The social dynamics of the Cape buffalo and the epidemiological implications

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The social dynamics of the Cape buffalo and the epidemiological implications

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DECLARATION

I hereby declare that the work has been completed by myself and no portion of the work contained within this Thesis has been submitted in support of any application for any other degree or qualification on this, or any other university or institution of learning.

Elodie Wielgus, 2020

GENERAL ABSTRACT

Although the ecology of the Cape buffalo is reasonably well understood, the social dynamics occurring within and among groups are less known, despite the important implications for both buffalo ecology and management, and intra and interspecies disease transmission. This thesis aims to better understand the social behaviour of Cape buffalo across several populations in sub-Saharan Africa using a combination of GPS tracking data and genetic markers. This thesis quantifies the dynamics of interactions within and among neighbouring buffalo groups and examines the influence of seasonality and inter-population variance on these dynamics. I also investigate the influence of sex on the dispersal ability, in order to better understand the spread of pathogens among populations. To go further, I examine the impact of intragroup dynamics on a directly transmitted pathogen spread as a model to link the host social organisation and pathogen transmission. This thesis reveals different social dynamics within and among groups, although consistent among the study populations. Results show that buffalo form relatively distinct groups occupying unique and separated home ranges, with minimal overlap, independently on the season. Direct contacts (*i.e.* the use of the same space at the same time) among groups were rare while indirect contacts (*i.e.* the use of the same space at different times or through an intermediate vector, here the mosquito) occurring within one month were more frequent, with serious implications for indirectly transmitted pathogens in the population. These results suggest a behavioural avoidance or a territorial behaviour occurring throughout the year. It appears that both males and females disperse among neighbouring groups, but females could be more likely to disperse among populations than males. Within groups, individuals form very unstable dyadic associations. These fission-fusion dynamics varied seasonally, with fission patterns lasting 1 to 3 days before individuals merge again for an equivalent average duration. However, it seems that the way individuals interact with each other within groups only slightly affects the transmission of a directly transmitted pathogen. This study is one of the first to quantify the degree of fission-fusion dynamics and intergroup encounter in the Cape buffalo, and to relate these dynamics to variations in environmental conditions across several populations. Therefore, this thesis contributes to the understanding of buffalo social systems and their relation to the environment, a growing issue at the wildlife-livestock interfaces given the economic costs due to pathogen transmission with cattle.

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CONTENTS

CHAPTER 1

INTRODUCTION

1 The growing issue of infectious diseases

There was optimism that the war on infectious diseases was over in the 1970s, but humans are still faced with challenges of pandemics and emerging diseases and the recent pandemic caused by the COVID-19 has once again increased the burden of infectious diseases. Many pathogens can infect both humans and animals (multihost pathogens) and pathogens can be transmitted between the parties. Around 60% of emerging and re-emerging infectious diseases in humans are caused by animal pathogens (zoonoses), particularly from wildlife (Cleaveland et al. 2001, Bengis et al. 2004, Jones et al. 2008). Zoonotic diseases pose considerable risks to public health and the economy around the world (Bengis et al. 2004, Schneider et al. 2009). For example, the Severe Acute Respiratory Syndrome (SARS) outbreaks in 2002-2003 initiated by zoonotic transmission from bats via palm civets caused more than 900 deaths across 29 countries (WHO 2003). Infectious diseases also have substantial negative effects on the health of both domestic and wild animals (Cleaveland et al. 2001, Taylor et al. 2001, Jones et al. 2008). In domestic animals, infectious diseases can have devastating effects on the livelihoods of livestock farmers by decreasing animal production (mortality) and national economies by limiting international trade (Latif et al. 2001). Although wildlife is frequently thought of as a conduit for transmitting infections to humans and domestic animals, the reverse is also true and 80% of domesticated animal pathogens can infect wildlife (Cleaveland et al. 2001). This threatens the environment when diseases transmitted from domestic animals cause the death of wild animals (Pastoret et al. 1988, Kock et al. 1999, Smith et al. 2009). For example, the expansion of livestock production promoted the spread of the rinderpest morbillivirus, which was first introduced by humans in Ethiopia, and caused significant damages to wild animal populations. African buffalo (*Syncerus caffer*) populations have been devastated by rinderpest, with the most several collapse occurring in the 1890s, with mortality rates estimated at 90-95% across the continent (Mack 1970, Sinclair 1977, Ryan et al. 1998, Winterbach 1998, Smitz et al. 2014). The potential disease transmission between domestic and wild animals, particularly livestock, intensifies the risk of infectious diseases in animals and the associated negative impacts. In the United States, the total cost for rabies prevention in humans and pets has been estimated at between USD 230 million and 1 billion annually (Rupprecht et al. 1995, Sterner and Sun 2004), and the national brucellosis eradication program has cost about USD 3.5 billion between 1934 and 1997 (Sriranganathan et al. 2009 in Kiros et al. 2016). In Cameroon, around Waza National Park, the economic losses due to livestock diseases were equivalent to the losses due to predators (Bauer et al. 2001) whilst in the Maasai Steppe, Tanzania, livestock mortality due to diseases is 10 times higher than due to predation (Ogutu et al. 2005, Kissui 2008).

Nowadays, concerns about infectious pathogens are increasing with cumulative effects of land development (*e.g.* habitat loss, environmental pollution), globalization and climate change (Smith et al. 2009). For example, the increasing encroachment of human activities on wildlife habitats and the international trade of wildlife has led to an increase in interactions between humans, domestic animals and wildlife, which creates more possibilities for transmission of pathogens. Intensive agriculture favours the transmission of infectious diseases in livestock, as more individuals are congregated in small spaces (Gilchrist et al. 2007). The expansion of human settlements can also promote exposure to certain non-human vectors and hosts of vector-borne diseases (Vora 2008). Understanding how disease spreads through, and among intra- or inter-specific populations is thus of growing interest to veterinary services, farmers, and conservationists for issues related to human health, economy and food security.

2 Contacts in epidemiology and pathogen spread

Mathematical models have been important in understanding the diffusion phenomena of a pathogen in both human and animal populations (Stehlé et al. 2011, Bjørnstad 2018). Without going into too much detail, the SIR and SEIR compartmental models are the most widely used (Figure 1). S represents the number of susceptible individuals (healthy who can become infected), E the number exposed (infected but not yet infectious), I the number of infectious and R the number recovered. In these epidemiological models, the frequency of contact of a susceptible individual with an infected individual, *i.e.* with the pathogen, is one of the most important parameters affecting the probability of infection of susceptible individuals as well as the diffusion capacity of a pathogen (Lloyd-Smith et al. 2005, Bansal et al. 2007, Smieszek 2009). A susceptible individual (S) can contract the pathogen (S -> E) in a period of *t* with a transmission rate of infection (β_t), function of the probability of pathogen transmission given contact and the contact rate (Smieszek 2009). After contracting the disease, a susceptible individual becomes exposed but is not infectious during an incubation period. These exposed individuals enter the infectious state at a rate σ, with σ^{-1} representing the mean latent period of the disease (E -> I) and can transmit the disease to the susceptible individuals during their infectious period. The infectious individuals become recovered (I -> R) according to the recovery rate γ.

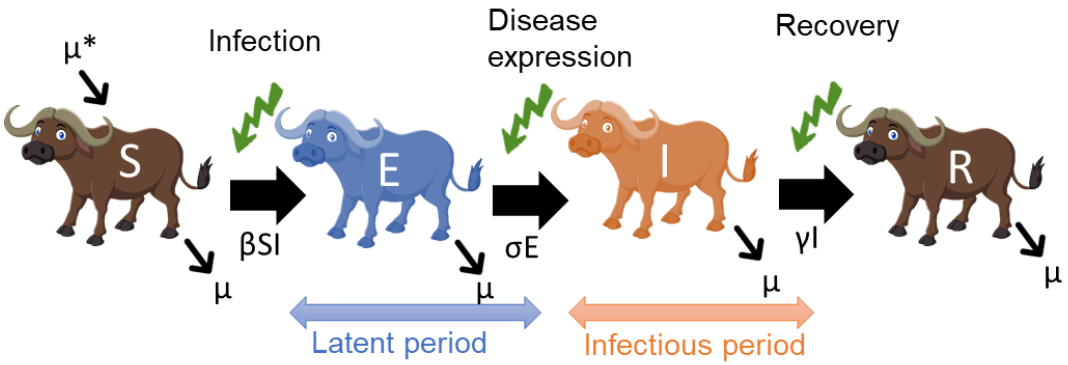


Figure 1. An SEIR compartmental model showing the evolution of states, according to the transmission rate of infection β; the recovery rate γ; and death/birth rates μ and μ*. To simplify models, death/birth rates are usually not considered. When permanent immunity is acquired, this reduces to an SEIR model, but in the case of reversible immunity, the model becomes an SEIRS model. In the case of density-dependent transmission (the host density in the population influences the number of potentially infectious contacts), the infection force governing the transition from a S state to an I state is equal βI, but when the transmission is frequency-dependent (the number of hosts in the population does not influence the number of potentially infectious contacts, *e.g.* sexually transmitted diseases), the infection force is βI/N, N being the population size.

Infectious diseases spread through transmission routes that vary along a spectrum from direct transmission, where close contacts between an infected and a healthy individual are required (*i.e.* at the same place and at the same time, Keeling 1999, Altizer et al. 2003, Hamede et al. 2009) to indirect transmission, when pathogens occupy some intermediate reservoir or vector between hosts (*e.g.* a host of another species or an environmental reservoir like soil or water), making spatial overlap between individuals a more important requirement than temporal overlap (Dougherty et al. 2018). A pathogen is treated as directly or indirectly transmitted in relation to both the duration of time it can survive in the environment outside of hosts and its ability to disperse in the environment separated from host movement (*e.g.* using a vector, like the Rift Valley Fever virus with the mosquito). Many pathogens have several transmission pathways. Traditional epidemiological models assumed that the contact rates are homogeneous between all individuals in the population (Anderson and May 1991), which means that no heterogeneity in the mixing pattern was considered. However, contact patterns are usually heterogeneous among individuals for human and animal populations (*e.g.* fission-fusion dynamics), and this variation can impact the probability, size and persistence of disease epidemics (Lloyd-Smith et al. 2005, Bansal et al. 2007, Smieszek 2009). Although the definition of what is a relevant contact for disease transmission can vary according to the pathogen of interest (*i.e.* mode of transmission), understanding how the individuals of a population interact with each other, via a set of behaviours (*e.g.* dispersal, social interactions), is essential for building computational models of infectious disease transmission and providing the best recommendations

concerning disease management (Hamede et al. 2009, Craft and Caillaud 2011, Stehlé et al. 2011, Reynolds et al. 2015).

3 Social systems, dispersal and contact patterns

The contact patterns of a population, whether defined as direct (*i.e.* the use of the same space at the same time, which does not necessarily mean physical contact) or indirect (*i.e.* the use of the same space at different times or through an intermediate host), certainly depend on animal movements and social systems. Free-living animal populations can live according to a solitary system, where individuals avoid each other and only meet during the breeding season, or "randomly" due to the environmental constraints, *e.g.* in response to spatial heterogeneity in food resource availability (Mcloughlin et al. 2000, Mattisson et al. 2013, Guilder et al. 2015, Elbroch and Quigley 2017). Alternatively, they can live in social groups of variable size, composition and dynamics depending on the species, population density or environmental conditions (Hill and Lee 1998, Sundaresan et al. 2007, Vander Wal et al. 2013).

3.1 The benefits and costs of sociality

The causes and consequences of sociality have been examined extensively in many species within both an ecological and evolutionary framework (Dunbar 1974, 1987, Jarman 1974). Group formation confers many benefits to group members, including reduced risk of predation and infanticide, improved foraging efficiency, *e.g.* via increased hunting success for predators, information sharing (*e.g.* about location of resources) and assistance in parental care (Hamilton 1971, Van Orsdol 1984, Clark and Mangel 1986, review in Krause and Ruxton 2002). In prey species, grouping can decrease predation risk for any individual through an enhanced ability to detect predators by collective vigilance, cooperative defence, a higher probability of escape or a lower probability of being selected as potential prey by dilution and confusion effects (Caraco et al. 1980, Turner and Pitcher 1986, Dehn 1990, Childress and Lung 2003). Individuals in groups can also spend less time being vigilant and allocate more time to other activities such as foraging, which improves the foraging efficiency at the individual level (Powell 1974, Caraco 1979, Underwood 1982, Elgar 1989, Lima 1995, Childress and Lung 2003).

Despite the apparent benefits, all animal species do not live in groups, which suggests that group living incurs costs as well as benefits. Indeed, while group size can be advantageous to minimize the predation risk, it also makes the group more detectable by predators (Vine 1973, Lindstrom 1989, Krause and Godin 1995, Hebblewhite and Pletscher

2002). Groups may also have negative impacts on individual foraging efficiency due to increasing competition for food, which can force groups to travel further and to spend more time feeding, or due to more intense aggressive interactions among group members (Caraco 1979, Chapman 1990, Molvar and Bowyer 1994, Olupot et al. 1994, Majolo et al. 2008). The spatial proximity between individuals promotes the transmission of pathogens and parasites (Caillaud et al. 2006, Rifkin et al. 2012). Moreover, to ensure group cohesion, animals must synchronize their activities (Conradt and Roper 2000, Jacobs et al. 2011) and this constraint may be costly because individual group members can compromise their own nutritional needs (*e.g.* metabolic requirements due to their reproductive status) to maintain spatial cohesion with their conspecifics. For example, in some cases, individuals may have to shorten their resting time to travel with the rest of the individuals in their group, whilst in other cases, individuals may be forced to wait for the whole individuals have finished feeding before moving.

3.2 *Group cohesion and individual trade-off*

Given the benefits and costs of group living, each individual is confronted to a trade-off between its own nutritional and social needs, and those of the group (*i.e.* synchronize the activities to maintain spatial cohesion and benefit from the presence of the conspecifics, Conradt and Roper 2005). However, when the group size increases or when the intrinsic differences (*e.g.* in sex, age) among individuals become too large, the needs can be very different among all group members (*e.g.* individuals with higher body mass spend more time to feeding, and lactating females forage longer than nonlactating females, Ruckstuhl and Neuhaus 2002). Consequently, the costs for maintaining group cohesion for each individual increase and individuals may cope with a compromise between pursuing its own interests (by leaving the group) or staying with preferred conspecifics at some cost (Jacobs et al. 2011). Maintaining group coordination also requires individuals to make common decisions, such as about the direction of travel or the next activity, which can generate a conflict of interest (Conradt and Roper 2005, Bourjade and Sueur 2010). These conflicts represent another factor that may lead to the departure of certain individuals from the group.

3.3 *Consequences of trade-offs: Dispersal and fission-fusion dynamics*

In the light of the compromises and decisions that group members must constantly make, group cohesion may decrease when the group size or within-group competition for food increases, and the group may therefore split. One sub-group can decide to move in one direction while the other one decides either to stay in the current zone or to move in another direction (Kerth et al. 2006, Ramos-Fernández et al. 2006). Group splitting can be on a long-

term scale, *i.e.* the groups that have split do not merge again. A classic example is when juveniles move away from their natal group for reducing sexual competition, avoiding inbreeding and finding suitable habitats (natal dispersal, Greenwood 1980, Cockburn et al. 1985, Wahlström and Liberg 1995, Sweitzer and Berger 1998). Adults can also leave permanently their group to join another one or a different population to find a new reproduction site, avoid within-group competition or improve their social status (Bowler and Benton 2005, Clutton-Brock and Lukas 2012, Marjamäki et al. 2013). Some categories of individuals could be more likely to initiate a movement. For example, males and females typically display large differences in terms of dispersal distances and/or dispersal rates, which is called sex-biased dispersal. Female-biased dispersal is more common in bird species, whereas mammals are typically male-biased, except primates where the female dispersal is more widespread (Greenwood 1980, Strier 1994, Clarke et al. 1997, Engelhaupt et al. 2009, Lebigre et al. 2010).

When splitting occurs on a short-term scale, this flexibility in social behaviour is defined as “fission-fusion societies” (Kummer 1971) or “fission-fusion dynamics” (Aureli et al. 2008). The term “fission-fusion” was first introduced by Kummer (1971) to describe the social organization in some non-human primate societies where group size changed frequently through the splitting (fission) and merging (fusion) of the group according to both the activity of group members and the distribution of resources. In animal societies, fission-fusion group dynamics refer to “the extent of variation in spatial cohesion and individual membership in a group over time” and vary along three dimensions: the temporal variation in spatial cohesion, subgroup size and subgroup composition (Aureli et al. 2008). According to this framework, any animal system can be characterized by its degree of fission-fusion group dynamics along a gradient of group stability, and fission frequency can vary according to taxa, environment and social structure. Kangaroos (*Macropus sp.*, Best et al. 2013, 2014), many ungulate species (*e.g.* European roe deer *Capreolus capreolus*, Pays et al. 2007, onagers *Equus hemionus khur*, Sundaresan et al. 2007, chamois *Rupicapra pyrenaica*, Pépin and Gerard 2008, bison *Bison bison*, Fortin et al. 2009), bats (Kerth and König 1999, Popa-Lisseanu et al. 2008) and many primates (*e.g.* baboon *Papio cynocephalus*, Henzi et al. 1997, black-and-white ruffed lemurs *Varecia variegata*, Baden et al. 2016, spider monkey *Ateles geoffroyi*, Pinacho-Guendulain and Ramos-Fernández 2017) form highly unstable and fluid subgroups, which are often merging together and splitting apart, which themselves are grouped into larger social groups. Subgroups vary in size and composition, while the whole group is stable in size, composition, and occupied home range. More complex social systems can be described by the hierarchical organization of social structures subject to fission and fusion events. For example, elephants (*Loxodonta africana*, Wittemyer et al. 2005, Archie et al. 2006) and giraffes (*Giraffa Camelopardalis*, Bercovitch and Berry 2010, VanderWaal et al. 2014) form

multilevel societies where cohesive groups temporarily join each other and form sub-communities, which themselves could be grouped into communities.

The drivers of fission-fusion dynamics are generally poorly understood, but are likely to be linked to short-term changes in irregular social and environmental conditions, such as in predation pressure, reproductive opportunities or in resource availability (Isvaran 2007, Couzin and Laidre 2009, Kelley et al. 2011, Bond et al. 2019). For example, in bottlenose dolphins *Tursiops aduncus*, the high degree of fission-fusion reflects an adaptation to heterogeneity in the distribution of prey resources, with dolphins spreading out in smaller groups to reduce intraspecific competition for food when resources are limited and aggregating in larger groups when food is abundant and predation risk is high (Connor et al. 2000, Heithaus and Dill 2002).

3.4 Establishing contact patterns using tracking and genetic tools

Direct observations of individuals using standard behavioural sampling methods provide the best empirical evidence and have been used in several instances to measure the social structure (*e.g.* Altmann 1974, Chapman 1990, Geffen et al. 1999). The degree of fission-fusion dynamics can be derived through the recording of group size and composition over time, as well as any fission and fusion events among subgroups (van Schaik 1999, Bercovitch and Berry 2012). Movements and social structure can also be described using capture-mark-recapture (CMR) methods. Capture-mark-recapture methods are often employed to document dispersal, and thus the social structure at population scale (*e.g.* Favre et al. 1997, Helfer et al. 2012). However, both direct observations and CMR methods have their limitations: (1) they can be very time consuming, (2) the number of individuals and groups that can be studied is limited, (3) the direct observations may be problematic depending on the environment in which the individuals are monitored (difficulty to observe in dense forests) or depending on the species studied (being scarce, nocturnal and/or shy) and (4) they are usually spatially and temporally restricted and reveal only partially the patterns of individual movements, and thus the social structure. Long-distance dispersal may be difficult to detect with these methods when individuals move out of the sampling area.

The use of new wildlife monitoring technologies, such as GPS and proximity loggers can overcome some of these issues by providing a more complete picture of movements of individuals or groups (Kays et al. 2015). Some studies have used GPS tracking data to estimate home range overlap as a proxy of contact, because of the difficulty of estimating rates of intraspecific interactions (*e.g.* Millspaugh et al. 2000). Even if the hypothesis of a positive correlation between home range overlap and interaction rate seems reasonable,

the strength of this association has rarely been evaluated (Schauber et al. 2007, Robert et al. 2012). In recent years, GPS and proximity loggers are becoming increasingly popular for studying complex social structures: GPS data allow researchers to have simultaneous locations of individuals with great accuracy (Podgórski et al. 2014, Elbroch and Quigley 2017, Lesmerises et al. 2018) whilst proximity loggers, which record when individuals are close to each other according to *a priori* defined spatial threshold, provide a more direct measure of contact rates (*e.g.* Ji et al. 2005, Hamede et al. 2009, Walrath et al. 2011). Both technologies allow researchers to determine when, and for how long, two animals have been in proximity and, therefore, describe the contact structure relevant for a directly or indirectly (only for GPS) transmitted infectious disease. However, they cannot discriminate among types of interactions (agonistic vs. affiliative) as direct observations do, and do not allow monitoring of the size and composition of subgroups over time. The telemetry devices are particularly essential for species that are hard to observe visually in their natural environment or that move over large spatial scales. These technologies can, however, be expensive since they require many individuals to be monitored simultaneously, especially for studies on social behaviour. The use of GPS loggers commonly requires the capture of individuals to place GPS tags (on collars, for example) and this needs certain logistics and qualified people (*i.e.* to anaesthetize) in the field. Another limitation is related to the battery size and memory size that are limited by animal weight and size. Researchers generally need to make a trade-off between sampling rate and battery life. Collecting data can also be challenging. While in some cases it is possible to download data remotely from tags, in other cases tags must be retrieved to download the data, either by recapturing animals or by having a remote drop-off system. Finally, the location errors can sometimes be very large, especially in densely vegetated habitats, which require intensive corrections before using the data. Despite these challenges, the actual rapid development of better, lighter and cheaper technologies should offer new opportunities to track more individuals and from a wider range of species (Haddadi et al. 2011, Kays et al. 2015).

Some behaviours beyond social structure can be examined using genetic tools, such as movements over larger temporal and spatial scales and sex-biased dispersal (Ji et al. 2001, Engelhaupt et al. 2009, Frantz et al. 2010, Vander Wal et al. 2012). These behaviours are determinants in disease spread within a population but also among populations. Whilst movement tracking technologies allow researchers to explore social structure at a relatively short-time scale (in general, around 1-2 years depending on the battery lifetime of the GPS collars or proximity loggers), the use of genetic tools describes phenomena occurring on a time scale of the individual's life or on the evolutionary time scale. Molecular genetic markers provide new insights for characterizing social and population structure in species for which behavioural and movement data are either hard to collect or absent. This method consists in quantifying variability between individuals within a DNA sequence, such as in

mitochondrial DNA (mtDNA), or in allele frequencies at one or more loci, such as at microsatellites (Prugnolle and de Meeus 2002) or single nucleotide polymorphisms (SNPs, Aguillon et al. 2017). The most common method for quantifying movements among groups or populations consists of assessing the fixation index (F_{ST}) as a measure of genetic differentiation among groups/populations based upon autosomal neutral markers. A high genetic differentiation between populations means low potential for dispersal between them. The use of sex-specific markers (*e.g.* maternally inherited mtDNA or paternally inherited non-PAR regions of the Y-chromosome), either alone or in combination with bi-parentally inherited markers (*e.g.* autosomal microsatellites or SNPs) provide valuable information regarding sex-specific gene flow (Palo et al. 2004, Eriksson et al. 2006, Hammond et al. 2006, Wang et al. 2019). These approaches can reveal sex differences in gene flow within a generation, and thus give information on interactions and mixing among groups or populations. For example, a strong male sex-bias in dispersal patterns revealed by genetic analyses has the potential to generate matrilineal social groups because members of the female sex remain in the natal group over consecutive generations. However, it is worth to mention that the bi-parentally inherited markers should be only used to measure sex-biased dispersal before mating of the individual having dispersed because allele frequencies are equally distributed between males and females in the offspring. In other words, the signal of a sex-biased dispersal may not be detected using biparental markers (Goudet et al. 2002).

4 The African buffalo

The African buffalo (*Syncerus caffer*, Sparrman 1779) is a ruminant mammal, belonging to the *Bovidae* family and the subfamily Bovini, and is the largest and most massive of the African bovids. The African buffalo is currently considered a single species, with important morphological variations throughout its geographical range (*e.g.* in body size, weight, fur colour, horn shape and size) leading to a subdivision into four subspecies: Cape buffalo (*S. c. caffer*), forest buffalo (*S. c. nanus*), West African savanna buffalo (*S. c. brachyceros*) and Central African savanna buffalo (*S. c. aequinoctialis*, East 1998). The African buffalo occupies a wide range of habitats, from open grasslands to rainforests (Sinclair 1977, Prins 1996, Melletti et al. 2007a, Megaze et al. 2013). In the past, the African buffalo occurred throughout sub-Saharan Africa, but its geographical distribution and population size have greatly decreased since the nineteenth century, as a result of habitat loss, poaching, disease outbreaks and climatic events (Cornélis et al. 2014). The majority of buffalo populations are now confined to protected areas and managed hunting areas (East 1998,

Figure 2). The African buffalo is now considered as “near threatened” by the IUCN (IUCN 2019).

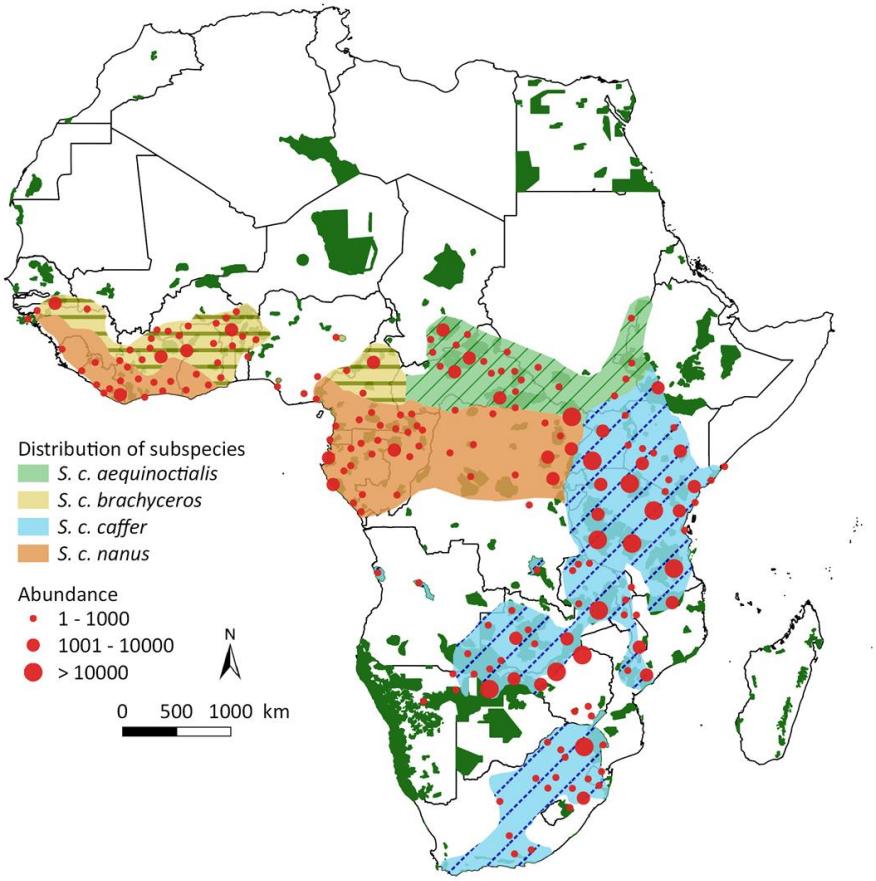


Figure 2. Distribution of the four African buffalo subspecies and their abundance in relation to protected areas (green). Data from East (1998).

The African buffalo is a key species with a high economic value. It has attracted the attention of hunters since the beginning of European settlement in southern and eastern Africa, and as a member of the ‘Big-Five’, buffalos have since been highly sought after as an animal trophy (Prins 1996, Munag’andu et al. 2006). The African buffalo is also a preferred species for bushmeat, as a source of protein and income in many African countries (Mfunda et al. 2010, Alexander et al. 2012, Prin 2014). During the last few decades, the African buffalo has also gained important value for eco-tourism and is popular on viewing and photographic safaris (Van der Merwe et al. 2004). Buffalos also play an important ecological role: as bulk grazers, they facilitate the opening up of habitats, which benefits more selective species or short-grass grazers (Prins 1996, Munag’andu et al. 2006, Eby et al. 2014). However, the African buffalo carries many pathogens such as foot and mouth virus, bovine tuberculosis, brucellosis and tick-borne diseases such as theileriosis, that can easily pass from one species to another (Bengis et al. 2002, Kock 2005, Dion et al. 2011, Caron et al. 2013, de Garine-Wichatitsky et al. 2013, Gorsich et al. 2015). Due to their close taxonomic relationship, buffalos represent the main threat for pathogen

transmission to cattle (Bengis et al. 2002, Kock et al. 2014). Additionally, as grazers and ruminants of similar size, buffalo and cattle have similar ecological niches and tend to utilize the same type of resources (*i.e.* forage and water, Hofmann 1989), leading to possible competition between them (Augustine et al. 2011, Odadi et al. 2011, Valls-Fox et al. 2018). In areas where buffalo and cattle live sympatrically, shared use of resources creates opportunities for buffalo-cattle contacts (*i.e.* direct, at the same time; indirect, at different times) and therefore pathogen transmission. Although buffalos usually avoid cattle, seasonal profiles in contact risk between buffalo and cattle are observed, with higher contact rate during the dry season when both water and forage resources are depleted or when cattle range further into protected areas in search of food (Kock 2005, Zengeya et al. 2015, Valls-Fox et al. 2018).

The ecology of the African buffalo is reasonably well understood (*e.g.* resource requirements, habitat use and selection, Sinclair 1977, Mloszewski 1983, Taylor 1985, Prins 1996), but the literature concerning its social behaviour is comparatively sparse. The current knowledge on the social behaviour of the African buffalo mainly comes from monographs (doctoral theses and works) focusing on the Cape buffalo and is often descriptive (Grimsdell 1969, Sinclair 1977, Mloszewski 1983, Prins 1996, Ryan 2006). The African buffalo is a highly social species forming groups (usually call 'herds') subject to fission (splitting) and fusion (merging) events. The fission-fusion dynamics vary with subspecies and environmental conditions (see below, Eltringham and Woodford 1973, Sinclair 1977, Prins 1996) and the definition of a herd can be problematic. Therefore, throughout the thesis, I use the term 'group', rather than 'herd', to define the set of individuals with fixed membership and size that share the same home range. A 'subgroup' is defined as a part of individual group members that exhibit fission and fusion events, leading to frequent changes in subgroup size and composition over time. I define the term 'population' as the assemblage of buffalos living in the same protected area. Forest buffalo typically occur in small groups rarely larger than 20, with little switching between groups and fission patterns that last 1-2 days before subgroups merge again (Melletti et al. 2007b, Korte 2008). West African savanna buffalo live in groups of approximately 50 individuals with very little interaction between groups (Cornélis et al. 2011). The group size of Cape buffalo is among the largest reported for this species since it can live in large groups up to 2000 individuals, but its group size varies across its distribution (Sinclair 1977, Prins 1996). Most studies of Cape buffalo in southern and eastern Africa have identified groups with permanent members that periodically subdivide due to fission-fusion dynamics but consistently occupied identifiable home ranges (Prins 1996, Cross et al. 2005a, Ryan et al. 2006). Even though there is more research on the social behaviour of the Cape buffalo than in the other subspecies, there are still important knowledge gaps particularly with respect to sociality and group behaviour, and the potential risks for pathogen transmission. This thesis will seek to address four

important knowledge gaps in the Cape buffalo, which relate to sociality and the potential for the spread of pathogens.

The first knowledge gap relates to the absence of understanding of fission-fusion patterns at fine temporal scale, and the ecological drivers of such patterns. Much of the previous research on fission-fusion dynamics in the Cape buffalo is mainly based on the seasonal variation of subgroup size and composition (Prins 1996). For example, in Chobe National Park (Botswana), Cape buffalos formed larger subgroups during the dry season, when resources are more limited (Halley et al. 2002), but the opposite was reported in Serengeti National Park (Tanzania, Sinclair 1977) and Klaserie Private Nature Reserve (South Africa, Ryan et al. 2006). However, no study focused on quantifying the characteristics of fission-fusion patterns, such as the frequency of fission and fusion events as well as the duration of subgroups, which directly influence the variation in subgroup size and composition.

The Cape buffalo is usually considered as non-territorial species, but studies investigating space sharing between neighbouring groups have reported contrasting results. At Lake Manyara NP (Prins 1996), in Chobe NP (Halley et al. 2002) and at Klaserie Private Nature Reserve (Ryan et al. 2006), groups tended to occupy distinct and exclusive home ranges with little overlap whilst in the Rwenzori National Park (Uganda, Grimsdell 1969) and in Sengwa Wildlife Research Area (Zimbabwe, Conybeare 1980), strong space overlap has been reported between home ranges of neighbouring groups. Few studies have compared overlap between neighbouring groups across seasons and investigated the contact patterns between groups, and this constitutes the second knowledge gap. Cross et al. (2004) observed contacts between neighbouring groups within a 2-year period, but without quantifying them. To my knowledge, only Bennitt et al. (2018) examined the patterns of direct contacts (*i.e.* at the same time within a small spatial window) between buffalo groups and the influence of environmental variables on contact patterns within a study site. Yet, although poorly understood, fission-fusion patterns *within* groups and contact patterns *between* groups are essential for understanding and predicting the spread of pathogens at varying social and spatial scales (Bastos et al. 2000, Corner et al. 2003, Craft 2015).

The third knowledge gap is related to the lack of understanding the role of dynamic contact patterns in disease dynamics in the Cape buffalo. Traditional epidemiological models assumed that contact patterns are homogeneous among all individuals in the host population (Anderson and May 1991). Although there is now more research on contact patterns and their influence on pathogen transmission in wild animal species (Drewe 2010, Chen et al. 2014, Reynolds et al. 2015), in the Cape buffalo, only Cross et al. (2004) investigated the influence of contact patterns *within* groups on pathogen dynamics. However, this study was based on an association index calculated on a monthly scale. This may lead to misleading predicted pathogen dynamics, as it ignores the short-term

interactions that change due to the ecology and social behaviour (*i.e.* fission-fusion behaviour), which could have an important effect on the pattern of pathogen transmission (Volz and Meyers 2007).

