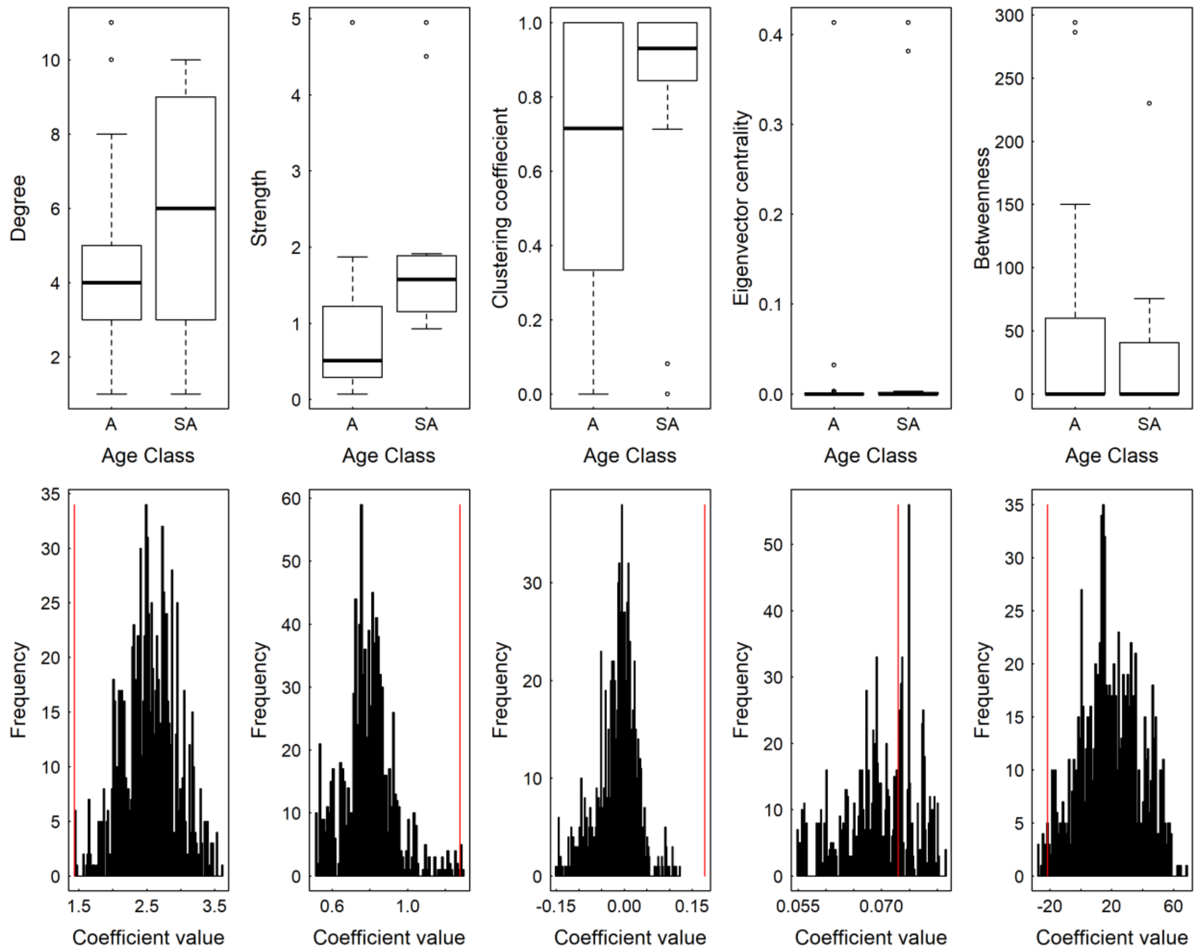

Figure 5.7 The difference between adults (A) and sub-adults (S) in Ol Pejeta Conservancy for the network metrics; degree, strength, clustering coefficient, Eigenvector centrality and betweenness (above), and the distribution of coefficient values from 1000 random networks (black histograms). Red vertical lines represent the observed coefficient values from linear regression models.

Appendix 3

The effect of female network position on inter-calving interval length and p-value estimation from null model permutations for Meru National Park and Lewa Wildlife Conservancy

Table 5.10. Mean inter-calving interval (ICI) length (years) and individual network metrics for the 16 adult female white rhinoceros in Lewa Wildlife Conservancy and the 11 adult female white rhinoceros in Meru National Park included in the analyses.

Female	Population	Mean ICI length	Degree	Strength	Betweenness	Eigenvector centrality	Clustering coefficient
Schini	Lewa	2.18	4	0.34	0	2.57^{-09}	1.00
Naserian	Lewa	2.19	4	0.33	294	7.90^{-04}	1.00
Lucille	Lewa	2.27	5	0.42	286	8.21^{-06}	0.57
Ramadhan	Lewa	2.30	3	0.38	0	4.40^{-16}	1.00
Natal	Lewa	2.31	10	1.87	60	2.49^{-08}	0.66
Queen	Lewa	2.38	5	0.67	0	1.24^{-03}	0.86
Tumbili	Lewa	2.55	2	1.22	0	6.32^{-06}	0.74
Jakwai	Lewa	2.55	8	0.67	7	7.96^{-09}	1.00
Jacho	Lewa	2.59	3	0.20	0	8.26^{-10}	0.81
Songare	Lewa	2.61	2	0.17	0	2.01^{-17}	1.00
Tale	Lewa	2.63	3	0.24	0	1.06^{-14}	1.00
Rinta	Lewa	2.70	1	0.25	0	2.10^{-29}	1.00
Wakesho	Lewa	2.83	4	1.43	3	5.30^{-14}	0.00
Titilei	Lewa	3.35	6	4.95	0	0.41	0.55
Rosie	Lewa	3.68	6	1.86	76	2.87^{-03}	0.71
Ngura	Lewa	4.72	1	0.07	0	1.62^{-10}	0.00
Tana	Meru	2.19	14	0.96	30	0.142	0.66
Makena	Meru	2.21	5	1.46	0	0.272	1.00
Monicah	Meru	2.25	1	0.13	0	0.004	0.00
Jenifer	Meru	2.27	14	1.42	96	0.223	0.72
Irine	Meru	2.47	13	1.24	169	0.103	0.43
Makhamesa	Meru	2.71	18	2.12	35	0.337	0.73
Rosie	Meru	2.73	6	1.22	20	0.011	0.63
Martina	Meru	2.89	10	1.45	32	0.137	0.60
Dorte	Meru	2.99	10	0.84	3	0.127	0.82
Nafula	Meru	3.05	7	0.65	31	0.079	0.59
Helen	Meru	3.94	6	0.45	14	0.043	0.55

Appendix 4

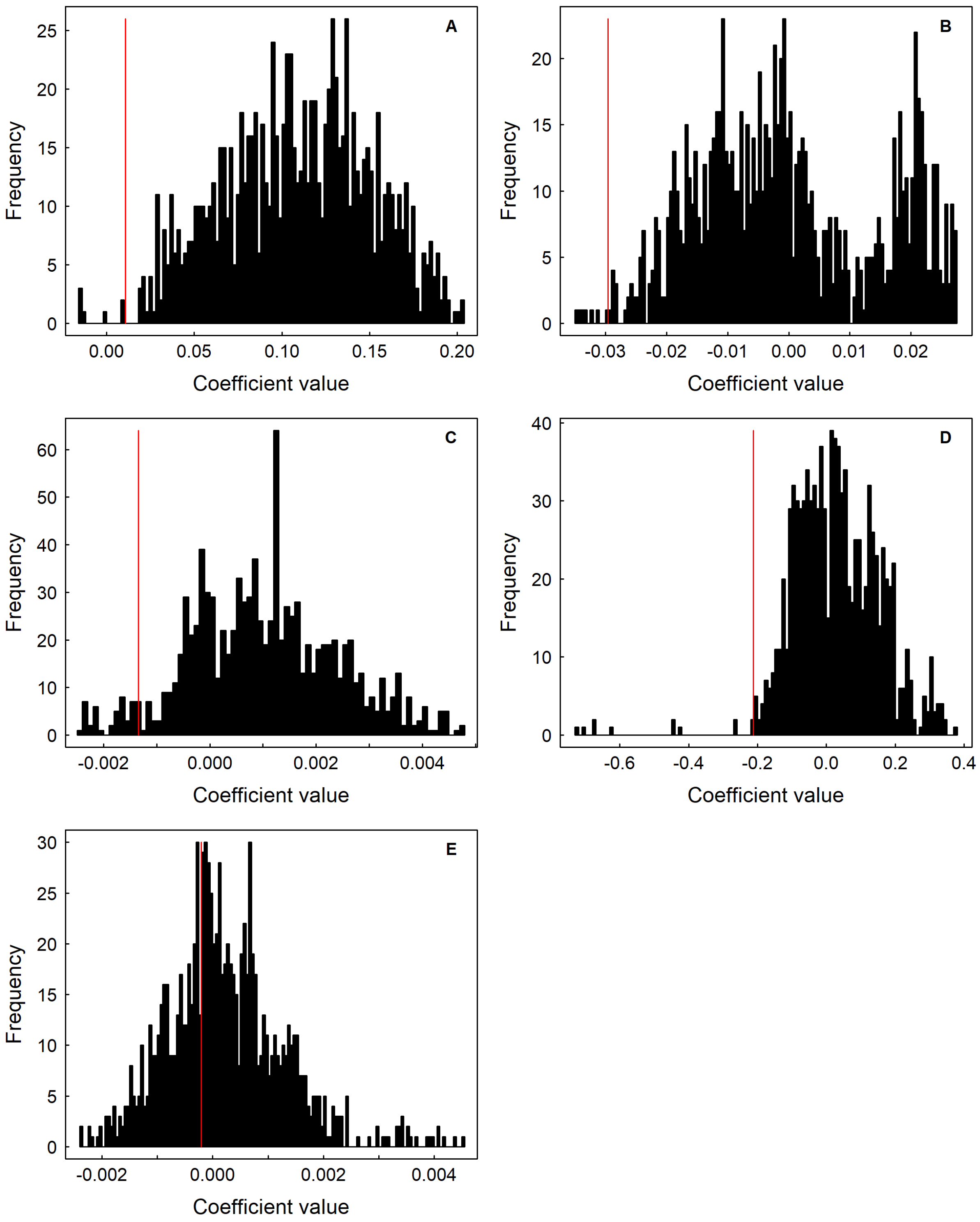

Figure 5.8 Pre-network data permutation tests showing the distribution of network metric coefficient values from 1000 random networks (black histograms) for the linear regression models used to predict female inter-calving interval length in Meru; (a) clustering coefficient (b) strength (c) degree (d) Eigenvector centrality, and (e) betweenness. Red vertical lines represent the observed coefficient values from linear regression models. Significance was determined (for P<0.025) when fewer than 2.5% of the random values are greater than the observed coefficient value, or more than 97.5% of the observed coefficient value.

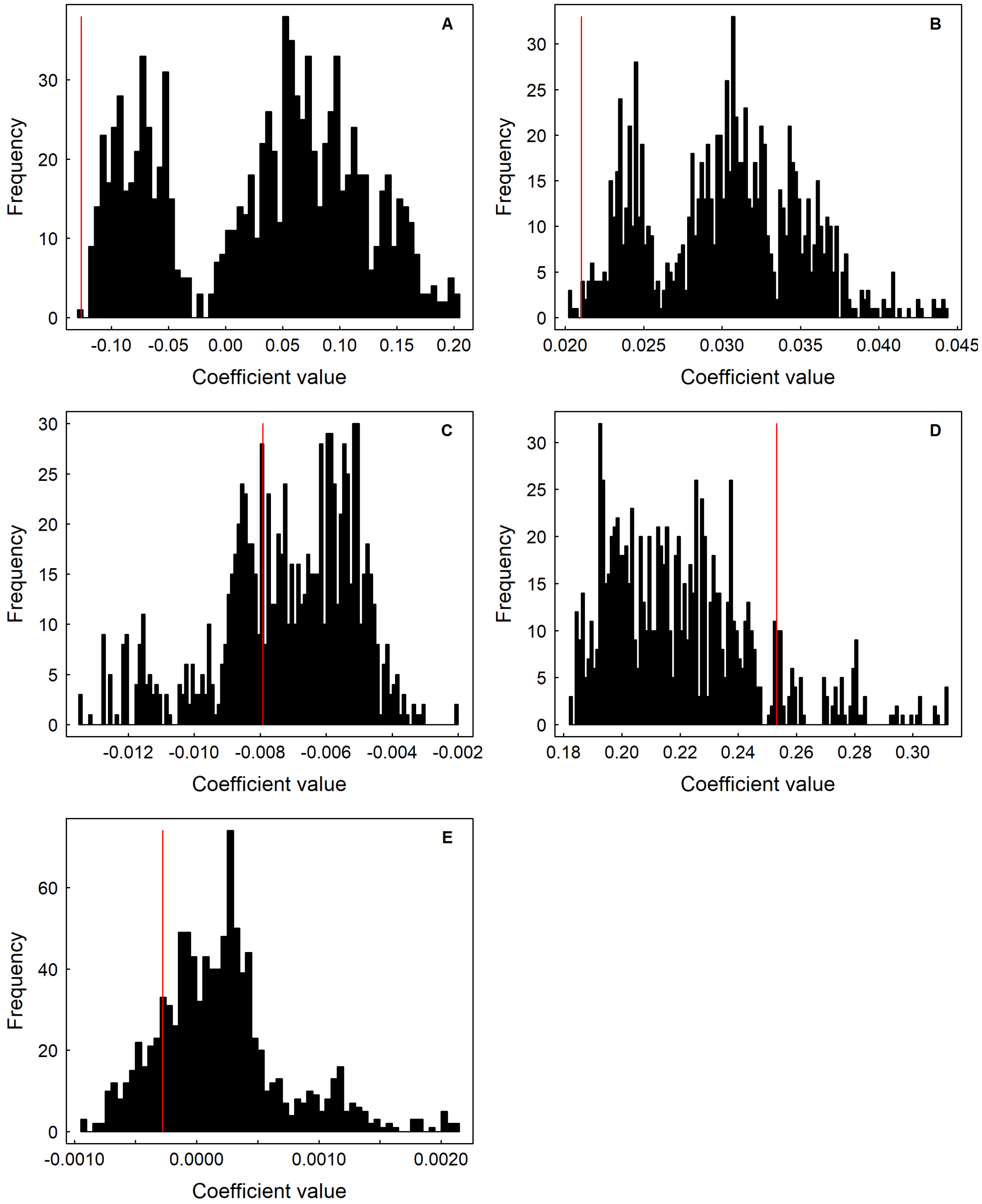

Figure 5.9 Pre-network data permutation tests showing the distribution of network metric coefficient values from 1000 random networks (black histograms) for the linear regression models used to predict female inter-calving interval length in Lewa; (a) clustering coefficient (b) strength (c) degree (d) Eigenvector centrality (e) betweenness. Red vertical lines represent the observed coefficient values from linear regression models. Significance was determined (for P<0.025) when fewer than 2.5% of the random values are greater than the observed coefficient value, or more than 97.5% of the observed coefficient value.

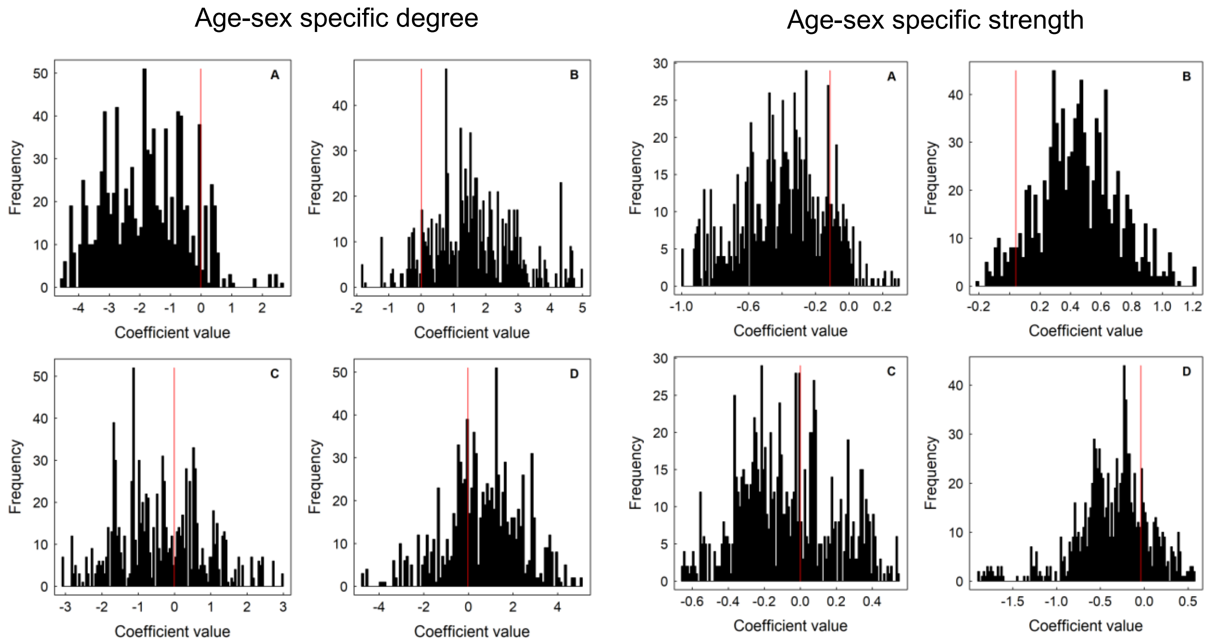

Figure 5.10 Pre-network data permutation tests showing the distribution of coefficient values from 1000 random networks (black histograms) for the age-sex specific degree (left), and age-sex specific strength (right), linear regression models used to predict female inter-calving interval length in Meru; (a) adult males (b) adult females (c) sub-adult males (d) sub-adult females. Red vertical lines represent the observed coefficient values from linear regression models. Significance was determined (for P<0.025) when fewer than 2.5% of the random values are greater than the observed coefficient value, or more than 97.5% of the observed coefficient value.