Finally, so far, male Cape buffalos were thought to be native dispersers and females were gregarious with a strong fidelity to their group and limited intergroup movements (*i.e.* dispersion, Sinclair 1977, Prins 1996). However, both genetic and observational studies now highlight the dispersal ability of both female and male Cape buffalos (Halley et al. 2002, Van Hooft et al. 2003, Naidoo et al. 2014, Caron et al. 2016). The use of GPS collars has made it possible to record long-distance dispersal in females among populations (Halley et al. 2002, Naidoo et al. 2014, Caron et al. 2016). Most genetic studies on the Cape buffalo have been carried out at the population level (national parks and game reserves, Simonsen et al. 1998, Van Hooft et al. 1999, 2000, 2002, Smitz et al. 2013, 2014). At the group level, only Van Hooft et al. (2003) explored the dispersal capacity and the differences between sexes using genetic tools to my knowledge. Telemetry studies support frequent switches among groups within a local population (Halley et al. 2002, Cross et al. 2004, Roug et al. 2020). Despite abundant evidence that dispersal is common in both male and female Cape buffalos, no studies have explored if there are differences in the dispersal patterns between different populations (*e.g.* due to different social or environmental environments).

5 Questions and research objectives of the thesis

In this thesis, I address the knowledge gaps relating to contact patterns *within* (*i.e.* fission-fusion patterns) and *between* Cape buffalo groups (*S. c. caffer*), and their moderators. Furthermore, to reduce the research gap related to sex-biased dispersal at population and group levels, I conduct an exploratory analysis of the dispersal capacity of both males and females *between* groups and *between* populations. Overall, this thesis explores the temporal and spatial distribution of individuals relative to each other throughout three organisational levels: within groups, among groups and among populations. To go further, this thesis examines the impact of contact patterns *within* groups on a directly transmitted pathogen spread as a model to link the host social organisation and pathogen transmission. In addition to improving our fundamental knowledge of the social behaviour of the Cape buffalo (*e.g.* what is a group), these results aim to better understand the transmission of pathogens within buffalo populations. The questions and objectives of this thesis are the following:

Question 1 – Do fission-fusion dynamics **between buffalo individuals** vary according to seasons, distribution of resources in the landscape and geographical regions?

Objectives: This part of the study included the use of long-term GPS tracking in three populations living in savanna environments. I quantified the frequency at which fission and fusion events occurred and their duration between buffalo dyads and investigated the environmental conditions (habitat structure, distance to water) in which such events happened. This analysis provides preliminary insights into the environmental factors determining the degree of fission-fusion dynamics. I compared the degree of fission-fusion dynamics and the location where such events occurred across seasons and sites. This question is addressed in Chapter 3.

Question 2 – Do the contact patterns **between buffalo groups** vary according to geographical region, season and distribution of resources in the landscape?

Objectives: Based on long-term GPS tracking in two populations living in contrasting environmental conditions, I quantified the frequency and the duration of direct (*i.e.* at the same time, at the same place) and indirect contacts (*i.e.* at different times), compatible with the transmission of various pathogens, between buffalo dyads belonging to neighbouring groups. I then investigated the environmental conditions under which such contacts happened in relation to the habitat structure and the distance to water to determine the importance of environmental conditions in social dynamics between groups. I compared the frequency and duration of contacts and the location of contacts across seasons and sites to explore whether the geographical region influences the between-group dynamics. This question is treated in Chapter 4.

Question 3 – Does sex influence the likelihood of **dispersal** among populations and groups?

Objectives: From an approach combining genetic and movement data in 10 populations, I investigated whether dispersal was sex-biased in the Cape buffalo. Using both sex-specific and bi-parentally inherited markers, I calculated multiple genetic indexes, such as the genetic differentiation levels and the relatedness indexes, and the correlation between genetic and geographical distances, to reveal differences in migration rates between sexes at population and group levels. As the genetic markers cannot give information about the characteristics of dispersal events, I used GPS data to describe the dispersal events (*e.g.* distance). This question is treated in Chapter 5.

Question 4 – Do the intensity, heterogeneity and temporal dynamic of interactions in a healthy buffalo group influence the **diffusion of a pathogen** within this group?

Objectives: Using the long-term GPS tracking in two populations, I built a dynamic system of networks representing buffalo direct contacts within a group. A dynamic system of

homogenous (*i.e.* random) contact networks was also produced to assess the role of heterogeneity in contact structure on the pathogen dynamics. The spread of a pathogen along these interactions within both the dynamic heterogeneous and homogeneous contact networks was simulated using an SEIR model. I used a hypothetical pathogen based on the characteristics of the Foot-and-Mouth Disease Virus (FMDV) with direct transmission. I investigated the dynamics of the pathogen across seasons, sites and types of network (homogeneous vs. heterogeneous). This question is addressed in Chapter 6.

CHAPTER 2

THE STUDY POPULATIONS AND GENERAL SAMPLING

In this thesis, I benefited from data entirely collected in 11 Cape buffalo populations across Mozambique, Zimbabwe, Botswana and South Africa between 2007 and 2016. The study populations were located in protected areas, in habitats varying from the tropical rainforest in Mozambique to mixed woodlands and riparian forests in South Africa, Zimbabwe and Botswana (Figure 1, Ryan et al. 2016). The data used in this thesis had been previously collected either for epidemiological and ethological monitoring or for telemetry studies in order to investigate buffalo habitat use and selection and were exclusively based on indirect observation methods, which were GPS tracking, remote sensing and genetic sampling. In this chapter, the data used in this thesis and the data pre-processing are described along with information on data collection. More detailed descriptions of specific data collection protocols and analyses are given in the Methods section of each chapter. The terms related to the socio-biology of the Cape buffalo defined in Chapter 1 are reminded in Box 1.

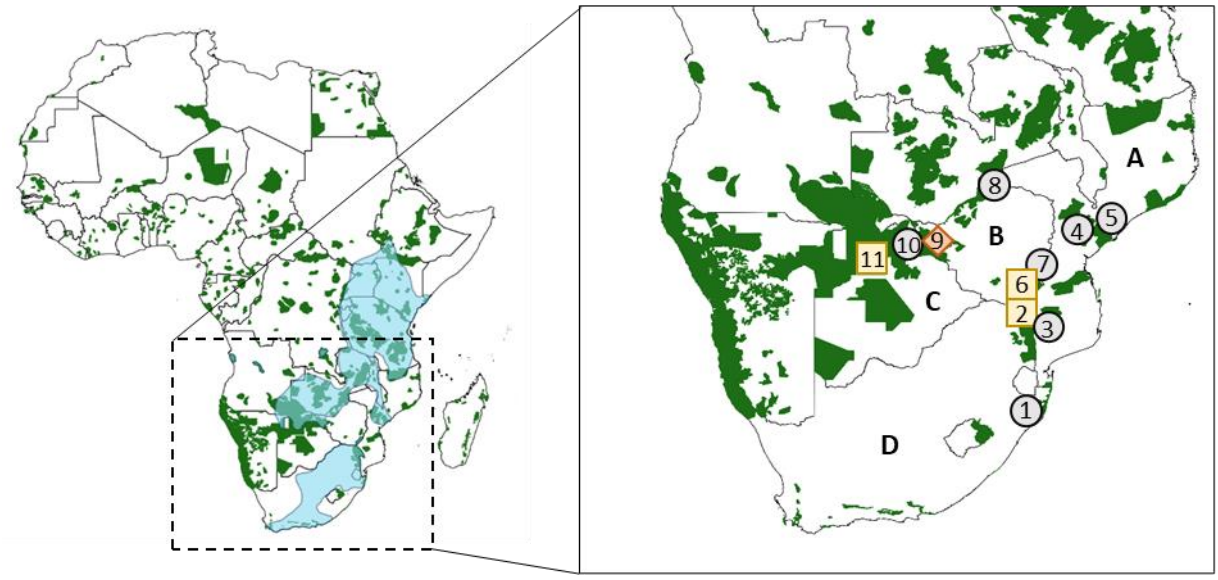


Figure 1. Map of Africa representing the 11 populations analyzed in this thesis. Light blue shapes on the left map represent the actual distribution of the Cape buffalo according to the IUCN Antelope Specialist Group, 2008. Green zones correspond to the protected areas (East 1998). A. Mozambique, B. Zimbabwe, C. Botswana, D. South Africa. 1. Hluhluwe-iMfolozi (960 km²), 2. Kruger (18 989 km²), 3. Limpopo (11 230 km²), 4. Gorongosa (4 000 km²), 5. Marromeu (11 270 km²), 6. Gonarezhou (5 053 km²), 7. Malilangwe (405 km²), 8. Mana Pools (6 766 km²), 9. Hwange (14 620 km²), 10. Chobe (11 700 km²), 11. Okavango Delta (16 000 km²). The symbols indicate the type of data collected in each population: circle = only genetic data; square = both telemetry and genetic data; diamond = only telemetry data.

Box 1. Definition of terms related to socio-biology of the Cape buffalo that I use throughout this thesis.

- *Population*: all buffalos living in the same protected area, including national parks and game reserves (*i.e.* possibly several groups of buffalos).
- *Group*: the assemblage of individuals with fixed membership and size that share most of their home range.
- *Subgroup*: a part of individual group members that exhibit fission and fusion events, leading to frequent changes in subgroup size and composition over time.

1 The GPS tracking data

I used GPS data previously collected in 4 study areas to examine the fission-fusion patterns (Chapter 3), the intergroup contact patterns (Chapter 4), to describe the dispersal events (Chapter 5) and build an intragroup social network for understanding pathogen dynamics (Chapter 6):

(1) southern Gonarezhou National Park and Malipati safari area (conservation area) adjacent to Sengwe communal land in the South-East Lowveld of Zimbabwe (22° 00' S, 31° 30' E);
(2) northern Kruger National Park in north-eastern South Africa, on the border between Zimbabwe and South Africa along the Limpopo River, connecting the northern part of the park to the Sengwe communal land adjacent to the Gonarezhou NP (22° 253' S, 31° 13' E);
(3) Hwange National Park (mainly the northern and eastern regions) and Sikumi Forest in the north-west of Zimbabwe (19° 00' S, 27° 10' E);
(4) the south-eastern area of the Okavango Delta in northern Botswana (22° 00' E – 18° 50' S).

The GPS data in the first three study areas had been collected by Cirad and its partners (including CNRS, IGF, SANParks). These three areas were selected for their proximity to human populations as part of PhDs in ecology and epidemiology aimed at exploring the sharing of space between buffalos and cattle, their contact patterns and the phenomena of pathogen transmission between the 2 species (Miguel 2012, Valls Fox 2015). The GPS data from the population of Okavango Delta were collected as part of Emily Bennitt's PhD (2012), which aimed to examine the ecology of the Cape buffalo, such as habitat selection, migratory behaviour and movement patterns (non-exhaustive). Depending on the study

design developed in each study area and the requirements for my research questions, I was forced to adapt the dataset of GPS locations to each of my research questions (see Table 1). While a large number of individuals followed in the same group was necessary to explore the contact patterns within groups (Chapters 3 & 6), examining the intergroup contact patterns (Chapter 4) required few GPS collars in the same group, but in many different neighbouring groups.

1.1 *Capture and collaring*

Depending on site, available capture team and material and experience, buffalos were captured either directly from helicopter or using a boma. In the first case, buffalo groups were sighted from a light airplane (cheaper) or directly from the helicopter; then, one or more buffalo were selected given the protocol requirements (*e.g.* adult females) to be tele-anesthetised. Once asleep the helicopter would land close to the one or more buffalos and, with or without the support of a ground team, would process to sampling (*e.g.* blood sample, a small piece of tissue (ear) and/or hair, see section 3) and collaring. The other method consisted in building a funnel-type boma (diameter 400 m), where buffalo groups were pushed inside using a helicopter (Figure 2). Later, once calm, a group team would enter the boma to dart selected individuals (la Grange 2006) and proceed to sampling and collaring. As adult males can leave the group temporarily and join bachelor groups, cows were primarily selected to be collared in order to reflect the movements of groups (Sinclair 1977, Mloszewski 1983, Prins 1996). During the capture event, age of individuals was defined based on tooth wear (juvenile: 0-2.5 years, subadult: 2.5-4.5 years old and adult: >4.5 years old, Grimsdell 1973, Taylor 1988) All animals were observed returning to their group after the darting operation. All field operations conformed to the permits and legal requirements of the countries in which they were carried out.

Figure 2. The elaboration of a boma.

A total of 16 capture sessions was carried out to place the collars. The movements of 82 buffalos in 19 groups were monitored using 95 GPS collars between December 2007 and June 2016. Of the 95 collars placed, 13 of them were replaced on the same individuals (in Gonarezhou and Kruger NPs) at a later capture session to extend data coverage, which explains the difference between the number of GPS collars placed and the number of buffalos followed (see Table 1). The collars were equipped with Very High Frequency (VHF)

transmitter, allowing animals to be located using conventional telemetry equipment. GPS loggers were scheduled to acquire locations at synchronous times (the top of the hour) every hour.

Table 1. Summary statistics of the deployment of 95 GPS collars in 19 groups in Hwange National Park, Gonarezhou National Park, Kruger National Park and Okavango Delta from 2007 and 2016. All buffalos monitored were adult females (A) or subadult females (SA, see text for details). I defined group membership *a posteriori* by calculating home range overlap (see Chapters 3 & 4).

Study area	Group	Total number of different buffalos	Deployment of GPS collars according to the age class		Chapters in which the data are used
Gonarezhou National Park	G1	6	10/2008	6 A	3, 4, 5 & 6
			11/2009	4 A	
	G2	6	10/2008	6 A	
			11/2009	2 A	
Hwange National Park	G1	8	08/2009	3 A	3
			11/2012	4 A	
			12/2013	1 A	
	G2	8	08/2009	5 A	
			11/2012	3 A	
	G3	3	11/2012	3 A	
	G4	1	11/2012	1 A	
Kruger National Park	G1	20	06/2010	2 SA	3, 4, 5 & 6
			07/2011	3 A + 4 SA	
			10/2013	6 A + 6 SA	
	G2	4	06/2010	1 A + 1 SA	
			07/2011	2 A + 2 SA	
	G3	9	06/2010	1 A + 1 SA	
			07/2011	2 A	
			10/2013	3 A + 3 SA	
	G4	2	06/2010	1 A + 1 SA	
			07/2011	2 A	
Okavango Delta	G1	3	12/2007	1 A	4
			10/2008	1 A	
			06/2009	1 A	
	G2	2	12/2007	2 A	
	G3	2	12/2007	2 A	
	G4	1	12/2007	1 A	
	G5	2	10/2008	1 A	
			06/2009	1 A	
	G6	2	06/2009	2 A	
	G7	1	06/2009	1 A	
	G8	1	10/2009	1 A	
	G9	1	10/2009	1 A	

1.2 *Data pre-processing*

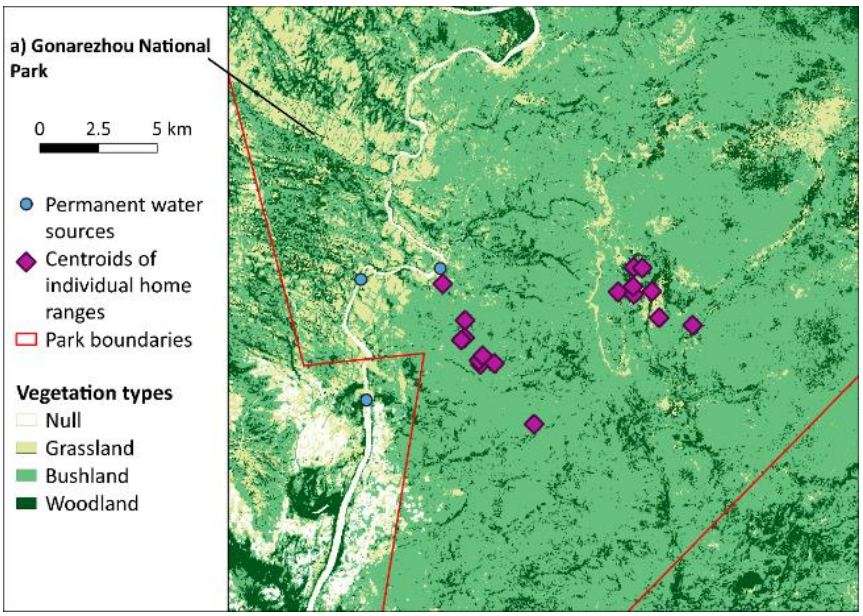
I projected the locations, originally acquired in decimal degrees, in Universal Transverse Mercator (UTM) coordinates with the WGS84 datum, using the 'rgdal' package in R (R Development Core Team 2016). The UTM grid cells corresponding to the study sites were: UTM 34S for Okavango Delta, UTM 35S for Hwange NP and UTM 36S for Gonarezhou and Kruger NPs. I screened the GPS locations successfully acquired for erroneous fixes following the established technique by Bjørneraas et al. (2010). This approach identifies locations arising from unrealistic movement pattern by using specified thresholds for distance, speed and turning angles between two recorded locations. Here, I applied the following criteria: Δ = 100,000 m; μ = 10,000 m; α = 3,000 m/h; θ = -0.95. Some of the GPS locations were acquired with a delay compared to the time the GPS was programmed to take the location. In order to limit the impact of acquisition delays on the subsequent analyses (*e.g.* inter-individual distance to identify contact), I corrected the acquisition delays according to the following rules: if the location was taken within 5-min interval from programmed acquisition time, I kept the location fix and repositioned it at the scheduled time (*i.e.* the top of the hour), otherwise, I calculated the location for the programmed acquisition time by linear interpolation. This was particularly essential for Chapter 3 in order to have locations at the same time between individuals to determine fission and fusion events. This method was, however, not applied in Chapter 4 as the approach used did not require locations at regular intervals and simultaneous between individuals.

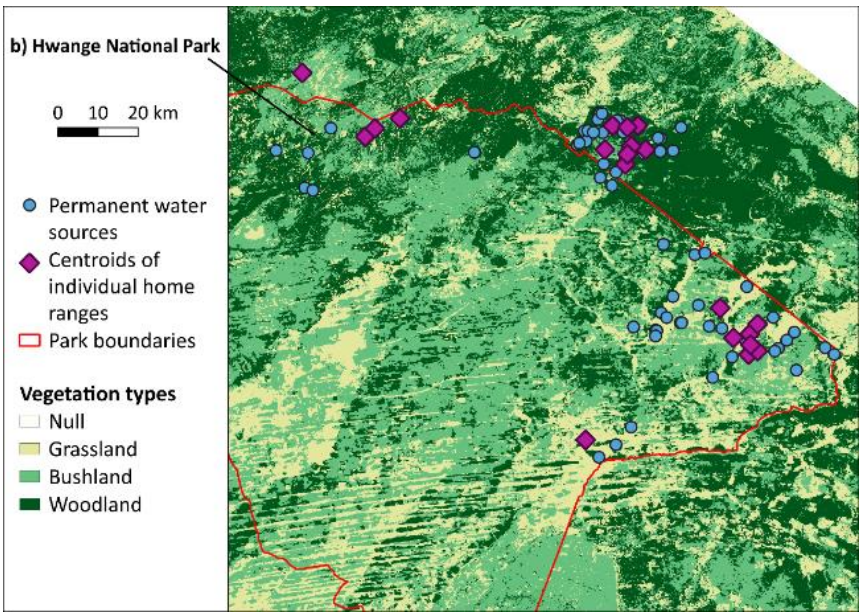
2 The environmental variables

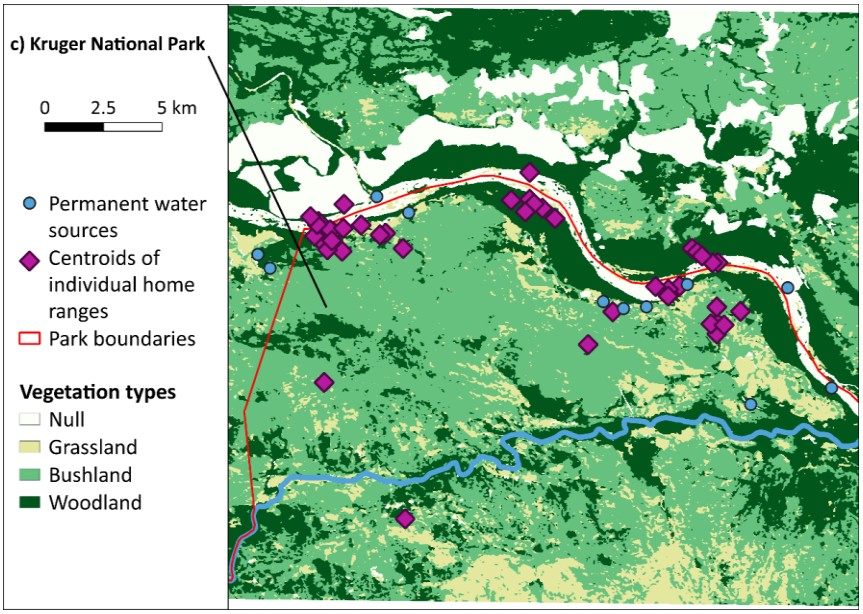
As the availability of resources is commonly cited to affect buffalo habitat selection (Sinclair 1977, Ryan et al. 2006, Valls-Fox et al. 2018), I used two environmental variables (habitat structure and distance from water) to examine whether fusion and fission events (Chapter 3) and contacts between neighbouring groups (Chapter 4) occurred in specific areas. Simplified vegetation maps were adapted from an unpublished map for Gonarezhou NP, Pretorius and Pretorius (2015) for Kruger NP, Arraut et al. (2018) for Hwange NP and Bennitt et al. (2014) for Okavango Delta. The original land cover classes, as well as the number of classes, were different across the study areas. For comparative purposes between the study areas, I combined the original classes into three broad classes of natural vegetation according to woody cover and availability of grasses, the main food for buffalo: (1) grassland, including areas dominated by grassland, or bushed grassland with sparse vegetation, (2) bushland, which consists of shrubs and bushed areas, (3) woodland, encompassing deciduous, evergreen or riverine forests. The non-vegetated or non-natural

vegetation land cover classes were re-classified as “null” as well as cloud cover. As the type (polygon vs. raster) and spatial resolution of the original maps also differed, I converted them to raster layers with 30-m resolution using the software R (Figure 3). I plotted the GPS coordinates of each buffalo location onto the habitat map of the corresponding study area and I extracted the habitat type (*i.e.* grassland, bushland or woodland) in which the location occurred (Chapters 3 & 4).

In Gonarezhou NP and Hwange NP, I identified the permanent waterholes, *i.e.* providing water in both dry and wet seasons, following the systematic monitoring of artificial and natural water pans within the home ranges of Cape buffalo groups studied here. This monitoring was implemented at the same periods as the deployment of the GPS collars (2011 in Gonarezhou NP and 2013-2014 in Hwange NP). In Kruger NP, I recorded the location of every permanent waterhole from Google Earth (Google Inc., Mountain View, CA) using photographic capture taken at different times of the year. In Okavango Delta, consistent with Bennitt et al. (2018), I used the vegetation class ‘Secondary floodplain’ as the location of permanent water sources since it is the only habitat that is flooded all year round (Bennitt et al. 2018, Figure 3). In each study site, the location of permanent water sources was used to generate a raster layer representing the distance to permanent water for each pixel (50-m resolution) in the study site. I plotted the GPS coordinates of each buffalo location onto the raster layer of the corresponding study area and I extracted the distance to permanent water in which the location occurred (Chapters 3 & 4).




b) Hwange National Park
0 10 20 km
Permanent water sources
Centroids of individual home ranges
Park boundaries
Vegetation types
Null
Grassland
Bushland
Woodland


c) Kruger National Park
0 2.5 5 km
Permanent water sources
Centroids of individual home ranges
Park boundaries
Vegetation types
Null
Grassland
Bushland
Woodland

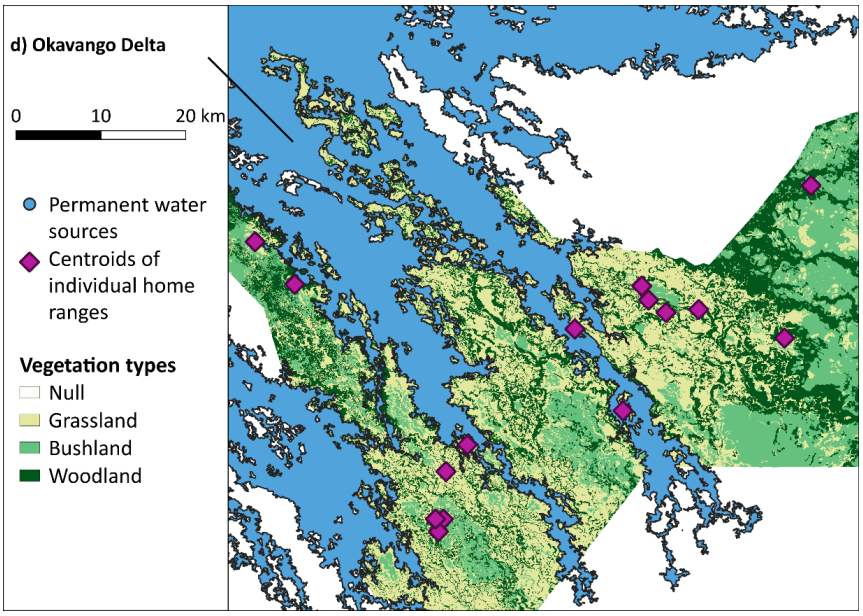

d) Okavango Delta
0 10 20 km
Permanent water sources
Centroids of individual home ranges
Vegetation types
Null
Grassland
Bushland
Woodland

Figure 3. Vegetation maps and permanent water sources for the 4 study areas. For a better reading, I only show the centroid of the individual home range rather than their contours. Home range centroid was calculated as the mean of longitude and latitude from all locations of the individual and represents the centre of the individual's home range.

Since the existing literature reports seasonal variation in habitat use and selection by buffalos as well as in group size and composition due to variation in resource availability (Sinclair 1977, Halley et al. 2002, Halley and Mari 2004, Turner et al. 2005, Ryan et al. 2006, Valls-Fox et al. 2018), I investigated the fission-fusion patterns and contact patterns *between* groups across seasons (Chapters 3, 4 & 6). I used the rainfall patterns to define 2 distinct seasons. Annual rainfall across the 4 study sites is similar with around 600 mm for Hwange NP, and 500 mm for Gonarezhou NP, Kruger NP and Okavango Delta (Gertenbach 1980, McCarthy et al. 1998, Chamaillé-Jammes et al. 2006, Gandiwa et al. 2016). The distribution of rainfall within the year is also similar between sites, with most rain falling between November and March. To avoid transitional periods and for seasonal comparisons, I restricted my analyses to the core of the wet and dry seasons. I defined these periods according to fixed dates based on similar rainfall patterns between the sites: the core wet season is the period running from January 1st to March 31st (n = 90 days) and the core dry season from August 15th to October 31st (n = 78 days) for all sites.

3 The genetic data

I used genetic data to explore sex-biased dispersal in the Cape buffalo (Chapter 6). The genetic data have been collected, analyzed and previously published by a PhD student (Smitz et al. 2013, 2014) examining the population genetic structure and evolutionary history of the African buffalo. The original dataset consisted of 264 *S. c. caffer* samples, with 178 females and 86 males, and was collected in 6 countries (South Africa, Mozambique, Zimbabwe, Botswana, Zambia and Angola). The samples (*i.e.* blood, a small piece of ear, hair or dung) were genotyped by N. Smitz at 14 variable autosomal microsatellite loci [TGLA227, TGLA263, ETH225, ABS010, BM1824, ETH010, SPS115, INRA006, BM4028, INRA128, CSSM19, AGLA293, ILSTS026, DIK020 described by Van Hooft et al. (1999) and Greyling et al. (2008)]. Additionally, 73 males were also genotyped at three Y-chromosomal microsatellites (UMN1113, INRA189, UMN0304- described by Van Hooft et al. 2007). The microsatellite amplification and genotyping are detailed in Smitz et al. (2014). Individuals in two populations (Gonarezhou and Hluhluwe-iMfolozi) were also sequenced using mitochondrial *D-loop* (control region). I read and aligned these mtDNA sequences available on the National Institutes of Health (NIH) genetic sequence database (GenBank- JQ780553.1 - JQ780600.1) using MEGA 10.0 (Tamura et al. 2011), with

corrections by eye. Newly sequenced samples led to the identification of a 580-bp overlapping region. To examine sex-biased dispersal (Chapter 5), I selected the populations in which both males and females were sampled, as well as those with a sample size > 5 among the populations sampled by Smitz et al. (2013, 2014). Finally, for my thesis, I used a dataset including 205 individuals genotyped at the 14 autosomal microsatellites, 68 males genotyped at the three Y-chromosome microsatellites and mtDNA sequences for 48 individuals.

CHAPTER 3

ARE FISSION-FUSION DYNAMICS CONSISTENT AMONG POPULATIONS? A LARGE-SCALE STUDY WITH CAPE BUFFALO

Abstract

Fission-fusion dynamics allow animals to manage costs and benefits of group living by adjusting group size. The degree of intraspecific variation in fission-fusion dynamics across the geographical range is poorly known. During 2008-2016, 38 adult female buffalos were equipped with GPS collars in three populations of Cape buffalo located in different protected areas (Gonarezhou National Park and Hwange National Park, Zimbabwe; Kruger National Park, South Africa) to investigate the patterns and environmental drivers of fission-fusion dynamics between pairs of buffalo (dyad) among populations. I estimated home range overlap and fission and fusion events between buffalo dyads. I investigated the temporal dynamics of both events at daily and seasonal scales and examined the influence of habitat and distance to water on event location. Fission-fusion dynamics at dyad level were generally consistent across populations: fission and fusion periods between dyads lasted on average between less than one day and three days. However, I found seasonal differences in the underlying patterns of fission and fusion between dyads, which point out the likely influence of resource availability and distribution in time on social dynamics: during the wet season, buffalo dyads split and associated more frequently and were together or separated for shorter periods. Whereas habitat structure did not have a significant influence on fission and fusion locations between dyads, my results suggest that water sources might act as hotspots of events during the dry season only in areas with low water availability. This study is one of the first to quantify fission-fusion dynamics between dyads in a single species across several populations with a common methodology. This underlines the question of the behavioural flexibility of fission-fusion dynamics among environments.

1 Introduction

Identifying the factors that drive social organization is central to understanding the ecology and evolution of animal populations. Animal social organizations range from solitary, where individuals meet occasionally and for mating during the breeding season, to systems whereby animals live in stable groups with individuals remaining together over several years (Clutton-Brock 2016). Groups can also be much more fluid, with regular splitting (*i.e.* fission) and merging (*i.e.* fusion) of subgroups, and the degree of fission-fusion dynamics between group members can be seen as a characteristic of any social system (Aureli et al. 2008).

Moderate to high levels of fission-fusion dynamics have been reported in a range of taxa (bats: Kerth and König 1999, cetaceans: Connor et al. 2000, primates: Lehmann and Boesch 2004, large mammalian herbivores: Archie et al. 2006, Fortin et al. 2009, Bercovitch and Berry 2010, fish: Kelley et al. 2011, macropods: Best et al. 2013). Decisions to split or merge are thought to be related to spatial and temporal variation in the costs and benefits of grouping, *e.g.* changes in resource availability, competition (Chapman 1990, Pépin and Gerard 2008), predation risk (*e.g.* through habitat structure, Hill and Lee 1998, Fortin et al. 2009), activity synchronization (Conradt and Roper 2000) or in the risk of disease or pathogen transmission (Kashima et al. 2013).

Most studies on fission-fusion dynamics published to date have either focused on describing dynamics in a single population (*e.g.* Lehmann and Boesch 2004) or comparing fission-fusion dynamics in populations of different species living in the same area (*e.g.* Parra et al. 2011). Little is known about the variability of fission-fusion dynamics among populations of a given species (*e.g.* Kelley et al. 2011). As heterogeneity in the environment across the geographical range of a species can influence social behaviour (Baden et al. 2016), fission-fusion dynamics may vary among populations. Comparing fission-fusion dynamics from several populations located in different areas would provide insight into the behavioural flexibility of a species to adjust to heterogeneous environmental constraints. Standardized comparative studies would also allow a better determination of the factors influencing fission-fusion dynamics at the species level.

Cape buffalo live in large (up to 1500 individuals) mixed-sex groups, of primarily females and their offspring, subadults of both sexes, and a small proportion of adult males (Sinclair 1977, Prins 1996). Group refers to the assemblage of individuals with stable membership and size that share most of their home range. Each group occupies a home range that overlaps very little with other groups (Sinclair 1977, Prins 1996, Chapter 4). Within these large groups, subgroups of individuals split and merge regularly, leading to frequent changes in subgroup size and composition. The critical characteristics of these so-called fission-fusion patterns, such as duration of subgroup splitting, and merging remain

mostly unknown (but see Bennitt et al. 2018). The factors that appear to drive group dynamics in the Cape buffalo remain unclear with conflicting results from different studies. In Chobe National Park (Botswana), buffalos formed larger subgroups during the dry season, when resources are more limited (Halley et al. 2002) but the opposite was reported in Serengeti National Park (Tanzania, Sinclair 1977) and Klaserie Private Nature Reserve (South Africa, Ryan et al. 2006). In Lake Manyara National Park (Tanzania), buffalo groups tended to exhibit fission-fusion patterns strongly related to group size: large groups split more frequently than smaller ones (Prins 1989). Finally, changes in buffalo group dynamics living in Addo Elephant National Park (South Africa) are related to predation, with buffalos aggregating into larger subgroups following the reintroduction of lions into the park (Tambling et al. 2012).

In order to better understand the patterns and drivers of fission and fusion in the Cape buffalo, I employed a comparative approach incorporating data collected over wet and dry seasons across three distinct populations living in similar environmental conditions (Gonarezhou National Park and Hwange National Park, Zimbabwe; Kruger National Park, South Africa). Much of the previous research on fission-fusion dynamics in the Cape buffalo, and generally on other species, is based on the observation of how the size and composition of subgroups change over time (Prins 1996, Aureli et al. 2008). In this study, I took a different approach by studying fission-fusion dynamics at the individual level, using GPS tracking data. This approach is increasingly used (*e.g.* Loretto et al. 2017, Lesmerises et al. 2018, for buffalo see Bennitt et al. 2018) as it provides detailed information on when and where two individuals are together but does not provide information on subgroup size and composition. I, therefore, used GPS tracking data to quantify the time that pairs of buffalo (dyads) spent together and the frequency and duration of fission and fusion events between buffalo dyads. Since the existing literature reports seasonal variation in subgroup and group size, I explored seasonal changes in fission-fusion dynamics between buffalo dyads but given the contradictory results of previous studies (see above), I refrained to make specific predictions. Building on our knowledge of the species' ecology and on consistent results from previous studies, I also specifically tested the predictions that (i) fission and fusion events between dyads would occur more during the periods when Cape buffalos are more active, *i.e.* early in the morning and late afternoon because conflicts of interest in the upcoming activities or directions would be higher (Cornélis et al. 2011, Valls-Fox et al. 2018); (ii) Cape buffalo dyads would be more likely to meet (fusion event) and remain together in open habitats, as large herbivores are commonly found in large groups in open habitats where visibility is higher (Jarman 1974, Isvaran 2007, Pays et al. 2007), facilitating social cohesion, reducing predation risk against ambush predators and, possibly for grazers, where forage is more abundant; and (iii) the scarcity of water during the dry season would increase the probability that buffalo meet, and remain together for some time, near

water points. I reveal new insights into Cape buffalo fission-fusion dynamics between dyads and provide one of the first studies demonstrating the consistency of fission-fusion dynamics across populations.

2 Materials and methods

2.1 Study areas

The study was conducted across three sites: the eastern region of Hwange National Park (14 620 km², HNP, Zimbabwe), the southern part of Gonarhezou National Park (5 053 km², GNP, Zimbabwe), and in the north of Kruger National Park (18 989 km², KNP, South Africa; Figure 1). Across the three study areas, the vegetation is a mosaic of bushland savanna, open grassland and woodland (GNP: Gandiwa and Zisadza 2010, HNP: Chamaillé-Jammes et al. 2006, KNP: Gertenbach 1983). Annual rainfall across the three sites is similar with around 600 mm for HNP, and 500 mm for GNP and KNP. The distribution of rainfall within the year is also similar between sites, with most rain falling between November and March (GNP: Gandiwa et al. 2016, HNP: Chamaillé-Jammes et al. 2006, KNP: Gertenbach 1980). During the wet season, grass water content is high, and water is widely distributed in the landscape across numerous natural and artificial pans (HNP, KNP) or rivers (GNP, KNP). During the dry season, most natural pans dry up and water distribution differs between sites. In GNP, water is only available in a few pools in the main river; in HNP, only artificial pumped waterholes provide water; in the north of KNP (Pafuri region), water is provided by a few permanent rivers and some pools that persist along the Limpopo river (GNP: Zvidzai et al. 2013, HNP: Chamaillé-Jammes et al. 2007, KNP: Purdon and van Aarde 2017).

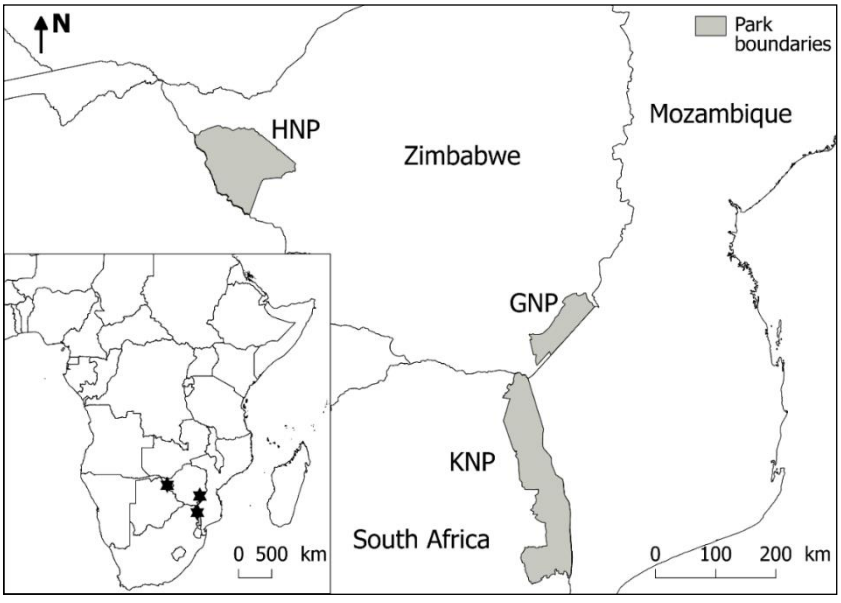


Figure 1. Location of the three study sites: Gonarezhou National Park (GNP) and Hwange National Park (HNP) in Zimbabwe, and Kruger National Park (KNP) in South Africa.

2.2 Environmental covariates

I used one unpublished and two published vegetation maps (KNP: Pretorius and Pretorius 2015, HNP: Arraut et al. 2018), each covering a study area and using different vegetation classes, to create simpler and more homogeneous maps for the comparative analyses. I combined the original land cover classes into three broad habitat types: (1) grassland, including areas dominated by grassland, or bushed grassland with sparse vegetation, (2) bushland, which consists of shrub and bushed areas, and (3) woodland, encompassing deciduous, evergreen or riverine forests. In HNP and GNP, the location of permanent waterholes was obtained exhaustively from project collaborators whilst in KNP locations were recorded from Google Earth.

Within the three study sites, due to the presence of numerous natural pans at all sites, it was difficult to quantify water availability outside of the core dry season. Because of this and to avoid transitional periods, I restricted the analyses to the core of the wet and dry seasons. I defined these periods according to fixed dates based on the similar rainfall patterns between the sites (GNP: Gandiwa et al. 2016, HNP: Chamaillé-Jammes et al. 2006, KNP: Gertenbach 1980): the core wet season (hereafter called wet season) is running from January 1st to March 31st (n = 90 days) and the core dry season (hereafter called dry season) from August 15th to October 31st (n = 78 days) for all sites. I considered water as a non-limiting factor in the wet season (Cornélis et al. 2011, Bennitt et al. 2014).

2.3 Capture and collaring

Between 2008 and 2016, 47 adult female Cape buffalo were tracked across the three study areas (GNP: n = 12, HNP: n = 20, KNP: n = 15) using GPS collars. We focused on adult females, as adult males leave subgroups and groups more often (Sinclair 1977, Prins 1996). On average, the collared female buffalos travelled between 4 (KNP) and 7 km (GNP and HNP) per day. All animals were captured by authorized personnel using established techniques (la Grange 2006) and were observed returning to their subgroups after collaring operations. All field operations were conducted in accordance with the legal and permit requirements of the countries in which they were carried out.

The data acquisition periods extended from October 2008 to May 2011 in GNP, from April 2010 to January 2016 in HNP, and from June 2010 to July 2015 in KNP. Duration of the tracking varied between 19 and 1013 days (median = 486) across individuals and GPS loggers were scheduled to acquire locations at synchronous times (the top of the hour) every hour. As some GPS locations were acquired with a small delay compared to the time the GPS was programmed to take the location, I corrected the acquisition delays. The location was retained if it was taken within a 5-min interval from the programmed acquisition

time, and I repositioned the location by linear interpolation otherwise. I computed fix success rate (*i.e.* the proportion of scheduled times for obtaining a GPS fix that resulted in successful acquisition of a GPS fix) within each season within each year for each individual and I retained GPS data from 38 collared individuals for which the fix success rate was higher than 90%. These individuals consisted of 10 groups: 2 in GNP, 4 in HNP and 4 in KNP. The number of collared cows in each group varied between 1 and 7 (GNP groups, $n_1 = 4$, $n_2 = 6$; HNP groups, $n_1 = 7$, $n_2 = 6$, $n_3 = 1$, $n_4 = 1$; KNP groups, $n_1 = 5$, $n_2 = 2$, $n_3 = 5$, $n_4 = 1$). The individuals selected had data for all days within the same season, and of these, 31 were tracked in both wet and dry seasons (GNP: $n = 10$, HNP: $n = 11$, KNP: $n = 10$) and 7 in only one season (HNP: $n = 4$, KNP: $n = 3$). This global dataset was used for a preliminary analysis (see section *Definition of association and fission-fusion events* below*)*, before some data selection processing for subsequent analyses (see *Statistical analyses* section).

2.4 Estimation of home ranges and home range overlaps

To estimate home range overlap (HRO) between individuals, I considered seasonal home ranges (HR) as the 90% utilization distribution during the dry and wet seasons for each year. Utilization Distributions (UD) were computed using the Movement-Based Kernel Density Estimation method (MKDE, Benhamou and Cornélis 2010) implemented in the 'adehabitatHR' package in R (Calenge 2007). Home range overlap between individuals was estimated using the Bhattacharyya's affinity index (Benhamou et al. 2014). The index accounts for variation in the intensity of HR use and can take values from 0 (no overlap) to 1 (identical space use).

2.5 Definition of association and fission-fusion events

Fusion and fission events were defined as the point in space and time at which two individuals merged and split up, respectively. Each fusion and fission event led to a period where individuals were together or separated, respectively (hereafter called 'together' or 'separated' periods, respectively). To quantify individual association patterns and define fission and fusion events between dyads, I calculated the distance between synchronous locations for every dyad that shared space (HRO > 0) for a given season (GNP: $n = 104$, HNP: $n = 20$, KNP: $n = 47$). Two buffalos were defined as being together if they were located simultaneously within a 1 km distance from each other. This distance threshold was determined using the group definition proposed by Cross et al. (2005a): a mixed-sex group is a set of individuals that are within 1 km of one another. At this same distance, Polansky et al. (2010) showed that female buffalos synchronized their movements, thus giving an estimate of the maximum diameter of a subgroup. As the activity synchronization among

group members is essential to ensure group cohesion, the result of Polansky et al. (2010) confirms that beyond 1 km, subgroups are likely to split. Bennitt et al. (2018) identified fusion events when collared buffalo were within 300 m of each other. Most recorded interindividual distances in my three sites occurred at these short distances (0-300 m: 74.27 % of all distances between dyads < 1 km apart), but the 1-km distance threshold was more consistent with field observations where buffalo subgroups spread over great distances (> 800 m) when travelling and arriving at a water point (pers. obs.). To minimize the number of false fission or fusion events resulting from infrequent erroneous locations, I also considered that two buffalos were together when their distance was ≥ 1 km for ≤ 2 h. The influence of the chosen distance (d_{th}) and time (t_{th}) thresholds on further analyses was examined using sensitivity analysis (Appendix 1). The sensitivity analysis indicated that the results would be qualitatively robust to changes in the values of d_{th} within the 800 m – 1.5 km range. Lowering t_{th} would change the absolute number of fission and fusion events (Appendix 1) but is unlikely to alter the qualitative conclusions of the study. To calculate the proportion of time spent together, I created for each dyad a binary vector of association, with value 'T' when individuals were together and 'S' when they were separated. When one value was missing between two association values ('T' or 'S') (*i.e.* the location of at least one of the two individuals had not been recorded), I substituted the missing value by the value of the previous hour (GNP: 0.44 % of the data, HNP: 0.31 % of the data, KNP: 0.97 % of the data). From these association vectors, I derived (1) the proportion of time that two individuals spent together (the number of times two individuals were together divided by the total number of association values for these two individuals during the entire season), (2) the timing and location of fission and fusion events between dyads and (3) the duration of periods that dyads spent together and separated (number of consecutive hourly time steps defined as 'together' and 'separated', respectively). I defined fusion events as the S_{t-1} -> T_t transition, from being separated (S) at time *t-1* to being together (T) at time *t*. Conversely, fissions are the opposite transition: T_{t-1} -> S_t. I excluded the periods containing at least one missing timestamp when calculating the duration of periods. The occurrence of fusion events was used to calculate the number of fusion events (by definition, the number of fission events is equal) per dyad per month as the total number of fusion events per dyad divided by the number of months of simultaneous tracking.

2.6 Statistical analyses

Animals from neighbouring groups can occasionally be in the vicinity of one another by chance (*e.g.* by randomly using the same resource patches at the same time). To avoid qualifying these events as within-group fission-fusion events, I restricted the analyses to dyads that spent a given amount of time together. To determine an appropriate cut-off value,

I investigated how the proportion of time that two individuals spent together was related to their HRO. I fitted a generalized (quasibinomial) additive mixed model with the proportion of time spent together as the response variable, and seasons (dry vs. wet), sites (GNP, HNP vs. KNP) and their interaction, and HRO as explanatory variables. From this preliminary analysis, I restricted the subsequent analyses to dyads that spent ≥10% of their time together (see Figure 2). Dyad identity was used as a random effect in all subsequent analyses that were conducted in a hierarchical (*i.e.* mixed) modelling framework.

I investigated the stability of HRO and proportion of time spent together across seasons at the dyad level. For each dyad with data for at least one dry and one wet season, I calculated the differences in HRO and proportion of time spent together between the dry season and the wet season (value $_{\text{dry season}}$ – value $_{\text{wet season}}$). To test whether these differences differed from 0 and varied between sites, I used two linear mixed models: the response variable was either (1) the seasonal difference in HRO or (2) the seasonal difference in the proportion of time spent together. The site was the unique explanatory variable in both models.

I then explored whether characteristics of the fission-fusion dynamics between buffalo dyads (*i.e.* the number of fusion events per month and the duration of 'together' and 'separated' periods) varied across sites and seasons. I fitted three generalized linear mixed-models with negative binomial distributions of errors: the response variable was either (1) the number of fusion events per month, (2) the duration of every 'together' period, or (3) the duration of every 'separated' period. Sites, seasons and their interaction and HRO were the explanatory variables. To analyze the distribution of fission and fusion events across the diel cycle, I ran two generalized additive mixed models with cubic splines and Poisson distribution of errors, with the number of (1) fission events or (2) fusion events per hour of the day per month as the response variables. The explanatory variables were site, season and their interaction and the time of the day.

Finally, I explored whether fission and fusion events and 'together' and 'separated' periods occurred in areas of the landscape differing in terms of distance to water (during the dry season) or vegetation type (during dry and wet seasons). The spatial location of fission and fusion events was defined as the average of the spatial coordinates of both individuals of the dyad. To describe the habitat of each individual of a dyad when they were 'together' or 'separated', I grouped, for each individual, all 'together' locations and all 'separated' locations, respectively. I calculated utilization distribution (90% UD using the MKDE approach) for those, resulting in one 'together' UD and one 'separated' UD for each individual of a dyad. I generated 300 random points/km² in each UD. The vegetation class and distance to the nearest water point were extracted at each fission and fusion location and each point drawn in the UDs. I used a generalized linear mixed model with a negative binomial distribution of the residuals, including distance to water as the response variable

and location type (*i.e.* fission event, fusion event, 'separated' and 'together' locations) and the site as explanatory variables. In addition, I compared the proportion of fusion and fission events taking place in each vegetation class to the proportion of 'separated' and 'together' points in each vegetation class. The comparisons were explored by fitting three generalized (binomial) linear mixed models, *i.e.* one for each vegetation class, and in each model, the response variable was whether the location occurred in the corresponding vegetation class (scored 1) or not (scored 0). The explanatory variables were site, season and their interaction and the variable indicating the location type. Here I explored the habitat structure both of periods when dyads were together and periods when they were separated in order to understand whether two individuals were more likely to be together or not in specific areas and because exploring the locations where two individuals are together does not give any information on the locations where these two individuals may be found separated. For example, even though two individuals spent 25% of their time together in grasslands, this result does not mean that they were 75% of their time separated when they were in grasslands. This result only indicates that the remaining 75% of their time spent together took place outside of the grasslands (in my case, bushlands and woodlands). Note that the results I present give the proportion of each habitat class within the locations of fission events, fusion events, 'together' and 'separated' periods rather than the proportion of fusion locations, fission locations, 'together' locations and 'separated 'locations' within each habitat class.

For each above-mentioned analysis, I used the Akaike Information Criterion corrected for small sample size (AICc) to test whether a simpler model, nested in the full model, would be more parsimonious (Burnham and Anderson 2002). Model sets are presented in Table 1. I considered the most parsimonious model to be the model that had both a ΔAICc < 2 and the lowest number of explanatory variables (Arnold 2010). The goodness-of-fit measure of the models was estimated by the adjusted R-squared (Wood 2017) for generalized additive models (Table 1, analyses 1, 7 and 8), and by the marginal pseudo-R-squared (Nakagawa et al. 2017) for generalized linear mixed models (Table 1 – analyses 2-6, 9 and 10) using the 'performance' package (Lüdecke et al. 2020). Analyses were conducted using the 'lme4' (Bates et al. 2015), 'mgcv' (Wood 2011) and 'glmmTMB' (Brooks et al. 2017) packages for R v. 3.3.2 (R Development Core Team 2016).

3 Results

Table 1. Summary of the candidate models fitted for each analysis. Response variables were modelled as a function of different combinations between HRO, site (GNP, HNP or KNP), season (dry or wet season), time of day and event type (fission event, fusion event, together periods and separated periods). Dyad identity was included as a random intercept in all models. For analyses 4–6, HRO was included in some models as an explanatory variable to control for the positive relationship between the number of fusion events or duration of 'together' and 'separated' periods and HRO, as HRO positively affects the total time that two buffalos spent together (analysis 1).

For each model the degree of freedom (df), deviance = -2*loglikelihood (-2LL), difference in AICc values between the best fit and model$_i$ (ΔAICc), model fit estimated by the adjusted R-squared (Wood 2017) for GAMMs (analyses 1, 7 and 8 below), and the marginal pseudo R-squared (Nakagawa et al. 2017) for GLMMs (analyses 2 to 6, 9 and 10 below) – Higher values indicate better model fit in both cases. The ranking was based on the ΔAICc. The best model, *i.e.* which had both a ΔAICc < 2 and the lowest number of explanatory variables, is shown in bold for each analysis. s(variable): explanatory variable with a spline effect.

Model	*df*	-2LL	ΔAIC_c	Adj. R^2 / Pseudo $R^2_{marginal}$
1. Relationship between proportion of time spent in the same subgroup and home-range overlap				
s(HRO) + site	**7**	**805.05**	**0.0**	**0.93**
s(HRO) + site + season	8	802.97	0.05	0.93
s(HRO) + site*season	15	788.52	1.0	0.93
s(HRO)	5	833.06	23.8	0.89
s(HRO) + season	6	833.14	26.0	0.90
null	3	1110.63	297.2	0.00
season	4	1112.06	300.7	0.00
site	5	1113.20	303.9	0.01
site + season	6	1114.52	307.3	0.01
site*season	8	1113.21	310.3	0.01
2. Seasonal changes in home range overlap				
null	**3**	**-52.2**	**0**	**0.00**
Site	5	-52.5	4.7	0.01
3. Seasonal changes in proportion of time spent in the same subgroup				
null	**3**	**378.9**	**0**	**0.00**
Site	5	375	1.0	0.12
4. Number of fusion events				
HRO + season	**5**	**440.3**	**0**	**0.39**
HRO + site + season	7	436.5	0.9	0.40
HRO + site*season	9	436.4	5.7	0.40
season	4	478.0	35.5	0.23
site + season	6	474.4	36.4	0.25
site*season	8	473.9	40.7	0.25
HRO	4	484.9	42.4	0.26
HRO + site	6	484.0	46.0	0.27
null	3	520.4	75.6	0.00
site	5	519.2	78.9	0.02
5. Duration of periods in the same subgroup				
Site + season	**6**	**15760**	**0**	**0.10**
HRO + site + season	7	15760	0.2	0.11
Site*season	8	15760	3.6	0.10
HRO + Site*season	9	15760	3.9	0.11

Season	4	15780	16.3	0.04
HRO + season	5	15780	17.2	0.04
HRO + site	6	15820	57.3	0.06
Site	5	15820	57.3	0.06
Null	3	15830	66.7	0.00
HRO	4	15830	67.1	0.00
6. Duration of periods in a different subgroup				
HRO + site + season	**7**	**16290**	**0**	**0.20**
HRO + site*season	9	16290	3.4	0.20
HRO + season	5	16310	9.1	0.15
Site + season	6	16360	62.2	0.17
Site*season	8	16360	65.5	0.17
HRO + site	6	16360	70.5	0.17
Season	4	16380	80.4	0.06
HRO	4	16380	82.7	0.10
Site	5	16440	140.6	0.12
null	3	16460	161.6	0.00
7. Occurrence of fusion events during the diel cycle				
null	**2**	**7389.06**	**0.0**	**0.00**
Site	4	7392.29	7.2	0.00
Season	3	7429.67	42.6	0.03
Site + season	5	7437.61	54.6	0.04
Site*season	7	7436.94	57.9	0.04
s(Time of day) + site*season	8	7458.14	81.1	0.11
s(Time of day)	3	7471.55	84.5	0.09
s(Time of day) + site	5	7475.06	92.0	0.09
s(Time of day) + season	4	7498.97	113.9	0.12
s(Time of day) + site + season	6	7507.75	126.7	0.12
s(Time of day) + site * season	8	7507.81	130.8	0.12
8. Occurrence of fission events during the diel cycle				
null	**2**	**7355.63**	**0**	**0.00**
Site	4	7358.68	7.1	0.00
s(Time of day)	3	7369.03	15.4	0.07
s(Time of day) + Site	5	7372.90	23.3	0.07
season	3	7393.70	40.1	0.03
Site + season	5	7400.68	51.1	0.04
Site*season	7	7399.58	54.0	0.03
s(Time of day) + season	4	7412.09	60.5	0.10
s(Time of day) * site * season	8	7411.90	68.4	0.14
s(Time of day) + site + season	6	7421.24	73.7	0.11
s(Time of day) + site*season	8	7421.52	78.0	0.11
9. Distance to water				
Type*site	**13**	**5997000**	**0.0**	**0.60**
Type + site	7	5998000	677.4	0.60
Type	5	5998000	757.8	0.01
Site	4	6029000	31915.9	0.60
null	2	6029000	31999.1	0.00
10. Habitat structure				
Grassland				
Type + site*season	**10**	**2416246**	**0.0**	**0.11**
Site*season	7	**2416628**	**376.0**	0.11
Type + site + season	8	2429397	13147.0	0.09

Type + season	6	2429420	13166.0	0.02
Site + season	5	2429891	13635.0	0.09
Season	3	2429915	13655.0	0.02
Type + site	7	2447079	30827.0	0.07
Type	5	2447099	30843.0	0.00
Site	4	2447627	31369.0	0.07
null	2	2447647	31385.0	0.00
Bushland				
Type + site*season	**10**	**3642600**	**0.0**	**0.25**
Site*season	7	3642625	19.0	0.25
Type + site + season	8	3648911	6307.0	0.25
site + season	5	3648937	6327.0	0.25
Type + Season	6	3649034	6426.0	0.01
season	3	3649059	6445.0	0.01
Type + site	7	3665492	22886.0	0.24
Site	4	3665529	22917.0	0.24
Type	5	3665611	23001.0	0.00
null	2	3665648	23032.0	0.00
Woodland				
Type + site*season	**10**	**2984964**	**0.0**	**0.12**
Type + site + season	8	2985014	46.0	0.12
Type + season	6	2985051	79.0	0.00
Site*season	7	2985253	283.0	0.12
Site + season	5	2985293	319.0	0.12
Season	3	2985330	352.0	0.00
Type + site	7	2985514	544.0	0.12
Type	5	2985550	576.0	0.00
Site	4	2985779	803.0	0.12
null	2	2985816	836.0	0.00

3.1 Relationship between the proportion of time spent together and home range overlap

Home range overlap and the proportion of time spent together by two individuals were positively and non-linearly related (Figure 2). With a few exceptions, the very small proportion of time spent together (< 10%) was associated with a small to moderate HRO (< 0.4). Moderate time spent together (10% < < 50%) could be associated with widely different HRO (0.5 < < 0.9). Individuals spending more than 50% of their time together always had a very large HRO (>0.8). The most parsimonious model between the proportion of time that two buffalos spent together and HRO fit the data well and included the effect of the site only (Table 1 – analysis 1), suggesting that the season had little influence on this relationship.
All subsequent analyses were restricted to dyads that spent ≥ 10% of their time together in at least one season.

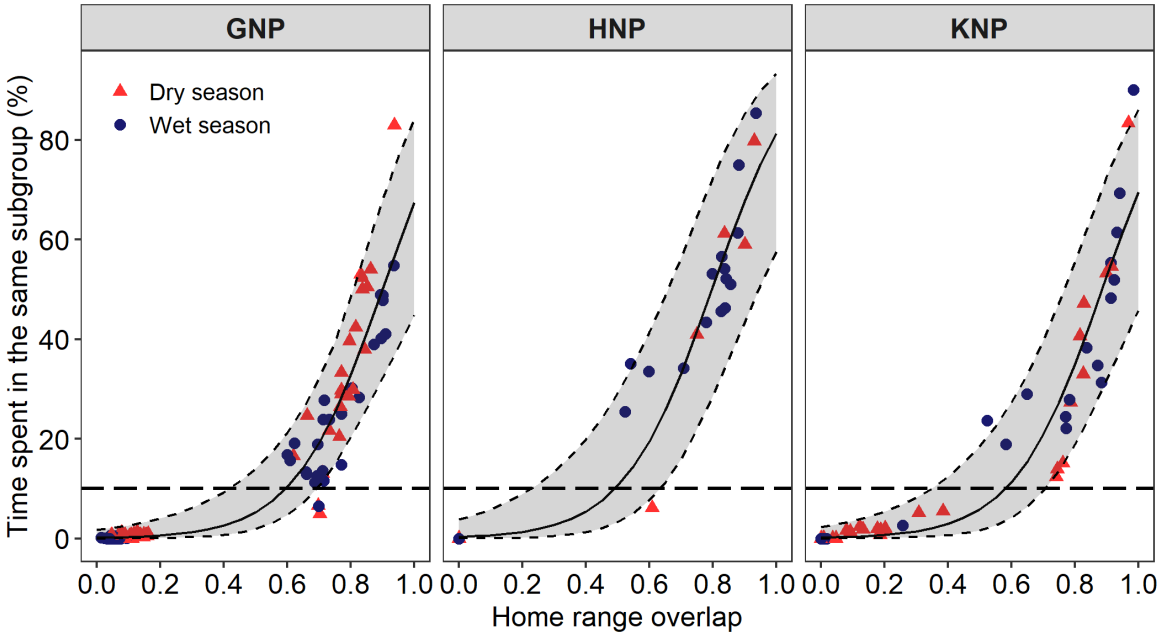


Figure 2. Relationship between the time spent together and home range overlap among pairs of Cape buffalos according to the study sites in dry (red) and wet (blue) seasons. Points in corresponding colours are the observed values for each dyad per year and season. Although the most parsimonious model did not include the effect of season (Table 1), the observed values are given per season for information. Solid lines represent the predictions from the model and grey dashed lines represent 95% confidence intervals. The horizontal black dashed line indicates the cut-off value of 10% of time spent together.

3.2 Seasonal stability of home range overlap and association patterns

The observed seasonal changes in HRO and in the proportion of time spent together are plotted on Figure 3. The most parsimonious models explaining seasonal changes in both the HRO and in the proportion of time spent together across all sites were the null models (Table 1 – analyses 2-3). The seasonal change estimated for HRO (± SE) was 0.01 ± 0.02 (95%CI: -0.03, 0.06) and that for the proportion of time spent together (± SE) was 5.75 ± 3.87 % (95%CI: -1.83, 13.33).

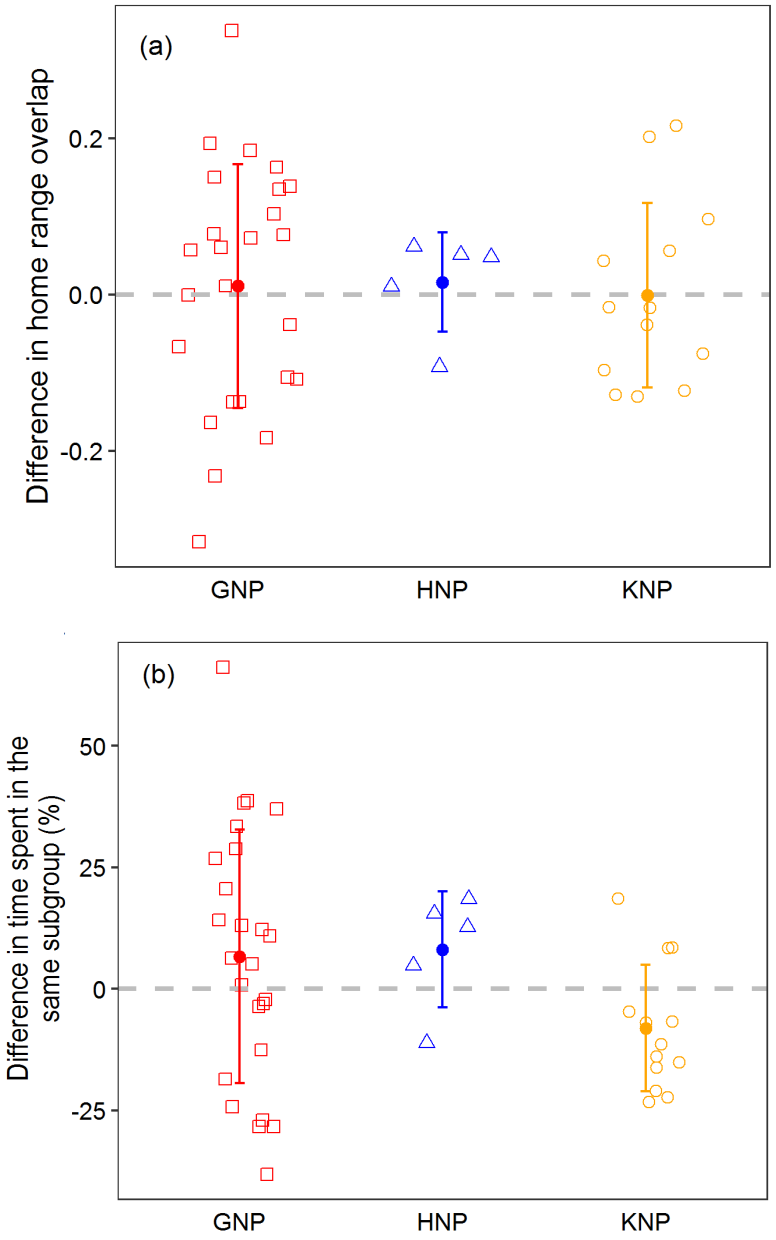


Figure 3. Differences in (a) HRO between two individuals and (b) the proportion of time that two individuals spent together between the dry season and the wet season in each site. Each open dot represents observed data for one dyad; the filled symbols denote observed means and the whiskers denote standard deviations (SDs) for each site. Grey dashed line indicates no seasonal difference. A positive value means that two individuals spent more time together/had more HRO during the dry than during the wet season. Conversely, a negative value means that two individuals spent less time together/had less HRO during the dry than during the wet season. This analysis required data for at least one dry season and one wet season for each dyad, which explains why the number of dyads is reduced compared to the other analyses.

3.3 Frequency of fusion events and duration of periods

Mean ± SD number of fusion events per month was 5.73 ± 1.86, 4.04 ± 1.28, and 5.54 ± 2.49 during the dry season in GNP, HNP, and KNP, respectively, and 9.83 ± 4.28, 8.22 ± 8.09, and 10.30 ± 3.92 during the wet season in GNP, HNP, and KNP, respectively. The most parsimonious model included the effect of HRO and season (Table 1 – analysis 4),

indicating that the frequency of fusion events between dyads was higher in the wet than in the dry season (Figure 4).

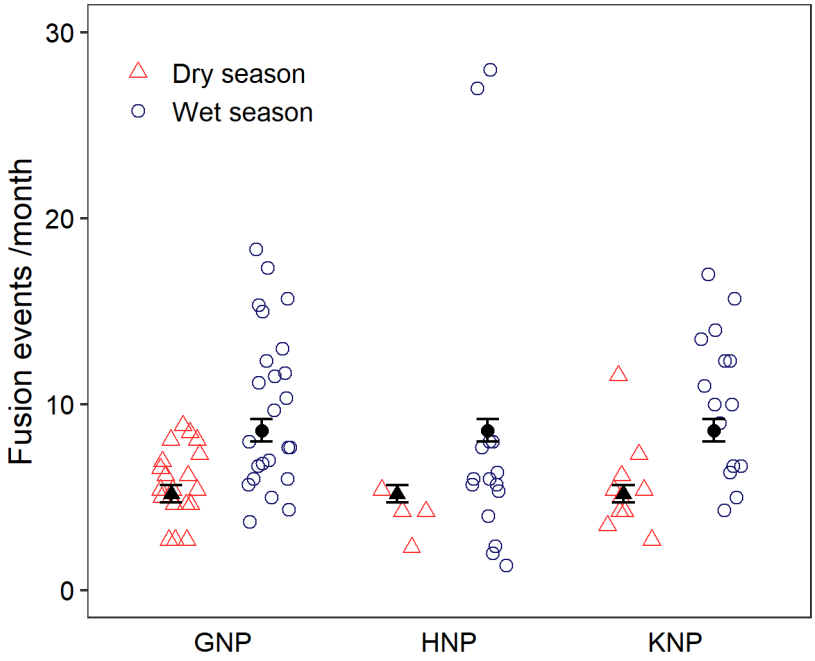


Figure 4. Effects of the study site and season on the number of fusion events per month per dyad. The open symbols give the observed values; the filled symbols denote means and the whiskers indicate SEs.