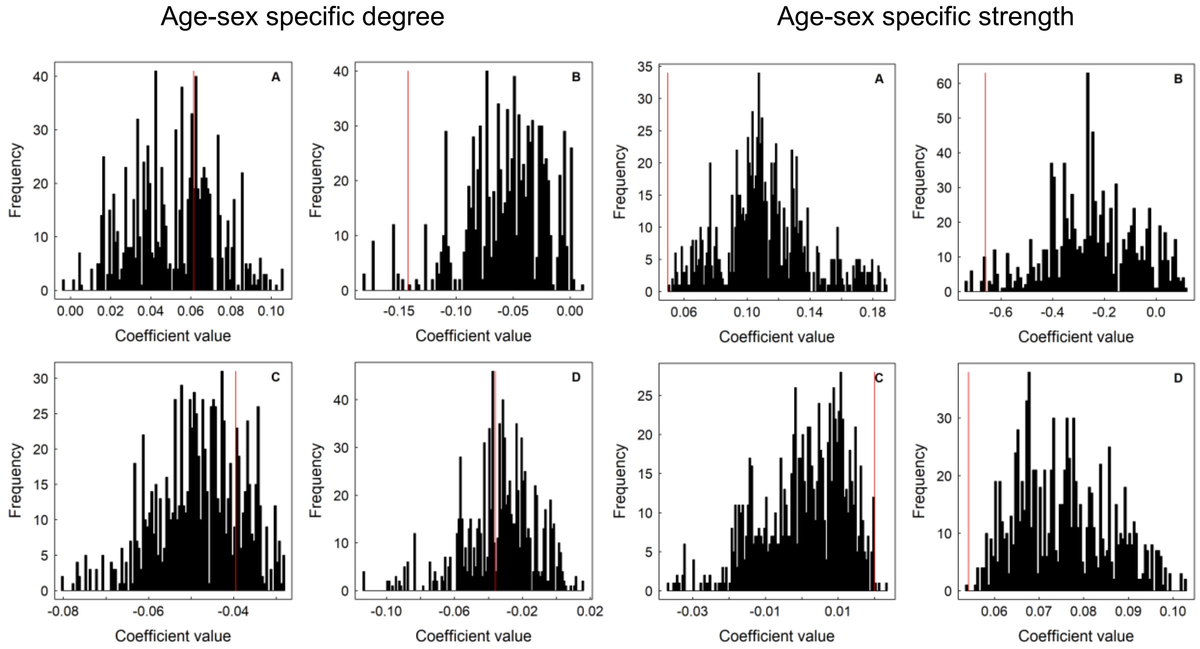

Figure 5.11 Pre-network data permutation tests showing the distribution of coefficient values from 1000 random networks (black histograms) for the age-sex specific degree (left), and age-sex specific strength (right), linear regression models used to predict female inter-calving interval length in Lewa; (a) adult males (b) adult females (c) sub-adult males (d) sub-adult females. Red vertical lines represent the observed coefficient values from linear regression models. Significance was determined (for P<0.025) when fewer than 2.5% of the random values are greater than the observed coefficient value, or more than 97.5% of the observed coefficient value.

Table 5.11. Pre-network permutation results for variable coefficient values (CV) and *P-values* for the linear regression models used to predict female inter-calving interval length. *P-values* were calculated from the proportion of random CV values that were either larger or greater than the observed CV value from the linear regression model, and represent the effect size of each metric on inter-calving interval length. Significance was determined when the observed CV value was less than 2.5%, or more than 97.5%, of the random CV values, i.e. p<0.025 conveys statistical significance.

	Meru			**Lewa**		
Metric	**CV observed**	**Mean CV random**	**P-value**	**CV observed**	**Mean CV random**	**P-value**
Network metrics						
Clustering coefficient	0.011	0.109	**0.007**	-0.126	0.030	**<0.001**
Strength	-0.030	0.000	**0.007**	0.021	0.030	**0.006**
Degree	-0.001	0.001	0.046	-0.008	-0.007	0.340
Eigenvector centrality	-0.213	0.027	**0.012**	0.253	0.220	0.101
Betweenness	0.000	0.000	0.338	0.000	0.000	0.162
Age-sex-specific degree						
Adult males	-0.015	-0.018	0.422	0.061	0.051	0.360
Adult females	0.003	0.009	0.314	-0.143	-0.056	0.029
Sub-adult males	-0.007	0.002	0.648	-0.040	-0.048	0.224
Sub-adult females	-0.024	0.015	0.032	-0.036	-0.033	0.401
Age-sex specific strength						
Adult males	-0.112	-0.078	0.249	0.050	0.112	**<0.001**
Adult females	0.041	0.051	0.346	-0.661	-0.250	**0.022**
Sub-adult males	0.000	0.028	0.452	0.020	0.001	**0.003**
Sub-adult females	-0.040	-0.035	0.536	0.054	0.075	**0.001**

6 SOUTHERN WHITE RHINOCEROS (*CERATOTHERIUM SIMUM SIMUM*) HABITAT USE AND RANGING BEHAVIOUR ACROSS POPULATIONS: INSIGHTS INTO DENSITY-DEPENDENT REPRODUCTION AND ECOLOGICAL CARRYING CAPACITY

Abstract

Understanding the ecological moderators of reproduction and population persistence is fundamental to the conservation management of endangered taxa. Due to the ongoing threat from poaching, many southern white rhinoceros, *Ceratotherium simum simum*, populations are confined within small sanctuaries. Differences in population density, inter-specific competition and resource availability between populations are likely to influence white rhinoceros habitat use and reproductive success, and this may lead to differences in ecological carrying capacity between sites. This study investigated the ecological variables associated with white rhinoceros habitat across four populations in Kenya, and examined how variation in resource availability related to ranging behaviour and breeding performance. The results demonstrate that white rhinoceros habitat is characterised by high grass cover, both shorter grass and trees, and low elevation, and they displayed a preference for swamp habitat. Core range size showed significant variation between populations and seasons; core ranges were smallest in the population with the highest density, and within this population, they were smaller during the extreme dry season. Despite differences in the area of optimal habitat available per individual, reproductive performance was high across all populations, suggesting white rhinoceros were below carrying capacity for their respective areas. However, disproportionately large ranges in one population suggested carrying capacity was lower at that site, whilst compressed ranges in another population suggested suitable habitat was limited. The results of this work provide important information on white rhinoceros habitat use and ranging behaviour that can help to guide habitat management and estimates of ecological carrying capacity for rhinoceros populations across Africa.

6.1 INTRODUCTION

An animal's reproductive success is driven by both intrinsic and extrinsic factors (Bronson, 1989). Whist intrinsic factors are those relating to an individual, such as age and genotype, extrinsic factors relate to an animal's environment (Ungerfeld and Bielli, 2012). In large mammals, food availability is an important extrinsic mediator of female reproductive success (White, 1983; Stephens and Krebs, 1986; McNamara and Houston, 1994), as pregnancy and lactation are energetically highly demanding (Bronson, 2009). For example*,* areas containing high-quality forage are associated with increased reproductive success in female roe deer, *Capreolus capreolus* (Mcloughlin et al., 2007), and greater infant survival in North American elk, *Cervus elaphus* (Long et al., 2016). Whilst home range site selection and habitat characteristics play an important role in reproduction, population density and inter-specific competition further mediate food availability and reproductive success (Rachlow and Berger, 1998; Bonenfant et al., 2009), and individuals tend to distribute themselves in relation to resource abundance in order to maximise their fitness (Bjørneraas et al., 2012).

Resources are often unevenly distributed across large spatial and temporal scales (Herfindal et al., 2009). For example, rainfall is the primary driver of plant productivity in grassland savannahs, and its variability in time and space is reflected in the temporal and spatial distribution of patches of green forage (McNaughton, 1984). This has led to considerable debate about whether rangeland resource degradation is mediated by equilibrium dynamics, whereby herbivore density and grazing pressure primarily drive forage availability (Illius and O'Connor, 1999), or non-equilibrium dynamics, whereby systems with high climactic variability are largely influenced by stochastic abiotic factors (Ellis and Swift, 1988; Behnke and Scoones, 1993). The latter suggests that density-dependent regulation rarely moderates herbivore populations, as they spend most of their time recovering from drought effects (Derry and Boone, 2010). More recent studies suggest a continuum between equilibrium and non-equilibrium states (Briske et al., 2003; Derry and Boone, 2010), and that the mechanisms driving vegetation dynamics are largely site-specific (Sullivan and Rohde, 2002).

The cost of utilising available habitat in one location, or at one point in time, may greatly exceed that of another, and this can lead to dissimilar habitat selection among populations of the same species (Herfindal et al., 2009; Bjørneraas et al., 2012), known as functional response in habitat selection (Mysterud and Ims, 1998). For example, reindeer, *Rangifer tarandus*, in overgrazed areas prioritise grass quantity, whereas those in areas of abundant grass prioritise quality (Hansen et al., 2009). In savannah systems, large species with relatively low metabolic requirements, such as buffalo, *Syncerus caffer*, only have selective diets during the dry season, whilst smaller species with high protein requirements, such as impala, *Aepyceros melampus*, are almost always selective for plant parts (Jarman and Sinclair, 1984). Knowledge of a species' habitat use across different ecological conditions can thus be used to uncover patterns of habitat utilisation, and identify resources or features of 'intrinsic habitat value', which are fundamental to reproduction and survival (Mcloughlin et al., 2007). This may be particularly important for the conservation management of slow-breeding, mammalian herbivores confined to fragmented habitat patches or protected areas, as the inability to disperse in response to resource depletion may limit reproduction and population persistence.

Due to the ongoing threat from poaching, southern white rhinoceros, *Ceratotherium simum simum*, populations require intensive conservation management to remain viable. The establishment of rhinoceros sanctuaries have played a major role in their protection across Africa (Emslie and Brooks, 1999; Knight et al., 2015). However, confinement within small areas limits their natural dispersal, and management intervention is often required to minimise the influence of restricted dispersal on population demography and behaviour (Rachlow and Berger, 1998). Additionally, biotic factors, such as variation in population density and inter-specific competition, and abiotic factors, such as fluctuations in rainfall and plant productivity, may further influence their population dynamics (Fernandez-Gimenez and Allen-Diaz, 1999).

With a body mass of over 1000kgs, white rhinoceros are termed megaherbivores (Owen-Smith, 1988): species that have a disproportionate impact on vegetation compared to smaller herbivores under top-down control from predation (Owen-Smith, 1987). With the exception of the hippo, *Hippopotamus amphibious*, white rhinoceros are the only megaherbivore that exist solely on a diet of grass, and their wide mouth makes them adapted to feeding on short grasses (Owen-Smith, 1975; Waldram et al., 2008). Their repeated grazing of short grass patches maintains highly nutritious 'grazing lawns' (Vesey-

Fitzgerald, 1965). Consequently, white rhinoceros are regarded as both ecosystem engineers and a keystone species (Owen-Smith, 1988; Jones et al., 1994; Waldram et al., 2008); they remove coarser grasses and expose high quality young growth, thus indirectly facilitating other herbivores with specific feeding preferences (Jarman and Sinclair, 1984). As white rhinoceros are hind-gut fermenters, they use a strategy of bulk feeding, allowing them to tolerate grass of a lower nutritional quality than smaller herbivore species or ruminants (Jarman and Sinclair, 1984; Waldram et al., 2008). Whilst resource partitioning between herbivores with different body sizes or digestive strategies can reduce inter-specific competition (Jarman and Sinclair, 1984), when resources are limited, such as during a drought, habitat overlap becomes more apparent, and this can lead to increased inter-specific competition (Hempson et al., 2015). As many small, intensively managed reserves support a high density of herbivores, often due to the provision of artificial water sources, this can increase grazing pressure beyond natural levels (Knight, 1995).

The concept of 'ecological carrying capacity' (McCullough, 1992), specifies that the number of animals a given area can support is related to resource availability. There is a linear, positive relationship between annual rainfall and grass production in most African savannahs (Lamprey, 1983), and thus annual rainfall and the spread of rainfall throughout the year influence white rhinoceros food availability (Owen-Smith, 1990). Both intra- and inter-specific competition can further affect resource availability and ecological carrying capacity, (Adcock, 2001), as overgrazing can reduce grass cover and species composition, and increase invasive species and soil degradation (Van der Linde et al., 2017). Therefore, variation in resource availability and competition between populations of white rhinoceros may lead to differences in ecological carrying capacity between areas of a similar size, and this may cause reproductive disparity between populations.

When populations of large mammals reach a high density in relation to resource availability, breeding performance is likely to decline; birth intervals, age at first calving and mortality increase, and population growth rate slows or declines (Hitchins and Anderson, 1983; Owen-Smith, 1988, 1990; Adcock, 2001; Stewart et al., 2005; Bonenfant et al., 2009). Breeding performance can therefore reflect ecological carrying capacity (Adcock, 2001). However, as rhinoceros have long gestation periods, they can often overshoot ecological carrying capacity before density-dependent impacts on breeding performance are apparent (du Toit et al., 2006). Adult home range size can thus be used to provide early insights on the ecological carrying capacity of rhinoceros conservation areas (Adcock, 2001). Research on black rhinoceros, *Diceros bicornis*, has shown that ecological carrying capacity declines alongside the availability of suitable browse, and this is correlated with a major increase in average home range size (Hitchins, 1969, 1971; Brooks, 1979; Emslie, 1999; Adcock, 2001).

Most of our understanding of white rhinoceros ranging patterns originates from high-density populations in South Africa, in either unfenced savannahs (Owen-Smith, 1973; Shrader and Perrin, 2006; Shrader et al., 2006), or large fenced reserves (Pienaar et al., 1992, 1993; White et al., 2007). Few studies have examined white rhinoceros habitat characteristics or ranging patterns in small reserves (with the exception of Thompson et al., 2016), or at low densities (notable exceptions are Pienaar et al., 1993; Rachlow et al., 1999; Thompson et al., 2016), and due to conflicting results, the impact of population density on ranging behaviour remains unclear. White rhinoceros spatial patterns in Matobo National Park, Zimbabwe (Rachlow et al., 1999), and Kruger National Park, South Africa (Pienaar et al., 1993), suggest home ranges tend to be larger in low-density populations. However, range estimates in Welgevonden Game Reserve, South Africa (Thompson et al., 2016), were substantially smaller, despite a comparatively low population density, and this was attributed to the heterogeneous terrain of the reserve. This suggests differences in habitat composition and resource distribution could influence white rhinoceros ranging patterns, and this may be related to ecological carrying capacity. Furthermore, as white rhinoceros grouping patterns (see Chapter 5) and reproductive output (Rachlow and Berger, 1998) have been linked to population density, differences in resource availability and competition may also mediate social behaviour and breeding performance.

Poaching rates in Kenya have been substantially lower than in other white rhinoceros range countries (Emslie et al., 2019), and this is largely due to their strict protection within small, fenced sanctuaries. However, due to the high growth rate of Kenyan populations, there are management concerns that some reserves are exceeding ecological carrying capacity. An understanding of white rhinoceros habitat use across varying population densities and ecological conditions is required to provide guidance for the management of small populations, and inform estimates of ecological carrying capacity, to ensure populations remain viable over the long-term.

The aim of this chapter was to identify important features of white rhinoceros habitat across four distinct populations in Kenya, and to determine how differences in ecology and resource availability relate to ecological carrying capacity and female reproductive success. The first objective was to determine the ecological variables associated with white rhinoceros habitat across populations, to identify key habitat features or resources likely to be important for reproduction and survival. With knowledge of objective one, objective two was to determine how important habitat features differ between populations. With knowledge of objective two, objective three was to assess how ranging patterns and population performance relate to differences in habitat and population density. The final objective of this chapter was to use one of the study populations to determine any potential seasonal differences in habitat associations and ranging patterns.