Mean ± SD duration of 'together' periods was 35.6 ± 71.6, 88.4 ± 127, and 39.9 ± 65.2 during the dry season in GNP, HNP, and KNP, respectively, and 18.9 ± 29.6, 38.5 ± 70.1, and 23.6 ± 40.4 during the wet season in GNP, HNP, and KNP, respectively. The most parsimonious model included effects of both season and site (Table 1 – analysis 5), indicating that periods were shorter in the wet than in the dry season and were the highest in HNP, intermediate in KNP, and the lowest in GNP (Figure 5a).

Mean ± SD duration of 'separated' periods was 71.9 ± 118.0, 60.6 ± 97.9, and 47.0 ± 103.0 during the dry season in GNP, HNP, and KNP, respectively, and 42.7 ± 80.9, 20.9 ± 55.0, and 22.9 ± 42.7 during the wet season in GNP, HNP, and KNP, respectively. The most parsimonious model included the effect of HRO, season and site (Table 1 – analysis 6). Therefore, the more space that two individuals shared, the shorter the periods during which they were separated. Independently to HRO, periods that two individuals spent separated were shorter in the wet than in the dry season and were the longest in GNP, intermediate in KNP, and the lowest in HNP (Figure 5b, Table 1 – analysis 6).

Overall, the effects of site and season explained only a small amount of the variability in the duration of both types of periods (pseudo-R^2 in Table 1 – analysis 5-6), suggesting that these variables may only slightly affect the duration of periods spent together or separated. Both types of periods were on average short but very variable (Figure 5).

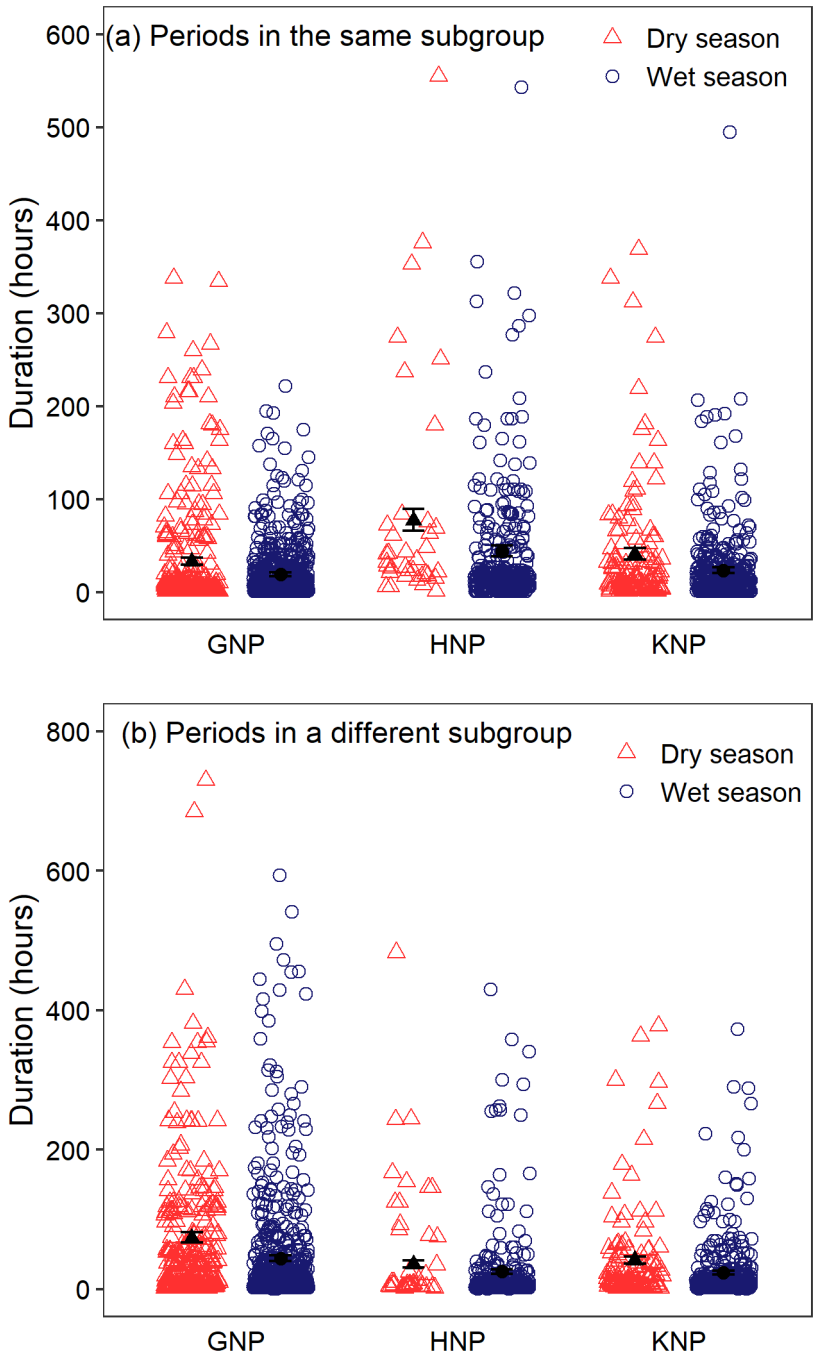


Figure 5. Effects of the study site and season on the duration of (a) every 'together' period and (b) every 'separated' period. The open symbols give the observed values; the filled circles denote means and the whiskers indicate SEs.

3.4 *Occurrence of fusion and fission events during the diurnal cycle*

Both fission and fusion events occurred at any time of the day but occurred more frequently in the early morning (04h00–07h00) and from mid-afternoon to the early evening (15h00–19h00, not shown). However, the most parsimonious models on the occurrence of fission and fusion events between dyads at diurnal cycle were the null models, suggesting that fission and fusion events occurred at any time of the day in all sites and both seasons (Table 1 – analyses 7-8).

3.5 *Environmental characteristics of fission and fusion events*

The mean distance to water ± SD of fission and fusion events and locations where individuals were together or separated are plotted in Figure 6. The most parsimonious model of distance to water included the interaction effect between site and type of location (Table 1 – analysis 9), indicating that fission and fusion locations occurred farther away from the water in GNP than those in HNP and KNP (Table 1 – analysis 9). At all sites, fusion events tended to occur slightly closer to water than fission events, especially in GNP. However, the pseudo-R^2 values indicated that the type variable improved the model fit only negligibly (Table 1 – analysis 9), suggesting that distance to water only slightly influenced the location of fusion and fission events and 'together' and 'separated' periods. Distance to water at fusion and fission locations was very variable and on average was not distinct to the ones when individuals were together or separated (Figure 6).

The distribution of buffalo locations among vegetation types varied strongly between sites (Figure 7). For all vegetation classes, the most parsimonious models included the type of location and the interaction between site and season (Table 1 – analysis 10). However, pseudo-R^2 values (Table 1 – analysis 10) showed that the inclusion of these variables led only to a small improvement of model fits. In general, seasonal effects were small and the vegetation at fusion and fission locations did not differ much from the one that in areas where individuals were together or separated, apart from in the dry season in HNP (Figure 7).

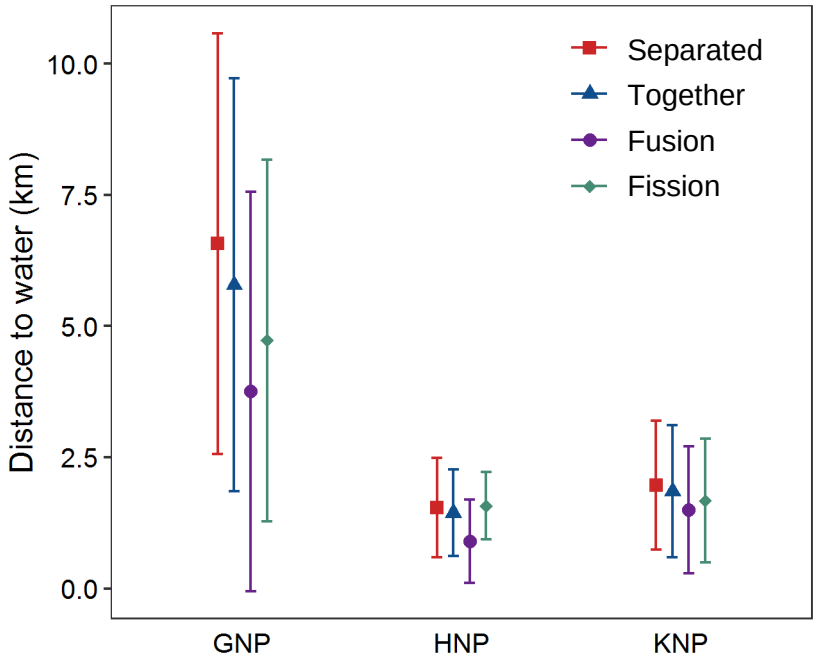


Figure 6. Distance to water of fission and fusion locations, and during periods when individuals of a dyad were together or separated. See text for details. The analysis was conducted during the dry season only. The points denote the observed means and the whiskers denote SDs.

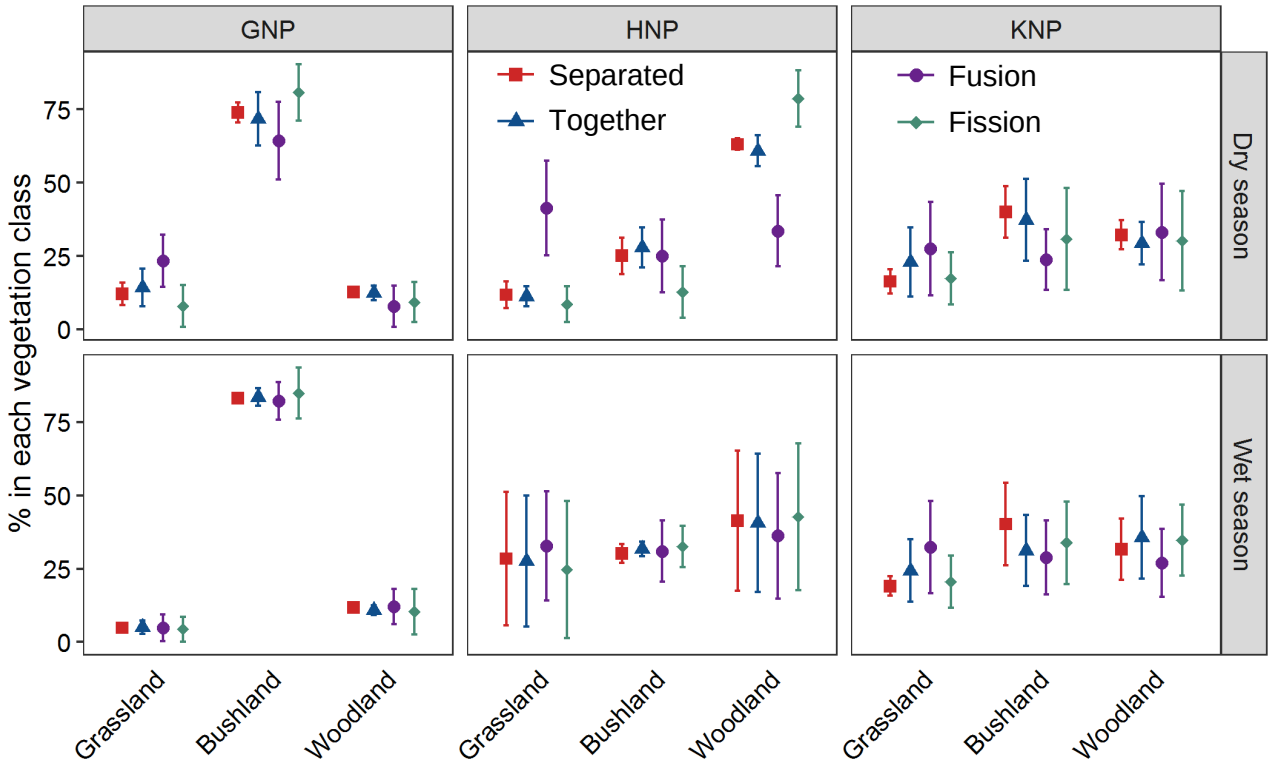


Figure 7. Percentage of each vegetation type among fission and fusion locations, and during 'together' and 'separated' periods. See text for details. The points denote the observed means and the whiskers denote SDs. The figure gives the proportion of each habitat class within fusion locations, fission locations, locations where dyads were together and locations where they were separated. For example, for a given dyad, the proportion of 'together' periods taking place in the grasslands was calculated as the number of locations in the grasslands where the dyad was together divided by the total number of locations where the dyad was together regardless of the habitat (*i.e.* grasslands, bushlands and woodlands).

4 Discussion

As the factors hypothesized to drive fission-fusion dynamics may vary across populations, it is expected that the levels and patterns of fission-fusion dynamics may also vary. However, variability in fission-fusion dynamics across natural populations is currently known only from comparisons between independent studies that have used different approaches (Furuichi 2009, Coles et al. 2012, Baden et al. 2016), or from experimental studies that investigate social dynamics in artificial settings (Kelley et al. 2011). Standardized comparative studies conducted *in natura* are essential for understanding how social, ecological and demographic factors influence patterns of fission and fusion. Here I address this important issue, by investigating the fission-fusion dynamics between dyads across three Cape buffalo populations living in similar environmental contexts. Patterns of fission and fusion between dyads were generally similar across all three populations suggesting that localized effects have little influence on adult female social dynamics in the species.

At all sites, the relationship between the time that two individuals spent together and the extent to which home range overlapped was positive and consistent across seasons. I found a site effect on this relationship but, as this effect was small and only marginally improved model fit, I considered that the pattern was generally consistent across sites. However, the predictive power for a specific dyad might be low at all sites, as the proportion of time spent together remained highly variable for any given home range overlap, in particular when the overlap was large. Some of this unexplained variability might be linked to non-random associations that could not be controlled for when the GPS collars were deployed. Whilst this study was conducted on adult females and therefore variability in association patterns is not linked to age/sex differences, female Cape buffalos may form preferred associations with close kin, as previously reported in species with fluid fission-fusion dynamics (elephants *Loxodonta africana,* Archie et al. 2006, eastern grey kangaroo *Macropus giganteus*, Best et al. 2014, and bottlenose dolphins *Tursiops aduncus*, Frère et al. 2010). Body condition may also affect the association patterns, as Cape buffalos in Lake Manyara National Park (Tanzania) located in the rear of the group, where conditions are worst, tended to split off more frequently from the group (Prins 1996). Possibly, variation in fission-fusion dynamics among the three studied populations could be due to differences in group and/or subgroup size. However, as the study design was originally developed for telemetry studies (*e.g.* habitat selection) or to track the transmission of pathogens, it was not necessary to consider the temporal variation of group size (but the group size during the capture was usually recorded) and recording subgroup size over time using GPS technology was not possible.

Fusion and fission events between dyads appeared to happen frequently in all populations with, on average, 5.7 to 10.3 fusion events per month per dyad depending on site and season (see Fig. 5) and periods when two individuals were together or separated lasting between 18 to 88 h and 20 to 71 h on average, respectively (see Fig. 6). It is, however, important to note that when assessing the duration of fusion and fission event between dyads, I only considered events where the association level (*i.e.* together or not) between two individuals was known throughout the period. Thus, long events were more likely to be excluded because they could include more missing data, which may have biased the estimate of the mean event duration. Cape buffalos usually rest in the middle of the day and are most active during the early morning and afternoon (Cornélis et al. 2011, Megaze et al. 2013, Valls-Fox et al. 2018). During these periods, individuals are more likely to differ in their activities, with some individuals engaging in foraging activities, whilst others are moving to other food patches. Although inspection of the data suggested a slight trend for fission and fusion events to occur more during these periods (not shown), such diel patterns were not retained in the most parsimonious models, showing that there are no important cycles of fission-fusion dynamics throughout the day. It is thus not clear why individuals

split, and the same question arises about why individuals fused regularly. This could be because the resource is limited and heterogeneously distributed in semi-arid areas such as my study sites. Cape buffalos could afford to congregate in areas where high-quality resources are abundant, or conversely, be forced to come together when foraging patches are limited. The regular fusions could also be because of an intrinsic need to regroup (for instance, to obtain information, Fortin and Fortin 2009).

A significant site effect was observed in the analysis describing the duration of 'together' periods. This was likely due to my large sample size, as the magnitude of this site effect was small. These slight differences between sites could be real, but also be due to small inter-annual variations in fission-fusion dynamics between years, as not all sites were surveyed during a similar period. The number of dyads tracked in each site during the common period (from June 2010 and May 2011) was too small, preventing me from testing such an effect. Overall, my results point towards similar fission-fusion dynamics between dyads across all study populations, which differ strongly from the one observed in a population in the Okavango Delta (Botswana, Bennitt et al. 2018). In general, the authors reported longer 'together' periods than those observed in my study and lower fission and fusion rates between dyads: the mean duration of 'together' periods varied from 60 to 75 hours according to seasons (except in one wet season where mean duration was 7.5 h, my study – from 18 to 88 h) and the number of fusion events per month varied between less than 1 and 3 (from 3 to 12 for the whole season based on dyads that spent more than 10% of their total time together). I consider it unlikely that methodological differences in the definition of fission and fusion events (see Bennitt et al. 2018) could account for differences between this study and mine. This is particularly true as the authors used a distance threshold of 300 m, compared to 1000 m in this study, as a threshold for defining a fusion event. The use of a similar threshold between the two studies would have led to even larger differences. This comparison suggests a greater instability of dyads in my populations and points towards resource conditions as being a driver of fission-fusion dynamics of female Cape buffalos. GNP, HNP and KNP are dominated by wooded semi-arid savannas, whereas the area of the Okavango Delta where Bennitt et al.'s (2018) study took place is at the border of an alluvial plain where food quality and possibly water availability is greater. Future research should be conducted to further compare the environments of my sites and the Okavango Delta, such as the predation pressure, the size and distribution of food patches, the forage quality and the access to water, which could be responsible for the variation in social dynamics between dyads observed between my sites and in the Okavango Delta.

The observed seasonal differences in the frequency of fusion events and the duration of both types of period hint at the role of resource condition as a driver of fission-fusion dynamics between dyads. At my study sites, despite the absence of seasonal

changes in home range overlap or the proportion of time that two buffalos spent together, Cape buffalos usually split and associated more frequently and were separated or together for shorter periods during the wet season when resource availability was high. As large Cape buffalo groups split more frequently than smaller ones (Prins 1989), one could hypothesize that in the wet season individuals occur in larger, more fluid subgroups than in the dry season when they would occur in smaller, more stable subgroups. An increase in subgroup size during the wet season has been shown in other species with fission-fusion dynamics (spider monkeys *Ateles belzebuth belzebuth*, Shimooka 2003, blackbuck *Antilope cervicapra*, Isvaran 2007, Thornicroft's giraffe *Giraffa camelopardalis*, Bercovitch and Berry 2010 and in Cape buffalo, Sinclair 1977). This would suggest that Cape buffalos have evolved a strategy to limit intra-group competition for food during the dry season while trying to benefit from larger aggregations (*e.g.* protection against predators for newborns), at least temporarily, in the wet season when food competition is reduced. Additionally, Cape buffalos are in much poorer body condition during the dry season than the wet season (Beechler et al. 2009), reflecting an increased susceptibility to diseases during this period (Ezenwa and Jolles 2011). Being in smaller subgroups during the dry season could help to reduce pathogen transmission between individuals. During the wet season, the cost of social cohesion is expected to be lower, yet I found that dyads were together for shorter amounts of time. Why they stay together for shorter durations during the wet season remains unexplained but could be linked to resource availability. As resources are highly available, buffalo dyads may prefer to split more often and stay together for a shorter time to exploit available habitat more efficiently. Conversely, the low resource availability in the dry season could force buffalo dyads to congregate in the few patches where resources are plentiful and stay longer in these areas.

Much of the research on fission-fusion dynamics published to date has relied on direct observations and the recording of temporal changes in subgroup size, but these are often conducted on a small number of groups (Lehmann and Boesch 2004, Baden et al. 2016, Pinacho-Guendulain and Ramos-Fernández 2017). The lack of data on subgroup size is a limitation in this study but using GPS tracking technology offers an individual viewpoint by describing the fission-fusion dynamics of dyads in various groups at several sites using a unified analysis. While I had a large sample size of locations through the use of GPS devices, it is worth noting that the constraints associated with this technology (*e.g.* deployment costs) have limited the number of individuals to be monitored simultaneously within the same group. Fission and fusion events involving non-collared animals have not been recorded, but it is unlikely that the behaviour of those animals was highly different from the collared Cape buffalos and that the biases related to sample size were heterogeneous across sites and seasons. Consequently, the differences observed across sites and seasons should remain valid. There is a need to collect more movement data from

individuals from the same group to compare and confirm or not my results. Even though GPS data collected every hour provide large location data sets and allow accurate measurements of fission and fusion frequency (Body et al. 2015), these data remain relatively coarse and it is not possible to identify exactly when or where fusion or fission events of dyads occur. Although this factor may have influenced the precise location of fusion and fission events in this study, it is unlikely that increasing the resolution of locations would have greatly affected the results on the frequency and duration of fusion and fission events. Given the gregarious behaviour of the species, I expected dyads to spend a lot of their time together, so it is unlikely that an accurate measure of the duration of fusion and fission events would change the average duration by site and season. Despite these limitations, GPS tracking provides new information about whether local environmental conditions affect where fission and fusion events occur and whether space use differs when individuals of a given dyad are together or not. In particular, the data allow the testing of the expectation that water sources should act as hubs where fission and fusion events occur. I expected this because (i) dyads may meet as they come to drink (which, irrespective of the actual decision process leading to the encounter, would be identified as a fusion event according to my approach); (ii) individuals initiate new activity bouts after drinking, and this could create conflicts between individuals leading to fission; (iii) water sources are dispersed in the landscapes during the dry season and the buffalos need to drink twice a day (Valls-Fox et al. 2018), providing an easy opportunity to meet. However, in HNP and KNP, there was no evidence of biologically meaningful differences in distance to water between location of fission and fusion events, when buffalo dyads were together or separated in the dry season. This observation agrees with findings in Cape buffalos living around the Okavango Delta area during the same period of the year, where the distance to permanent water between fission and fusion events did not vary (Bennitt et al. 2018). In contrast, in GNP, fusion events tended to occur closer to water than fission events and periods when dyads were together or not. This could be explained by the fact that, compared to my study areas in HNP and KNP, and to the Okavango Delta site studied by Bennitt et al. (2018), water in GNP is only available in a few waterholes during the dry season, increasing the probability that individuals use the same water sources. Therefore, I tentatively suggest that water sources may act as focal spots where fusion and fission events occur in protected areas when water availability is low.

I also did not observe any general link between vegetation type and location of fission and fusion events. Habitat characteristics differed between sites, mostly between HNP/KNP and GNP where bushland is more widespread. Within sites, fission and fusion events were not more likely to occur in one habitat type compared to habitats used at other times. The exception was in the dry season in HNP, where the location of fusion events was more likely to occur in grasslands. As in open habitats, such as grasslands, visibility

increases, facilitating predator's detection and visual contacts, Cape buffalos may prefer to join in these habitats, as noted in many herbivores (*e.g.* blackbuck, Isvaran 2007, Thornicroft's giraffe, Bercovitch and Berry 2010), but why this would only happen in HNP is unclear. Grasslands are common around waterholes in HNP, but the results on the location of fusion events regarding distance to water (see above) suggest that fusion events did not occur closer to water in HNP.

5 Conclusions

This study provides the most comprehensive description of the dynamics of association patterns in the Cape buffalo reported so far. Cape buffalos in Hwange, Gonarezhou and Kruger National Parks form associations based on a shared home range but loose temporal associations. These associations occur for generally short periods, and levels of fission-fusion dynamics of dyads are generally consistent across populations, with no obvious environmental determinants, although in areas with low water availability water sources might act as hotspots of fusion events. Strikingly, I found variability in fission-fusion dynamics across dyads within the same population, suggesting that further studies should now focus on identifying the factors underlying this heterogeneity. Such studies will be critical for (i) gaining a better understanding of drivers of fission-fusion dynamics across species (Sueur et al. 2011a), and (ii) improving our ability to understand and predict the consequences of social dynamics on other biological processes, such as the transmission of important pathogens (*e.g.* tuberculosis) that is a key concern in Cape buffalo populations (de Garine-Wichatitsky et al. 2010a).

6 Appendices

Appendix 1. Sensitivity analysis

The use of a distance threshold could easily lead to spurious breaks in association patterns when distances beyond the threshold are recorded for a short period. This can occur either because the distance between the individuals is close to the threshold and sometimes just above for a short, non-biologically meaningful duration, or because the GPS location for at least one of the individuals has a significant error. Such conditions are unlikely to be biologically meaningful in the context of this study, and I therefore also considered a time threshold t_{th}, considering that two individuals were still together if the inter-individual distance was $\geq d_{th}$ for a duration $\leq t_{th}$.

To choose the most appropriate values for t_{th} and explore the effect of a $d_{th} = 1000$m on further analyses, I evaluated how robust the estimations of (i) the proportion of time that

dyads spent together and (ii) the number of fusion events per month per dyad, were to changes in d_{th} and t_{th} values. I did this at each study site and investigated d_{th} values ranging from 100 m to 3100 m and t_{th} values ranging from 2 h to 6 h. I thus calculated (i) the proportion of total time that dyads spent together and (ii) the number of fusion events per month per dyad for each combination of d_{th} and t_{th} values (see main text for further explanation). I explored the relationships between the proportion of time spent together or the number of fusion events per month and the values of d_{th}, for each value of t_{th} using generalized additive mixed models (GAMMs).

The proportion of time that dyads spent together and the number of fusion events per month were not very sensitive to the value of t_{th} in the three sites, except in HNP for low values of d_{th} where the number of fusion events per month varied greatly with t_{th} (Figures S1b & S1e). The proportion of time spent together was most sensitive to d_{th}, resulting in greater time spent together as d_{th} increased in all sites (Figures S1a-c). This was expected because, as d_{th} increases, extra locations are accounted for as being time spent together. The relationship between the number of fusion events and d_{th} is more complex and differs between sites. In HNP and to a lesser extent in KNP, increasing d_{th} decreased the number of fusion events observed (Figures S1e-f). This was expected because, as d_{th} increases, buffalos are considered together for longer periods, leading to a reduced number of fusion events. The differences in the shape of the relationship between HNP and KNP suggest that dispersion of individuals within the groups differ, with animals being more dispersed in HNP. Unexpectedly, in GNP, increasing d_{th} increased the number of fusion events detected (Figure S1d). I explain this observation by the regular proximity of the two groups studied, which share space significantly. As d_{th} increases, times when groups were in close proximity likely became counted as a fusion event.

In the light of these results, a d_{th} value of 1000m for the analyses seemed to be able to account for the effect of small-scale dispersion of individuals in HNP (which was not of interest here). The choice of d_{th} did not influence the number of fusion events calculated in KNP, and it would affect the results for GNP only moderately, in a way that could be understood thanks to this sensitivity analysis. As, at this d_{th} value, the proportion of time that dyads spent together and the number of fusion events were little sensitive to the value of t_{th} in the three sites, I selected the minimal t_{th} value, *i.e.* 2h, for the analyses presented in the main text. Note that overall, this sensitivity analysis showed that moderate changes in the values used for defining these thresholds would not alter the results qualitatively.

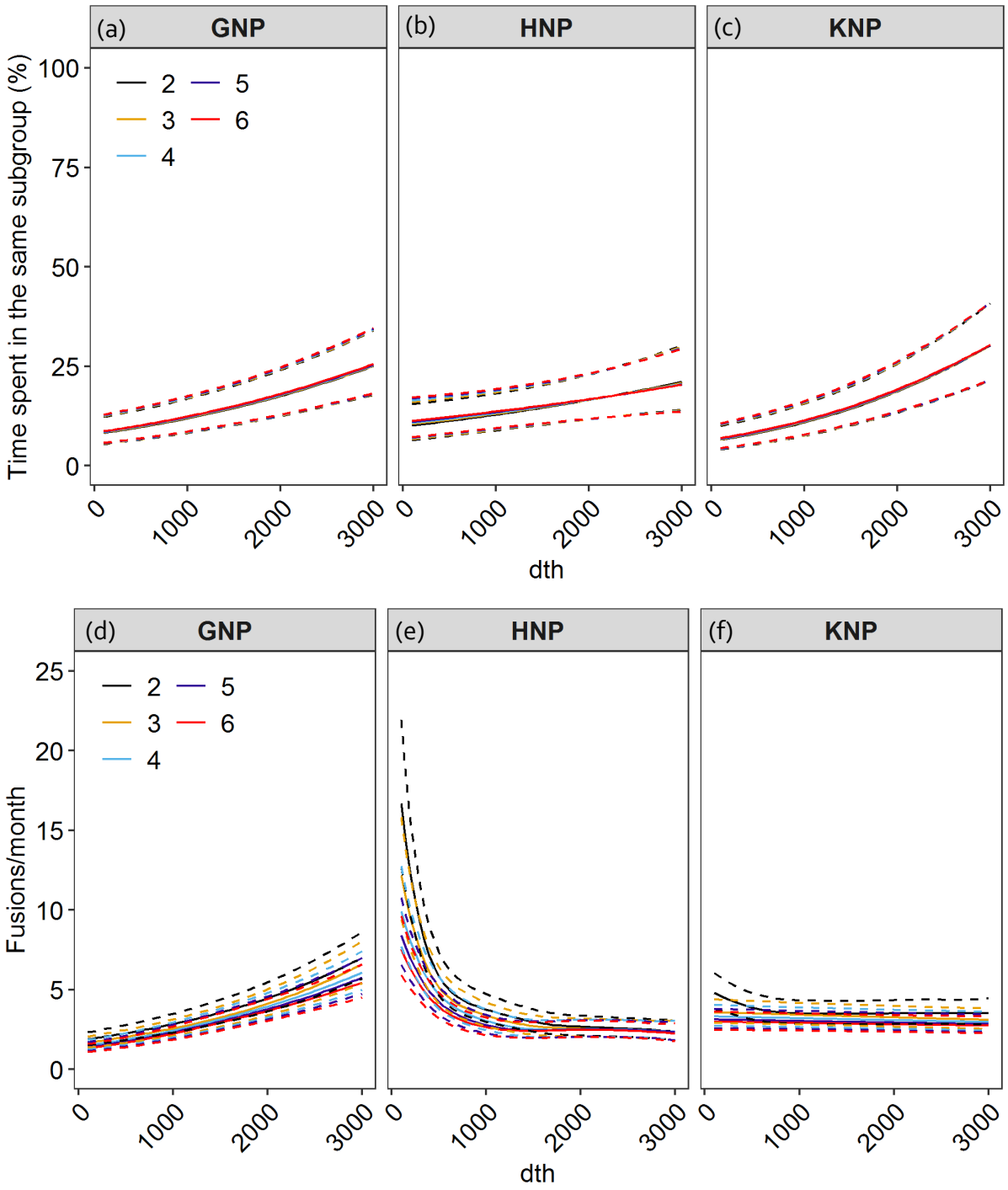


Figure S1. Results of the sensitivity analyses for each site. (a), (b), (c): Changes in the proportion of time that dyads spent together with changes in d_{th} and t_{th} ; (d), (e), (f): Changes in the number of fusion events per month per dyad with changes in d_{th} and t_{th}. Solid lines represent the predictions from the GAMMs fitted to the original data and dashed lines represent 95% confidence intervals. The colours of line correspond to the different value of t_{th} (red: t_{th} = 2; green: t_{th} = 3; blue: t_{th} = 4; purple: t_{th} = 5; orange: t_{th} = 6).

CHAPTER 4

INTER-GROUP CONTACTS IN THE CAPE BUFFALO AND RISK FOR PATHOGEN TRANSMISSION

Abstract

In social species, the transmission and maintenance of infectious diseases depend not only on the contact patterns between individuals within groups but also on the interactions between groups. In southern Africa, the Cape buffalo (*Syncerus caffer caffer*) is a vector for many pathogens that can infect nearby livestock. Whilst intra-group contact patterns of buffalo have been relatively well described, how groups interact with each other and risks for pathogen transmission remain poorly understood. I used telemetry data on 10 individuals from different groups in two populations in contrasting environments across southern Africa (Kruger National Park and Okavango Delta). Direct (*i.e.* the use of the same space at the same time) and indirect (*i.e.* the use of the same space at different times or through an intermediate vector) contact patterns were explored between individuals from neighbouring groups with variable spatiotemporal windows compatible with the transmission of pathogens carried by the Cape buffalo: bovine tuberculosis, brucellosis and Rift Valley Fever. I investigated spatial behaviour between buffalo dyads from neighbouring groups, using the overlap and proximity of their home ranges, and quantified contact rate and duration. I also examined the influence of habitat and distance to water on the location of contacts. In both study populations, neighbouring buffalo groups were highly spatially segregated in both the dry and wet seasons. Inter-group contact patterns were characterized by very few direct and short-term indirect contacts and were generally consistent across populations and seasons, suggesting a species-specific behaviour. The results highlight the importance of dry season water availability in driving the dynamics of Cape buffalo inter-group contact patterns and the risk of indirect pathogen transmission. The results from this study have important implications for the future modelling of pathogen dynamics in a single host, and the ecology and management of the Cape buffalo at the landscape level.

1 Introduction

How animals distribute themselves and move across a landscape has a strong influence on how animals interact, which in turn affects the dynamics of infectious diseases (White et al. 2017, Dougherty et al. 2018). Resource availability influences habitat selection and use, with individuals often sharing space in areas where resources are abundant (*e.g.* Jarman 1974, Brashares and Arcese 2002, Kolbe and Weckerly 2015) or when restricted, around key-limiting resource patches (*e.g.* waterholes in semi-arid areas, Redfern et al. 2003). The simultaneous use of common space promotes the spread of pathogens transmitted directly, *e.g.* by aerosols (Keeling 1999, Altizer et al. 2003, Hamede et al. 2009) or indirectly via the environment, *e.g.* through contaminated materials such as faeces (Dougherty et al. 2018). Understanding how individuals share space and interact with their conspecifics, either directly or indirectly, is thus essential for developing realistic epidemiological models and to develop effective interventions to manage infectious diseases (Craft 2015, Reynolds et al. 2015).