6.2 METHODS

6.2.1 *Study populations*

White rhinoceros populations from four reserves in Kenya were included in this study; Ol Pejeta Conservancy, Lewa Wildlife Conservancy, Meru National Park and Lake Nakuru National Park (hereafter referred to as Ol Pejeta, Lewa, Meru and Nakuru). Average daily temperatures across the reserves range from 11-29°C during the warmest months (between January and March), and from 12-26°C during the coolest months (between June and August). Peak rainfall usually occurs during the long rains, between late March and May, and the short rains, between October and December, in all four reserves. Data were collected in all reserves between June and August, in the years 2017, 2018 and 2019, as this time-period was expected to capture habitat use when resource availability was low-moderate (after the long rains). To provide an understanding of the differences in habitat use when resources are most limited, additional data were collected in Meru during February-March 2018, the extreme dry season (before the long rains). Full details of data collection periods and study sites are provided in Chapter 4.

6.2.2 Sites utilised by white rhinoceros

To determine the areas being utilised by rhinoceros, study sites were searched daily following the methodology described in Chapter 5 (section 5.2.2). When a group was located (See Chapter 5 for definition of a group), all individuals were identified (see Chapter 5 for identification methods), their activity was recorded (feeding, resting, moving, drinking, wallowing, interacting) and one GPS point was recorded and assigned to all group members. Individuals within the vicinity, but over 50m from another rhinoceros, were assigned their own GPS point. The GPS location of the observer was recorded, and the group's direction was determined using a compass. The distance from the observer to the group was estimated by eye. As the observer was most often within 50m of the rhinoceros group, distance estimations were thought to be relatively accurate.

6.2.3 Habitat characteristics data collection

Vegetation plots were carried out at 20 locations where rhinoceros were observed feeding, and at 20 control locations, for each study site except Lewa, where, to account for the widespread distribution of rhinoceros, 25 feeding plots and 25 control plots were carried out. Additionally, 30 feeding and 30 control plots were carried out in Meru during February-March 2018, for seasonal comparison. A 500x500m grid was overlaid on all location points using the software QGIS (The QGIS Development Team, 2020), and a maximum of one feeding location per grid square was selected to ensure feeding sites of several individuals were sampled. A random number generator was used to select grid squares and the feeding location within each grid square to use for a plot. If there were not enough independent grid squares, those containing more than one point were randomly reselected, and an additional feeding location was also used, providing it was >100m from any other plot. In Nakuru, white rhinoceros feeding locations were largely clustered on one plain, at the southern tip of the lake. Therefore, a 100x100m grid was used for initial grid square selection, and random points were only selected if they were >100m from another plot.

Control plots were generated using the '*generate random points*' function in QGIS, and a 100m buffer around all sighting locations. To ensure control plots were evenly distributed across reserves, only one point per 500x500m grid square, and points >100m from any other plot (control or feeding), were used. In Ol Pejeta, only the eastern half of the reserve was used to generate control points, as the white rhinoceros only resided in this half of the reserve, both before and during the study. Furthermore, areas not accessible to rhinoceros, such as the fenced endangered species enclosure in Ol Pejeta and lake boundaries in Nakuru, were omitted from the areas used to generate random points. This ensured that control plots were generated in areas rhinoceros could potentially utilise.

Circular plots with a diameter of 22.6m (the nominal diameter of a 1/25 ha circular plot), were marked out using measuring tapes running from north to south and east to west (sensu Estes et al., 2008). The GPS point was used as the centre point for control plots. For feeding plots, the noted distance and direction from the GPS point to the observed rhinoceros group was paced out, and this location was used as the plot centre point. The number and species of any invasive plants, the number and species of any tree seedlings (defined as <0.5m in height), and any herbivore dung present within the plot boundaries was identified, and species totals were recorded. The height and species of the three tallest trees (measured using a clinometer) and the species and diameter at breast height (DBH) of all trees with a DBH >7.5cm were recorded (Estes et al., 2008). To provide a measure of ground cover, at every meter on the cross transect, in both north to south and east to west directions, a 10cm diameter circular area was assessed for the presence or absence of grass, dry grass, bare ground, herbs and shrubs, and the tallest piece of grass (cm) was recorded. Canopy cover at each metre was estimated by assessing the proportion of sky covered by tree canopy, when standing at full height and looking upwards through inverted binoculars. To improve consistency, the same person (SS) always estimated canopy cover. Field guides (Dharani, 2006; van Oudtshoorn, 2012), and the expertise of local park rangers and field scientists were used to assist with all plant and dung identification.

The grass species with the highest percentage cover in the plot was recorded as the dominant grass species, and each plot was assigned a grazing value from 1-3 based on the palatability and productivity of the dominant grass species, following classification by Oudtshoorn (2012). For grass species not included in Oudsthoorn (2012), a grazing value was assigned based on descriptions of crude protein content, digestibility and use for fodder, collated from multiple sources (Tussie, 2004; Quattrocchi, 2006; Heuzé et al., 2015, 2016; Stubbendieck et al., 2017; Dowsett et al., 2018; Fletcher and Ryan, 2020). Plot grazing value was based on the dominant grass species, as it was often not possible to identify all species within a plot, mainly due to low ground cover and the absence of inflorescences.

6.2.4 Topography variables

A 30m resolution *ASTER* Global Digital Elevation Model (*GDEM*) from NASA's Earth Science Data and Information System (*ESDIS*), was used to obtain elevation and slope values for each vegetation plot in *QGIS* (The QGIS Development Team, 2020). Elevation values were adjusted relative to each reserve, as whether rhinoceros utilise higher or lower elevations relative to those available was the interest of this study. Within reserves, low elevations are likely to be more nutrient-rich than high elevations (Cromsigt and te Beest, 2014), and thus relative elevation may relate to the nutrient content of grass in each plot. Relative elevations were determined from the true plot elevation, minus the minimum plot elevation recorded in the respective reserve. Therefore, the datum was 0m, and all elevations were relative to this.

6.2.5 Ecological variables associated with white rhinoceros habitat

A binomial linear mixed effect model (*GLMM*), including population as a random effect, was used to identify the characteristics of habitat associated with white rhinoceros feeding locations. Variable Inflation Factors (VIFs) were used to assess multicollinearity between predictor variables, and only variables with VIF's <2 were retained in the model (Zuur et al., 2010). All other logistic regression assumptions were met; including linearity of independent variables with log odds, and the presence of no influential outliers (Cook's D >3.0). Transformations, including Log_{10} and square root (√) were used to adjust variables with uneven variances or skew, and to improve their linear relationship with log odds. Model selection based on *AIC* indicated there were several models within 2*ΔAIC* of the best model, suggesting several competing candidate models. Therefore, model averaging was incorporated, using 2*ΔAIC* as the threshold (Burnham and Anderson, 2002). The package *lme4* (Bates et al., 2015) was used to generate the initial binomial GLMM, and the package *MuMIn* (Barton, 2019) was used for model selection and model averaging. All statistical analysis was carried out in R version 3.6.2 (R Core Team, 2016).

6.2.6 Differences in habitat between populations

6.2.6.1 Differences in overall ecology

Nonmetric multidimensional scaling (NMDS) ordination, using the *Bray-Curtis distance* as the dissimilarity measure, was used to visualise differences in all topography and vegetation plot variables between populations, for both control and feedings sites, using the *vegan* package in R (Oksanen et al., 2019). Prior to analysis, all variables were standardised using a square root transformation. Permutational analysis of variance (*PERMANOVA*) was used to test whether populations showed significant variation in their topography and vegetation plot variables, using the "*adonis2*" function in *vegan*. The *RVAideMemoire* package (Hervé, 2020), was used to conduct post-hoc pairwise comparisons, to identify which populations were significantly different from each other. Analyses were conducted separately for control and feeding plots, to identify differences in the areas utilised by rhinoceros, as well as differences in the areas available.

6.2.6.2 Differences in important habitat features

To investigate how the important features of white rhinoceros habitat differed between populations, the ecological variables associated with white rhinoceros habitat (identified in Objective 1) were compared across population feeding sites. As all habitat variables violated the assumptions of parametric statistics, *Kruskal-Wallis tests* were used to determine differences between populations. Post-hoc *Mann-Whitney U tests*, with a *Bonferroni* correction to account for multiple comparisons, were used to identify which populations were significantly different from one another.

6.2.7 Range size, resource availability and population performance

6.2.7.1 Range size

Range estimates for adults and sub-adults were determined using GPS data recorded during rhinoceros searches. A maximum of two GPS locations were assigned to an individual for each day, to improve the precision of range estimations, whilst minimising the risk of autocorrelation. Individual range size was determined using kernel density estimations in the R package *adehabitatHR* (Calenge, 2006), and the fixed kernel method. Range estimates were only calculated for adult and sub-adults with at least 10 GPS locations, to improve their accuracy (Börger et al., 2006). Calves were omitted from the analysis, as their ranging patterns are not independent of their mother's. As less than 15% of the Lewa population had >10 location records, GPS locations recorded by park rangers during data collection were used to supplement locations for each individual. As these were based on nearby geo-referenced locations, some GPS coordinates were identical. Therefore, to reduce spatial autocorrelation, only unique GPS locations were used. Supplementary location data was not available for the other populations.

Probability contours are used to estimate the likelihood of locating an individual, and the smoothing factor controls the level of variation around the density estimate (Worton, 1989; Börger et al., 2006). The smoothing factor was calculated using the reference (*href*) method, as it is more conservative than the least square cross validation method (*lscv*) (Börger et al., 2006), which can be highly variable at small sample sizes (Hemson et al., 2005), and produce fragmented ranges (Börger et al., 2006). The 50% probability contours were used to provide an estimate of core range size; i.e. heavily utilised areas likely to be defended by territorial males (Thompson et al., 2016). Whilst estimates across one month are unlikely to represent an animals entire home range, to allow comparison with previous home range studies, 95% probability contours were also calculated and referred to as "seasonal ranges" (Pienaar et al., 1993). To improve the accuracy of range estimates, areas not accessible to rhinoceros, and reserve boundaries, were excluded using clipped shapefiles in QGIS (The QGIS Development Team, 2020).

As inner isopleths are more precise and produce more accurate range estimates (Anderson, 1982; Erran Seaman and Powell, 1996), only 50% kernel density estimates were used for statistical analysis. A linear mixed effects model, including population as a random effect, was used to assess the influence of age-class (adult/sub-adult) and sex on core range size across populations. A *Kruskal-Wallace test* was used to determine whether mean core range size was significantly different between populations. Post-hoc *Mann–Whitney U tests,* with a Bonferroni correction, were used to determine significant differences between populations. *One-way ANOVA's* were used to determine whether mean core range size differed between populations for each age-sex class, and post-hoc *Tukey tests* were used to identify significant differences. For all analyses, range size was $\log_{10}$ transformed to fit a normal distribution, *Shapiro-Wilk* tests were used to check the normality of residuals, and *Bartlett tests* were used to check homogeneity of variance. As there was only one adult male and no sub-adult females in Nakuru, and only one sub-adult female in Ol Pejeta, these populations were excluded from the respective statistical analyses. A *t-test* was used to compare sub-adult female core range size between Meru and Lewa.

Home range size has been used to assess ecological carrying capacity in black rhinoceros (Adcock, 2001). However, as it was not possible to calculate long-term home ranges for the study populations, mean core range size was used to explore the relationship between range size, forage availability and ecological carrying capacity. As white rhinoceros are typically a gregarious species (Owen-Smith, 1973; Shrader and Owen-Smith, 2002), group size may also relate to resource availability and intra-specific competition. To explore the relationship between resource availability and grouping patterns, data on group compositions recorded during rhinoceros searches were used to calculate mean observed group size in each population. Observations of territorial males were excluded, as they are mostly solitary, and only associate with females passing through their territory (Owen-Smith, 1975; Chapter 5).

6.2.7.2 The habitat composition of core use areas

The habitat composition of each reserve was determined from AFRICOVER land cover classifications (Di Gregorio and Latham, 2009). As Lake Nakuru has increased dramatically in size during recent years, the area of the lake was amended using Google Earth satellite imagery to draw a polygon around the current lake perimeter. Areas of permanent swamp not included in AFRICOVER land cover classifications were also incorporated into land cover maps using the same method. The total area of each habitat type was determined, excluding major fenced areas inaccessible to rhinoceros. To determine the habitat composition of areas heavily utilised by rhinoceros, 50% kernel density range estimates were combined into one ‘core use area’, and the total area of each habitat type encompassed within the core use area was determined for each population. Habitat selectivity in relation to relative abundance was determined using Jacob’s correction of Ivlev’s selectivity index (Jacobs, 1974):

$$J = \frac{r - p}{(r + p) - 2rp}$$

Where r is the proportion of a particular habitat type within the core use area, and p is the proportion of that habitat type available within the study site. Habitat types with a selectivity index value between 0.5 and 1 were considered ‘preferred’, whilst those between -0.5 and -1 were considered ‘avoided’. Habitat types with a selectivity index value between -0.5 and 0.5 were categorised as ‘no preference’.

6.2.7.3 Resource availability

White rhinoceros population density was used to provide a measure of intra-specific competition, and median dung counts for herbivore species associated with white rhinoceros feeding locations were used to provide a measure of potential inter-specific competition. To quantify the area of habitat likely to be suitable for white rhinoceros at each study site, the total area of 'open' habitat (i.e. habitats likely to have substantial grass cover) per rhinoceros was determined from land cover maps, based on AFRICOVER habitat classifications (Di Gregorio and Latham, 2009). Habitats classified as *shrub savannah, tree and shrub savannah, swamp, open low shrubs, open shrubs, very open trees* or *open trees*, were considered open habitats. Median grass cover and grass height at feeding sites were used to provide more fine-scale measures of food availability within populations. Mean annual rainfall and range in monthly rainfall were used to provide measures of grass production and the variation in grass production across the year. Rainfall data were obtained from previous studies and reports (Chege et al., 2006; Georgiadis et al., 2007; Onyancha et al., 2016; Ogutu et al., 2017), and when not available, from *en.climate-data.org*, using data collected between 1982 and 2012 from the nearest weather station to the study site. *Solanum incanum* is considered a local invasive in the reserves, and its presence is associated with overgrazing (Ng'weno et al., 2010). Therefore, the median number of *Solanum incanum* at feeding sites was used as a measure of invasive species presence and grazing pressure.

6.2.7.4 Population performance

To examine breeding performance, demographic data were used to determine mean female inter-calving interval length, mean age at first calving and population growth rate. To capture current population performance, inter-caving intervals (the length of time between the birth of one calf and the next) were based on a female's most recent birth interval. Mean female age at first calving and annual population growth rate were determined within a three-year window from 2016-2018, to provide recent estimates of breeding performance. It was not possible to determine mean age at first calving for the Ol Pejeta population, as all adult females first calved before 2016, and demographic data were limited. There were no demographic data available for the Nakuru population, and therefore it was not possible to calculate any measures of population performance.

6.2.8 Seasonal differences in habitat use

The Meru population was used to investigate differences in white rhinoceros habitat use between two data collection periods; when resources availability was expected to be low-moderate (July-August), and when resource availability was expected to be very low, during the extreme dry season (February-March). *T-tests* and *Mann-Whitney U tests* were used to compare the ecological variables associated with white rhinoceros habitat (identified in Objective 1) between the two data collection periods, depending on the distribution of the data. Individual core ranges were calculated using GPS location data obtained in February-March, following the methodology described under section 6.2.7 (*Range size*). A *Mann–Whitney U* test was used to compare mean core range size between data collection periods, and *t-tests* were used to compare age-sex specific differences.

6.3 RESULTS

A total of 170 vegetation plots were used to compare ecological variables between populations (Ol Pejeta=40, Nakuru=40, Lewa=50, Meru=40). On average, each individual core range (50% kernel density estimate) contained 3.8 feeding plots (mean: Ol Pejeta=10.6; Nakuru=9.9; Lewa=3.4; Meru=4.2), and 87% of feeding plots were within individual core ranges (Ol Pejeta=100%; Nakuru=80%; Lewa=96%; Meru=70%). A total of 100 vegetation plots were used to compare ecological variables between seasons in Meru (P1=40; P2=60). On average, each individual core range contained 3.2 feeding plots (mean: P1=4.2; P2=2.6), and 65% of feeding plots were within individual core ranges (P1=70%; P2=60%).

6.3.1 Ecological variables associated white rhinoceros habitat

White rhinoceros feeding sites were associated with areas with greater grass cover, more *Solanum incanum*, shorter grass and trees, and lower elevation (Figure 6.1, Table 6.1). Feeding sites were also associated with lower shrub cover, and more zebra, buffalo and giraffe dung, but these were not reliable predictors across all populations, as confidence intervals crossed zero. See Appendix 1 for within population associations for the nine ecological variables identified in Table 6.1.

Table 6.1. Averaged model parameters explaining the characteristics of white rhinoceros habitat across the four populations. All variables were $\log_{10}$ transformed, with the exception of grass height and elevation, which were √ transformed, and grass cover, which had no transformation applied. Lower and Upper CI represent the 95% confidence intervals, and RVI represents the relative variable importance.

Predictor	Coefficient estimate	Standard error	Lower CI	Upper CI	RVI
Grass cover	4.608	1.031	2.587	6.629	1.000
Solanum count	1.123	0.565	0.015	2.231	0.575
Zebra dung count	0.966	0.594	-0.198	2.130	0.526
Buffalo dung count	0.721	0.477	-0.215	1.657	0.521
Giraffe dung count	0.627	0.579	-0.509	1.763	0.380
Shrub cover	-1.340	0.903	-3.110	0.429	1.000
Mean tree height	-1.562	0.691	-2.917	-0.207	1.000
Elevation	-2.075	0.780	-3.604	-0.546	1.000
Mean grass height	-2.635	0.896	-4.392	-0.879	1.000

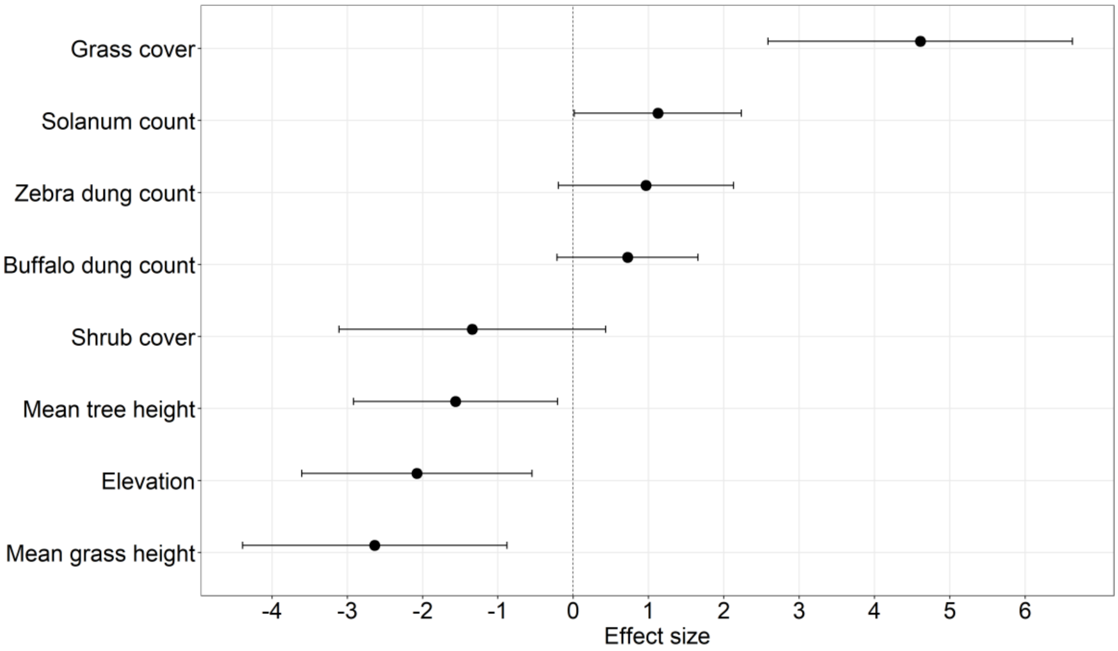

Figure 6.1. Average effect sizes (coefficient averages) and 95% confidence intervals for the averaged model predictors with an RVI>0.5, used to determine the characteristics of white rhinoceros preferred habitat. All predictors were standardised prior to analysis, meaning effect sizes are comparable between variables. See Table 6.1 for full model output.

6.3.2 Differences in habitat between populations

6.3.2.1 Differences in overall ecology

There was a significant difference in the ecological characteristics of feeding sites (*PERMANOVA*: F=20.39, R^2=0.43, DF=3,81, p=0.001) and control sites (F=19.20, R^2=0.42, DF = 3,81, p=0.001) between populations (Figure 6.2, see also Appendix 2).

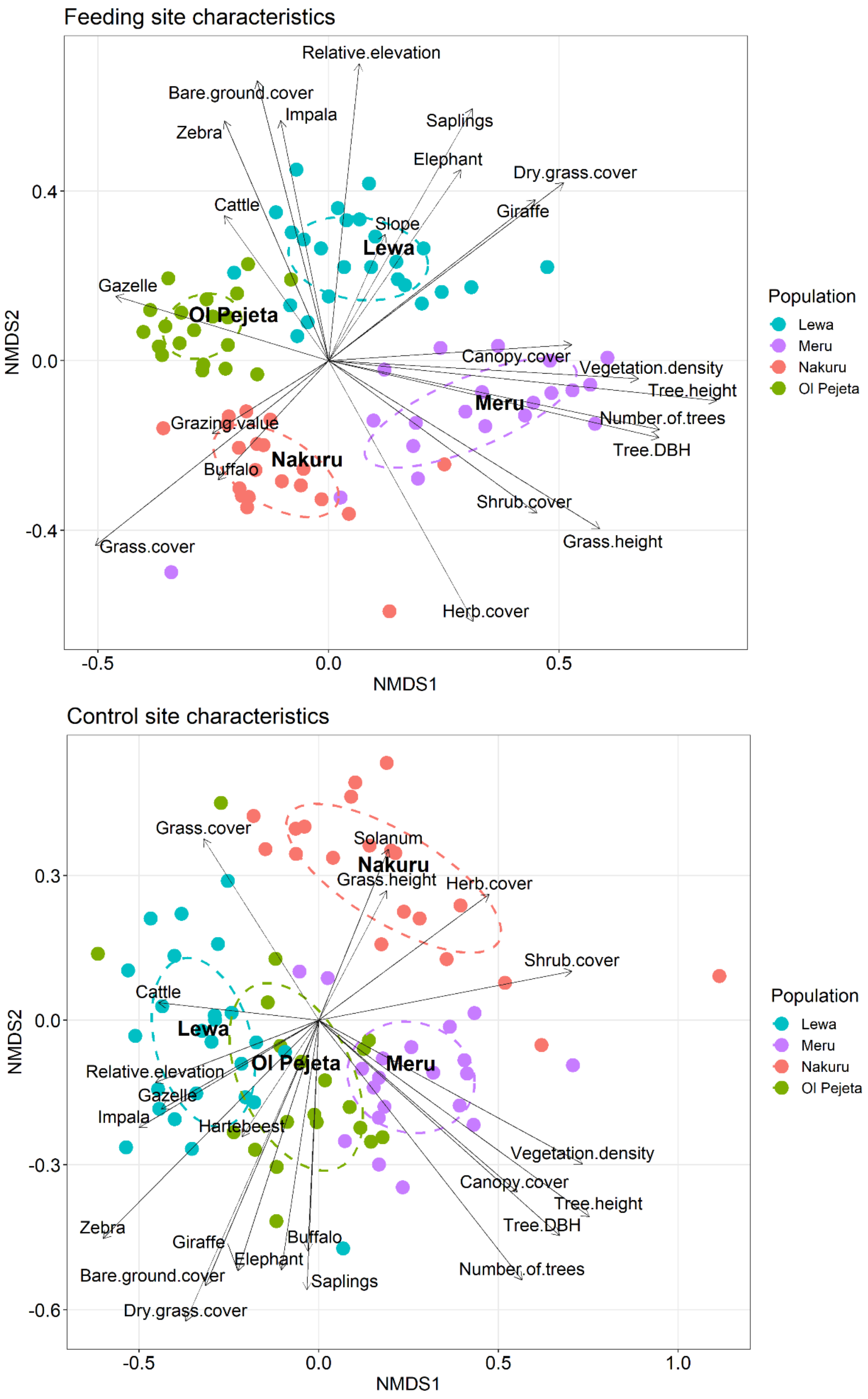

Figure 6.2. NMDS (nonmetric multidimensional scaling) ordination diagram of the four populations based on dissimilarity in their vegetation, topography and herbivore species, for feeding sites (top) and control sites (bottom). Dashed polygons represent the standard deviation for plots in that population, and labelled arrows demonstrate the variables that have a significant effect (p<0.05) on population dissimilarity. See Appendix 2 for full NMDS results.

Post-hoc pairwise comparisons conveyed that both feeding sites and control sites were significantly different between all four populations (p=0.001). In particular, both feeding and control sites in Meru had larger trees (height and DBH), taller grass, and denser vegetation than those in the other study populations, whilst both feeding and control sites in Lewa and Ol Pejeta had greater bare ground and dry grass cover. Inter-specific associations with gazelle, zebra and cattle were more apparent in Ol Pejeta, whilst associations with zebra, cattle, elephant, giraffe and impala were apparent in Lewa. An association with buffalo was characteristic of feeding sites in Nakuru, whilst high *Solanum incanum* cover was characteristic of control sites in Nakuru.

6.3.2.2 Differences in important habitat features

The ecological variables associated with white rhinoceros habitat (Objective 1, Table 6.1) showed substantial variation across population feeding sites (Table 6.2; see Appendix 3 for Kruskal-Wallis results and post-hoc Mann–Whitney U comparisons). Feeding sites in Ol Pejeta had shorter grass than those in all other populations, and more zebra dung than feeding sites in Nakuru and Meru. Feeding sites in Meru had both taller grass and trees, and greater shrub cover, than feeding sites in all other populations. Feeding sites in Lewa were at a greater relative elevation than those in all other populations, and feeding sites in Ol Pejeta and Nakuru had greater grass cover than those in Meru and Lewa.

Table 6.2. Feeding plot median ± interquartile range (IQR) for the nine variables associated with white rhinoceros habitat across populations, and significant post-hoc Mann–Whitney U differences (with a Bonferroni correction). See Appendix 3 for results from Kruskal-Wallis comparisons between sites, and significance levels for post-hoc pairwise Mann–Whitney U comparisons. Post-hoc significant differences between populations are indicated in the final column; Ol Pejeta (OP), Meru (M), Nakuru (N) and Lewa (L). 'A' indicates a significant difference with all populations. For example, feeding site grass cover was significantly greater in Ol Pejeta and Nakuru compared to Meru and Lewa.

Predictor	**Lewa**		**Nakuru**		**Ol Pejeta**		**Meru**		**Post-hoc sig differences**
	Median	**IQR**	**Median**	**IQR**	**Median**	**IQR**	**Median**	**IQR**	
Grass cover (%)	78	15	100	3	100	0	85	17	OP>L,M; N>L,M
Solanum count	2.00	9.00	13.50	93.25	24.50	62.00	9.50	23.00	OP>L
Zebra dung count	8.00	18.00	2.00	2.25	15.50	6.25	0.50	5.00	OP>M,N; L>M,N
Buffalo dung count	7.00	10.00	11.50	14.50	7.50	4.25	4.00	4.75	-
Giraffe dung count	2.00	5.00	0.00	0.00	0.00	1.00	2.00	3.25	L>OP; M>OP
Shrub cover (%)	0	0	0	5	0	4	12	12	M>A
Tree height (m)	0.00	1.58	0.00	0.00	0.00	0.00	2.75	4.68	M>A
Relative elevation (m)	169.00	83.00	14.50	23.00	57.00	23.50	40.50	26.50	L>A; OP>M,N
Grass height (cm)	29.15	18.40	30.98	18.47	7.90	1.78	44.26	22.38	A>OP; M>A

6.3.3 Range size, resource availability and population performance

6.3.3.1 Range size differences between populations

Across populations, the mean core range size for males was smaller than for females, but the effect was only weak (Table 6.3). Neither age-class nor the interaction between sex and age-class had an effect on core range size (Table 6.3).

Table 6.3. Fixed effects explaining white rhinoceros mean core range size (50% kernel density estimates) across the four populations. Population was included as a random effect and core range size was $\log_{10}$ transformed to improve normality. Mean core range size (km^2) ± standard deviation (SD) is provided for each predictor category. Lower and Upper CI represent the 95% confidence intervals.

Predictor	Category	Mean core range size (km^2; SD)	Coefficient estimate (Lower CI, Upper CI)	Standard error
Sex	Females	11.13 (14.84)	-0.470 (-0.903, -0.034)	0.517
	Males	8.75 (8.79)		
Age-class	Sub-adults	10.62 (12.56)	0.015 (-0.421, 0.446)	0.223
	Adults	9.65 (12.62)		
Sex*Age-class	Adult female	11.62 (14.87)	0.383 (-0.250, 1.019)	0.326
	Adult male	5.71 (4.07)		
	Sub-adult female	10.14 (15.15)		
	Sub-adult male	10.97 (10.58)		

There was a significant difference in the size of individual core ranges between populations (χ^2 =37.65, DF=3, p<0.001; Table 6.4; Figure 6.3); white rhinoceros in Ol Pejeta (Figure 6.4a) had larger core ranges than those in Meru (Figure 6.5a) and Lewa (Figure 6.5b), and individuals in Lewa had larger core ranges than those in Meru. Adult male core range size also differed significantly between populations (F=11.69, df=2,15 p<0.001), mirroring the differences observed across all individuals. Whilst Nakuru was not included in the statistical analysis, the adult male in Nakuru had a core range similar in size to the adult males in Ol Pejeta (Figure 6.3, Table 6.4). There was also a significant difference in adult female core range size between populations (F=19.47, df=3,34, p<0.001); adult females in Meru had smaller core ranges than those in all other populations, and adult females in Ol Pejeta had larger core ranges than those in all other populations (Table 6.4). Sub-adult female core range size was larger in Lewa compared to Meru (t=2.97, p=0.012), and sub-adult male core range size did not differ between populations (χ^2=2.75, df=3, p=0.432). Whilst the sub-adult female in Ol Pejeta was omitted from the analysis, it had a much larger core range than those in other populations (Figure 6.3, Table 6.4).

Table 6.4 **Mean (±SD) 95% and 50% kernel density range estimates (KDE; km^2) for all individuals and each age-sex class within populations, and significant post-hoc pairwise comparisons**. Significant differences between populations are indicated in the final column; Ol Pejeta (OP), Meru (M), Nakuru (N) and Lewa (L). For example, adult males in Ol Pejeta had larger 50% KDE's than adult males in Lewa and Meru. See Appendix 4 for significance levels for post-hoc pairwise comparisons. 50% KDE's for sub-adult females in Ol Pejeta, and adult males in Nakuru, were based on one individual, and thus were excluded from analyses.