Space-sharing between conspecifics is strongly driven by social systems. Solitary animals generally avoid each other apart from during breeding, in instances of territorial conflicts or “randomly” due to the environmental constraints, *e.g.* in response to spatial heterogeneity in food resource availability (Mattisson et al. 2013, Elbroch and Quigley 2017). In contrast, social species often form groups in which associations between individuals, and therefore the use of common space, vary depending on whether the group is stable over a long period or subjected to fission-fusion dynamics (Aureli et al. 2008). Irrespective of the factors mediating sociality, individuals within groups usually spend a significant amount of time together, which increases the potential for pathogen transmission within social groups (Altizer et al. 2003, Chapter 3). At the landscape level, the spread of infectious diseases is also dependent on movements and interactions between neighbouring groups distributed throughout the landscape (Cross et al. 2005b, Daversa et al. 2017, Podgorski et al. 2018). Many herbivore species do not defend territories but occupy home ranges that can vary seasonally due to changes in resource abundance and distribution (Owen-Smith et al. 2010). Spatial use between groups of ungulates varies according to species and ecological context, ranging from non-exclusive home ranges but with possible time avoidance (*e.g.* mountain gazelle *Gazella gazella gazella*, Geffen et al. 1999) to exclusive home ranges (*i.e.* with little overlap between home ranges of groups, *e.g.* impala *Aepyceros melampus*, Murray 1982 and Roosevelt elk *Cervus elaphus roosevelti*, Kolbe and Weckerly 2015). Although integrating within-group interactions is central to managing infectious diseases (Blanchong et al. 2007, Grear et al. 2010), information about interactions among groups should also be taken into account, as these

interactions could have major consequences on spread and maintenance of infectious diseases at the landscape level (Thrall et al. 2000).

The Cape buffalo (*Syncerus caffer caffer*) offers a unique opportunity to explore interactions between groups and the implications for the spread of disease. Buffalo groups consist primarily of females and their offspring, subadults of both sexes, and a small proportion of adult males. Adult males can temporarily leave the group to live alone or in small bachelor groups (Sinclair 1977, Prins 1996). The relatively recent availability of telemetry data has enabled the examination of within-group social structure across several populations in relation to habitat variables (Chapter 3). However, social dynamics between groups and the moderators on inter-group contacts remain poorly understood. One study emphasized marked spatial segregation between neighbouring West African savanna buffalo *S. c. brachyceros* groups with few direct contacts between groups (W Regional Park, West Africa, Cornélis et al. 2011). Understanding the factors mediating intergroup contacts in the Cape buffalo may offer opportunities to further understand pathogen transmission at the landscape level. Buffalos carry many transmissible pathogens of economic concern, including foot-and-mouth disease, tick-borne diseases (*e.g.* theileriosis), bovine tuberculosis, brucellosis and Rift Valley Fever (Bengis et al. 2002, de Garine-Wichatitsky et al. 2010b, Caron et al. 2013, Gorsich et al. 2015). Most pathogens are carried asymptomatically by buffalos and do not pose a threat to the population's survival (Caron et al. 2003, Michel and Bengis 2012). However, they pose a serious threat when transmitted to cattle. Due to their close taxonomic relationship, buffalos represent the main threat for pathogen transmission to cattle (Bengis et al. 2002, Kock et al. 2014). Although buffalos usually avoid cattle, seasonal profiles in the risk of contact are observed, with higher spatial overlap and contact rate during the dry season when both water and forage resources are depleted or when cattle range further into protected areas in search of food (Kock 2005, Miguel et al. 2013, Zengeya et al. 2015, Valls-Fox et al. 2018). In cattle, infectious diseases inflict substantial economic losses, by decreasing livestock production or by constraining international trade. Based on 35 priority diseases, Grace et al. (2015) estimated the costs associated with livestock mortality at USD 9 billion a year in 34 countries in Africa and in Kenya, the foot-and-mouth disease caused high mortality losses in cattle with costs estimated at USD 230 million (FAO 2016), but only a part of these cases can be attributed to buffalo-cattle pathogen transmission. The risk of pathogen spillover into domestic and human populations is increasing with the extensive buffalo/cattle/human interfaces occurring where natural habitats are encroached by human settlements (Kock et al. 2014). Thus, understanding social behaviour between buffalo groups can help to apprehend the spread of pathogens into buffalo populations and the risk of spillover into domestic ruminant populations. For example, identifying the location of contacts between buffalo groups can help managers to manipulate the landscape so that each group can access key-resource

patches without having to share it with another group, and avoiding using these areas for cattle.

This study aimed to quantify and compare the spatial behaviour and contact patterns between neighbouring groups in Cape buffalo populations. I used location data from Global Positioning System (GPS) collars on Cape buffalos from two populations living in contrasting environmental conditions, *i.e.* a semi-arid savanna environment and a seasonally flooded environment. From GPS tracking, I quantified the contact patterns between buffalo dyads from neighbouring groups using different spatiotemporal windows, defining direct and indirect contacts (*i.e.* in the same area at the same time and at different times, respectively) compatible with the intraspecific transmission of important pathogens. Here, I focus on three pathogens with different modes of transmission responsible for bovine tuberculosis, brucellosis and Rift Valley fever, but the results of this study can be adapted to any other pathogen with a similar mode of transmission. Bovine tuberculosis (bTB) is most often transmitted by respiratory routes, but the disease can also spread by indirect contacts, as the virus *Mycobacterium bovis* can survive in faeces (Bengis et al. 1996, Tanner and Michel 1999, Michel et al. 2007). Brucellosis is mainly transmitted by direct or mucosal contact with a contaminated foetus, placentas or birthing fluids (Kiros et al. 2016). Rift Valley fever (RVF) is an infectious disease transmitted between animals through the bite of a female mosquito, usually *Aedes* and *Culex* spp. (Bengis et al. 2002). Buffalos play a dominant role in the maintenance of bTB and brucellosis in southern Africa, making them an important reservoir for these diseases, and are also amplification hosts for the RVF virus (Kock et al. 2014). Additionally, bTB, brucellosis and RVF are zoonotic diseases, *i.e.* transmissible to humans, and are therefore an important cause of public health concern (Alexander et al. 2012, de Garine-Wichatitsky et al. 2013). I explored seasonal changes in contact patterns and determined whether contacts occurred in specific areas in relation to resource availability. I explored whether contact patterns were similar or different between the two populations. I tested the hypotheses that (1) groups would be located closer to each other or have more overlapping home ranges during the dry season when water availability is lower, leading to more interactions and potential infectious contacts; (2) waterholes would be key areas for contacts during the dry season because limited water availability should force buffalo groups to share the same waterhole(s), and thus facilitate the transmission of pathogens. Additionally, I predicted that (3) the neighbouring groups in the seasonally flooded environment would be less constrained by water availability all year round, and thus less likely to interact with each other, compared to groups living in the savanna environment.

2 Methods

2.1 Study areas

Data used in this study were collected from two Cape buffalo populations in southern Africa. The first occupies an area at the border between Zimbabwe and South Africa, along the Limpopo River, linking the northern tip of Kruger National Park in South Africa (18 959 km², 30° 50' E – 22° 25' S) with the Sengwe communal land in Zimbabwe – a non-protected area (this population is hereafter called "KNP"). The second occupies the south-eastern area of the Okavango Delta (hereafter called "OD"), situated in northern Botswana, 15 000 km², 22° 00' E – 18° 50' S, Figure 1a). These two study sites are characterized by contrasting environmental conditions.

KNP is a semi-arid savanna primarily composed of woodland and bushland. Average annual rainfall is 450 mm, with distinct wet-dry seasons (Venter et al. 2003). Most rainfall occurs between November and March. During the wet season, grass water content is high, and water is widely distributed across the landscape in numerous natural and artificial pans and rivers. During the dry season, in my study area in the north, most natural pans have dried up and water is provided by a few permanent rivers and some pools that persist in and along the Limpopo River (Gaylard et al. 2003).

OD is an alluvial zone, consisting of permanent swamps, temporary floodplains, riverine woodlands and dry savannas that rarely flood (Ramberg et al. 2006). OD comprises a mosaic of protected lands. As in KNP, rainfall in the delta is seasonal, with an annual average of 490 mm falling mostly between November and March (McCarthy et al. 2000). Water is available all year round throughout the flooded areas. However, their extent varies seasonally: floodwaters rise from April to July and recede between August and November. Ephemeral pans are also widespread across the landscape and provide water during the wet season.

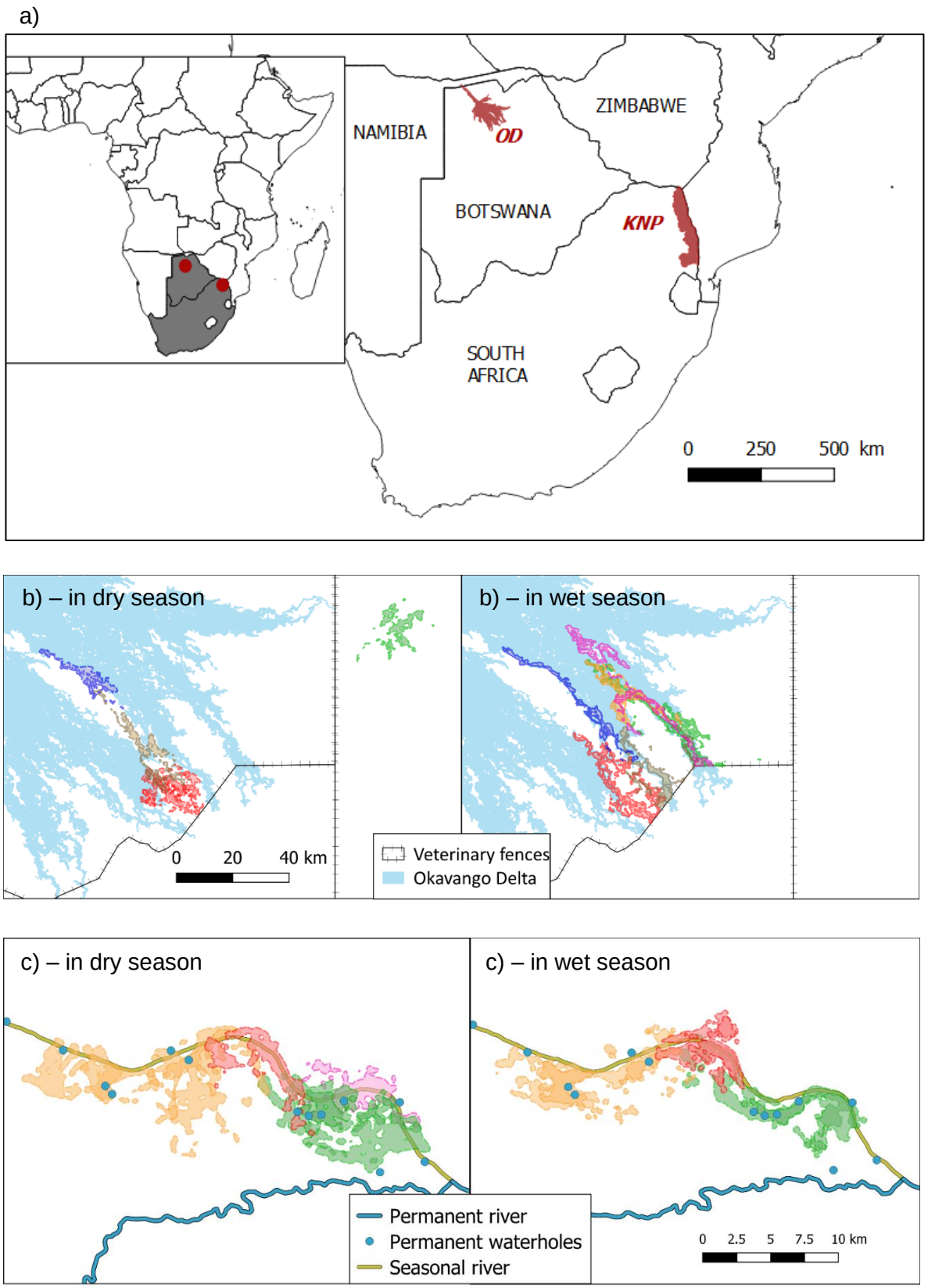


Figure 1. Location of study areas: Kruger National Park (KNP) in South Africa and Okavango Delta (OD) in Botswana. b) Locations of seasonal home ranges of the six study groups in OD and c) of the four study groups (from 6 individuals tracked at different years) in KNP during the dry (left) and wet (right) seasons.

2.2 Environmental covariates

Simplified vegetation maps were adapted from Bennitt et al. (2014) for OD and Pretorius and Pretorius (2015) for KNP. For comparative purposes, three broad habitat classes were defined according to woody cover and availability of grasses, the main food resource for buffalo: (1) grassland, including floodplains, areas dominated by grassland, or bushed grassland with sparse vegetation, (2) bushland, which consists of shrubby and bushy areas, and (3) woodland, encompassing deciduous, evergreen or riverine forests. The location of permanent water (*i.e.* rivers and waterholes) was recorded by Bennitt et al. (2015) for OD and from Google Earth at KNP (Figures 1b-1c). In both sites, due to the presence of numerous natural pans, it was difficult to quantify water availability outside of the core dry season. I, therefore, restricted the analyses to the core wet and dry seasons (hereafter called wet and dry season, respectively). I defined these periods based on the average rainfall patterns, which are similar between the sites (McCarthy et al. 2000, Venter et al. 2003). I defined the wet season as the period from the January 1st to March 31st (n = 90 days) and the dry season as the period between August 15th and October 31st (n = 78 days). Although water is available all year round, its availability and distribution change between wet and dry season, which affect movement and habitat use of buffalos (Cornélis et al. 2011, Bennitt et al. 2014). During the wet season, I considered water as a non-limiting factor in both sites.

2.3 Collaring and monitoring

Between 2007 and 2015, 31 adult female buffalos (KNP: n = 16, OD: n = 15) were tracked using GPS collars. As adult males can leave the group temporarily, cows were focused to study the movements of groups (Sinclair 1977, Prins 1996). All animals were captured by authorized personnel using established techniques (la Grange 2006) and were observed returning to their groups after collaring operations. All field operations were conducted following the legal and permit requirements of the countries in which they were carried out.

The data acquisition periods extended from June 2010 to July 2015 in KNP and from December 2007 to August 2010 in OD. Except for one collar that only acquired locations for a few hours after being deployed, the duration of the tracking varied between 54 and 1013 days (median = 383) across individuals. The GPS loggers were scheduled to acquire locations at 1-hour intervals, although a GPS fix was not always acquired when scheduled. I computed fix success rate within each season for each individual and I retained seasonal data from 23 individuals (KNP: n = 15, OD: n = 8) for which the success rate was > 80%.

2.4 Defining neighbouring groups

Buffalo cows live in large groups whose members occupy an identifiable and stable home range over time (Ryan et al. 2006, Wielgus et al. 2020). I thus identified pairs of Cape buffalo in the same groups based on high levels of home range overlap. To do so, I considered seasonal home ranges as the 90% utilization distribution during the dry and wet seasons (Börger et al. 2006). Utilization Distributions (UD) were computed using the Movement-Based Kernel Density Estimation method (MKDE, Benhamou and Cornélis 2010) implemented in the 'adehabitatHR' package in R (Calenge 2007). I examined the distribution of seasonal home range overlap between dyads (see below for home range overlap computation, Appendix 1), seeking breakpoint in distribution interpreted as indicating group membership. The distribution of seasonal home range overlap between dyads showed a set of pair with an home range overlap < 0.4 and a second set of pairs with an home range overlap > 0.6 (Appendix 1). For this reason, I considered individuals with seasonal home range overlap ≥ 0.6 to belong to the same group. I verified groupings based on both field observations and capture location, by assuming that 2 individuals captured in the same subgroup should belong to the same group. I thus explored spatial behaviour and contact patterns between six groups in OD and four groups in KNP. The movement of each group was represented by the movement of the individual with the most locations.

Exploring the contacts between individuals belonging to different groups only makes sense when individuals overlap in time and are neighbours in space and thus have adjacent (*i.e.* nearby or slightly overlapping) home ranges. To identify dyads with adjacent home ranges, I computed the minimum distance between the contours of seasonal home ranges within year, for each dyad. As buffalos can cover distances up to 8-10km in 24 hours (Sinclair 1977, Mloszewski 1983, Stark 1986, these data), I assumed that individuals whose home range limits were less than 10 km apart during the same season could still be using similar areas, albeit rarely. These rare contacts could still be important for understanding disease transmission. I considered that two individuals belong to neighbouring groups when they overlap in time and when either their seasonal home ranges overlapped or when the minimal distance between their seasonal home ranges was ≤ 10 km during at least one season. I ultimately analyzed data from 13 individuals (KNP = 6, OD = 7) and investigated the characteristics of contacts between nine pairs in KNP and 10 in OD (see Figures 1b-1c for home ranges of neighbouring study groups and Table 1).

Table 1. Number of simultaneous locations over an entire season at 5-min intervals for each dyad.

Site	Dyad identity (group membership)	Year	Number of simultaneous locations	
			Dry season	**Wet season**
OD	B1 (G1) – B2 (G2)	2008	N/A	26183
OD	B6 (G1) – B7 (G5)	2009	22224	N/A
OD	B6 (G1) – B7 (G5)	2010	N/A	22596
OD	B6 (G1) – B5 (G6)	2010	N/A	25704
OD	B6 (G1) – B5 (G6)	2009	22451	N/A
OD	B7 (G5) – B5 (G6)	2009	22224	N/A
OD	B7 (G5) – B5 (G6)	2010	N/A	22596
OD	B3 (G3) – B2 (G2)	2008	22451	N/A
OD	B3 (G3) – B4 (G4)	2008	22451	N/A
OD	B2 (G2) – B4 (G4)	2008	22451	N/A
KNP	B10 (G9) – B11 (G10)	2011	22451	N/A
KNP	B10 (G9) – B8 (G7)	2011	22451	N/A
KNP	B10 (G9) – B9 (G8)	2011	22451	N/A
KNP	B11 (G10) – B9 (G8)	2011	N/A	25907
KNP	B11 (G10) – B9 (G8)	2011	22451	N/A
KNP	B8 (G7) – B9 (G8)	2011	22451	N/A
KNP	B8 (G7) – B9 (G8)	2012	N/A	26195
KNP	B12 (G7) – B13 (G10)	2014	N/A	25907
KNP	B12 (G7) – B13 (G10)	2014	22450	N/A

Dyads were not all collared concurrently throughout seasons. N/A = not applicable.

2.5 Seasonal proximity and overlap of home ranges of neighbouring groups

To explore how neighbouring groups shared space across seasons, I measured the overlap in the seasonal home ranges between dyads from neighbouring groups using the Bhattacharyya's affinity index (Benhamou et al. 2014). The index accounts for variation in the intensity of home range use and varies from 0 (no overlap) to 1 (identical space use). I also explored seasonal variations in the minimum distance between the home range contours of dyads when home ranges did not overlap.

2.6 Definition of contact

Estimating potential contacts between animals is notoriously difficult with hourly GPS locations because at times some GPS fixes may have been missed, and contacts could have occurred between fixes. Traditionally, studies that attempt to estimate contacts between animals with one-hour GPS data use a relatively large spatial window to define contacts. This is to account that the tracked individual moves during the one-hour period between two recorded locations (*e.g.* Miguel et al. 2013). Here, I addressed this problem and reduced the risk of underestimated contacts by first interpolating each individual

trajectory using a continuous-time correlated random walk model, following the approach of Johnson et al. (2008) implemented in the R package 'crawl' (Johnson et al. 2008). Then, from these models, I predicted the location of individuals every 5 min and estimated contacts (see below) from the interpolated data.

I defined contact between 2 individuals as the presence of both individuals at the same place (defined by a spatial window) and at the same time (direct contact, within a short temporal window) or at different times (indirect contact, within a larger temporal window). To explore contact patterns between groups, I used various spatiotemporal windows defining direct and indirect contacts compatible with the modes of transmission of three important pathogens in buffalo: bovine tuberculosis, brucellosis and Rift Valley Fever, which are present in my two study areas with different prevalence levels (see Table 2). Bovine tuberculosis (bTB) can spread both by direct and indirect contacts, as the virus can survive in faeces for up to one month in natural conditions in southern Africa (Tanner and Michel 1999). Brucellosis is mainly transmitted by direct or mucosal contact with a contaminated foetus, placentas or birthing fluids (Kiros et al. 2016). Since the bacteria can persist in a bovine foetus for several weeks, or even months in temperate regions (Aune et al. 2011), the most limiting transmission factor seems to be the persistence of the contaminated foetus in the environment before being eaten by scavengers. To estimate the persistence of a foetus in the environment, de Garine-Wichatitsky et al. (unpublished data) placed, in November 2010, 10 mixed offal-meat bags (mimicking foetuses) inside Gonarezhou National Park, around Mabalauta region (Zimbabwe) and in open areas in Malipati Communal Land. The results showed that the bait bags persisted for 43h on average (range: 6h-71h) before being removed by scavenging carnivores such as domestic dog *Canis familiaris*, spotted hyena *Crocuta crocuta* and black-backed jackals *Canis mesomelas*. The main factors that may limit the transmission of RVF virus from mosquito to buffalos are the lifespan of mosquitoes and their ability to disperse. According to mark-release-recapture studies, female mosquitoes do not live for more than 3 weeks (Rodhain 1996, Ba et al. 2006). Estimating that buffalos spend an average of 4 days in an infectious state, as in other ruminants (Manore and Beechler 2015), a buffalo may be able to transmit the virus within one month of infection. Mosquitoes can fly over considerable distances, ranging from a few hundred meters up to 2500m (Shannon and Davis 1930, Wolfinsohn and Galun 1953, Ba et al. 2006).

For each pathogen, I selected relevant spatiotemporal windows to define contacts that could lead to infectious contacts and pathogen transmission, should one of the individuals excrete the target pathogen at the time of the contact (Table 2).

Table 2. Characteristics of selected pathogens transmitted between buffalos and corresponding spatiotemporal windows chosen to define contacts. The spatial windows consider the mode of transmission of the pathogen (*i.e.* at close proximity through the air or transmitted at a longer distance by a vector) and the time windows are defined as the time a site remains potentially infectious after contamination by an infected buffalo. [1]Rodwell et al. 2001, [2]Jori et al. 2013, [3]Chaparro et al. 1990, [4]Alexander et al. 2012, [5]Beechler et al. 2015, [6]Jori et al. 2015. na = no data.

Disease name	Pathogen	Prevalence (%) in buffalo at each site [95% CI] (*n* = Total number of buffalo sampled)	Mode of transmission	Spatial-window	Time-window	Contact name
Bovine tuberculosis (bTB)	*Mycobacterium bovis*	KNP_{north}: 1.5% [0.4–4.0] (*n* = 203)[1] OD: 2.9% [0.8–9.8] (*n* = 70)[2]	Inhalation of aerolized droplets	150m	0h	Direct contact
			Inhalation or ingestion of infected materials (*e.g.* faeces)	150m	0-31 days	Long-term indirect close contact
Brucellosis	*Brucella abortus*	KNP: 19.2% [na–na] (n = 406)[3] OD: 6% [3.0–9.0] (*n* = 247)[4]	Contact with or ingestion of infected foetus or other abortion products	150m	0-2 days	Short-term indirect close contact
Rift Valley Fever (RVF)	Rift Valley Fever virus	KNP_{north}: 3.6% [na – na] (*n* = 196)[5] OD: 9.7% [4.0–19.0] (*n* = 72)[6]	By the bite of a female mosquito (Aedes/Culex)	2500m	0-31 days	Long-term indirect contact at large spatial scale

2.7 Contact analysis

For each buffalo dyad and each spatiotemporal window, I identified the time and place of contacts. The location of an individual of a given dyad was defined as a pathogen-specific contact location when, during the previous period defined by the temporal window, at least one GPS location of the other buffalo in the dyad was within a distance lower than the spatial window. For instance, for brucellosis, the location of a buffalo was considered as a contact location when at least one GPS location of the other buffalo was located ≤ 150 m within the two days preceding the time of that GPS location. If several successive locations were defined as contacts, I considered these locations as a single contact and calculated its duration, as the duration of contacts is likely to be an important factor in pathogen transmission. Contact occurrence was used to calculate the number of contacts per dyad per month (hereafter called contact rate) as the total number of contact events divided by the number of months of simultaneous tracking.

2.8 Statistical analyses

As an individual could be represented in several dyads with individuals from different neighbouring groups, I used hierarchical (*i.e.* mixed) models with dyad identity as a random intercept. I first tested whether the home range overlap of dyads from neighbouring groups and the spatial proximity between their home ranges varied across seasons and sites. I ran two generalized linear mixed models (GLMMs) with (1) home range overlap and (2) distance between contours of home ranges as the response variables. In both models, I used a negative binomial distribution of errors and the explanatory variables were site, season and their interaction.

I then explored the number and duration of contacts between dyads of neighbouring groups across seasons and sites. As the contacts were described for 4 spatiotemporal windows (Table 2), I built one model for each spatiotemporal window, both for the number and duration of contacts. To account for overdispersion in the contact rates and durations, I fitted 8 negative binomial GLMMs with the contact rate as the response variable for 4 of them and the duration of every contact for the rest. The relatively small sample size for dyads displaying direct and short-term indirect contacts during the wet season in both sites did not allow to test the influence of the season and the site during the wet season on rate and duration of these contacts (Figures 3a-3b). I, therefore, explored the inter-site effect on duration and rate of direct and short-term indirect contacts only during the dry season. For analyses of long-term indirect contacts, I included site, season and their interaction as explanatory variables.

Finally, I explored how buffalos distributed themselves according to distance from permanent water in the dry season between sites and the probability of contact between dyads from neighbouring groups in relation to distance from permanent water sources (only in the dry season) and vegetation type (in the dry and wet seasons). As I considered water as a non-limiting factor during the wet season, I examined whether buffalo distribution according to distance to water differed between sites and whether the location of contacts was influenced by distance to water during the dry season only. I extracted the distance to the nearest permanent water source and the vegetation type for every buffalo GPS location. For each buffalo dyad, I then classified the locations of each of the two individuals as a contact or not depending on the different spatiotemporal windows. To test whether site affected buffalo distribution according to permanent water during the dry season, I used a GLMM with a Poisson distribution, distance to water as the response variable, and site as the explanatory variable. In this model, the random effect was buffalo identity. To determine whether distance to water and habitat type affected the probability of contact, I ran 4 GLMMs for the dry season GPS locations, *i.e.* one corresponding to each spatiotemporal window, with a binomial distribution of errors. In each model, the binary response variable was the location type, *i.e.* whether the location was a contact (scored 1) or not (scored 0), and the explanatory variables were the distance to water, associated vegetation type, site and the interactions between site and distance to water and between site and vegetation type. GLMMs for the wet season locations were similar without distance to water as explanatory variable, and the GLMMs were built only for long-term indirect contacts. The direct and short-term indirect contact analyses could only be done on dry season data due to the low number of these contacts in the wet season.

For each analysis, I tested whether a simpler model, nested in the full model, would be more parsimonious using the Akaike's Information Criterion corrected for small sample size (AICc, Burnham and Anderson 2002). Model sets are presented in Table 3. I considered the most parsimonious model to be the model that had both an ΔAICc < 2 and the lowest number of explanatory variables (Arnold 2010). The goodness-of-fit of the models was assessed using the marginal theoretical coefficient of determination (r^2) for the binomial GLMMs and the marginal lognormal r^2 for the negative binomial GLMMs using the MuMIn package (function r.squaredGLMM, Barton 2019). Statistical models were computed using the lme4 (Bates et al. 2015) and glmmTMB (Brooks et al. 2017) packages for R v. 3.3.2 (R Development Core Team 2016).

3 Results

Table 3. Summary of the candidate models fitted for each analysis. Response variables were modelled as a function of different combinations between site (KNP or OD), season (dry or wet season), distance to water and vegetation type (Grassland, Bushland, Woodland). Dyad identity was included as a random intercept in the models, except for analysis 5, where the random intercept was the buffalo identity. Direct and short-term indirect contacts were only statistically explored during the dry season due to the quasi-absence of these contacts during the wet season.
***Notes*: For each model, the degree of freedom (df), deviance = -2*loglikelihood (-2LL), the difference in AIC_c values between the best fit and $model_i$ (ΔAIC_c), model fit estimated by marginal r^2 (see text for details) – Higher values indicate better model fit. The ranking was based on the ΔAIC_c. The best model, *i.e.* which had both a $\Delta AICc < 2$ and the lowest number of explanatory variables, is shown in bold for each analysis.**

Model	*df*	-2LL	ΔAIC_c	$R^2_{marginal}$
1. Home range overlap				
null	**3**	**8.49**	**0.0**	**0.00**
site	4	8.27	3.0	0.06
season	4	8.46	3.2	0.01
site + season	5	8.25	6.8	0.07
site*season	6	8.24	11.2	0.08
2. Distance between home ranges				
season	**4**	**88.60**	**0.0**	**0.16**
site*season	6	82.86	2.4	0.24
site + season	5	87.43	2.6	0.27
null	3	250.20	158.4	0.00
site	4	248.80	160.2	0.15
3. Frequency of contacts				
Direct contacts (only in dry season)				
null	**3**	**25.13**	**0.0**	**0.00**
site	4	25.11	4.7	0.00
Long-term indirect contacts				
season	4	153.57	0.0	0.01
null	**3**	**157.89**	**1.8**	**0.00**
site + season	5	152.89	2.0	0.08
site	4	157.10	3.5	0.07
site*season	6	152.73	4.7	0.09
Short-term indirect contacts (only in dry season)				
null	**3**	**62.96**	**0.0**	**0.00**
site	4	61.93	1.9	0.12
Long-term indirect contacts at large spatial scale				
null	**3**	**148.95**	**0.0**	**0.00**
site	4	147.45	1.0	0.11
season	4	147.65	1.2	0.02
site + season	5	146.28	2.5	0.13
site*season	6	144.46	3.5	0.22
4. Duration of contacts				
Direct contacts (only in dry season)				
null	**3**	**88.30**	**0.0**	0.00
site	4	87.66	2.0	0.03

Long-term indirect contacts				
site	**4**	**2718.32**	**0.0**	**0.13**
site + season	5	2717.17	0.9	0.13
site*season	6	2717.10	2.9	0.13
null	3	2725.76	5.4	0.00
season	4	2725.47	7.2	0.00
Short-term indirect contacts (only in dry season)				
site	4	493.57	0.0	0.05
null	**3**	**497.45**	**1.7**	**0.00**
Long-term indirect contacts at large spatial scale				
null	**3**	**1588.32**	**0.0**	**0.00**
site	4	1588.31	2.1	0.00
season	4	1588.32	2.1	0.00
site + season	5	1588.31	4.2	0.00
site*season	6	1588.14	6.2	0.00
5. Distance to water during the dry season				
site	**4**	**140800000**	**0.0**	**0.76**
null	3	140800000	15.2	0.00
6. Occurrence of contacts according to distance to water and vegetation type in dry season				
Direct contacts				
Distance to water * site + Vegetation type * site	**9**	**4635.36**	**0.0**	**0.38**
Distance to water * site + Vegetation type	7	4653.86	14.5	0.35
Distance to water + Vegetation type * site	8	4665.17	27.8	0.35
Distance to water + Vegetation type	5	4676.54	33.2	0.10
Distance to water + Vegetation type + site	6	4675.84	34.5	0.34
Vegetation type * site	7	4688.42	49.1	0.31
Vegetation type	4	4695.04	49.7	0.04
Vegetation type + site	5	4693.97	50.6	0.31
Distance to water * site	5	4721.98	78.6	0.27
Distance to water	3	4746.82	99.4	0.01
Distance to water + site	4	4745.89	100.5	0.26
null	2	4752.43	103.1	0.00
site	3	4751.32	104.0	0.25
Long-term indirect contacts				
Distance to water * site + Vegetation type * site	**9**	**76956.00**	**0.00**	**0.11**
Distance to water + Vegetation type* site	8	77045.28	87.3	0.11
Distance to water* site + Vegetation type	7	77176.72	216.7	0.10
Distance to water + Vegetation type	5	77243.78	279.8	0.17
Distance to water + Vegetation type + site	6	77242.94	280.9	0.10
Distance to water * site	5	77657.48	693.5	0.09
Distance to water	3	77717.36	749.4	0.15
Distance to water + site	4	77716.72	750.7	0.09
Vegetation type* site	7	82069.20	5109.2	0.00

Vegetation type	4	82127.72	5161.7	0.00
Vegetation type + site	5	82127.70	5163.7	0.00
null	2	82302.04	5332.0	0.00
site	3	82302.02	5334.0	0.00
Short-term indirect contacts				
Distance to water * site + Vegetation type * site	**9**	**26066.96**	**0.00**	**0.14**
Distance to water + Vegetation type* site	8	26109.36	40.4	0.14
Distance to water* site + Vegetation type	7	26169.50	98.5	0.13
Distance to water + Vegetation type	5	26190.28	115.3	0.01
Distance to water + Vegetation type + site	6	26189.28	116.3	0.13
Distance to water * site	5	26574.68	499.7	0.13
Distance to water	3	26611.14	532.2	0.00
Distance to water + site	4	26610.18	533.2	0.14
Vegetation type* site	7	26841.88	770.9	0.14
Vegetation type	4	26878.32	801.4	0.00
Vegetation type + site	5	26877.66	802.7	0.14
Null	2	27146.58	1065.6	0.00
site	3	27145.94	1067.0	0.14
Long-term indirect contacts at large spatial scale				
Distance to water * site + Vegetation type * site	**9**	**142834.14**	**0.00**	**0.05**
Distance to water + Vegetation type* site	8	142857.70	21.6	0.05
Distance to water* site + Vegetation type	7	143418.38	580.2	0.05
Distance to water + Vegetation type	5	143422.86	580.7	0.04
Distance to water + Vegetation type + site	6	143421.46	581.3	0.05
Distance to water * site	5	143735.64	893.5	0.05
Distance to water	3	143740.10	8934.0	0.03
Distance to water + site	4	143738.84	894.7	0.04
Vegetation type* site	7	146967.16	4129.0	0.03
Vegetation type	4	147357.42	4513.3	0.00
Vegetation type + site	5	147356.94	4514.8	0.03
Null	2	147448.84	4600.7	0.00
site	3	147448.40	4602.3	0.03
7. Occurrence of contacts according to distance to water and vegetation type in wet season				
Long-term indirect contacts				
Vegetation type * site	**7**	**32722.68**	**0.00**	**0.05**
Vegetation type	4	32748.76	20.1	0.03
Vegetation type + site	5	32748.52	21.9	0.04
Null	2	33344.42	611.7	0.00
site	3	33344.28	613.6	0.01
Long-term indirect contacts at a large spatial scale				
Vegetation type * site	**7**	**93422.22**	**0.00**	**0.14**
Vegetation type	4	95124.16	1696.0	0.10
Vegetation type + site	5	95123.78	1697.6	0.12

Null	2	101477.56	8045.3	0.00
Site	3	101476.74	8046.5	0.03

3.1 Spatial behaviour between neighbouring groups

The observed values of the overlapping home range and the distance between home ranges between individuals from neighbouring groups are plotted on Figures 2a-2b, respectively. The most parsimonious model of home range overlap variation did not include the effects of site or season (Table 3 – analysis 1), suggesting that neighbouring buffalo groups had home ranges consistently overlap across seasons and sites (β ± SE = -2.68 ± 0.85, 95% CI = [-4.35, -1.02]). Although visual interpretation indicates that groups were further apart in the OD during the wet season (Figure 2b), model selection indicated no effect of site, but there was a seasonal effect (Table 3 – analysis 2). Groups were thus further apart during the wet season (β ± SE = 0.68 ± 1.14, 95% CI = [-1.56, 2.91]) compared to the dry season (β ± SE = -1.77 ± 1.14, 95% CI = [-4.02, 0.47]).