Age-sex class	Lewa		Nakuru		Ol Pejeta		Meru		Post-hoc sig. comparisons
	Mean (±SD)	N	Mean (±SD)	N	Mean (±SD)	N	Mean (±SD)	N	
95% KDE core range estimates (km^2)									
All individuals	29.01 (23.74)	64	45.93 (29.17)	9	104.90 (58.80)	9	10.19 (6.75)	20	NA
Adult males	16.98 (7.36)	14	56.79	1	52.84 (9.84)	2	5.16 (0.24)	2	
Adult females	29.34 (21.38)	19	45.83 (28.32)	5	124.53 (51.97)	4	8.28 (3.24)	10	
SA females	33.35 (25.62)	12	NA	0	188.78	1	11.03 (8.78)	6	
SA males	34.82 (30.24)	19	42.47 (41.51)	3	75.75 (61.34)	2	22.24(1.80)	2	
50% KDE core range estimates (km^2)									
All individuals	7.88 (6.95)	64	11.02 (9.01)	9	30.34 (18.83)	9	2.53 (1.56)	20	OP>M,L; L>M
Adult males	4.37 (1.80)	14	10.61	1	11.32 (2.56)	2	1.59 (0.18)	2	OP>M,L; L>M
Adult females	8.41 (6.55)	19	11.46 (9.08)	5	39.25 (15.10)	4	2.05 (0.88)	10	OP>L,M,N; L, N>M
SA females	8.78 (7.68)	12	NA	0	55.51	1	2.75 (1.98)	6	L>M
SA males	9.39 (8.66)	19	10.42 (12.60)	3	18.96 (14.59)	2	5.26 (0.52)	2	-

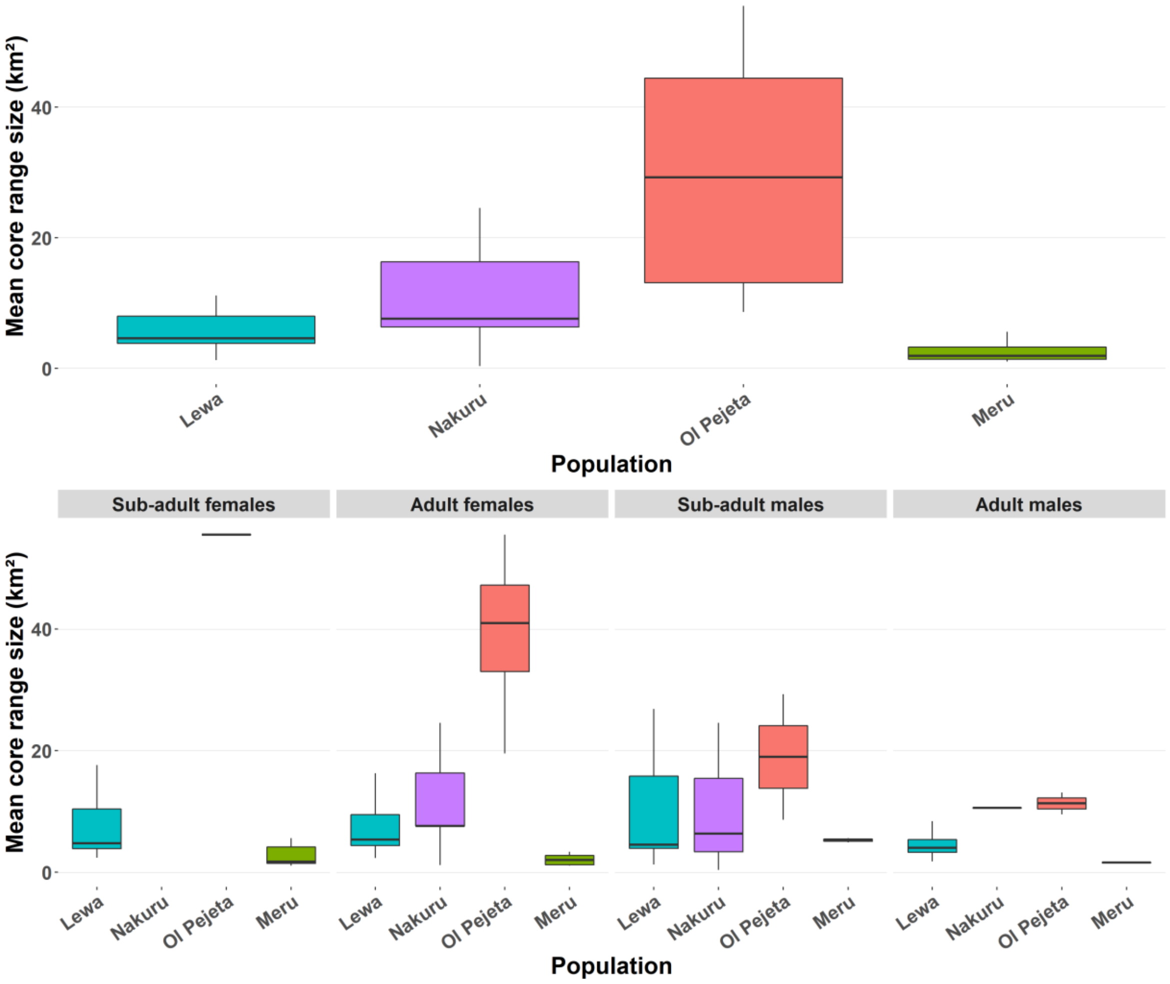

Figure 6.3 Mean 50% kernel density core range sizes in the four study populations for all individuals (top) and each age-sex class (bottom). Note that core range estimates for sub-adult females in Ol Pejeta, and adult males in Nakuru, are based on only one individual, and there were no sub-adult females in the Nakuru population at the time of data collection.

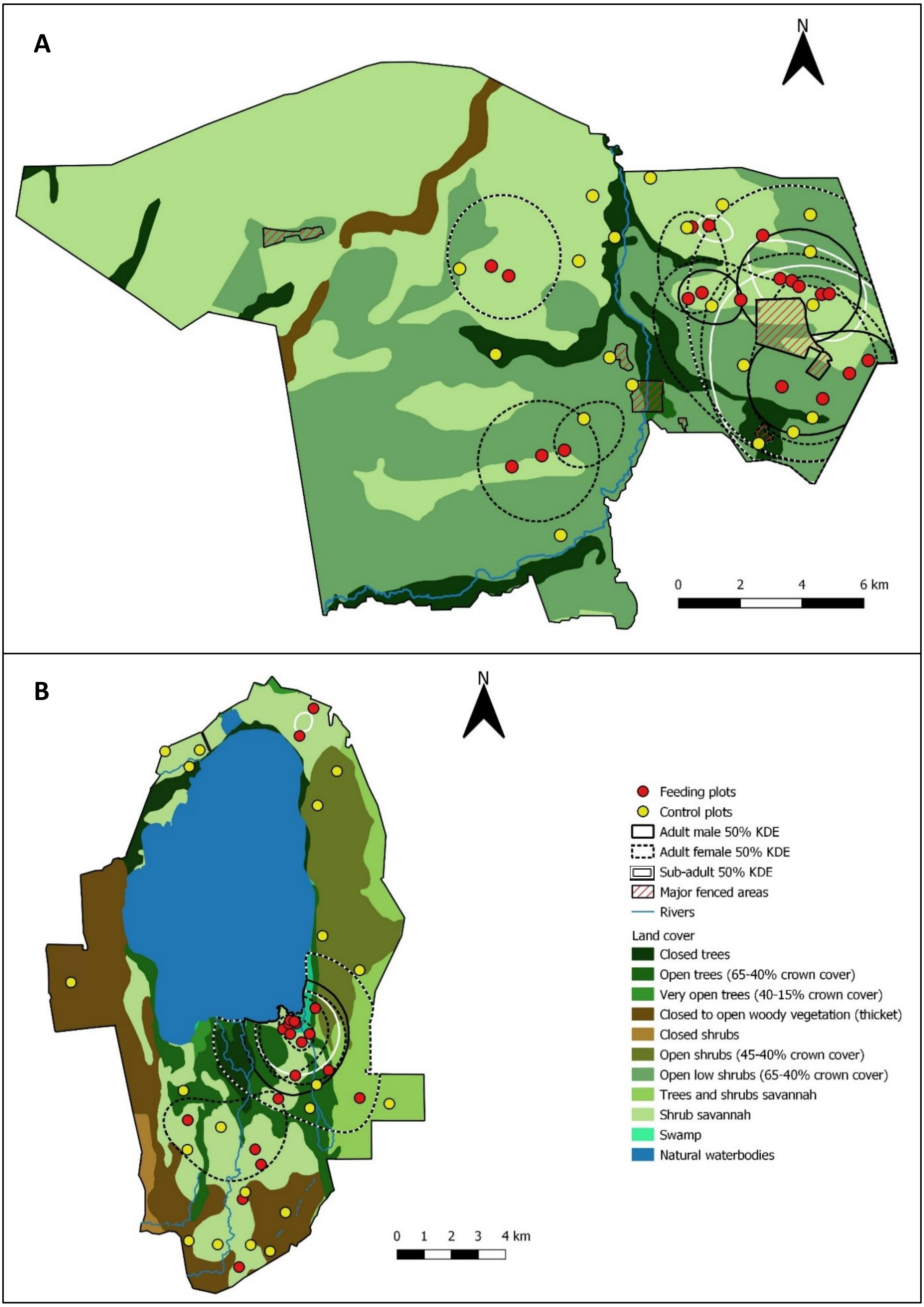

Figure 6.4. The location of vegetation plots and age-sex specific 50% kernel density estimate (KDE) core ranges within (A) Ol Pejeta Conservancy and (B) Lake Nakuru National Park. Vegetation classification and land cover were obtained from the AFRICOVER project (Di Gregorio and Latham, 2009).

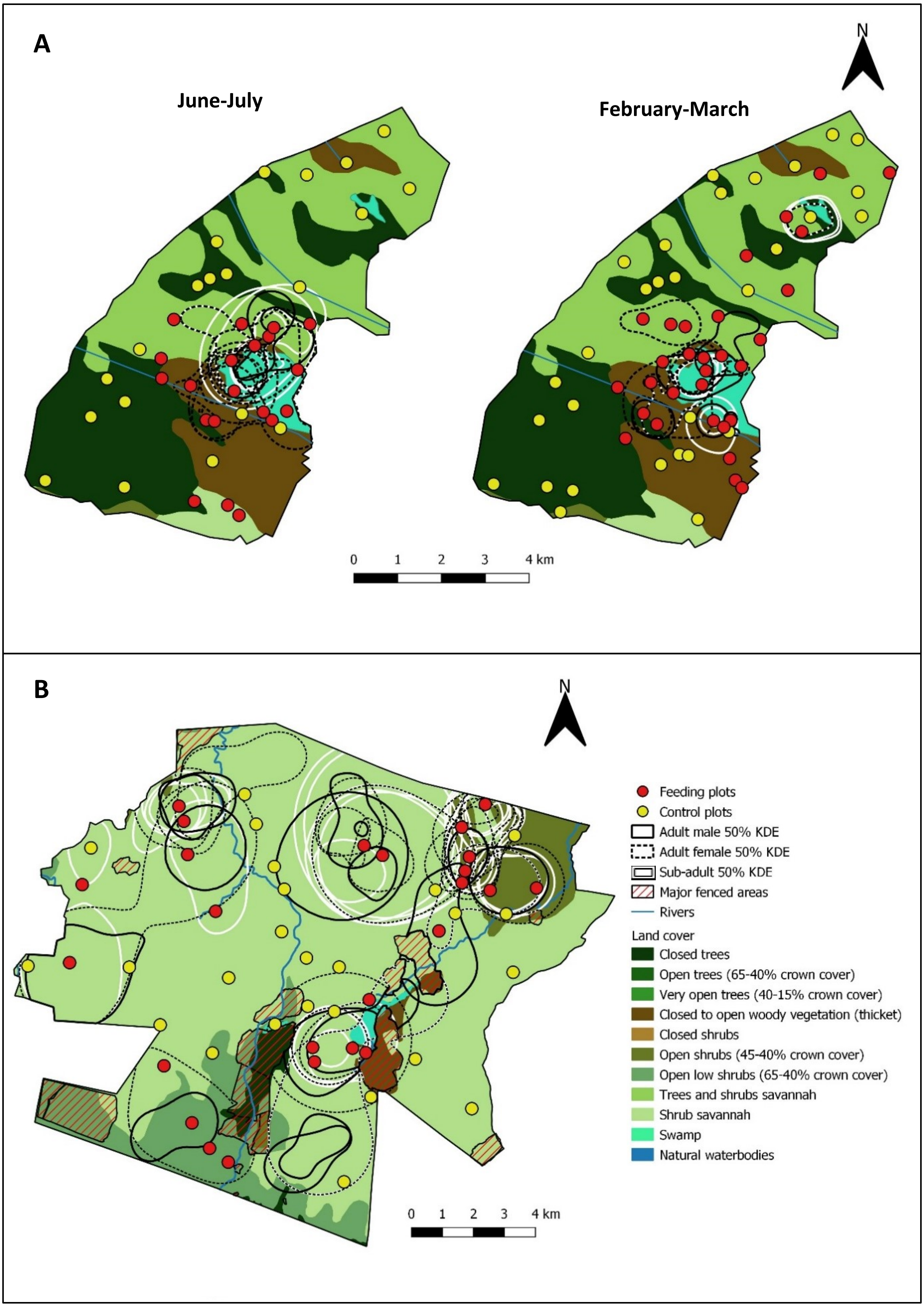

Figure 6.5. The location of vegetation plots and age-sex specific 50% kernel density estimate (KDE) core ranges within (A) Meru National Park (both June-July and February-March data collection periods) and (B) Lewa Wildlife Conservancy. Vegetation classification and land cover were obtained from the AFRICOVER project (Di Gregorio and Latham, 2009).

6.3.3.2 The habitat composition of core use areas

In both Nakuru and Meru, the number of white rhinoceros sightings per km^2 was greatest in *swamp* habitat, and white rhinoceros in both populations displayed a strong selectivity towards *swamp* habitat (Table 6.5). Although the greatest number of location sightings per km^2 was also within *swamp* habitat in Lewa, rhinoceros were not selective for any habitat type (Table 6.5). White rhinoceros in Nakuru displayed an avoidance of *very open trees, closed shrubs* and *closed to open woody vegetation*, whilst individuals in Ol Pejeta avoided *open trees* and *closed to open woody vegetation* (Table 6.5). Rhinoceros in Ol Pejeta had no habitat preference, although all sightings were within *shrub savannah* or *open low shrubs* (Table 6.5). Despite the relatively high number of sightings in *shrub savannah* habitat in Meru, rhinoceros avoided both *closed trees* and *shrub savannah* in relation to their abundance (Table 6.5).

Table 6.5. The number of white rhinoceros sightings per km^2 in each habitat type and Ivlev's selectivity index with Jacob's correction (J) for core area habitat composition. J>0.5 = Preference*; J<-0.5 = Avoidance**; J>-0.5 and <0.5 = No selectivity. Habitat types not present in a reserve are denoted by '-'.

Habitat type	**Lewa**		**Nakuru**		**Ol Pejeta**		**Meru**	
	Sightings	**Selectivity**	**Sightings**	**Selectivity**	**Sightings**	**Selectivity**	**Sightings**	**Selectivity**
Shrub savannah	1.14	-0.03	1.82	0.14	0.52	-0.15	4.85	-1.00**
Tree/shrub savannah	0.00	0.00	0.36	0.24	-	-	3.75	-0.29
Swamp	8.58	0.20	7.96	0.54*	-	-	27.38	0.66*
Open low shrubs	0.44	-0.05	-	-	0.12	0.20	-	-
Open shrubs	3.66	0.10	0.00	-0.28	-	-	-	-
Very open trees	-	-	0.00	-1.00**	-	-	-	-
Open trees	-	-	0.17	0.44	0.00	-1.00**	-	-
Closed shrubs	-	-	0.00	-1.00**	-	-	-	-
Closed-open vegetation	2.98	-0.13	0.00	-0.99**	0.00	-1.00**	5.02	-0.05
Closed trees	0.00	-0.05	0.00	0.18	0.00	-0.06	0.49	-0.94**

6.3.4 Population comparisons

Despite differences in potential inter-specific competition, population density and resource availability between populations, breeding performance measures indicated that all populations, for which demographic data were available (Lewa, Ol Pejeta and Meru), were performing well (Table 6.6). Rhinoceros in Meru were at the highest population density, had the lowest area of suitable habitat per individual, and typically experience the greatest range in monthly rainfall, yet, mean age at first calving and population growth rate demonstrate excellent breeding performance in this population (Figure 6.6). Rhinoceros in Meru also had the smallest core ranges, and formed the largest groups.

Table 6.6. Differences in competition, resource availability, behaviour and population performance between the four populations. Ecological population density was determined from the total area of suitable white rhinoceros habitat, i.e. 'open' habitat types according to AFRICOVER land cover (Di Gregorio and Latham, 2009). Population performance indicators marked with '+' indicate good performance, and those marked with '++' indicate excellent performance (du Toit, 2006).

		Lewa	**Nakuru**	**Ol Pejeta**	**Meru**
Potential competition	**Ecological population density** (rhinos/km^2 suitable habitat)	0.54	0.14	0.07	2.70
	Buffalo dung count (median ± IQR)	7.0 (10.0)	11.5 (14.5)	7.5 (4.25)	4.0 (4.75)
	Zebra dung count (median ± IQR)	8.0 (18.0)	2.0 (2.5)	15.5 (6.25)	0.50 (5.0)
Resource avaiability	**Feeding plot grass cover** (median ± IQR)	78% (±15%)	100% (±3%)	100% (±0%)	85% (±17%)
	Feeding plot grass height (median ± IQR)	29.15 (±18.4)	30.98 (±18.47)	7.90 (±1.78)	44.26 (±22.38)
	Mean annual rainfall (mm/year)	545[1]	869[2]	722[3]	700[4]
	Range in rainfall (mm/month)	7-124[1]	33-126[2]	23-133[5]	1-171[5]
	***Solanum incanum* count** (median ± IQR)	2.00 (±9.0)	13.50 (±93.25)	24.50 (±62.0)	9.50 (±23.0)
Behaviour	**Core range size** (km^2; mean ±SD)	7.9 (±7.0)	11.0 (±9.0)	30.3 (±18.8)	2.5 (±1.6)
	Observed group size (mean ±SD)	3.0 (±1.5)	2.3 (±1.3)	2.4 (±1.0)	3.2 (±1.9)
Population performance (2016-2018)	**Mean inter-calving interval** (years; mean ±SD)	2.65 (±0.70) +	Data not available	2.92 (±0.88) +	2.93 (±0.65) +
	Mean age at first calving (years; mean ±SD)	6.61 (±1.04) +	Data not available	Data not available	5.34 (±0.87) ++
	Annual population growth rate (% increase; mean ±SD)	7.63 (±1.6) ++	Data not available	9.51 (±2.9) ++	11.09 (±4.8) ++

[1 (Chege et al., 2006) [2] (Ogutu et al., 2017)[3] (Georgiadis et al., 2007) [4] (Onyancha et al., 2016) [5] En.climate-data.org

Whilst the abundance of zebra and buffalo dung at feeding sites indicated similar levels of potential inter-specific competition in Lewa and Ol Pejeta, feeding sites in Ol Pejeta had substantially more *Solanum incanum* than feeding sites in Lewa, suggesting overall grazing pressure is higher in Ol Pejeta. Mean annual rainfall is typically lowest in Lewa, and after Meru, Lewa had the smallest area of suitable habitat per rhinoceros, and the highest population density. Mean age at first calving was over one year older in Lewa compared to Meru, which may suggest Lewa is closer to ecological carrying capacity. In Nakuru, both buffalo dung and *Solanum incanum* count were high, and showed considerable variation, suggesting overall grazing pressure was high, and may be localised to particular areas.

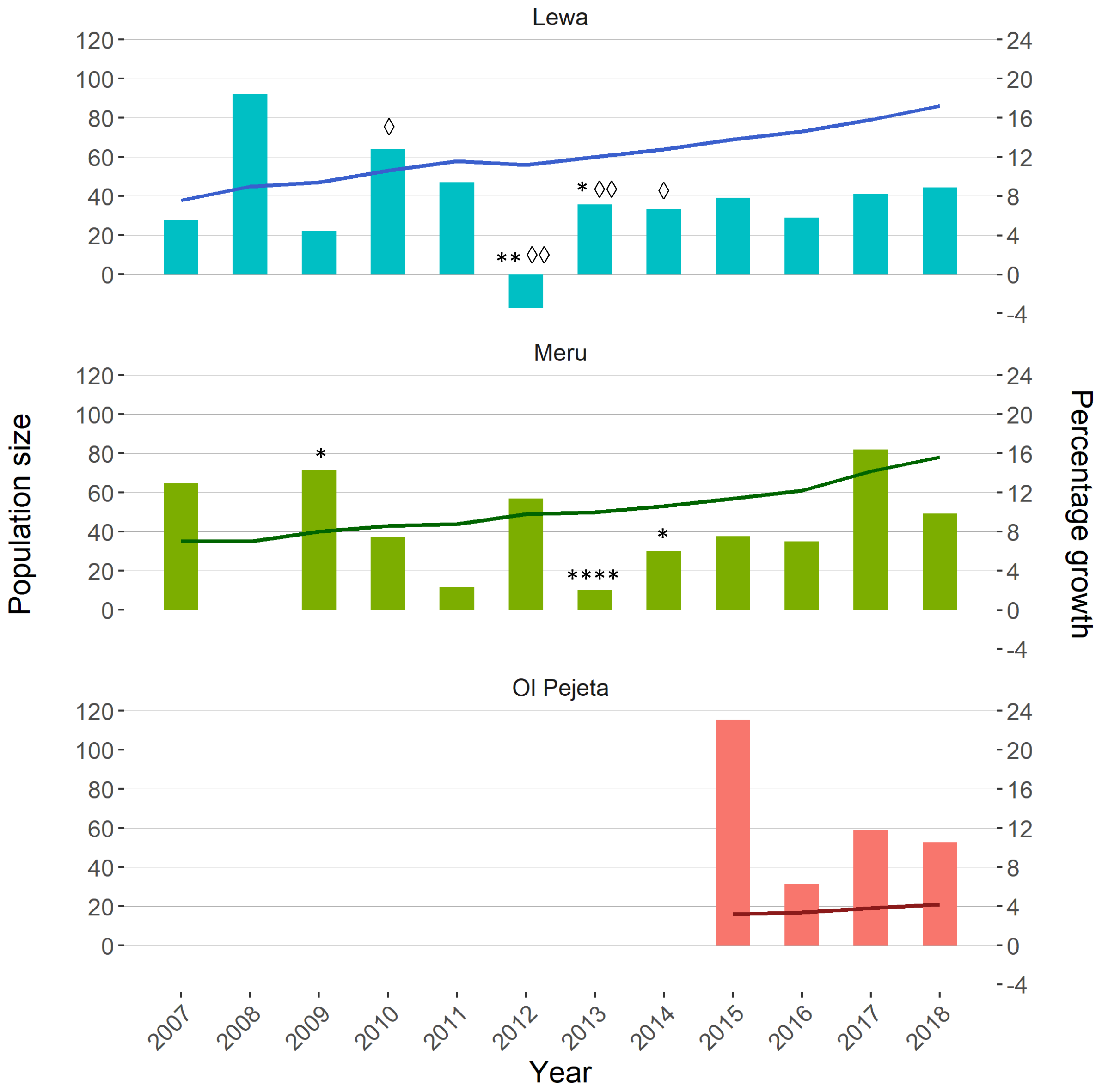

Figure 6.6. White rhinoceros population size (line plot) and percentage growth (bar plot) between 2007 and 2018 in Lewa and Meru, and between 2015 and 2018 in Ol Pejeta. Annual number of deaths due to poaching are denoted by "*" and annual number of translocations are denoted by "◊".

6.3.5 *Seasonal differences in habitat use*

Several ecological variables showed substantial variation between seasons (Table 6.7); feeding sites in February-March, the extreme dry season, were at a significantly higher elevation (t=-26.74, p=0.013), had significantly less *Solanum incanum* (U=271, p=0.047), and had significantly lower shrub cover (U=335, p<0.001), in comparison to feeding sites in June-July, when conditions were more favourable. See Appendix 5 for median values in control and feeding plots within seasons. There was also variation in mean core range size between seasons (Table 6.7); core ranges were significantly larger in June-July compared to February-March (U=62, P<0.001). Whilst there was no significant difference in adult male core range size detected between seasons (t=-2.53, p=0.052), core ranges were significantly smaller in February-March for adult females (t=-2.36, p=0.032), sub-adult females (t=-3.79, p=0.002) and sub-adult males (t=-9.79, p<0.001).

Table 6.7. Median ± interquartile range (IQR) for the nine ecological variables associated with white rhinoceros habitat across populations, and mean ± standard deviation (SD) age-sex class 50% kernel density estimate (KDE) range sizes (km^2), for white rhinoceros in Meru during the June-July and Feb-March seasons. Statistically significant differences between seasons are indicated as follows; * denotes significance at p<0.05, ** denotes significance at p<0.01, and ***denotes significance at p<0.001.

	Predictor	**June-July**		**February-March**	
Ecological variables		**Median**	**IQR**	**Median**	**IQR**
	Grass cover (%)	85	17	87	23
	Solanum count	9.50*	23.00	0.00*	3.75
	Zebra dung count	0.50	5.00	2.00	5.75
	Buffalo dung count	4.00	4.75	5.00	10.75
	Giraffe dung count	2.00	3.25	4.50	4.75
	Shrub cover (%)	12***	12	1***	2
	Tree height (m)	2.75	4.68	4.23	9.10
	Relative elevation (m)	40.50*	26.50	53.00*	23.00
	Grass height (cm)	44.26	22.38	36.91	18.21
50% KDE range sizes (km^2)		**Mean**	**SD**	**Mean**	**SD**
	All individuals	2.53***	1.56	0.88***	0.63
	Adult males	1.59	0.18	0.82	0.62
	Adult females	2.05*	0.88	1.27*	0.89
	Sub-adult females	2.75**	1.98	0.66**	0.45
	Sub-adult males	5.26***	0.52	0.75***	0.35

6.4 DISCUSSION

This study aimed to identify the ecological characteristics of white rhinoceros habitat across four populations in Kenya, and to determine how differences in ecology and resource availability relate to ecological carrying capacity and female reproductive success. The results show that high grass cover, both shorter grass and trees, and lower elevations, were key habitat characteristics across populations. However, these important feeding site characteristics differed substantially between populations. There were also differences in associations with other herbivore species between the study populations, suggesting variation in inter-specific competition may exist between sites. Core range size varied considerably between populations; core ranges were smallest in the population with the highest density (Meru), and largest in the population with the lowest density (Ol Pejeta). Whilst demographic performance indicators suggest all populations are performing well, differences in resource availability and grazing pressure may explain the variation in range size between populations. Seasonal differences in habitat use were also apparent; during the extreme dry season, individual core ranges in Meru were smaller, and feeding sites had lower shrub cover, fewer *Solanum incanum,* and were at a higher elevation, in comparison to feeding sites when resources were less limited.

Previous studies suggest that white rhinoceros graze grass species unselectively to maximise quantity (Perrin and Brereton-Stiles, 1999; Waldram et al., 2008), and are only selective for grass species during periods of food abundance (Wardjomto et al., 2019). Instead, they are selective for grass height, and preferentially graze short grasses (Owen-Smith, 1975; Waldram et al., 2008; Cromsigt and te Beest, 2014), most likely because it is more digestible and has a greater protein content compared to taller grass (Crampton and Harris, 1969; Mattson, 1980). The results of this study support this, as grass height and grass cover were both strong predictors of white rhinoceros feeding sites across populations; rhinoceros utilised areas with shorter grass and greater grass cover than control areas. Grass height was significantly shorter in Ol Pejeta in comparison to the other study populations, suggesting that rhinoceros in Ol Pejeta were utilising and maintaining ‘grazing lawns’ (Vesey-Fitzgerald, 1965). Grass cover also showed significant variation between populations; feeding sites in Nakuru and Ol Pejeta had greater grass cover than those in Meru and Lewa. This was reflected in the rainfall patterns across study sites; both Ol Pejeta and Nakuru typically experience more annual rainfall, and less seasonal variation in rainfall, in comparison to the other study sites. Rainfall patterns are thus likely to have a greater impact on resource availability in Meru and Lewa compared to Ol Pejeta and Nakuru.

Variation in rainfall may explain the differences in the relative elevation of feeding sites between both populations and seasons. As nutrients are transported down the catena, intensively grazed hotspots are often at lower elevations (Cromsigt and te Beest, 2014), and consequently, white rhinoceros tend to utilise areas of low elevation (Owen-Smith, 1975; Perrin and Brereton-Stiles, 1999), as found in Nakuru and Meru. However, when resources are limited, white rhinoceros are less selective for grass height or elevation, and may move into areas of higher elevation to utilise taller grasses (Owen-Smith, 1973). Feeding sites in Lewa were at a significantly higher relative elevation compared to those in the other study populations, and feeding sites in Meru were at a significantly higher elevation during the extreme dry season in February-March, in comparison to July-August, when conditions were cooler. As Lewa typically experiences the lowest annual rainfall across the study sites, this may suggest that rhinoceros in Lewa and Meru moved to areas of high elevation to search for food in response to dry conditions. Whist feeding sites in Ol Pejeta were also at a higher relative elevation than those in Nakuru or Meru, this can likely be explained by the high coverage of the *Euclea divinorum* tree in the valleys of Ol Pejeta, which limits grass cover in areas of low elevation (Kavwele et al., 2017).

The results of this study demonstrate that white rhinoceros generally fed in more ‘open’ areas; feeding sites typically had smaller trees and lower shrub cover than control areas, and rhinoceros avoided several closed and wooded habitat types. Whilst females with young calves may use areas with greater vegetation density to avoid predators (Owen-Smith, 1988), white rhinoceros generally show a preference for open areas (Kleynhans et al., 2011; Thompson et al., 2016). This is likely because grass cover is higher in areas where canopy cover and vegetation density are low, and therefore open areas are likely to have greater food availability. In both Nakuru and Meru, feeding sites were largely clustered around swamp habitat, and rhinoceros in both populations had a preference for swamp habitat, as also found in other studies (Patton et al., 2011). This is likely because swamps retain water for longer, and thus during the dry season, they not only provide more nutritious grass than surrounding savannahs or woodlands (Moss et al., 2011), but also provide wallows for thermoregulation. Across the study sites, Meru had substantially taller trees and greater shrub cover, and consequently, the smallest area of suitable habitat per rhinoceros. This suggests there may be few optimal feeding sites in Meru, and the severe core range overlap across the largest swamp further supports this.

Whilst the area of optimal habitat may be scarcer in Meru, grazing pressure appears to be much higher in the other populations. Resource partitioning theory suggests that other herbivore species utilising the same habitat patches as white rhinoceros present limited competition (Kleynhans et al., 2011). However, when resources are limited, niches may show more overlap, and consequently, more exploitative competition may occur (Hempson et al., 2015). Under dry conditions, grass grows more slowly, and therefore white rhinoceros may be in direct competition with other short-grass grazers when resources are limited. Both bare ground and dry grass were more prevalent at sites in Ol Pejeta and Lewa, suggesting that patches of green grass may have been limited, and grazing competition high.

As buffalo favour tall grasses, they may act as an indirect facilitator to white rhinoceros, modifying grassland habitat by trimming and trampling grasses to levels preferred by white rhinoceros (Perrin and Brereton-Stiles, 1999). Previous research suggests that when grazing resources are abundant, there is no competition evident between buffalo and white rhinoceros, as the two species are partitioned not only by grazing niche, but also by topography and gradient (Perrin and Brereton-Stiles, 1999). However, white rhinoceros feeding sites in Nakuru were strongly associated with buffalo dung counts, suggesting both species were utilising the same areas, and that buffalo may present a competitive threat to white rhinoceros when graze is limited. Furthermore, as the median grass height at feeding sites in Nakuru, Lewa and Meru was between 29cm and 44cm, this suggests that individuals were utilising taller grass patches than usually preferred by white rhinoceros (<10cm; Arsenault and Owen-Smith, 2008), most likely in response to dry season conditions. Therefore, during periods when graze is limited, rhinoceros are likely competing with tall grass grazers, such as zebra and buffalo (Perrin and Brereton-Stiles, 1999; Arsenault and Owen-Smith, 2008).

White rhinoceros feeding sites were also associated with high *Solanum incanum* cover. *Solanum incanum* is one of the most problematic weeds in East Africa, as it is toxic to livestock and a major threat to grazing (Ng'weno et al., 2010). *Solanum* cover was highest at feeding sites in Ol Pejeta and Nakuru, and it was a defining characteristic of control areas in Nakuru, suggesting rhinoceros may avoid areas with high *Solanum* cover in reserves with severe spread. This is likely because patches of grassland invaded by *Solanum* have lower forage biomass and nutritional quality in comparison to non-invaded patches, as *Solanum* limits the availability of light, water and nutrients to surrounding vegetation (Ng'weno et al., 2010). High levels of selective grazing can increase the dominance of less palatable plant species (Hobbs and Mooney, 1986), and therefore *Solanum* is associated with over-grazing (Ng'weno et al., 2010; Al-Rowaily et al., 2015). This suggests that grasslands in Nakuru and Ol Pejeta are potentially being over-grazed, and the nutritional content of their forage may be limited.

Variation in the availability of optimal habitat, and in particular, highly nutritious forage, between populations may have important consequences for white rhinoceros population dynamics (Hempson et al., 2015). Adult females are likely to derive nutritional benefits from increased access to mineral-rich grazing lawns when their energy demands are high, such as during the final stages of pregnancy, or when lactating (McNaughton, 1990). High quality graze can not only improve female body condition (Hempson et al., 2015), but can also improve pre- and post-weaning infant survival rates (Gaillard et al., 2000), and thus grazing lawns may play an important role in female reproductive success. Females in Meru, Lewa and Ol Pejeta had inter-calving intervals below 3 years long, and mean annual growth rates were all above 7%, which is indicative of good female fecundity and population performance (du Toit et al., 2006). Therefore, despite differences in population density and the availability of optimal habitat, female reproductive success appears to be high across these populations.

This differs from previous research on white rhinoceros in Matobo National Park, Zimbabwe, which found that female age at first calving and inter-calving interval length increased as population density increased (Rachlow and Berger, 1998). Whilst calving data suggests females in Meru (2.7 rhinos/km^2) reproduce earlier than females in Lewa (0.54 rhinos/km^2), at 5.5 and 6.5 years old respectively, both of these estimates were below those of the high density (0.83 rhinos/km^2) and low density (0.23 rhinos/km^2) populations in Matobo, at 7.5 and 10.1 years old, respectively (Rachlow and Berger, 1998). As reproductive success was also correlated with a decrease in female body condition in the Matobo population, this suggest that rhinoceros were above the ecological carry capacity of the reserve. Whilst female body condition was not included in this study, there were no density-dependent effects on female reproduction detected, suggesting that the Lewa, Meru and Ol Pejeta populations were below ecological carrying capacity. As demographic data were not available for Nakuru, it is unknown whether inter-specific competition and the abundance of *Solanum* have affected female reproductive success. The buffalo population in Nakuru is well above capacity, with almost 4000 individuals counted in 2014 (Ogutu et al., 2017), equating to approximately 44 buffalo/km^2 of suitable habitat. Therefore, the impacts of overgrazing and invasive species on female reproduction are likely to be more apparent in Nakuru, and require further investigation.