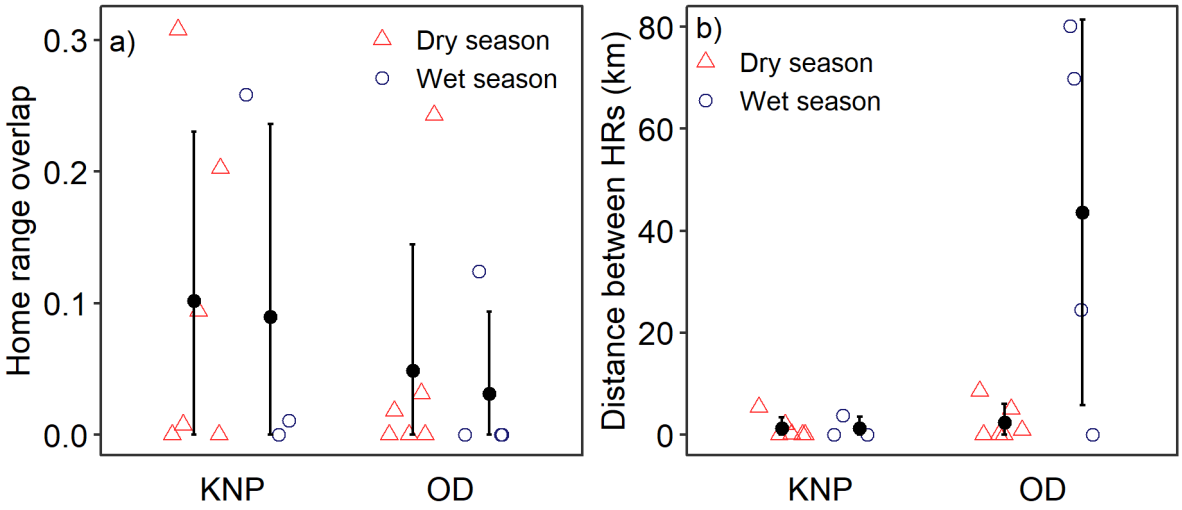


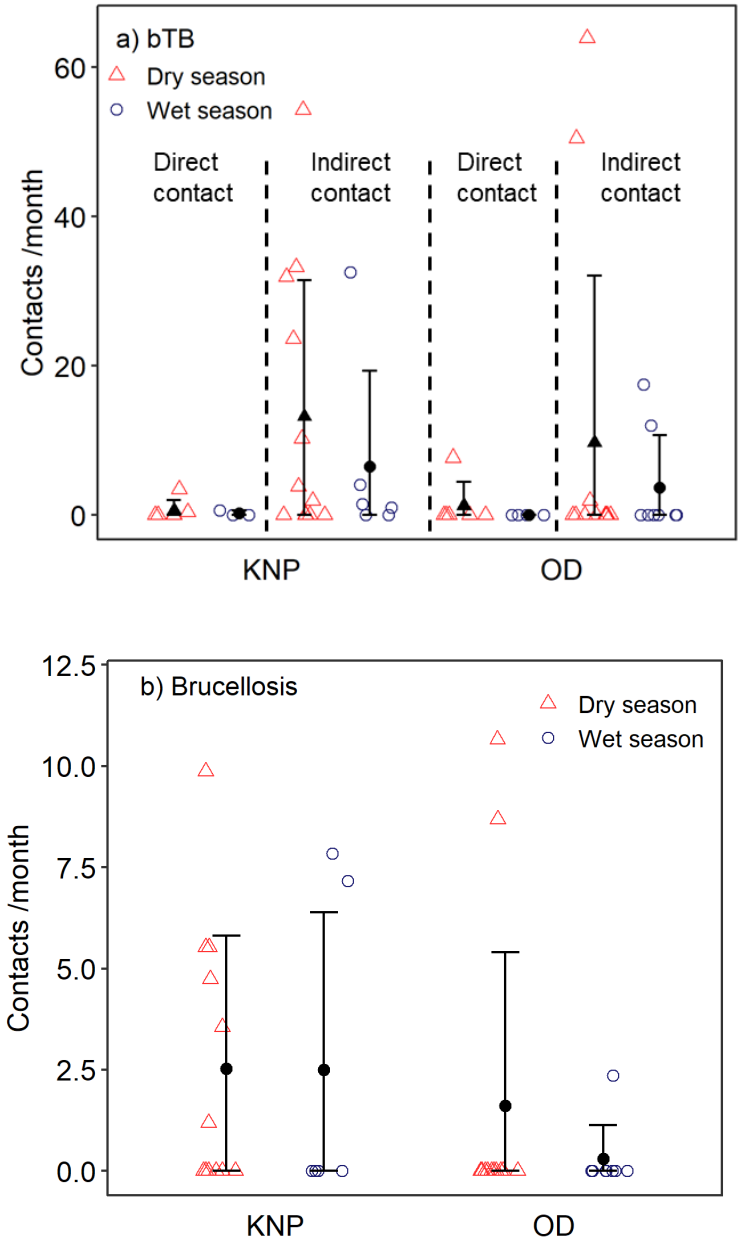
Figure 2. a) Home range overlap (Bhattacharyya's affinity index) and b) minimum distance between home ranges of buffalo dyads belonging to different groups by site and season. The observed values are given by open symbols. The filled symbols are mean values and the whiskers denote SDs.

3.2 Contacts characteristics

A total of 32 direct contacts were recorded, with 12 in KNP and 20 in OD (Figure 3a). Indirect contacts were more frequent, ranging from 177 for short-term indirect close contact (brucellosis, KNP: n = 121, OD: n = 56, Figure 3b), to 567 for long-term indirect close contact (bTB, KNP: n = 326, OD: n = 241, Figure 3a), and 176 for long-term indirect contacts at large spatial scale (RVF, KNP: n = 135, OD: n = 41, Figure 3c). The most parsimonious models for explaining contact rates were the null models, suggesting that buffalo groups

consistently interact directly and indirectly with each other across seasons and sites (Table 3 – analysis 3).

The observed values of the duration of intergroup contacts are plotted in Figure 4 by site and season. Model selection suggested that the duration of contacts was generally consistent across seasons and/or sites (Table 3 – analysis 4). The only exception is for the duration of long-term indirect contacts compatible with bTB transmission, where the most parsimonious model included the effect of site, but the difference between sites was minor (Table 5). Summary statistics of the most parsimonious models predicting contact rates and duration of contacts are given in Tables 4–5, respectively.



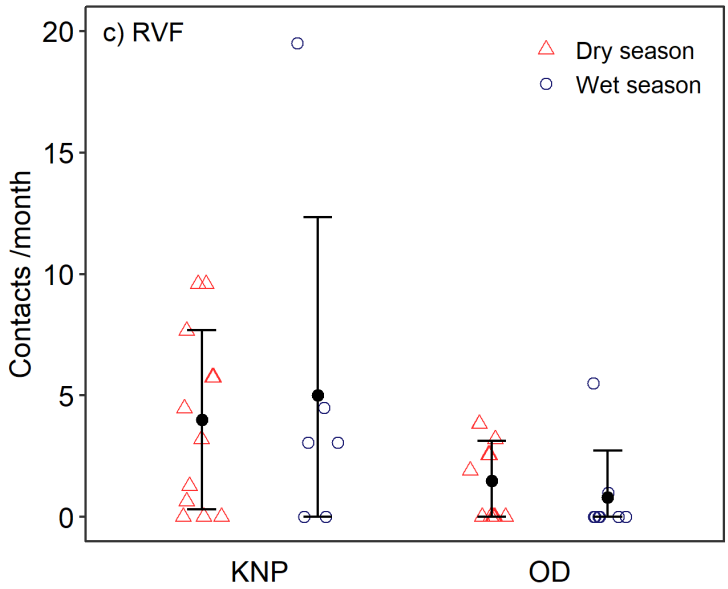


Figure 3. Direct and indirect contact rates between buffalo dyads belonging to neighbouring groups for each selected pathogen: a) bTB for direct and indirect contacts, b) Brucellosis and c) RVF, in relation to the site and the season. The observed values are given by open symbols. The filled symbols are mean values and the whiskers denote SDs. Note different y-axis scales.

Table 4. Coefficient (β) ± SE and 95% confidence intervals of the most parsimonious models explaining the direct and indirect contact rates between buffalo dyads belonging to neighbouring groups. Models explaining rates of direct and short-term indirect contacts were only based on dry season data.

	β ± SE	95%CI (lower, upper)
Direct contact		
(Intercept)	-3.83 ± 2.65	(-9.01, 1.36)
Long-term indirect close contact		
(Intercept)	-0.94 ± 1.33	(-3.55, 1.66)
Short-term indirect close contact		
(Intercept)	-5.00 ± 1.18	(-7.32, -2.67)
Long-term indirect contact at large spatial scale		
(Intercept)	0.28 ± 0.45	(-0.60, 1.16)

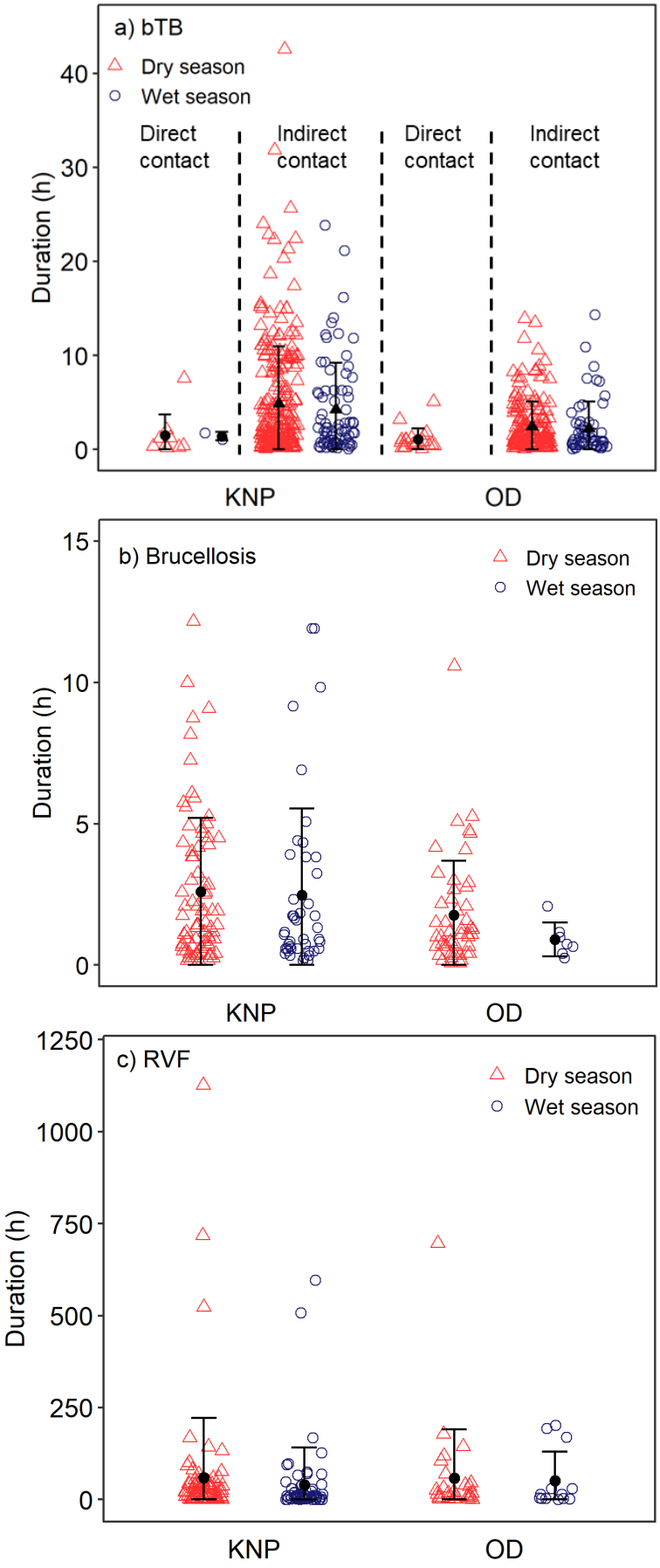


Figure 4. Duration of direct and indirect contacts (in hours) between buffalo dyads belonging to neighbouring groups for each selected pathogen: a) bTB for direct and indirect contacts,

b) Brucellosis and c) RVF, in relation to the site and the season. The observed values are given by open symbols. The filled symbols are mean values and the whiskers denote SDs. Note different y-axis scales.

Table 5. Coefficient (β) ± SE and 95% confidence intervals of the most parsimonious models explaining the duration of direct and indirect contacts between buffalo dyads from neighbouring groups. Models explaining the duration of direct and short-term indirect contacts were only based on dry season data.

	β ± SE	95%CI (lower, upper)
Direct contact		
(Intercept)	0.18 ± 0.20	(-0.21, 0.58)
Long-term indirect close contact		
(Intercept)	1.55 ± 0.07	(1.42, 1.69)
Site [OD > KNP]	-0.68 ± 0.10	(-0.88, -0.48)
Short-term indirect close contact		
(Intercept)	0.83 ± 0.11	(0.62, 1.05)
Long-term indirect contact at large spatial scale		
(Intercept)	3.64 ± 0.33	(2.99, 4.29)

3.3 Location of contacts

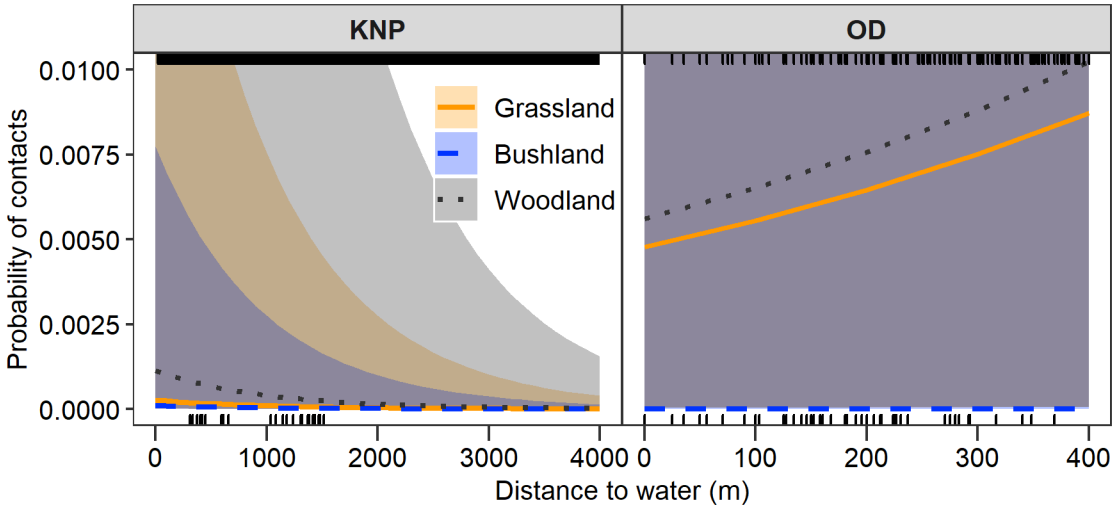
During the dry season, the distribution of buffalo in relation to distance to water varied between sites, as the most parsimonious model explaining the distance to the water of buffalos included a site effect (Table 3 – analysis 5). Buffalos were, therefore, closer to water in OD (odds ratio ± SE [95%CI]: 213.15 ± 52.13 [132.58 – 342.68] m) than in KNP (1787.90 ± 430.40 [568.22 – 5625.26] m).

I also found that the most parsimonious models that explained the probability of direct and indirect contact during the dry season included an interaction effect between site and distance to water, and site and vegetation type (Table 3 – analysis 6). However, the difference in the relationship between distance to water and probability of contact between sites could be simply due to the variation in the distribution of buffalo in relation to the distance to water (see above). In KNP, the probability of contact decreased with distance to water (Figure 5) whilst in OD, the relationship between the distance to water and probability of contact is less clear: the probability of long-term indirect contact at large spatial scale decreased with distance to water (Figure 5d) whilst the other contacts were more likely to occur when the distance to water increased (Figures 5a–5c). However, the effect of distance to water on the probability of contact in OD was weak, and with very large confidence intervals, which prevented me from assuming an effect of distance to water on the probability of contact in OD (Figure 5). Model selection indicated an effect of vegetation type in interaction with the site on the probability of contact (Table 3 – analysis 6). The minimal overlap in confidence intervals was for short-term indirect contact compatible with

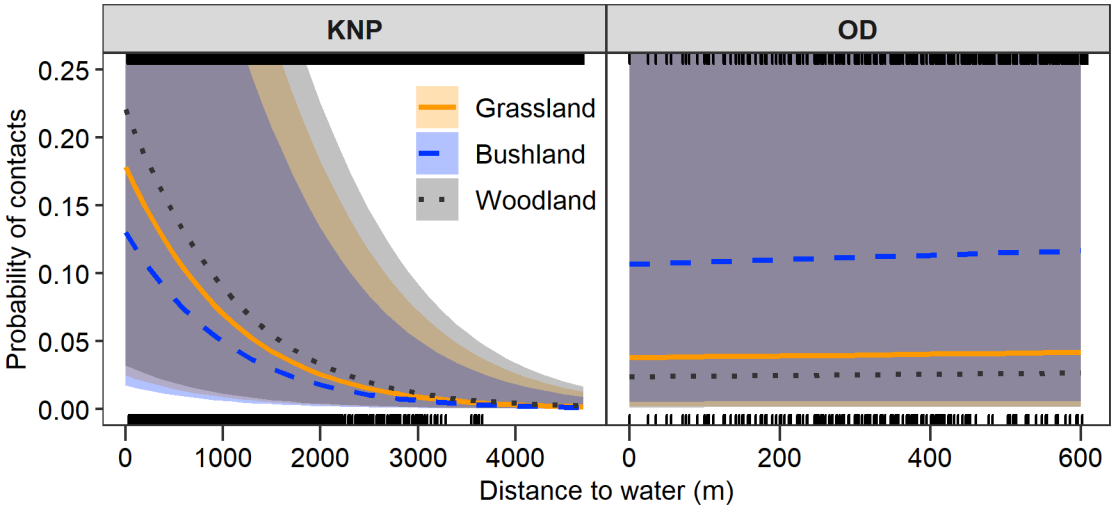
brucellosis transmission in KNP, where probabilities differed between vegetation types: contacts were more likely to occur in woodlands than in bushlands and grasslands (Figure 5c). For the other types of contact, I did not identify any vegetation types where contacts were more likely to occur due to the small difference in the probability of contact between vegetation types and the large overlap of the confidence intervals.

During the wet season, the vegetation type and the site affected the probability of long-term indirect contact (Table 3 – analysis 7). The influence of vegetation type on probability of contact for bTB was weak in both sites and with large confidence intervals considerably overlapping, which prevented me from identifying any vegetation types where these contacts were more likely to take place (Figure 5b). Similarly, I did not identify any vegetation types in OD where contacts compatible with RVF transmission were more likely to occur (Figure 5d). In contrast, in KNP, the probability of contact compatible with RVF transmission differed among vegetation types and the overlap between confidence intervals of different vegetation types was low, indicating that these contacts were more likely to occur in woodlands during the wet season (Figure 5).

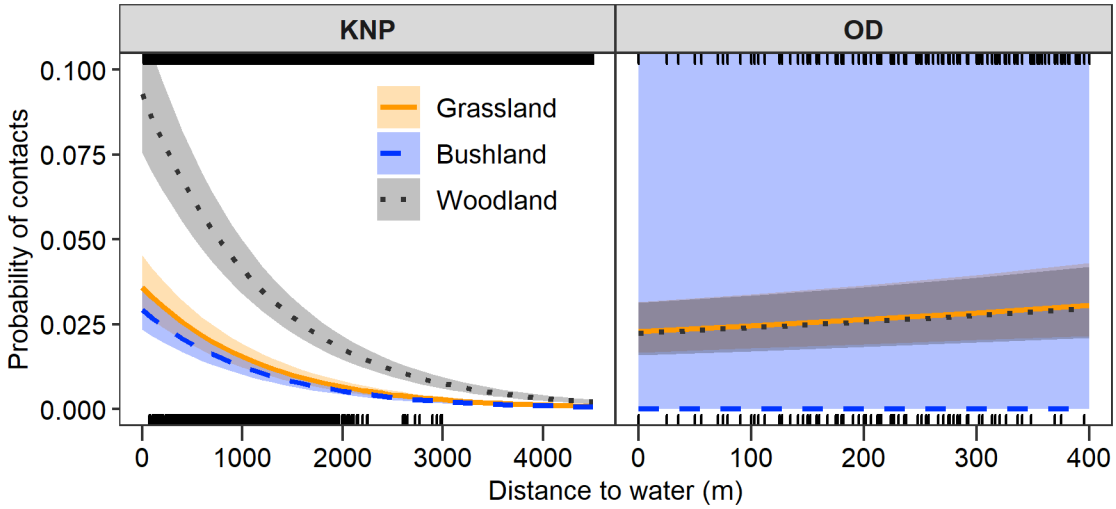
a) bTB direct contacts in dry season



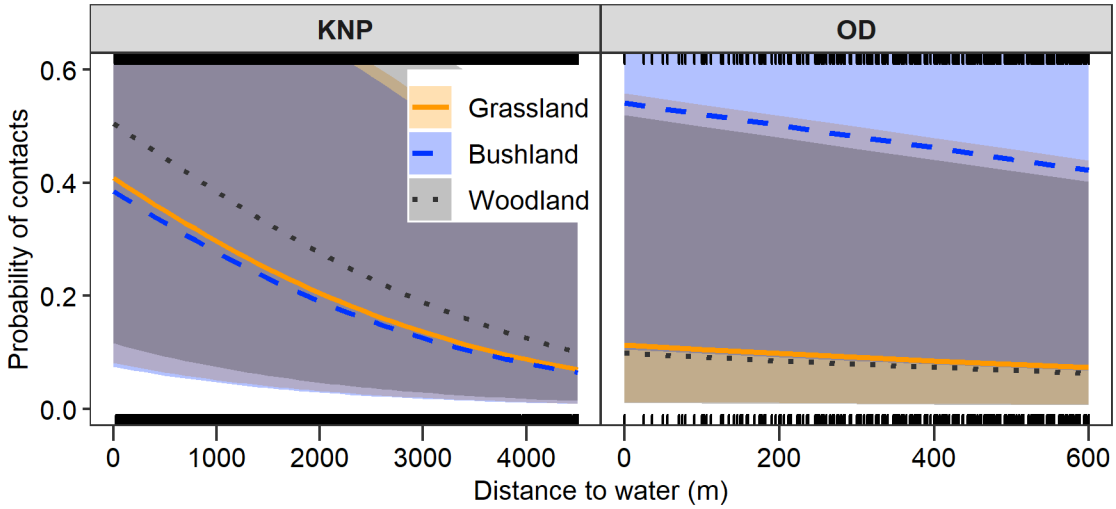
b) bTB long-term indirect contacts in dry season



c) Brucellosis short-term indirect close contacts in dry season



d) RVF long-term indirect contacts at large spatial scale in dry season



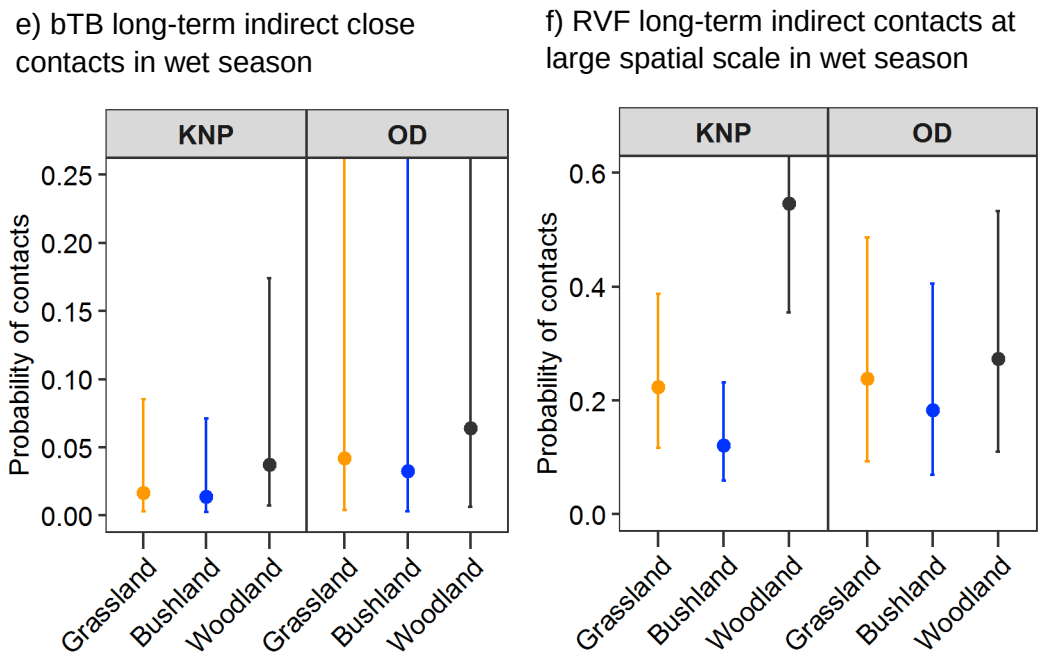


Figure 5. Predicted probability of direct and indirect contact according to site, distance to permanent water and vegetation type during the dry season (a-d) and according to site and vegetation type during the wet season, only for long-term indirect contacts (e-f). Shaded areas and error bars represent 95% confidence intervals. The distance to water during the dry season at the observed locations are plotted by tick marks, with marks at the bottom corresponding to the contact locations and marks at the top to the non-contact locations. Note the different y-axis and x-axis scales. a-d) Note that the confidence intervals considerably overlap between habitat types, explaining why the colours are not easily apparent.

4 Discussion

The spread of infectious diseases in natural populations is a spatial process facilitated by interactions amongst hosts (Altizer et al. 2003). For social species, understanding how groups interact with each other is crucial for predicting the spatial spread of pathogen at the population scale. In this chapter, I used GPS data to assess spatial behaviour and contact patterns between buffalo groups in two populations living in contrasting environmental conditions. Using bTB, brucellosis and RVF viruses as case studies to define contacts, I demonstrate that (1) contact patterns between buffalo groups are generally similar between seasons and sites, indicating a potential species-specific pattern, (2) direct contacts are very rare and (3) waterholes are key determinants of buffalo intergroup contact in semi-arid savannas, such as KNP, where water sources are scarce and patchily distributed. These findings could be particularly important for understanding and predicting the spread of pathogens in this species and the risks posed to other species, including cattle.

At the population scale, it is acknowledged that direct contacts critically affect pathogen transmission and, ultimately, disease prevalence. A recent study of the KNP Cape

buffalo population estimated that direct contact rates among individuals in the same group ranged from 2.7 to 17 per month and lasted, on average, 24h and 40h during the wet season and dry season, respectively (Wielgus et al. 2020). In this same population, I found that direct contacts between individuals from neighbouring groups were much rarer, on average 0.2 and 0.6 in the wet and dry season, respectively (0 and 1.3 in OD in the wet and dry season, respectively). The quasi-absence of contacts between neighbouring groups is consistent with previous work on the West African buffalo (Cornélis et al. 2011). Pathogens with a direct transmission mode like bTB, therefore, have a lower probability of spreading between groups and over large distances. Conversely, my findings highlight the importance of contacts between buffalo groups for the population-wide transmission of pathogens that persist in the environment for a long time or are vector-borne, such as bTB and RVF viruses (my study) and foot-and-mouth disease virus than can survive in the environment for up to 15 days (Miguel et al. 2013). Taken together, these results suggest frequent local extinction of pathogens with only a direct mode of transmission if the group size is not large enough or the transmission of pathogens cannot occur through other species. Bovine tuberculosis transmission opportunities would be much more frequent through the indirect route (*i.e.* through inhalation or ingestion of contaminated materials) than the direct route. For RVF, the involvement of a vector (*i.e.* mosquito) increases the factors that can influence the transmission such as vector capacity and density, and susceptible hosts (Chitnis et al. 2013, Manore and Beechler 2015).

I did not identify any vegetation types in OD where contacts were more likely to occur, but I found that woodlands in KNP may be favoured place for some indirect contacts, depending on the season. Additionally, I found that contacts were more likely closer to water holes, but only in KNP where water is more of a limiting factor. In the north of KNP, water is very scarce during the dry season with only one permanent river and some permanent pools remaining in a dry riverbed (Figure 1). Dry-season water availability constrains water-dependent buffalos to aggregate within a few kilometres from available water and therefore increases intergroup contacts. In contrast, in OD, the wetland system progressively dries up as the dry season progresses, but water remains available over a large area. I hypothesized that the higher abundance and wide distribution of water and productive forage across the landscape in OD would lead to fewer levels of contact between groups than in KNP, but the rate and duration of contacts did generally not appear to be affected by such environmental factors. The only exception was for long-term indirect contacts compatible with bTB transmission, which significantly lasted longer in KNP (mean ± SD: 4.7 ± 5.8h) than in OD (2.4h ± 2.7h), but the magnitude of this site effect was small. Based on these findings, I hypothesize that the structure of intergroup contact patterns is specific to the species, but that surface waterholes are hotspots for contact, and associated pathogen spread, during the dry season in areas where water availability is low.

In the northern areas of KNP, it was decided in 1994 to close more than half of the waterholes to limit the impact of elephants and facilitate co-existence between water-dependent and water-independent ungulates (Gaylard et al. 2003). As I showed that contacts tend to occur closer to water in KNP, efforts to reduce the number of water points may have contributed to the transmission of pathogens among buffalo groups. Notably, this may explain in part the progressive spread of bTB from southern KNP to adjacent Gonarezhou National Park, Zimbabwe, which occurred from the 1990s, corresponding approximately to the period when artificial waterholes were closed down (Caron et al. 2003). My results suggest that in the dry season, plans to control the spread of diseases within the KNP buffalo population should focus on the management of water availability. Managers can try to manipulate the landscape in such a way so that each group can access water without having to share it with another group. For instance, ensuring that the distance between waterholes is sufficiently large (> 5 km) should allow distinct buffalo groups to establish their home ranges with minimal overlap.

A potential limitation of this study is that the data were not collected during the same period in both populations. Although I used fixed dates for defining seasons, small differences in resource availability within seasons among years (*e.g.* drought year) could drive potential differences in observed spatial behaviour and affect interpretation. However, the similar contact patterns between populations and seasons suggest that this difference in the period of data collection does not affect the result. The aim of this study was not to estimate the total number of contacts between buffalo groups because this would have required excessive resources to equip all buffalos with GPS collars. Instead, I took advantage of the gregarious habits of buffalo that move in groups and use a similar home range (Sinclair 1977, Ryan et al. 2006) to capture the movements of the groups and to examine the factors moderating contact patterns. However, my data probably underestimate contact rates because (1) a buffalo from one group may have come into contact with several individuals from another group, (2) groups could have encountered small bachelor groups (Sinclair 1977, Hay et al. 2008), (3) buffalo groups are subject to fission-fusion dynamics (Bennitt et al. 2018, Chapter 3), which means that all individuals of the same group are not constantly together, (4) groups can be widely dispersed, for instance of several hundred meters when a buffalo group arrives at a waterhole (Chamaillé-Jammes and Wielgus, unpublished data) and (5) males are known to regularly switch from one mixed-sex group to another (Halley and Mari 2004, Turner et al. 2005), and can be key individuals in pathogen transmission between groups. The lack of GPS data on males is a limitation of this study, but collecting movement data for this sex class is challenging since males tend to break their collar within a few months of deployment, either intentionally or by accident during fights (Halley and Mari 2004, Caron et al. 2016). However, the biases

generated by this study are unlikely to have been heterogeneous across sites and seasons, and the comparisons of the trends in contact rate and duration thus remain appropriate.

Whilst assessing intergroup contacts is key to developing realistic models for the spread of pathogens at the population level, other types of interactions may also affect pathogen transmission and ultimately disease prevalence. In social species, intra-group contacts are particularly important for explaining the spread of many infectious diseases at the local scale (for buffalo Cross et al. 2004, Blanchong et al. 2007, Grear et al. 2010). In Cape buffalo, long-range dispersal of subadult females could be important in the spread of disease between groups and among distant populations (Caron et al. 2016). Pathogens infecting buffalo can also be transmitted to multiple sympatric host species in southern Africa, such as domestic cattle *Bos taurus* / *Bos indicus*, hippopotamus *Hippopotamus amphibius*, and wildebeest *Connochaetes taurinus* (Bengis et al. 2002, Miguel et al. 2013, Kiffner et al. 2014). In the populations studied here, the strong spatial segregation between buffalo groups means that inter-specific contacts might be more important in the spread of infection in buffalo populations than inter-group contacts (Holt et al. 2003, Keeling 2005). The difficulty of simultaneously studying contact networks among several species makes it difficult to estimate interspecific contact rates and the relative importance of these contacts in pathogen transmission (but see Kiffner et al. 2014 for a study on social structure of multi-host systems, including buffalo, on a seasonal scale). Nonetheless, this study is, to my knowledge, the first study to quantify potentially infectious contacts between Cape buffalo groups in multiple populations. These findings could be particularly important for understanding and predicting the spread of pathogens in the species (by improving epidemiological models) and help in the management of economically important diseases.