Whilst their impact on reproduction remains unclear, both resource availability and population density very likely explain the differences in white rhinoceros range size between populations. Across the study populations, core range size increased as population density decreased. Rhinoceros in Ol Pejeta were at the lowest density (0.07 rhino/km^2), and had significantly larger core ranges than those from both Lewa and Meru, whilst rhinoceros in Meru were at the highest population density (2.70 rhino/km^2), and had significantly smaller core ranges than rhinoceros in Lewa and Ol Pejeta. Previous studies also suggest white rhinoceros range size tends to increase with decreasing population density (Owen-Smith, 1975; Pienaar et al., 1993; Rachlow and Berger, 1998). However, female core ranges in Meru (2.05km^2) were substantially smaller than those recorded at a similar population density (approximately 2.65 rhinos/km^2) in Hluhluwe-iMfolozi Game Reserve, South Africa (5km^2; White et al., 2007). Whilst the same study used a different method (Neighbourhood analysis) to calculate male territory sizes, mean range estimates for males were very similar (4.79km^2) to those calculated in this study (5.16km^2). Thompson et al (2016) also found white rhinoceros range sizes smaller than those reported in previous studies with comparable population densities, and attributed these differences to the heterogeneous terrain of the reserve, which likely reduced the area of suitable habitat. This may also explain the compressed ranges for females in Meru, as only 23.7km^2 of the sanctuary contained suitable white rhinoceros habitat. Female ranges were significantly larger than male ranges, as also found in several previous studies (Owen-Smith, 1975; Pienaar et al., 1993; Rachlow et al., 1999; White et al., 2007), and this may explain why the effects of range compression are more apparent in females. Whilst there is currently no evidence of density-dependent declines in female reproduction in Meru, severe range compression and overlap may increase the frequency of territorial disputes and intra-specific competition, which may result in a greater number of injuries and fatalities in the future.

On the other hand, the seasonal ranges of females in Ol Pejeta (0.07 rhinos/km^2; 124.5km^2 range size) were substantially larger than estimates for females in the low-density population in Matobo (0.03 rhinos/km^2; 59km^2 range size ;Rachlow et al., 1999). Though also larger, male seasonal range size in Ol Pejeta (52.3km^2) was more similar to male range size in Matobo (36km^2 ;Rachlow et al., 1999). In reindeer, individual home range size is negatively correlated with food availability (Hansen et al., 2009), and in black rhinoceros, home range size is negatively correlated with availability of suitable browse (Hitchins, 1969; Brooks, 1979; Clubb et al., 2008), and this has been linked to a reduction in ecological carry capacity (Adcock, 2001; Reid et al., 2007). Females in Ol Pejeta may therefore encompass larger ranges than expected for their population density due to poor quality habitat, most likely caused by over-grazing and *Solanum incanum*.

Conversely, female and sub-adult ranges in Meru were significantly smaller when resources were more limited, during the extreme dry season in February-March. Similar seasonal differences in range size have also been recorded in black rhinoceros in Hluhluwe-Umfolozi Park; ranges were smaller during the winter, when there is less rainfall, in comparison to the summer (Reid et al., 2007). This is likely because rhinoceros are confined to areas with greater water retention when conditions are dry. Due to their differing diets, dry conditions are likely to have a greater impact on white rhinoceros resource availability, as grass dries out more quickly than browse (Ferreira et al., 2019).

Whilst seasonal variation in range size further suggests that resource availability influences ranging patterns in white rhinoceros, the large ranges of females in Ol Pejeta and Nakuru may also be attributed to mate selection (White et al., 2007). As also observed in this study, females occupy ranges that overlap with numerous breeding males (Owen-Smith, 1975; Thompson et al., 2016). At the time of this study, there were only two breeding males in Ol Pejeta, and just one in Nakuru. Therefore, the large core ranges of adult females in these populations may also be attributed to attempts to seek new mating partners. Notably, one adult female of 16 years old in Ol Pejeta, and one adult female of 9 years old in Nakuru, were yet to produce any calves. The oldest female that had not yet calved across both Lewa and Meru was just 6.6 years old. Consequently, inbreeding avoidance may also be limiting female reproduction in these populations.

Overall, this chapter demonstrates the importance of understanding habitat utilisation and ranging patterns across different ecological conditions for the conservation management of threatened species. The results of this chapter have provided a first understanding of white rhinoceros habitat use and ranging behaviour in Kenya, and have identified key habitat characteristics and inter-specific associations that may influence reproduction and population viability. Variation in range size between populations and seasons suggests that both density and resource availability influence white rhinoceros ranging patterns, and increased grazing pressure and invasive species cover may necessitate an increase in range size, and thus reduce ecological carrying capacity. As all populations demonstrated good reproductive performance, this suggests that current population densities are having little impact on female reproduction. This information is not only applicable to the management of white rhinoceros in Kenya, but can also be used to guide conservation planning, habitat protection and estimates of ecological carrying capacity in small white rhinoceros populations across Africa. The results of this chapter are also likely to be relevant to the conservation of other threatened species, such as Grevy’s zebra, *Equus grevyi*, which utilise the same habitat as white rhinoceros.

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6.6 APPENDICES

Appendix 1

Table 6.8 Median variable values for control and feeding plots in each reserve and the statistical significance of differences using Mann–Whitney U tests. P-values were adjusted for multiple comparisons using the false discovery rate correction. * denotes significance at p<0.05, ** denotes significance at p<0.01, and ***denotes significance at p<0.001.

Variable	Lewa		Nakuru		Ol Pejeta		Meru	
	Control	Feeding	Control	Feeding	Control	Feeding	Control	Feeding
Grass cover (%)	59**	78**	99	100	94**	100**	52**	85**
***Solanum incanum* count**	0.00	2.00	22.50	13.50	2.00	24.50	0.00	9.50
Zebra dung count	10.00	8.00	0.00	2.00	3.00*	15.50*	0.00	0.50
Buffalo dung count	2.00	7.00	1.00*	11.50*	6.00	7.50	3.50	4.00
Giraffe dung count	1.00	2.00	0.00	0.00	0.00	0.00	1.50	2.00
Shrub cover (%)	0	0	16	0	4	0	8	12
Tree height (m)	0.00	0.00	3.40*	0.00*	3.85***	0.00***	8.40	2.75
Relative elevation (m)	186.00	169.00	47.00	14.50	47.00	57.00	62.50	40.50
Grass height (cm)	31.94	29.15	52.66	30.98	15.94**	7.90**	60.12	44.26

Appendix 2

Table 6.9. NMDS values and significance (p-values<0.05) for the ecological variables driving dissimilarity between the study sites, in both feeding and control areas.

Variable	Feeding sites			Control sites		
	NMDS1	NMDS2	P-value	NMDS1	NMDS2	P-value
Bare ground cover	-0.155	0.661	0.001	-0.315	-0.550	0.001
Buffalo dung count	-0.240	-0.281	0.004	-0.031	-0.479	0.001
Canopy cover	0.528	0.038	0.001	0.553	-0.357	0.001
Cattle dung count	-0.226	0.342	0.001	-0.446	0.036	0.002
Dry grass cover	0.510	0.420	0.001	-0.371	-0.624	0.001
Elephant dung count	0.287	0.450	0.001	-0.104	-0.518	0.001
Gazelle dung count	-0.462	0.153	0.001	-0.439	-0.185	0.001
Giraffe dung count	0.448	0.380	0.001	-0.225	-0.520	0.001
Grass cover	-0.506	-0.436	0.001	-0.321	0.376	0.001
Grass height	0.589	-0.397	0.001	0.189	0.268	0.009
Grazing value	-0.253	-0.172	0.018	-	-	-
Hartebeest dung count	-	-	-	-0.214	-0.242	0.009
Herb cover	0.314	-0.616	0.001	0.474	0.261	0.001
Impala dung count	-0.104	0.567	0.001	-0.501	-0.223	0.001
Number of trees	0.718	-0.162	0.001	0.566	-0.539	0.001
Relative elevation	0.066	0.701	0.001	-0.455	-0.129	0.001
Saplings	0.313	0.595	0.001	-0.034	-0.559	0.001
Shrub cover	0.452	-0.359	0.001	0.704	0.101	0.001
Slope	0.123	0.298	0.018	-	-	-
Solanum count	-	-	-	0.193	0.354	0.002
Tree DBH	0.717	-0.181	0.001	0.670	-0.447	0.001
Tree height	0.842	-0.094	0.001	0.753	-0.407	0.001
Vegetation density	0.672	-0.042	0.001	0.734	-0.298	0.001
Zebra dung count	-0.226	0.566	0.001	-0.601	-0.453	0.001

Appendix 3

Table 6.10. Kruskal-Wallis results comparing the difference in important ecological variables in feeding plots between populations, and Mann–Whitney U post-hoc comparison significance (with a Bonferroni correction).

	Post-hoc significance				
Variable (Kruskal-Wallis results)	**Population**	Lewa	Meru	Nakuru	Ol Pejeta
Grass cover $\chi^2=53.91$, DF=3, $p<0.001$	Lewa	-	0.543	<0.001	<0.001
	Meru	0.543	-	<0.001	<0.001
	Nakuru	<0.001	<0.001	-	0.695
	Ol Pejeta	<0.001	<0.001	0.695	-
Grass height $\chi^2=51.09$, DF=3, $p<0.001$	Lewa	-	0.026	1.000	<0.001
	Meru	0.026	-	0.040	<0.001
	Nakuru	1.000	0.040	-	<0.001
	Ol Pejeta	<0.001	<0.001	<0.001	-
Tree height $\chi^2=42.45$, DF=3, $p<0.001$	Lewa	-	0.001	0.409	0.005
	Meru	0.001	-	<0.001	<0.001
	Nakuru	0.409	<0.001	-	0.484
	Ol Pejeta	0.005	<0.001	0.484	-
Shrub cover $\chi^2=30.58$, DF=3, $p<0.001$	Lewa	-	<0.001	0.277	0.195
	Meru	<0.001	-	0.012	0.001
	Nakuru	0.277	0.012	-	1.000
	Ol Pejeta	0.195	0.001	1.000	-
Elevation $\chi^2=54.36$, DF=3, $p<0.001$	Lewa	-	<0.001	<0.001	<0.001
	Meru	<0.001	-	0.077	0.035
	Nakuru	<0.001	0.077	-	<0.001
	Ol Pejeta	<0.001	0.035	<0.001	-
***Solanum* count** $\chi^2=11.39$, DF=3, $p=0.010$	Lewa	-	1.000	0.145	0.008
	Meru	1.000	-	1.000	0.525
	Nakuru	0.145	1.000	-	1.000
	Ol Pejeta	0.008	0.525	1.000	-
Zebra dung count $\chi^2=37.14$, DF=3, $p<0.001$	Lewa	-	0.006	<0.001	0.937
	Meru	0.006	-	1.000	<0.001
	Nakuru	<0.001	1.000	-	<0.001
	Ol Pejeta	0.937	<0.001	<0.001	-
Giraffe dung count $\chi^2=33.82$, DF=3, $p<0.001$	Lewa	-	1.000	<0.001	0.003
	Meru	1.000	-	<0.001	0.006
	Nakuru	<0.001	<0.001	-	0.057
	Ol Pejeta	0.003	0.006	0.057	-

Appendix 4

Table 6.11. Mann–Whitney U (with Bonferroni correction) significance comparing the core range size of white rhinoceros between the four different study populations.

Population	Lewa	Meru	Nakuru	Ol Pejeta
Lewa	-	<0.001	1.000	<0.001
Meru	<0.001	-	0.070	<0.001
Nakuru	1.000	0.070	-	0.102
Ol Pejeta	<0.001	<0.001	0.102	-

Table 6.12. Tukey test results comparing mean core range sizes for adult males and adult females between the different populations. Core range size was $\log_{10}$ transformed to fit a normal distribution.

Age class	Populations	Difference	Lower	Upper	P-value
Adult male	Lewa-Meru	0.93	0.14	1.72	0.021
	Ol Pejeta-Meru	1.95	0.90	3.00	0.001
	Ol Pejeta-Lewa	1.02	0.23	1.81	0.012
Adult female	Lewa-Meru	1.27	0.55	1.98	<0.001
	Nakuru-Meru	1.41	0.41	2.42	0.003
	Ol Pejeta-Meru	2.97	1.88	4.06	<0.001
	Nakuru-Lewa	0.15	-0.78	1.07	0.972
	Ol Pejeta-Lewa	1.70	0.69	2.72	<0.001
	Ol Pejeta-Nakuru	1.56	0.32	2.79	0.009

Appendix 5

Table 6.13. Median values (± interquartile range) for the ecological variables associated with white rhinoceros habitat in control and feeding plots for the February-March season in Meru. Mann–Whitney U tests were used to determine whether there was a statistically significant difference (at p<0.05) between control and feeding plots for each variable. *P-values* were adjusted for multiple comparisons using the false discovery rate correction. There were no statistically significant differences identified.

Variable	**Control plot** (n=30)	**Feeding plot** (n=30)
Grass cover (%)	80 (29)	87 (23)
Solanum incanum count	0.00 (1.00)	0.00 (3.75)
Zebra dung count	0.00 (3.00)	2.00 (5.75)
Buffalo dung count	2.50 (4.75)	5.00 (10.75)
Giraffe dung count	2.50 (5.25)	4.50 (4.75)
Shrub cover (%)	4 (13)	1 (2)
Tree height (m)	9.14 (6.14)	4.23 (9.10)
Relative elevation (m)	64.50 (36.00)	53.00 (23.00)
Grass height (cm)	44.30 (23.22)	36.91 (18.21)

7 DISCUSSION

7.1 INTRODUCTION

The main aim of this thesis was to identify the social and ecological factors that influence reproduction in female white rhinoceros to improve the conservation management of in situ and ex situ populations. The first objective was to determine whether the European captive white rhinoceros population is currently self-sustaining and viable, and to identify the key factors limiting population growth. The second objective was to identify whether aspects of captive management and social conditions are related to female breeding success in captivity. The third objective was to use social network analysis to describe and analyse the structure of in situ white rhinoceros populations, and to determine whether social connectivity influences female reproductive success. The final objective of this thesis was to identify important features of white rhinoceros habitat across four in situ populations in Kenya, and to determine whether differences in ecology and population density are related to reproduction and ecological carrying capacity.

This chapter summarises the key results from this thesis, and evaluates the social and ecological factors that are likely mediating female reproductive success in captive and wild white rhinoceros populations. This chapter also highlights new insights on white rhinoceros social structure derived from this thesis, and their relevance to the conservation management of both in situ and ex situ white rhinoceros populations. Finally, this chapter provides suggestions to improve female breeding success in captivity and maximise population performance in the wild, as well as directions for future research.

7.2 SUMMARY OF KEY CHAPTER RESULTS

Chapter 2: The reproductive performance and future viability of European captive southern white rhinoceros (Ceratotherium simum simum)

Using long-term demographic data and population viability analysis (PVA), the results from this chapter demonstrate that the European captive white rhinoceros population is not only demographically unsustainable, but is also threatened by low genetic diversity. The population is projected to decline at a rate of approximately 2% per year under current demographic parameters, and the key factor limiting population growth is the low proportion of females calving each year, as on average, just 10% of females calve annually. The delayed onset of breeding in females further exacerbates this, as the mean age at first reproduction was 13.5 years old in captive females, almost double that of wild females, at 7.3 years old. High infant mortality rates are also of concern, as on average, 18% of calves are either stillborn or die during infancy. Furthermore, severe reproductive skew is apparent in both males and females in the captive population, suggesting the genetic diversity of the population is likely very low. The proportion of females calving annually must increase to a minimum of 17% to prevent further population decline, and more individuals must contribute towards the captive gene pool to increase the genetic diversity of the population.

Chapter 3: Group composition influences socio-sexual behaviours and breeding success in captive female southern white rhinoceros (Ceratotherium simum simum)

Using breeding data from the European white rhinoceros studbook and a multi-institutional comparison, the results from this chapter show that institutions housing larger sized groups had greater breeding success (i.e. a greater proportion of females calved) than those housing smaller groups. Adult females were also more likely to calve when housed alongside a breeding female, than when not. Results from a questionnaire survey on a sample of the European population suggest that adult females were more receptive to a breeding bull (i.e. allowed the bull to mount) if they were housed in groups with a lower mean age. The results also demonstrate that females were more likely to copulate with a bull if they were housed in larger sized groups and alongside a breeding female. Factors unrelated to captive management were also associated with female breeding success; females that were born in the wild, or were younger, were more likely to exhibit reproductive behaviour, copulate and become pregnant, than captive-born or older females.