How Cape buffalo groups interact with each other and how site and season influence contact patterns have also implications for the socio-spatial organization of the species. The present study provides evidence for spatial segregation and short-term behavioural avoidance between neighbouring buffalo groups in two geographically distinct populations. Home ranges of buffalos from neighbouring groups had little to no overlap, with direct contacts and short-term indirect contacts rare and short in duration. The tendency to use exclusive home ranges has already been observed in several buffalo populations, such as the one at Chobe riverfront (study based on the dry season, Botswana, Halley et al. 2002), the one of Klaserie Private Nature Reserve (South Africa, Ryan et al. 2006) and the one in Lake Manyara National Park (Tanzania, Prins 1996). In a West African buffalo population living in W Regional Park, two neighbouring groups had very little direct contact within a 500 m spatial window, and for less than an hour despite the quite large overlap (21 %) of their home ranges (Cornélis et al. 2011). The low overlap and few contact rates I observed during the dry season are, however, surprising and do not support the hypothesis that low water availability during this season could have forced buffalo groups to contract their home

ranges around the same water sources (Ryan et al. 2006, Cornélis et al. 2011). Nevertheless, although there was no seasonal variation in home range overlap between dyads from neighbouring groups, the distance between home ranges of neighbouring groups varied seasonally. The model selection did not show a site effect, but home ranges of dyads from neighbouring groups in OD tended to be further apart during the wet than the dry season. This is probably because unlike KNP, the Okavango Delta's environment provides available space and abundant resources to allow some groups to disperse and use the available habitat more efficiently (Bennitt et al. 2016). In OD, during the dry season, buffalos may gather on seasonal floodplains (Bennitt et al. 2014), which provide water and fresh food and may explain the closer proximity of home ranges of neighbouring groups during the dry season. Although the spatial segregation observed in my populations suggests some territoriality, the quasi-absence of direct contact suggests that physical encounters with active interactions are not the mechanism by which segregation is maintained. Avoidance between groups may be achieved through non-aggressive territorial signs, such as scent markings facilitated by faeces, vocalizations, emitted by individuals to maintain group cohesion and order (Mloszewski 1983), or may simply be due to a passive avoidance of patches used by other groups through spatial memory (Riotte-Lambert et al. 2015). To understand the mechanisms underlying behavioural avoidance, spatiotemporal windows could be used to assess visual and direct and indirect olfactory contacts (*e.g.* faeces, marking) between groups, but there is currently a lack of empirical data to estimate these spatiotemporal windows. It is unclear why neighbouring groups did not use the same areas at the same time or in a short time interval, but this may be to limit competition for resources or because areas used by other animals appeared to be less profitable (Benhamou and Riotte-Lambert 2012) or to limit pathogen transmission. Overall, the spatial arrangement of home ranges of neighbouring buffalo groups and the few direct and short-term indirect contacts suggest that interactions between groups might act as a high-level constraint on habitat selection, in addition to the availability of resources, which are commonly cited to affect buffalo habitat selection (Sinclair 1977, Ryan et al. 2006, Winnie et al. 2008).

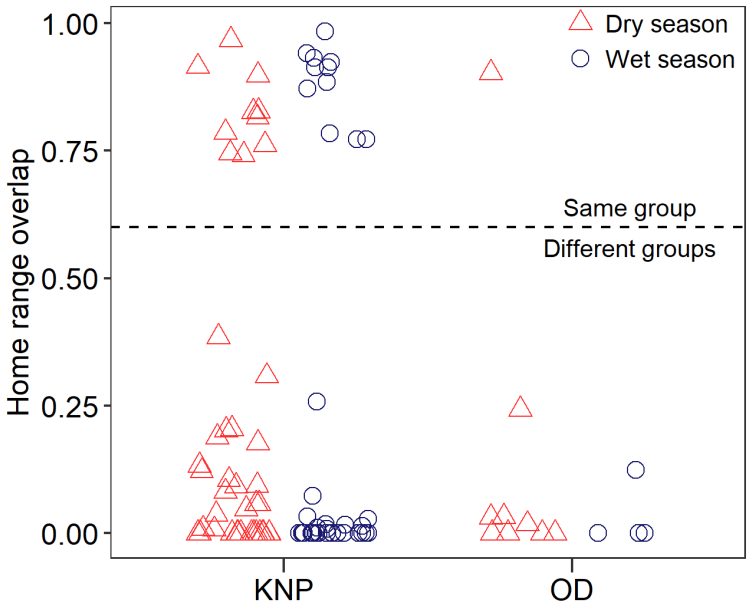
5 Conclusions

This study is one of the first to describe contact patterns between buffalo groups, compatible with the transmission of important pathogens in buffalo, in two populations living in contrasting environmental conditions. The contact patterns between groups are generally consistent across populations, supporting the idea that how neighbouring groups interact with each other is defined by the species behaviour rather than by environmental conditions.

Whilst direct contacts between groups are very rare, this study highlights the importance of long-term indirect contacts for the transmission of some pathogens between buffalo groups, and thus at the population level. Additionally, in areas with low water availability, water sources might act as hotspots of contacts between groups, and ultimately for spread of pathogens. The availability of telemetry data allowed a greater understanding of intra (Chapter 3) and intergroup contact patterns (this chapter). Although recent studies on the social structure of multihost systems, including buffalo, allow predictions about the interspecific social links of buffalo (Kiffner et al. 2014, Meise et al. 2019), further studies should now focus on exploring contact networks in these systems at fine temporal scale (*i.e.* contact rate and duration), including between buffalo and cattle (Miguel et al. 2013), to better understand pathogen spread at a larger, regional, scale.

6 Appendices

Appendix 1. Home range overlap (Bhattacharyya's affinity index) between individuals belonging to the same group or different group according to site and season (red triangle = dry season, blue circle = wet season). The dashed line corresponds to a home range overlap = 0.6 and divides the dyads belonging to the same group from the dyads belonging to different groups.



Appendix 2. Space-use and contact patterns between 2 neighbouring groups in Gonarezhou National Park.

Two adjacent groups were tracked in the southern part of Gonarezhou National Park (5 053 km², Zimbabwe), but this low sample size has prevented from exploring the intra-site variability for each analysis (*i.e.* one dyad). Results for space use and contact patterns for this dyad are given for information, but no statistical analyses have been performed (see Table below). The landscape of the study area is similar to that in Kruger NP: the vegetation is characterized by bushland savanna, open grassland and woodland and mean annual rainfall is around 500 mm, with most rain falling between November and March (Gandiwa et al. 2016). Water availability in the dry season is lower than in Kruger NP, with only a few perennial pools in the main river providing water (Zvidzai et al. 2013). Each group was tracked by fitting one GPS collar on one adult female from January 2009 to December 2009. GPS locations were acquired every hour.

The home range overlap between the 2 individuals from neighbouring groups was 0.14 during the dry season and 0.04 during the wet season. The table below indicates the contact rate (*i.e.* number of contacts per month) and contact duration between the 2 individuals from neighbouring groups. No direct contact was observed in both seasons between the 2 individuals.

Contacts time-space window	Number of contacts /month (mean ± SD)		Duration of contacts in hour (mean ± SD)	
	Dry	Wet	Dry	Wet
Direct contact – bTB	0	0	Na	Na
Long-term indirect contact – bTB	18.2 ± 11.3	5.6 ± 0.0	1.9 ± 2.0	1.2 ± 1.4
Short-term indirect contact – Brucellosis	3.8 ± 0.3	0.2 ± 0.2	1.5 ± 1.1	1.0 ± na
Long-term indirect contact at large spatial scale – RVF	13.4 ± 0	15.3 ± 5.8	29.0 ± 29.6	18.7 ± 29.4

Note that the mean duration of direct contacts is Na because there was no direct contact.

CHAPTER 5

FEMALE DISPERSAL IN THE CAPE BUFFALO CONFIRMED BY GENETIC MARKERS AND GPS TRACKING

Abstract

Sex-biased dispersal is an important life-history trait, influencing species' social organization and genetic structure, and has important management implications, especially for disease spread. Dispersal in the Cape buffalo is usually reported to be biased towards males. Females have strong fidelity to their natal groups, but conflicting field data show that females can also disperse. In this study, I combined GPS tracking data and three genetic markers to investigate the sex differences in dispersal rates at two organizational levels: among populations and among groups within populations. From published data, 14 autosomal microsatellites and two sex-linked markers (mitochondrial DNA sequences and three Y-chromosome microsatellites) were used to infer patterns of dispersal. I found low levels of genetic differentiation among populations with a strong isolation-by-distance pattern of genetic variation. Females undertook long-distance dispersal events (among populations), but also short-distance dispersal events (among neighbouring groups). My results also suggest that dispersal is female-biased when happening among populations, but not at the smaller organizational level (among groups within a local population), where males could disperse as much as females. Finally, the results suggest that sex differences may differ from environmental conditions, generating spatial variation in sex-specific dispersal rates and/or distances. Selective pressures are thus likely to depend on spatial scale considered, but also social and environmental factors that may differ between populations. However, alternative explanations to my results are also possible and further analyses are needed to understand the ultimate causes of sex-biased dispersal distances and rates in the Cape buffalo.

1 Introduction

Dispersal is a key life-history trait in animals that has relevant effects on both dynamics and genetics of species. Inbreeding avoidance, reducing mate and resource competition or finding usable habitats are the main selective forces that promote this behaviour (Cockburn et al. 1985, Bowler and Benton 2005, Lebigre et al. 2010, Clutton-Brock and Lukas 2012). In animal societies, males and females generally display large differences in terms of dispersal rates and/or dispersal distances; this is called sex-biased dispersal (Greenwood 1980). Sex-biased dispersal is widespread in many species, with male-biased dispersal more common in mammals (*i.e.* males have higher dispersal rates than females), whilst the reverse pattern is more widespread in birds (Greenwood 1980, Cockburn et al. 1985, Strier 1994, Clarke et al. 1997, Engelhaupt et al. 2009, Lebigre et al. 2010). Counter-examples exist such as in the European roe deer (*Capreolus capreolus*), where both sexes disperse at the juvenile stage in a similar proportion (Wahlström and Liberg 1995). Furthermore, sex-bias in dispersal rates and/or distances can also vary with geographical scale (Ji et al. 2001, Fontanillas et al. 2004). Dispersal is important in the management and conservation of natural populations, allowing recolonization of empty habitat patches, demographic rescue and maintenance of genetic diversity through gene flow (Greenwood 1980, Nelson 1993, Neve et al. 1996), but has important implications for disease spread (Mazé-Guilmo et al. 2016, Daversa et al. 2017).

Detecting and quantifying dispersal levels can be challenging and depend on the employed method. By providing detailed patterns of individual movement, field-based approaches such as capture-mark-recapture have been used in several instances to document the ability of individuals to disperse in space and the sex-biased rates (Favre et al. 1997, Helfer et al. 2012). Because these approaches are limited in space and time, the detection of long-distance dispersal can be difficult. Technology advances (*e.g.* GPS, biologging, Kays et al. 2015) have facilitated the study of dispersal rates over broad spatial and temporal extents and at increasingly fine resolutions (Spaan et al. 2019). However, these techniques require the immobilization of individuals, limiting the number of individuals that can be studied. Relatively recent advances in genetic techniques and their increasing accessibility offer new promising alternatives to indirectly explore dispersal (Prugnolle and de Meeus 2002). These methods benefit from not requiring intensive field observations and are relevant for studying sex dispersal levels, for example, based on the differences in genetic structure across sexes (review in Prugnolle and de Meeus 2002, Fontanillas et al. 2004, Wang et al. 2019). Given their different contribution in estimating levels of dispersal, a combination of GPS and genetic data should provide detailed insight into dispersal and population connectivity (Helfer et al. 2012).

Cape buffalos live in mixed-sex groups that vary in size between 10 to more than 1500 individuals (Sinclair 1977, Prins 1996). Groups are primarily made up of females and their offspring, subadults of both sexes, and a small proportion of adult males. Both genetic and observational studies found that almost all males leave their native groups before reaching sexual maturity (Sinclair 1977, Prins 1996, Van Hooft et al. 2003). In adulthood, they move regularly between mixed-sex groups and bachelor groups according to the seasonal mating opportunities, forage availability and predation avoidance (Sinclair 1977, Prins 1996, Halley and Mari 2004). Whilst primary literature generally considers females as gregarious with a strong fidelity to their group and limited intergroup movements (*i.e.* dispersion, Sinclair 1977, Prins 1996), more recent observational and genetic studies highlighted the dispersal of adult and immature females. The use of GPS collars has made it possible to record long-distance dispersal in females among populations (Halley et al. 2002, Naidoo et al. 2014, Caron et al. 2016). Genetic evidence also suggests that long-distance dispersal of females is not uncommon. For example, Simonsen et al. (1998) found little genetic structure in mitochondrial DNA inherited from the mother or microsatellite (nuclear) loci among buffalo populations in 11 localities in eastern and southern Africa. Most genetic studies on the Cape buffalo have been carried out at the population level (national parks and game reserves, Simonsen et al. 1998, Van Hooft et al. 1999, 2000, 2002, Smitz et al. 2013, 2014). At the group level, only Van Hooft et al. (2003) explored the dispersal capacity and the differences between sexes to my knowledge. Based on mitochondrial DNA and microsatellites collected in two populations, they estimated that 5-20% of female buffalos older than two years of age dispersed between groups per generation (7 years) against close to 100% for males. Telemetry studies support frequent switches among groups within a local population (Halley et al. 2002, Cross et al. 2004, Roug et al. 2020). Despite abundant evidence that dispersal is common in both male and female Cape buffalos, no studies have explored whether there are differences in the sex-biased dispersal patterns between different populations.

In this chapter, I used GPS and genetic data collected over a seven-year study in 10 southern African populations to assess the pattern of dispersal behaviour in the Cape buffalo at two organizational levels: among populations and among groups within local populations. Specifically, I explored the following three questions: (1) Is there genetic differentiation between populations? (2) Is there isolation by distance pattern amongst buffalo populations? and (3) Is there sex bias in dispersal at both group and population levels? I used bi-parentally inherited markers (14 microsatellite loci) and sex-linked markers (three Y-chromosomal microsatellites and 580-bp of mitochondrial DNA D-loop region) to (i) calculate the genetic differentiation levels between populations and the correlation between genetic and geographical distances using the bi-parentally inherited markers, (ii) compare the population genetic structure of the three markers and (iii) calculate the

relatedness and/or assignment indices separately for the sexes between populations and between groups using the bi-parentally inherited markers. I used GPS data collected on females to examine whether there is concordance between the results of telemetry and genetic. I described the dispersal events for this sex (*e.g.* distances travelled, timing and duration) between populations and between groups. With these data, I aim to improve our understanding of the characteristics of dispersal events of Cape buffalos.

2 Methods

2.1 Genetic data

In this study, I had access to published data of genetic markers from 264 Cape buffalos, sampled from 19 study sites in 6 countries of southern Africa (Smitz et al. 2013, 2014). The samples consisted in blood, a small piece of ear, hair or dung samples. All individuals were of known sex. Further details of how animals were sexed, DNA samples collected, DNA extracted and genotyping methods can be found in Smitz et al. (2013, 2014). The original dataset consisted of individuals genotyped for three different genetic markers: (1) all individuals were characterized using 14 autosomal microsatellite loci developed in cattle (TGLA227, TGLA263, ETH225, ABS010, BM1824, ETH010, SPS115, INRA006, BM4028, INRA128, CSSM19, AGLA293, ILSTS026, DIK020 described by Van Hooft et al. 1999 and Greyling et al. 2008); (2) within this sample set, 86 males were genotyped at three Y-chromosomal microsatellites (UMN1113, INRA189, UMN0304 described by van Hooft et al. 2007); and (3) 48 buffalo mtDNA sequences for the D-loop region. I read and aligned the mtDNA sequences using MEGA 10.0 (Tamura et al. 2011), with corrections by eye. Newly sequenced samples led to the identification of a 580-bp overlapping region.

For this study, I omitted the samples from four study areas, representing 49 individuals because none or only one male was sampled [‘Hwange’, ‘Manguana’, ‘Niassa’ and ‘Victoria Falls’ in Smitz et al. (2013, 2014)]. The samples previously collected in the study sites ‘Kruger’, ‘Sengwe’ and ‘Crooks Corner’ were grouped into a single population (hereafter referred to as ‘Kruger’) for further analyses because monitoring with GPS collars has revealed that individuals from those sites belonged to neighbouring groups with overlapping home ranges (Chapters 3 & 4). Finally, the dataset used for this study comprised 205 individuals from 10 populations (n_{male} = 80; n_{female} = 125) genotyped at 14 autosomal microsatellite loci, 68 males genotyped at three Y-chromosomal microsatellites, and 48 mitochondrial DNA sequences (see Figure 1, Table 1).

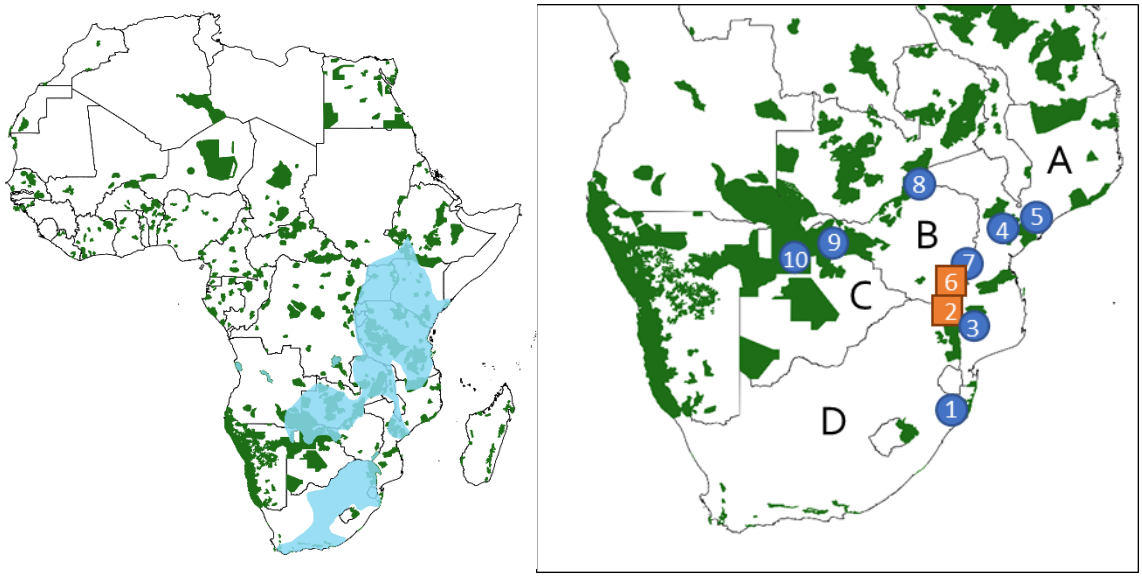


Figure 1. Map of Africa representing the 10 populations analyzed in this chapter. Light blue shapes on the left map represent the actual distribution of the Cape buffalo according to the IUCN Antelope Specialist Group, 2008. Green zones correspond to the protected areas (East 1998). A. Mozambique, B. Zimbabwe, C. Botswana, D. South Africa. 1. Hluhluwe-iMfolozi, 2. Kruger North, 3. Limpopo, 4. Gorongosa, 5. Marromeu, 6. Gonarezhou, 7. Malilangwe, 8. Mana Pools, 9. Chobe, 10. Okavango Delta. The squares represent the localities where genetic and telemetry data were collected while the circles indicate the localities where only genetic data were collected.

Table 1. Sampled populations and genetic markers genotyped. This table summarizes the sample origin (country and sampling locality) and sample size per locality for each sex and each kind of genetic marker involved in the present study.

Population	ID Fig.1	Autosomal microsatellites			Y-chromosomal microsatellites	mtDNA		
		N_{female}	N_{male}	Total	N_{male}	N_{female}	N_{male}	Total
South Africa								
Hluhluwe-iMfolozi	1	8	12	20	12	7	12	19
Kruger	2	32	12	44	12			
Mozambique								
Limpopo	3	3	2	5	2			
Gorongosa	4	3	4	7	3			
Marromeu	5	14	7	21	7			
Zimbabwe								
Gonarezhou	6	27	10	37	8	16	13	29
Malilangwe	7	14	6	20	6			
Mana Pools	8	2	8	10	8			
Botswana								
Chobe	9	11	10	21	4			
Okavango delta	10	11	9	20	6			

2.2 *Estimating sex-biased dispersal among populations*

a) Isolation-by-distance and comparison between mitochondrial DNA, Y-chromosome and autosomal microsatellites

To investigate potential differences in dispersal rates between females and males in the Cape buffalo, I compared the population genetic structure (F_{st}) of the three Y-linked microsatellites (paternal marker), 580-bp of mtDNA D-loop sequences (maternal marker) and 14 autosomal loci (biparental marker). Higher level of genetic distances (F_{st}) in maternally inherited markers than paternally or biparentally inherited markers usually indicates females' philopatry and therefore, male-biased dispersal (Prugnolle and de Meeus 2002). I calculated F_{st}, the proportion of genetic variation among populations, in Arlequin 3.5 (Excoffier and Lishcer 2010) for each of the three genomic regions. For autosomal loci, overall and population pairwise F_{st} were calculated for all available individuals (n = 205) sampled in 10 populations based on microsatellite allele frequencies. For Y-chromosome, overall and population pairwise F_{st} were calculated based on haplogroup frequencies for the sub-sample of 68 males that were genotyped at the three Y-markers. For mtDNA, overall F_{st} was calculated based on haplotype frequencies for a sample of 48 individuals in two populations. I tested the overall F_{st} using Markov-chain approximation with 100 000 steps and 10 000 dememorization steps.

I also tested for isolation by distance by investigating the correlation between genetic distances (F_{st}, based on microsatellite data) and geographical distances among the 10 populations. I measured the geographical distances among populations using R, v. 3.6.0 (R Development Core Team 2019). Then, I assessed the correlation between genetic and geographical distance matrices with 95% confidence interval (CI) using Mantel's tests in Arlequin 3.5 (Excoffier and Lishcer 2010) with 10 000 permutations.

b) Sex differences based on microsatellite loci

To further understand sex-biased dispersal, I compared multiple genetic indices between males and females based on biparentally inherited loci (14 autosomal loci, Goudet et al. 2002) sampled on 205 individuals from 10 populations (n_{male} = 80; n_{female} = 125). For the set of females and the set of males, I quantified mean assignment index (*mAIc*) and variance of the assignment index (*vAIc*). I used the methods implemented in FSTAT v.2.9 (Goudet 2001) to measure the values of *mAIC* and *vAIC* and to determine the statistical significance of differences in these within-population indices using 10 000 randomizations. I used one-sided tests and females were chosen *a priori* as the most philopatric group based on previous research suggesting the limited movement of females (Van Hooft et al. 2002). Additionally, I calculated mean values of relatedness within populations between the sexes in Coancestry 1.0 (Wang 2011), using two likelihood estimators (TrioML and DyadML) and

one moment estimator (Queller and Goodnight's) with 1,000 bootstraps (Queller and Goodnight 1989, Milligan 2003, Wang 2007). Differences in the dispersal between the sexes should result in significant dissimilarity in the population genetic parameters. Mean assignment index and relatedness are expected to be higher in the philopatric sex, whereas the variance of the assignment index should be lower (see Goudet et al. 2002 for further explanation).

c) Fine-scale analyses in two populations

Because allele frequencies and genotypes between philopatric individuals and dispersers can be better estimated with more samples, I also examined the sex-biased dispersal in the two largest sampled populations: Gonarezhou (including 37 individuals) and Kruger (44 individuals). Using biparentally markers, I evaluated relatedness between the sexes in each population using Coancestry 1.0 (TrioML, DyadML and Queller and Goodnight's index).

2.3 Estimating sex-biased dispersal among groups

I explored sex-biased dispersal at the group level using genetic data in only 2 geographically distinct populations (Gonarezhou and Kruger) because the GPS tracking of female buffalos (presented in part in Chapter 3) allowed to identify group membership. I used GPS locations collected between 2008 and 2015 on 47 female buffalos (total across the sites). Of the 47 buffalos, 27 were adult females (12 in Gonarezhou and 15 in Kruger), because their behaviours are generally representative of those of the group and were thus appropriate for identifying study groups (see below). Twenty subadult females were also tracked in Kruger, precisely to explore the dispersal behaviour of individuals of this age class (Caron et al. 2016). Male buffalos tend to lose their collar within a few months of deployment, either intentionally or by accident during fights (Halley and Mari 2004, Caron et al. 2016).

The data acquisition periods extended from October 2008 to December 2012 in Gonarezhou and from June 2010 to July 2015 in Kruger. GPS loggers were scheduled to acquire locations at synchronous times every hour. The computation of the home ranges of adult females identified 6 groups: 2 in Gonarezhou and 4 in Kruger (see Chapters 3 & 4). The resulting home ranges were consistent with the view that groups were spatially separated with little overlap in their home ranges between groups at the time scales at which tracking collar data were collected. All groups had multiple capture locations (because individuals formed subgroups that regularly merge) and multiple individuals were captured at each capture location. Using the location of individual captures, I determined the group membership of GPS-collared subadult females and individuals captured for genetic sampling but not for fitting a GPS collar (including males and females). An individual was

therefore assigned to a group when its capture location was the same as that of the GPS-collared adult females used in the group definition. When possible (*i.e.* GPS-collared subadult females), I verified groupings based on GPS locations. The number of collared adult and subadult females in each group varied between 4 and 19 (Gonarezhou groups: $n_1 = 9$, $n_2 = 8$ collared buffalos: Kruger groups: $n_1 = 19$, $n_2 = 6$, $n_3 = 9$, $n_4 = 4$ collared buffalos, Chapters 3 & 4).

After defining the 6 study Cape buffalo groups, I examined patterns of relatedness within and among groups. I estimated pairwise relatedness values based on biparental microsatellites for individuals sampled in the same population both within and between groups separately for each sex, but also for all individuals. I used Coancestry 1.0 to calculate the relatedness index of Queller and Goodnight (1989) with 1,000 bootstraps.

2.4 Dispersal events of female Cape buffalos

I also used GPS data from female Cape buffalos in Gonarezhou and Kruger to describe the characteristics of dispersal events. I determined females engaging in dispersal using time-series of x and y location values, and visual inspection of movement data in QGIS 3.0 (QGIS Development Team 2020). I identified the initiation point of dispersal by a steep increase in the value of x and y locations and the end point of dispersal by a plateau in x and y locations, suggesting that the animal potentially settles into a new group (Appendix 1). From dates of initiation and end points, I calculated the (1) dispersal duration as the number of days between initiation and end points, (2) the dispersal distance as both the straight-line distance from initiation point to end point and (3) the cumulative distance of the dispersal path. The cumulative distance was calculated as the sum of the Euclidean distances travelled between successive positions (*i.e.* the movement path) between the start and end points. I further calculated the ratio between cumulative dispersal distance and straight-line distance for each individual. I also calculated the average cumulative distance travelled within a 24-hour period for philopatric individuals to compare the movements between dispersers and philopatric individuals. For each disperser, I calculated the ratio between its cumulative dispersal distance and the average cumulative distance of the philopatric individuals on the same time scale (*i.e.* the average distance travelled by the philopatric individuals within one day was multiplied by the duration of the dispersal event of the disperser).

3 Results

3.1 Sex-biased dispersal among populations

a) Isolation-by-distance and comparison between mitochondrial DNA, Y-chromosome and autosomal microsatellites

The Mantel test detected a significant positive correlation between pairwise population genetic distances (F_{st}) based on microsatellite loci and geographical distances (R = 0.54, P = 0.001, Figure 2) among the 10 populations. Removing Hluhluwe-iMfolozi, the most isolated population, decreased this signal (R = 0.46, P = 0.01).

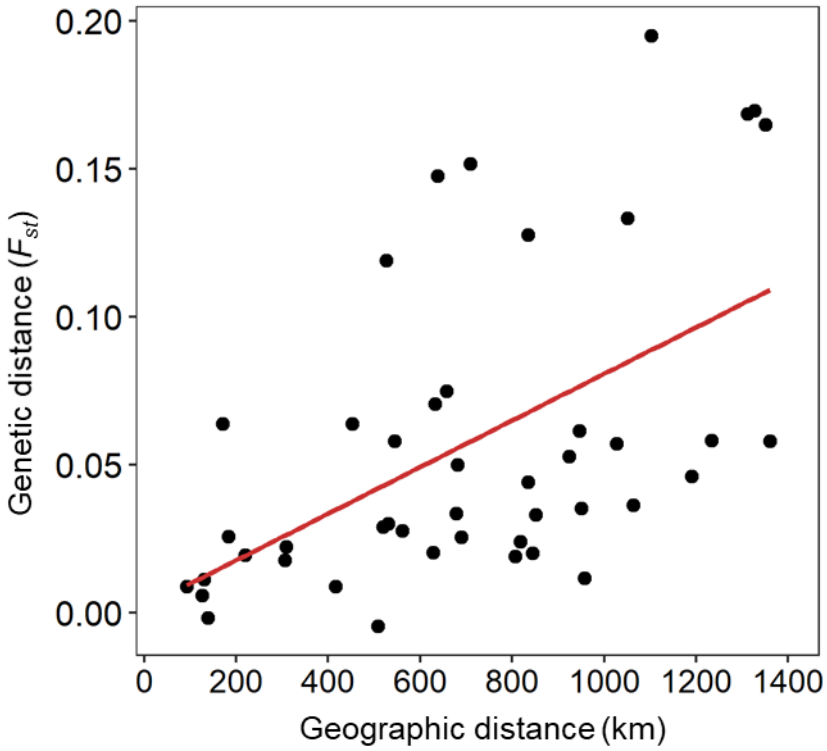


Figure 2. Correlation between pairwise geographical and genetic distance (F_{st}). The genetic distance (F_{st}) was based on microsatellite loci and calculated for all possible population pairs (see Table 2).

The pairwise F_{st} values from microsatellites estimated among 10 populations ranged from -0.004 to 0.19, whilst the Y-markers F_{st} values among the same populations ranged from -0.09 to 0.42 (Table 2). The comparison of genetic differentiation values between these two types of markers revealed that both overall F_{st} and pairwise F_{st} based on Y-markers (F_{st} = 0.21, p < 0.001) were higher than the values from autosomal microsatellites (F_{st} = 0.06, p < 0.001). Based on the comparison of genetic differentiation values between the three types of markers estimated from two populations, I found that F_{st} based on Y-markers (0.42, p < 0.001) was higher than the values from mtDNA markers (0.23, p < 0.001) and autosomal microsatellites (0.15, p < 0.001). Therefore, paternal markers showed greater genetic

Table 2. Population pairwise F_{st} values from autosomal microsatellites (above diagonal) and Y-chromosome microsatellites (below diagonal) for 10 Cape buffalo populations. An asterisk (*) indicates a significant difference between populations according to the exact test *p*-values with a significance level of 0.05.

	Chobe	Gonarezhou	Gorongosa	Kruger	Limpopo	Malilangwe	Mana Pools	Marromeu	Okavango Delta	Hluhluwe-iMfolozi
Chobe		0.03*	0.04*	0.04*	0.06*	0.02*	0.03*	0.06*	-0.002	0.17*
Gonarezhou	0.21		0.01	0.01*	0.03	0.01*	0.02*	0.06*	0.04*	0.15*
Gorongosa	0.15	0.32*		-0.004	0.03	0.02	0.03	0.06*	0.05*	0.13*
Kruger	0.12	0.17*	0.20		0.005	0.02*	0.03*	0.07*	0.05*	0.15*
Limpopo	0.00	-0.09	0.21	-0.03		0.02	0.02	0.07*	0.06*	0.12*
Malilangwe	-0.09	0.07	0.08	0.06	-0.09		0.03*	0.06*	0.01*	0.13*
Mana Pools	0.10	0.29*	0.26	0.20*	0.16	0.09		0.05*	0.02*	0.17*
Marromeu	0.11	0.28*	0.24	0.19*	0.14	0.10	0.20*		0.06*	0.19*
Okavango Delta	-0.05	0.22*	0.17	0.14*	-0.05	-0.02	0.13	0.13*		0.16*
Hluhluwe-iMfolozi	0.34*	0.42*	0.40*	0.32*	0.41	0.26*	0.38*	0.38*	0.33*	

structure among the two populations than maternal and biparental markers. This high difference may, however, be due to the inclusion of the population Hluhluwe-iMfolozi, which is significantly different from almost all populations (Table 2).

b) Sex differences based on microsatellite loci

The values obtained for the three relatedness indices were significantly different between sexes ($p < 0.001$, Table 3), with males showing higher relatedness values compared with females. Therefore, males were more related and had a greater probability of being residents than do females. By contrast, there was no significant difference in either the mean or the variance of assignment index between males and females (Table 3).

Table 3. Parameters of sex-biased dispersal for female and male Cape buffalos among 10 populations. *mAIc* and *vAIc*, the mean and the variance of the assignment index, respectively.

			Relatedness			
	mAIc	*vAIc*	TrioML	DyadML	Queller and Goodnight	*n*
Females	0.03222	14.00863	0.069106	0.092928	0.069291	125
Males	-0.05035	12.30827	0.11694	0.14551	0.1141	80
p-value	0.4344	0.3850	< 0.001	< 0.001	< 0.001	
	M = F	*M = F*	*M > F*	*M > F*	*M > F*	

c) Fine-scale analyses in two populations

Within the population Gonarezhou, I found that two out of the three relatedness values were significantly higher in males than in females (Table 4), similarly with the results from the 10 populations; therefore, males were more related within the population and had a greater probability of being philopatric. In contrast, there was no difference in the three relatedness values between the sexes in Kruger (Table 4).