Chapter 5: Age and sex-specific association patterns in southern white rhinoceros (Ceratotherium simum simum) and implications for female reproductive success

Using social network analysis, the results of this chapter demonstrate that white rhinoceros have a complex social structure similar to that of many fission-fusion species, characterised by a tendency to form strong associations within cliques. Network comparisons conveyed that inter-individual association rates and grouping patterns differed substantially between populations, suggesting population density or ecology influenced social structure. Analysis of individual social network metrics demonstrated that sub-adults associated more frequently, and were more likely to associate in cliques, than adults were. Using lagged association rates, the results of this chapter also demonstrate that white rhinoceros developed long-lasting associations with one another, persisting for at least seven months, and the temporal stability of associations was greatest between females. Analysis of network metrics in relation to mean inter-calving interval length suggests that female social connectivity is related to reproductive success, as female association frequency, connectedness within the population, and tendency to form strong social bonds within cliques, were related to inter-calving interval length. However, the relationships between female network metrics and inter-calving interval length varied between populations, suggesting population density or reserve ecology may also influence female association patterns.

Chapter 6: Southern white rhinoceros (Ceratotherium simum simum) habitat use and ranging behaviour across populations: insights into density-dependent reproduction and ecological carrying capacity

Using vegetation assessments across four distinct populations, the results of this chapter demonstrate that white rhinoceros habitat was characterised by high grass cover, shorter grass and trees, and low elevation, and that they displayed a preference for swamp habitat. The results of this chapter also demonstrate that core range size increased as population density decreased. Despite differences in the habitat characteristics, inter-specific associations and size of individual core ranges between populations, breeding data suggested that all populations were performing well. Whilst these results demonstrate that differences in reserve ecology and intra-specific competition had little impact on female reproduction at current population densities, they did influence core range size; white rhinoceros in Ol Pejeta encompassed larger ranges than expected for their population density, and rhinoceros in Meru had severely compressed ranges. The results from this chapter suggest that grazing pressure, invasive species cover and area of optimal habitat per individual may influence white rhinoceros range size and ecological carrying capacity, providing guidance for future management strategies aimed at maximising population performance.

7.3 LIMITATIONS AND OPPORTUNTIES FOR FUTURE RESEARCH

Whilst this thesis has provided important new insights on white rhinoceros social behaviour and ecology, and the way in which social conditions influence female reproductive success, there are some limitations to this research.

The population viability analysis conducted for chapter two was based on estimates of genetic relatedness by Reid et al., 2012, which are likely to be inaccurate due to the unknown genetic ancestry of the founding European captive population, and the assumption that wild-caught founders are unrelated. Whilst population viability was modelled under two scenarios, using the reproductive-age sub-population and the breeding sub-population, both are likely a gross under-estimation of the true genetic relatedness of the captive population. Nevertheless, despite using such highly conservative models, it is apparent that if the breeding sub-population does not increase, the genetic diversity of the European population is likely to dramatically decline.

The results from chapter five demonstrate that white rhinoceros social network structure differs between populations. Drawing comparisons across populations is notoriously difficult in the field of social network analysis, due to the many factors that can influence social network structure, such as population density, age and sex structure, predation pressure, or habitat composition (Croft et al., 2008; Farine and Whitehead, 2015; Muller et al., 2019). Whilst social networks were constructed using the same data collection methodology and analytical techniques across populations, and spatio-temporal effects were controlled for within populations, making network comparisons more valid (Farine and Whitehead, 2015), it remains difficult to determine whether population density or ecological factors (or both) drive the variation in social structure observed between the study populations.

The results from chapter six demonstrate that ranging patterns differed between seasons, which suggests that the structure of white rhinoceros social networks may also vary between seasons. As the data used to construct social networks were collected between June and August, they only provide a representation of white rhinoceros grouping patterns during one season (dry). When resources are limited or clustered around certain areas, higher rates of repeated social interaction are expected, and social network sub-groups typically become more defined, with a greater mean association strength between pairs of individuals (He et al., 2019). As Lewa experiences the driest conditions, this could explain why rhinoceros at this study site had the strongest social bonds, and the greatest tendency to form cliques (see Chapter 5), as individuals may have clustered around patchily distributed resources. Whilst conditions were also dry in Meru, mean bond strength was generally weaker (see Chapter 5). This instead may be a consequence of greater intra-specific competition and limited suitable habitat. Rhinoceros in Meru formed the largest groups, and frequent aggression was observed between individuals grazing in close proximity. Associating frequently with the same individuals, and maintaining strong social bonds, is likely more costly when there is less optimal foraging habitat available, and population density is high. Further long-term studies that can control for ecological features or population density are required to disentangle the factors driving the differences in white rhinoceros social structure between populations. This may be achieved using adjoining study populations, which differ in density, but where habitat composition remains contiguous across study sites.

The results from chapter five suggest that female inter-calving interval length is related to social network position. Whilst the study populations used for this analysis represent two of the largest white rhinoceros populations in Kenya (n=71 and n=96), the number of females that had calved at least twice and were observed more than five times during data collection represented a much smaller sample size (n=11 and n=16). Other studies have used similar sample sizes to determine reproductive correlates of individual network position; n=16 male chimpanzees, *Pan troglodytes* (Gilby et al., 2013), n=12 male Assamese macaques, *Macaca assamensis* (Schülke et al., 2010), n=14 male degus, *Octodon degus* (Wey et al., 2013). However, as the network measures correlated with female inter-calving interval were not uniform across populations, possibly due to population density or reserve ecology, the fitness benefits associated with social connectivity remain unclear, and warrant further investigation. Incorporating data on group compositions collected by rangers during routine monitoring may provide a more efficient way of collecting the long-term datasets required to conduct social network analysis on large white rhinoceros populations. In this study, ranger records were limited to the general area, or 'block', where rhinoceros were sighted during patrols, and it was not possible to determine whether individuals were in the same place at the same time. Therefore, the data collected by rangers were not appropriate for social network analysis. In order to utilise data collected by rangers for social network analysis, the GPS location, time, and distance between individuals should also be collected.

The data used in chapter six to identify the characteristics of white rhinoceros habitat across populations were based on vegetation plots carried out from June-August, and thus only provide an understanding of white rhinoceros habitat use during the dry season. This study has shown that habitat use and core range size differ between the extreme dry season in February-March, and the less intense dry season in June-August, following the long rains. This warrants a more long-term study on white rhinoceros habitat use throughout the year. However, as the ecological carrying capacity of rhinoceros areas is influenced by resource availability (Hitchins and Anderson, 1983; Adcock, 2001), investigating habitat use when resources are limited, as in this study, may be more informative for management when time or resources are limited, as this can ensure seasonal impacts on body condition, reproduction and survival are minimised. Further studies on white rhinoceros habitat use during periods when resources are severely limited, such as a drought, are thus likely to be important for their management.

Data on the abundance of other herbivore species in each reserve were not available, and this is likely to have influenced inter-specific association rates within populations. However, the purpose of this study was not to quantify inter-specific association rates, but instead to identify species that may increase grazing pressure and present a competitive threat to female white rhinoceros and their breeding success. The differences in potential inter-specific competition identified between reserves therefore provides direction for further research on the species associations most likely to influence female reproduction. Furthermore, as long-term demographic data were only available for the two larger study populations, it remains unclear whether a small population size and skewed age-sex structure impacts female white rhinoceros reproduction.

The genetic diversity in each population may also influence female reproductive success (Ruiz-López et al., 2012), and genetic relatedness could have affected white rhinoceros association patterns and ranging behaviour (Wittemyer et al., 2009; Brent et al., 2013; Carter et al., 2013). This study initially intended to use DNA obtained from dung samples to conduct microsatellite genotyping, and assess the influence of genetic relatedness and reproductive skew on population performance and social network structure. Whilst several DNA samples were successfully obtained during data collection, it was not possible to export the samples to the UK for microsatellite genotyping within the timescale of this study due to permitting issues, and thus the genetic aspect of this PhD had to be omitted. Further studies that incorporate genetic relatedness, as well as both ecological and social factors, may provide a better understanding of all of the factors that drive reproductive success in female white rhinoceros.

7.4 APPLICATIONS TO CONSERVATION AND FUTURE DIRECTIONS

7.4.1 Breeding management in captivity

The results of this thesis have highlighted important areas to direct future research related to maintaining viable populations of white rhinoceros in captivity. Genetic studies on the European captive white rhinoceros population are urgently required to establish accurate estimates of genetic diversity and pairwise relatedness. This information can not only be used to provide a more accurate assessment of the genetic viability of the population, but can also inform breeding management decisions to ensure inbreeding is minimised. Furthermore, the results from this thesis have uncovered that high infant mortality rates also play an important role in driving population decline in captivity, and thus the reasons why so many calves are stillborn or die during infancy requires further investigation.

The results from chapter three suggest that social conditions influence female white rhinoceros reproduction, and provide guidance on group structures that may promote breeding success in captivity. Females housed in large groups alongside a successfully breeding female were more likely to reproduce than those not, and females housed in groups with a younger mean age were more likely to exhibit reproductive behaviour in response to courtship advances from a bull. Manipulating group compositions accordingly may improve female reproductive success in captivity. As reproductive pathologies are associated with long non-reproductive periods and the ageing of the female reproductive tract (Hermes et al., 2006), ensuring that females reaching sexual maturity are transferred to large, young groups containing a breeding female may help to stimulate reproductive behaviours and breeding success before the onset of reproductive-tract issues.

Previous studies have discounted the possibility that pre-copulatory problems influence female white rhinoceros breeding success in captivity (Swaisgood et al., 2006). Yet, over 25% of females included in the questionnaire survey did not exhibit reproductive behaviours when paired with a breeding bull, and 35% did not copulate with the bull. This suggests that pre-copulatory complications also contribute towards low female breeding success in captivity, and the factors driving female reproductive behaviour require further investigation.

Chapter five demonstrates that familiarity is likely to be important to female white rhinoceros, as females in the wild have a tendency to form strong associations within cliques, and long-lasting relationships with associates. Whilst chapter three did not detect an effect of number of translocations on female breeding success in captivity, it is still possible that females become stressed upon separation from their social partners. Future studies that investigate changes in stress, through either hormone analysis or behavioural observations, after social groups are separated will provide a better understanding of the potential importance of familiarity to female white rhinoceros welfare and reproduction.

As the results of chapter five demonstrate that the fitness benefits associated with social connectivity differed between populations, possibly due to differences in population density and reserve ecology, space availability may also influence welfare and reproduction in captivity. However, the results from chapter three suggest that enclosure size had no effect on female breeding success. This may be because females in captivity are supplementary fed, and thus intra-specific competition is less likely to affect captive females. Nevertheless, females living in captivity may form dominance hierarchies (Metrione, 2010), which suggests that some degree of competition does exist within the captive environment. Monitoring the behaviour and reproductive success of females receiving disproportionate levels of aggression may help to identify group structures that reduce stress and promote group cohesion (Ha et al., 1999).

7.4.2 In situ population management

The information resulting from this work can also be used to guide the management of wild populations of white rhinoceros. Chapter five has provided a first understanding of white rhinoceros social network structure, and a baseline to monitor the way in which association patterns change in relation to fluctuations in population size or resource availability. Due to increasing anthropogenic pressures, disease outbreaks are becoming increasingly common, and social networks can be used to inform targeted disease management strategies that focus on vaccinating individuals most likely to further the spread of a disease (Silk et al., 2017). Furthermore, social networks can be used to monitor grouping patterns and identify inter-individual associations that are likely to become problematic. For example, high-density clusters of adult or sub-adult males may increase the likelihood of aggressive interactions between individuals, as more males fight to secure a breeding territory. Translocating males from high-density clusters could therefore reduce the number of injuries resulting from territorial disputes in the future. Ensuring social groups are not broken apart during routine translocations may also increase the social stability of newly established populations, which may improve female breeding success and population persistence (Shier, 2006).

The results from this work suggest that female social connectivity is related to breeding success, and the adaptive benefits of sociality are likely influenced by population density and habitat quality. Managing white rhinoceros social conditions in relation to the ecology of a site could therefore help to maximise population performance. As social network analysis revealed that adult females associated with multiple adult males during the study timeframe, this may suggest that mate choice is important to females. Therefore, in populations with limited mate choice, such as in the Nakuru population where there was only one adult male, it may be beneficial to import more adult males to improve mate choice.

The key features of rhinoceros habitat identified in chapter six provide guidance for the management of white rhinoceros conservation areas. White rhinoceros were associated with areas of low elevation, with high grass cover, and both shorter grass and trees. Whilst these habitat features are among those identified in previous studies related to white rhinoceros feeding ecology and habitat selection (Owen-Smith, 1975; Perrin and Brereton-

Stiles, 1999; Waldram et al., 2008; Cromsigt and te Beest, 2014), this study has identified habitat features common across four ecologically diverse sites. These habitat features are thus likely important to white rhinoceros reproduction and survival, and should be prioritised when assessing areas for reserve expansion, or when selecting new sites to establish populations.

The results from chapter six also demonstrate that the size of individual core ranges varied considerably between populations. As site-specific ecology and inter-specific competition are likely to influence the way in which rhinoceros utilise habitat, a ‘one size fits all’ approach may not be suitable to maximise population performance. Developing an understanding of ranging patterns and habitat use within populations can thus be used to identify factors likely to limit population performance, and those that should be prioritised for future management. For example, high *Solanum incanum* cover and inter-specific competition were identified as potential factors that may reduce female reproductive success in both Nakuru and Ol Pejeta. Focussing efforts on the eradication of *Solanum incanum* may help to alleviate grazing pressure, and investigating potential inter-specific competition with zebra, *Equus quagga* and *E.grevyi,* and buffalo, *Syncerus caffer*, during periods of resource scarcity may help to uncover whether high densities of other herbivores are likely to influence female reproduction. Furthermore, as rhinoceros exhibited a preference for swamp habitat in Meru and Nakuru, prioritising the maintenance, and possible expansion, of swamp habitat may be the best use of limited resources.

Whilst the results from chapter six demonstrate that reserve ecology and population density had little effect on female reproduction and population growth, the differences in core range size between populations is likely related to both population density and resource availability. Due to their long gestation periods, white rhinoceros may overshoot ecological carrying capacity before any reductions in breeding success are detected (du Toit et al., 2006). Therefore, monitoring changes in core range size, body condition, and the frequency of aggressive interactions, may provide early warning signs that a population is reaching ecological carrying capacity. In black rhinoceros, *Diceros bicornis*, home range size tends to increase as resource availability decreases (Hitchins and Anderson, 1983), and this can be used to indicate a population is reaching ecological carrying capacity (Adcock, 2001).

However, home ranges may also be compressed in high-density populations (Adcock, 2001). This is likely the case in the Meru population; individual core ranges were significantly smaller in Meru compared to those in other populations. In such cases, assessing the amount of optimal habitat available per individual may provide insights on whether a population is reaching ecological carrying capacity.

Whilst reproductive output was high in Meru between 2014 and 2016, suggesting the population is not under density-dependent regulation, population growth may be expected to slow due to the limited area of optimal habitat available per individual, and increased intra-specific competition. However, Meru National Park extended their rhinoceros sanctuary in 2018, after data collection for this study was complete, to encompass a total of 84km^2, and further swamp habitat. The results from chapter six suggest that this is likely to have increased carrying capacity considerably, and as such, it is unlikely that the population will face substantial declines in reproductive performance in the near future. An impact assessment investigating whether mean individual core range size and overlap have changed following the expansion of the sanctuary would help to confirm this.

Lastly, further work on the genetic relatedness of in situ populations will improve our understanding of the factors driving variation in white rhinoceros population performance. In particular, there have been no genetic studies on the Kenyan meta-population, and as this population was founded from a small number of individuals translocated from South Africa after a severe population bottleneck, it is likely that many individuals are highly inbred. A total of 116 dung samples were collected from white rhinoceros across the four study populations, and DNA was extracted from each sample and frozen. It is hoped that the samples can be retrieved in the near future, and microsatellite genotyping can be undertaken to determine paternity and pairwise relatedness within the study populations. This information can then be used to provide estimates of inbreeding, reproductive skew and population genetic diversity. Furthermore, estimates of pairwise relationships can be incorporated into social networks to provide an understanding of the role in which genetic relatedness plays in rhinoceros social structure and association patterns.

7.5 OVERALL CONCLUSIONS

This thesis demonstrates that the European captive white rhinoceros population is currently not self-sustaining, and urgent action is required to improve female reproductive output and the chances of population persistence. The results from this thesis have shown that white rhinoceros have a complex social structure in the wild, and female reproductive success in both captive and wild populations is related to social conditions. Considering female social conditions in the breeding management of white rhinoceros could therefore improve female reproductive success in captivity. Wild populations of white rhinoceros are currently under threat from illegal poaching, and thus populations should be managed to maximise breeding performance. This thesis has provided guidance on the habitat features likely to be important to white rhinoceros reproduction and population persistence, and those that should be prioritised for their ecological management. Overall, the results from this thesis provide important new insights on white rhinoceros social behaviour and ecology that can be used to improve their global conservation management.

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