Table 4. Relatedness for female and male Cape buffalos in Gonarezhou and Kruger. TrioML and DyadML: two likelihood estimators; Queller and Goodnight: one moment estimator. *p*-values indicate the confidence in difference between sexes with a significance level of 0.05.

	Relatedness			
	TrioML	DyadML	Queller and Goodnight	*n*
Gonarezhou				
Females	0.03699	0.04945	-0.02780	27
Males	0.07766	0.08902	-0.05018	10
p-value	0.0099	0.0301	0.4821	
Kruger				
Females	0.03058	0.04091	-0.02008	32
Males	0.02721	0.03764	-0.05240	12
p-value	0.6988	0.7525	0.1066	

3.2 Sex-biased dispersal among groups

The average pairwise relatedness was estimated both within and between groups to identify whether short-distance group switching occurred and whether this was different between the sexes. Due to small sample sizes, the *r* values were negative. In Kruger, when all individuals were included, average pairwise *r* within groups was not different from that between groups (within-group, $r = -0.023$, between-group, $r = -0.026$, $p = 0.86$). Similarly, by analysing each sex separately, average pairwise relatedness between females and between males within groups was not different from that between groups (females: within-groups $r = -0.026$, between-groups $r = -0.023$, $p = 0.86$; males: within-groups: $r = -0.088$, between-groups: $r = -0.043$, $p = 0.38$). In Gonarezhou, as genotyped males were all in the same group, I only calculated pairwise relatedness for all individuals and females. The relatedness between the females was not different whether they were in the same group or not (within-groups: $r = -0.051$, between-groups: $r = -0.065$, $p = 0.73$) as well as when I included all individuals (within-groups: $r = -0.025$, between-groups: $r = -0.068$, $p = 0.11$).

3.3 Dispersal events of female Cape buffalos

Based on radio-tracking data, four of the 57 female Cape buffalos collared in this study dispersed during monitoring; all of these were subadults in Kruger. Two of these travelled straight-line distances greater than 50 km during their dispersal period, supporting a long-distance dispersal among populations whilst the two other ones dispersed to neighbouring groups within the same population (Table 5). One female from Kruger temporary settles in Gonarezhou during dispersal for 55 days. All dispersal events occurred during the wet season (generally extending from November to March). By comparison, the average cumulative distance travelled by philopatric individuals within one day was 7.4 km in

Gonarezhou and 4.7 km in Kruger. The ratio between cumulative dispersal distance of the disperser and the average cumulative distance of the philopatric individuals on the same time scale ranged from 1.03 and 1.9.

Table 5. Summary of dispersal distances for four female Cape buffalos in Kruger.

Buffalo ID	Days monitored	Dispersal					
		Age (years)	Start date	End date	Duration (days)	Cumulative distance (km)	Straight-line distance (km)
B34560	149	2.5	23/12/2013	29/12/2013	6	53.4	12.5
B34565	395	4	06/01/2014	16/03/2014	68	610.1	90.4
B34568	176	4	25/02/2014	06/03/2014	9	75.0	51.7
B34569	453	3	20/03/2014	01/04/2014	12	58.0	10.5

Note: One female had multistage dispersal (B34565). For this female, temporary settlement movements were included in the cumulative distance and dispersal duration.

4 Discussion

In this study, I used GPS data and three types of molecular markers to examine sex-biased dispersal patterns in the Cape buffalo at two organizational levels. I found (i) low levels of genetic differentiation among Cape buffalo populations with a strong isolation-by-distance pattern of genetic variation, and (ii) the dispersal distances, just like dispersal rates, may differ among sexes. While my data suggest that both sexes disperse at similar rates between groups within a local population, on a larger spatial scale, *i.e.* among populations, females might disperse more than males. Overall, my results support the idea that Cape buffalos have good dispersal ability among populations and among groups. They also give a new example supporting the dispersal of females, refuting the presumed philopatric behaviour of this sex.

4.1 Low levels of genetic differentiation among populations

I found a low level of genetic differentiation among Cape buffalo populations (F_{st} = 0.06 based on autosomal microsatellites), especially among the closest populations, and these findings are consistent with previous studies. Simonsen et al. (1998) worked on 11 populations of Cape buffalo in eastern and southern African and found an overall F_{st} value of 0.098 based on mtDNA control region sequences and 0.085 when estimated with autosomal microsatellites. Van Hooft et al. (2000) recorded an overall F_{st} value of 0.059 based on autosomal microsatellites on nine African buffalo populations throughout Africa

(one population of *S. c. nanus*). More recently, Smitz et al. (2014) investigated the genetic structure of 16 Cape buffalo populations (including some of this study) and obtained pairwise F_{st} ranging from -0.013 and 0.196. Furthermore, Lorenzen et al. (2008) have concluded that the African buffalo has the weakest genetic structure of all African ungulates studied to date. Based on simulation data, Goudet et al. (2002) showed that relatedness is the most efficient measure to detect differences in dispersal between sexes when dispersal is high (more than 10%) while the variance in assignment index (*vAIc*) should be more efficient for low dispersal rates (less than 10%). The power to detect sex-biased dispersal with the mean in assignment index (*mAIc*) is intermediate (Goudet et al. 2002). In this study, the comparison of autosomal microsatellite-based indexes between sexes across populations showed that only the relatedness coefficient was significantly different between the sexes, which is consistent with high gene flow among populations. In addition, the telemetry data support the ability of females (no data on males) to engage in long-distance dispersal events. However, it is worth noting that the translocations that have taken place over the last decades among protected areas in southern Africa may have promoted gene flow among populations.

4.2 Sex differences dispersal at the population level

Here, the field-based GPS data on females revealed their ability to engage in long-distance dispersal events and this is supported by significantly different relatedness coefficients between sexes. According to the comparison of microsatellite-based indices across the 10 populations, I found that males were more related within populations than females. This pattern may be a consequence of a higher proportion of philopatric individuals being male, indicating a bias towards female dispersal. Mean assignment index and variance assignment index were not significantly different between sexes, which may be due to low statistical power caused by long geographical distance between populations (Goudet et al. 2002). Although non-significant, *vAIc* was larger for females than for males, indicating that the sample of females contained a higher mixture of residents and immigrants than that of males, offering further support that females disperse more. However, I must note that the mating will obscure sex-biased dispersal signal in biparental markers because allele frequencies are equally randomized between females and males in the offspring (Goudet et al. 2002). This may explain why some genetic indices are not significantly different between sexes. Despite the non-significance of some indices, most molecular statistics and field-based tracking data refute the traditional view of female group philopatry, which is in concordance with previous telemetry studies (Halley et al. 2002, Spaan et al. 2019).

The comparison of genetic differentiation between different molecular markers yielded fewer clear-cut results. Across 10 populations, I found higher level of genetic

differentiation for the three Y-linked microsatellites, which was about 3.5 times higher than the overall F_{st} for autosomal loci. When I compared the genetic differentiation between three molecular markers across Gonarezhou and Hluhluwe-iMfolozi (the only two populations where mtDNA sequences were available), I found that the F_{st} value for Y-linked microsatellites was 2.8 times higher than the overall F_{st} for autosomal loci and 1.8 times higher than for mtDNA. This might be interpreted as evidence for higher female than male dispersal rates, consistent with the results of my previous genetic analyses and GPS data. The differences might also reflect differences in effective population size between females and males. Indeed, a difference in F_{st} values between nuclear and sex-linked markers is expected even where there is no sex bias in gene flow because of differences in effective population size between nuclear, mitochondrial and Y genes (Prugnolle and de Meeus 2002). The effective population size of haploid markers (here, mtDNA and Y-linked microsatellites) is generally assumed to be four times less than in diploid markers. Therefore, the F_{st} values estimated with mtDNA and Y-linked chromosome are theoretically expected to be at least four times the F_{st} values estimated with microsatellite loci in the absence of sex-biased gene flow. Here, the ratio of F_{st} for Y-linked and autosomal microsatellites (3.5) suggests that differences in effective population size may explain the differences in F_{st} values between nuclear and Y-linked markers. Van Hooft et al. (2003) showed that female Cape buffalos have a much higher effective population size as compared to males. They suggested that the strong male dominance among groups is responsible for the lower male effective population size because a very small proportion of males reproduce. This may contribute to a higher variation in allele frequencies observed in females than in males. I also note that the values of genetic differentiation estimated for the three markers between Gonarezhou and Hluhluwe-iMfolozi were higher than values calculated across 10 populations. Hluhluwe-iMfolozi is a protected area in South Africa that has been completely isolated for about 100 years with low gene flow with other populations. Finally, even if the comparison of genetic differentiation between the different molecular markers tends to show a female-biased dispersal, in agreement with the dispersal pattern observed based on my previous analyses, the differences might only result from differences in effective population size.

The fine-scale analyses performed in two populations revealed differences in the pattern of sex-biased dispersal between the populations. Based on the comparison of microsatellite-based indices between sexes across the two populations (*i.e.* Gonarezhou and Kruger), I found that two out of three relatedness values were significantly higher in males than in females in Gonarezhou, whereas there was no difference in the relatedness values between sexes in Kruger. In other words, in Kruger, the dispersal rate for males and females would be similar, while in Gonarezhou, the proportion of immigrants would be higher in females than in males. Besides, females from the north Kruger have already been

observed to disperse to Gonarezhou (Caron et al. 2016). Differences in social and spatial environments between these two populations may be responsible for this variation in sex-biased dispersal. For example, Lane and Shine (2011) showed changes in the direction of sex-biased dispersal in two sea snake species (*Laticauda saintgironsi and L. laticaudata*) in the Pacific nation of New Caledonia, and hypothesized that this variation may be due to spatial variation in sex-specific resources. Matthysen (2012) suggested that increased population density can modify habitat quality, and thus promote dispersal of females. It is therefore likely that, depending on the ecological (*e.g.* resource distribution) and social factors (*e.g.* population density, group size) of the environment of the population, the dispersal rate and distance of males and females vary between populations. Similar intraspecific variation in the direction and/or degree of sex-biased dispersal has been noticed in the Eurasian badger (*Meles meles*, Frantz et al. 2010) and the roe deer (Wahlström and Liberg 1995). I therefore suggest that dispersal of the Cape buffalo depends, not only on organization level considered (*i.e.* population or group level), but also on the social and environmental context that can differ between populations. However, the lower level of relatedness in females than in males in Gonarezhou may also result from numerous translocations that have taken place over the last decades in this population (Smitz et al. 2014).

4.3 Sex differences dispersal at the group level

The comparison of relatedness values for females and males within and between groups in two populations suggests no difference in dispersal rates between sexes at group level. Neither males nor females were more related when they were in the same group than in different groups, supporting short-distance movements for both males and females. The GPS data on females also support the ability of females to disperse over short distances. Differences in dispersal distance between sexes are common in mammals (Ji et al. 2001, Fontanillas et al. 2004). However, it is not clear why the direction of sex-biased dispersal in the Cape buffalo differs according to the organizational level. Short movements may allow avoiding inbreeding or mating competition, whereas greater distances may be required to escape poor environmental conditions or to colonize empty territories. Dispersal events of females between neighbouring groups have already been recorded in northern Botswana (Halley et al. 2002). Although males likely disperse to neighbouring groups to reduce inbreeding and mating competition, pressures underlying short-distance female dispersal may be more difficult to understand. I tentatively suggest that short-distance movements could allow females to improve their social status within the group. Consistent with this hypothesis, Spaan et al. (2019) showed that females in poor body condition were more

likely to disperse, while Prins (1996) observed that individuals at the rear of the group are generally in the least favourable condition.

One limitation of this study is the small number of Cape buffalo groups that have been examined and the small number of individuals sampled in each group. Initially, the study design was developed either for telemetry studies (females selected) or for exploring genetic structure at the regional level. The authors therefore sampled a few individuals from many populations, whereas a group-wide study would require sampling a large number of individuals in a few groups within the same population. Therefore, the lack of significant difference in the relatedness values between individuals belonging to the same group and those belonging to different groups may be due to low sample size. There is a need to collect more genetic samples from individuals from the same group. In addition to the small number of individuals that have been sampled in each group, there is another limitation relating to male behaviour. Adult males are known to regularly switch between neighbouring groups within the population according to the seasonal mating opportunities, forage availability and predation avoidance (Sinclair 1977, Prins 1996, Halley and Mari 2004). Identifying group membership for males is thus challenging and males can reproduce in several groups. The similar relatedness values between individuals belonging to the same group and individuals belonging to different groups may simply be the result of the frequent changes of males between neighbouring groups rather than short-distance dispersal of females and males.

4.4 Characteristics of female dispersal events

The genetic and telemetry data showed that females can disperse between neighbouring groups whilst some of the females travel very long distances during dispersal. From telemetry data, four out of 47 females (8.5%) dispersed, which is lower to previous estimates of 14% and 19% for groups in southern Kruger National Park (travelling distances up to 110 km, Spaan et al. 2019) and 17.7% in Chobe groups (8 out of 45 females over distances up to 133km, Halley et al. 2002). In my study, the dispersing females were subadults whilst the two comparable studies (Halley et al. 2002, Spaan et al. 2019) were mostly based on adult females even though younger adult cows were more likely to disperse (Spaan et al. 2019). I found that two out of the four dispersing females had long-distance dispersal events, and the two other ones had short-distance dispersal, switching between neighbouring groups. These results are consistent with previous observations in Chobe, where both short- and long-distance group switching were noted but performed by adult cows (Halley et al. 2002). My genetic and telemetry data support that female Cape buffalos also contribute to gene flow within and among populations, and colonization and population expansion with short- and long-distance dispersal movements. This indicates that the dispersal capacity and

potential for dispersal are not limiting factors to either sex in a Cape buffalo population. Interestingly, with one exception, dispersal movements occurred quickly, and dispersers moved faster than philopatric individuals. The comparison of straight-line distance to cumulative movement distance also showed that cumulative movement distances were on average only 1.4 times (or 6.7 for the individual with 2 dispersal stages) longer than straight-line distances for the long-distance dispersal events, whilst cumulative distances for short-distance dispersal events were on average 4.3 – 5.5 times longer than straight-line distances. This comparison indicates that females engaged in long-distance dispersal events have faster and straighter movements than females engaged in short-distance dispersal events that explore and move from group to group before settling.

Despite the few dispersal events observed, all of them occurred during the wet season, consistent with results of Spaan et al. (2019). Since resources are abundant during this season, females are unlikely to disperse to avoid intragroup competition. By contrast, females may disperse to minimize inbreeding, in particular because all the females that have dispersed are subadults, *i.e.* before their first reproduction. However, the reasons for engaging in either long- or short-distance dispersal are unclear. Females that dispersed to neighbouring groups did so within Kruger NP. Females involved in long-distance dispersal undertook these events on communal lands (although one of them settled temporarily in Gonarezhou NP, Caron et al. 2016) whilst it may be easier for females to disperse within the park (*e.g.* low human disturbance, high resource availability).

The lack of GPS data on males is a limitation of this study. Males are believed to move between groups, but collecting movement data for this sex class is challenging since males tend to break their collar within a few months of deployment, either intentionally or by accident during fights (Halley and Mari 2004, Caron et al. 2016). Yet, movement data on males would allow a direct comparison of the dispersal patterns of males and females, by giving information on dispersal rate and distance. This may help to understand the mechanisms responsible for long and short-distance dispersal in both males and females.

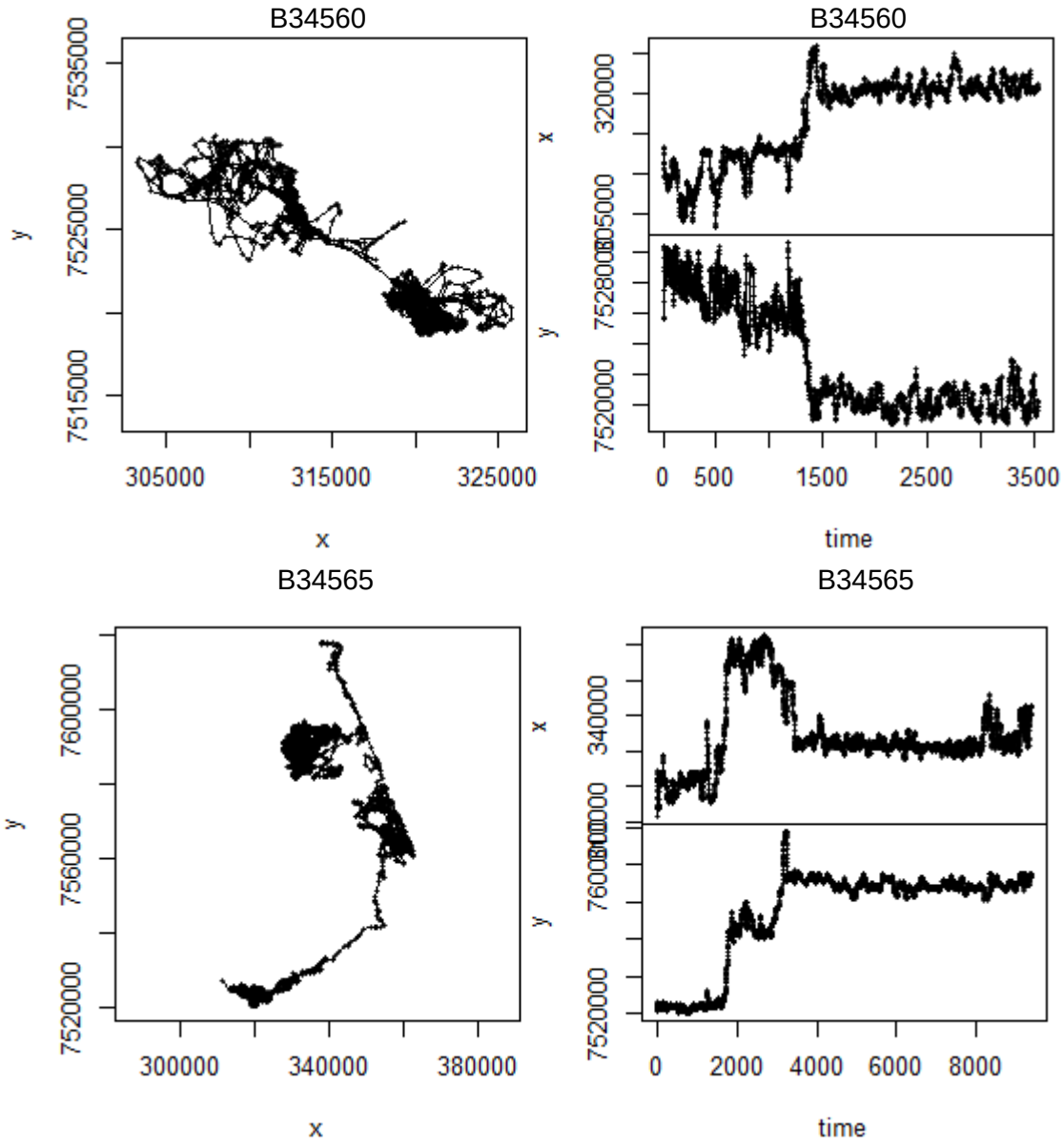
5 Conclusions

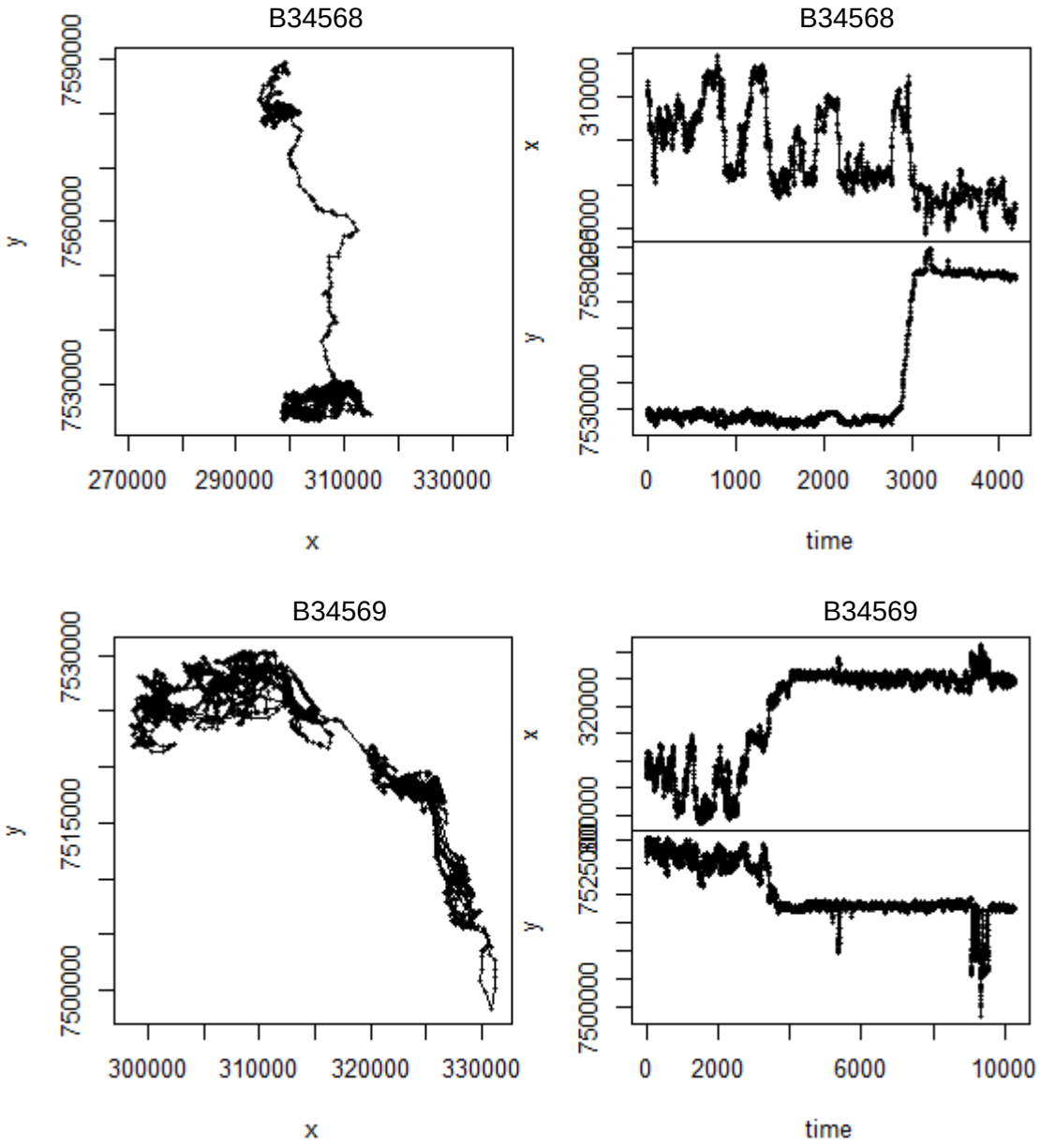
By combining GPS and genetic data, this study gives a well-supported example of Cape buffalo female dispersal between neighbouring groups or between populations. The originality of this work is that the direction of the sex-biased dispersal differ depending on the organizational level considered. Thus, the results suggest that dispersal is female-biased when happening among populations, but probably not at a smaller organizational level (among groups within a local population), where the lack of significant difference in relatedness values for males and females when they are in the same group or not suggests

a lot of mixing for both sexes. I tentatively suggest that selective pressures depend on the organizational level considered, but it was difficult to determine the underlying causation of potential sex differences in dispersal rates and distances solely based on current data. However, the results of this study should be taken carefully as alternative explanations for the observed results are also possible. Extensive field observations, notably using GPS collars on both males and females combined with an important collection of genetic data, are needed to understand the mechanisms responsible for dispersal (*e.g.* social and ecological factors), as well as the difference in the dispersal rate between the sexes.

6 Appendices

Appendix 1. Movement path and time-series of x and y locations of *n* = 4 dispersers, all of which are subadults. B34565 experienced exploratory movements before returning to its new home range.

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CHAPTER 6

MODELING PATHOGEN TRANSMISSION IN A WILD UNGULATE USING DYNAMIC CONTACT NETWORKS

Abstract

The spread of infectious diseases is highly dependent on contact patterns between individuals. In social species, contacts are largely contained within social groups, but diseases are unequally transmitted due to the individual differences in contact structure. In this chapter, I investigated the effects of temporal changes and heterogeneities in within-group contact patterns of the Cape buffalo on a directly transmitted pathogen using network modelling. In southern Africa, the Cape buffalo (*Syncerus caffer caffer*) plays an important role in the maintenance of many livestock diseases of economic and zoonotic concerns. It is thus vital to understand how contact patterns influence the spread of diseases in buffalo groups in order to design effective control measures and to prevent transmission to human and livestock populations. Based on empirical data from GPS collars on two Cape buffalo populations, I constructed a dynamic system of contact networks and then simulated pathogen spread across these networks. I used the epidemiological parameters of Foot-and-Mouth Disease Virus (FMDV) as an example. The contact networks were designed seasonally and for each population and included differences in the number and duration of contacts between individuals. I compared the spread of the epidemic to that in a dynamic system of random networks, where information about the heterogeneity in contact structure between individuals and temporal series of contacts were ignored. Results demonstrated that observed contact patterns in buffalo groups varied according to the season and the population. The contact structure slightly affected the pathogen dynamics within a group, but the speed of pathogen spread within a group was more dependent on the season during which the pathogen is introduced, although the outbreak size was similar between seasons. When the pathogen was introduced during the dry season, the pathogen spread faster and reached a larger number of individuals quicker. These results raise questions about the intragroup dynamics as a strategy for minimizing infection risk in the Cape buffalo and have important ecological and health implications for buffalos, humans and other animals like domestic livestock.

1 Introduction

The structure of contacts between individuals of the host species is a determining factor for the spread of infectious diseases in a population (Altizer et al. 2003, Vicente et al. 2007, Nunn et al. 2015). A better knowledge of host contact patterns is essential for predicting and controlling disease epidemics (Keeling 1999, Miguel et al. 2013, Craft 2015, Reynolds et al. 2015). Traditional epidemiological models assume that the contact patterns are homogeneous between all individuals in the host population (Anderson and May 1991), which means that no heterogeneity in the mixing pattern or in the duration or rate of contact is considered. However, contact patterns are usually heterogeneous among individuals in human and animal populations, and this variation can impact the probability, size and persistence of disease epidemics (Lloyd-Smith et al. 2005, Bansal et al. 2007, Smieszek 2009).

Contact patterns are strongly driven by the host's social system. In solitary animals, individuals avoid each other and are only into contact during the breeding season, when hostile individuals settle territorial conflicts or "randomly" due to environmental constraints, *e.g.* in response to spatial heterogeneity in food availability (Mattisson et al. 2013, Guilder et al. 2015). In contrast, social species typically form groups, which can be stable and persist over a long period of time. Contacts between individuals are largely contained within social groups and information and micro-organisms such as pathogens are disproportionally transmitted within social groups (Grear et al. 2010, Carne et al. 2013). One of the most complex social systems is characterized by fission-fusion dynamics, where subgroups within a larger group regularly merge and divide, varying in size and demographic composition (Aureli et al. 2008). Studies examining this phenomenon have usually focused on the quantification of group patterns over time (*i.e.* mainly based on temporal changes in subgroup size and composition) and/or the role of environmental or internal factors (*e.g.* age, sex, kinship, Cross et al. 2005a, Parra et al. 2011, Bercovitch and Berry 2012, Kashima et al. 2013, Pinacho-Guendulain and Ramos-Fernández 2017). There is still little research investigating how this flexibility in group dynamics can influence the fine-scale patterns of disease transmission (*i.e.* within a group). Mathematical models suggest that pathogen spread in an entire group is more limited when the group is organized into subgroups of individuals (Salathé and Jones 2010, Griffin and Nunn 2012).

Determining the contact structure of wildlife populations can be challenging, but new monitoring technologies have facilitated their quantification, greatly improving our ability to understand and characterize social behaviour (Krause et al. 2013, Kays et al. 2015). The heterogeneity in contact structure among individuals can be captured and analyzed using social network analysis (SNA, Craft 2015, Farine and Whitehead 2015, Silk et al. 2017).

Contacts between individuals that can promote pathogen transmission can be represented using networks, where individuals are represented as nodes, and interactions between them as edges and being used as a proxy of potentially infectious contacts (*e.g.* Carne et al. 2013). Network models can also be used to represent temporal instability of interactions representative of fission-fusion dynamics; this is often called "dynamic social networks" (Rubenstein et al. 2015). Rather than collapsing data over relatively long periods to capture associations (*e.g.* Hamede et al. 2009, Carne et al. 2014), several networks can be built on a fine temporal scale to represent temporal changes in contact structure. Network modelling is a powerful and essential method for understanding and predicting the dynamics of infectious diseases as it allows the simulation of pathogen spread across contact networks through time. These approaches have been widely used in the study of human diseases such as Severe Acute Respiratory Syndrome (SARS, Meyers et al. 2005) and more recently to investigate how contact patterns influence pathogen transmission in wild animal species (Drewe 2010, Chen et al. 2014, Reynolds et al. 2015).

In this study, I use empirical data from GPS collars and epidemiological modelling to explore pathogen spread within Cape buffalo (*Syncerus caffer caffer*) groups. Cape buffalos live in groups primarily consisting of females and their offspring, subadults of both sexes, and a small proportion of adult males. Adult males can temporarily leave the group to live alone or in small bachelor groups (Sinclair 1977, Prins 1996). Social groups of buffalos are unstable, with subgroups of individuals regularly splitting and merging ("fission-fusion dynamics", Sinclair 1977). Recent fine-scale telemetry studies in southern Africa have quantified and indicated more complex fission-fusion dynamics than previously thought (Bennitt et al. 2018, Chapter 3). Individuals within the same group shared on average 79 % of their home range but spent around 38 % of their total time together (Wielgus et al. 2020). However, the strength of association varied greatly among individuals, with pairs of buffalo forming short-term associations and pairs forming long-term associations, and the associations between individuals varied across seasons (Wielgus et al. 2020). These new insights into Cape buffalo group dynamics can impact the way pathogens are transmitted within groups and populations. Disease ecology in the Cape buffalo is of particular importance given the roles the species can play (*e.g.* as a maintenance host) in many livestock diseases. These diseases are generally of economic or zoonotic (when pathogens are transmitted from livestock to humans) importance associated to the overlap between buffalo and livestock home ranges in many areas (Kock et al. 2014, Valls-Fox et al. 2018). So far, to my knowledge, only Cross et al. (2004) used a social-network based approach to explore disease transmission in buffalo population, but the association networks were constructed at the monthly scale. Yet, association patterns vary over short periods of time (*e.g.* fusion events of dyads occurred on average every 1-3

day, Chapter 3), which could have an important effect on the pattern of pathogen transmission.

Here, I used a dynamic contact network approach to simulate pathogen spread in buffalo groups, in order to understand how the high flexibility in grouping patterns influenced the pathogen spread. I focused on foot-and-mouth disease virus (FMDV), a highly contagious virus that can be transmitted between buffalo and cattle with substantial economic losses due to productivity losses and costs associated with control (Dijkhuizen et al. 1995, Jori et al. 2009). FMDV is usually transmitted by direct routes through oral inhalation of viral particles during close contact between two hosts. Indirect transmission through contact with contaminated materials (*e.g.* ground, water) is also possible (Alexandersen et al. 2003), but this has never been quantified under natural conditions in a savanna ecosystem. In southern Africa, the Cape buffalo plays a dominant role in the maintenance of FMDV, acting as the main local reservoir (Guerrini et al. 2019). I began by describing the intra-group contact patterns of 39 radio-tracked Cape buffalo from 6 groups in 2 southern African populations by calculating contact rate and duration between dyads. I then produced a dynamic system of networks representing the contacts between buffalo dyads within the same group from GPS data. I employed a Suceptible-Exposed-Infected-Recovered network modelling approach to investigate the potential spread of FMDV in dynamic contact networks. The aims of this chapter were (1) to compare the observed contact network approach with the more traditional approach (*i.e.* when all individuals had the same probability of contact) to determine if the structure of the network (*i.e.* fine-scale temporal changes and heterogeneity in contact structure) impacted the pathogen spread, and (2) to compare the results of contact networks and predicted pathogen spread between the populations and seasons to understand the impact of the environmental context and seasonal environmental changes (*i.e.* mainly in resource abundance) on the threat of disease. I tested the predictions that (1) the heterogeneity in the contact structure between dyads would slow the pathogen spread and reduce the outbreak size (Cross et al. 2004, Stehlé et al. 2011, Nunn et al. 2015) because infections should be contained within the highest associated individuals, (2) forming subgroups would reduce pathogen risk, because infections would spread quickly within subgroups and die out before spreading to other subgroups (Salathé and Jones 2010, Griffin and Nunn 2012), and (3) the seasonal changes in resource abundance and distribution, which are responsible for variation in contact patterns (Chapter 3) should, in turn, affect the pathogen dynamics.

2 Methods

2.1 Study areas

Data used in this study were collected in two Cape buffalo populations in southern Africa (Figure 1). The first population (hereafter called “Gonarezhou”) lives in the southern part of Gonarhezou National Park (5 053 km², Zimbabwe). The second population (hereafter called “Kruger”) is at the border between Zimbabwe and South Africa, along the Limpopo River, linking the northern tip of the Kruger National Park in South Africa (18 989 km², South Africa) with communal lands in Zimbabwe.

The study areas were characterized by similar environmental conditions, containing a mix of bushland savanna, open grassland and woodland (Gertenbach 1983, Gandiwa and Zisadza 2010). Annual rainfall across the two study areas is similar with around 500 mm and the distribution of rainfall within the year is also similar between the populations, with most rainfall falling between November and March (Gertenbach 1980, Gandiwa et al. 2016). For seasonal comparisons, I defined two core seasons according to fixed dates based on similar rainfall patterns between the populations (Gertenbach 1980, Gandiwa et al. 2016), excluding the transitional periods between typically wet and dry seasons: the core wet season was the period running from January 1st to March 31st (*n* = 90 days) and the core dry season from August 15th to October 31st (*n* = 78 days).

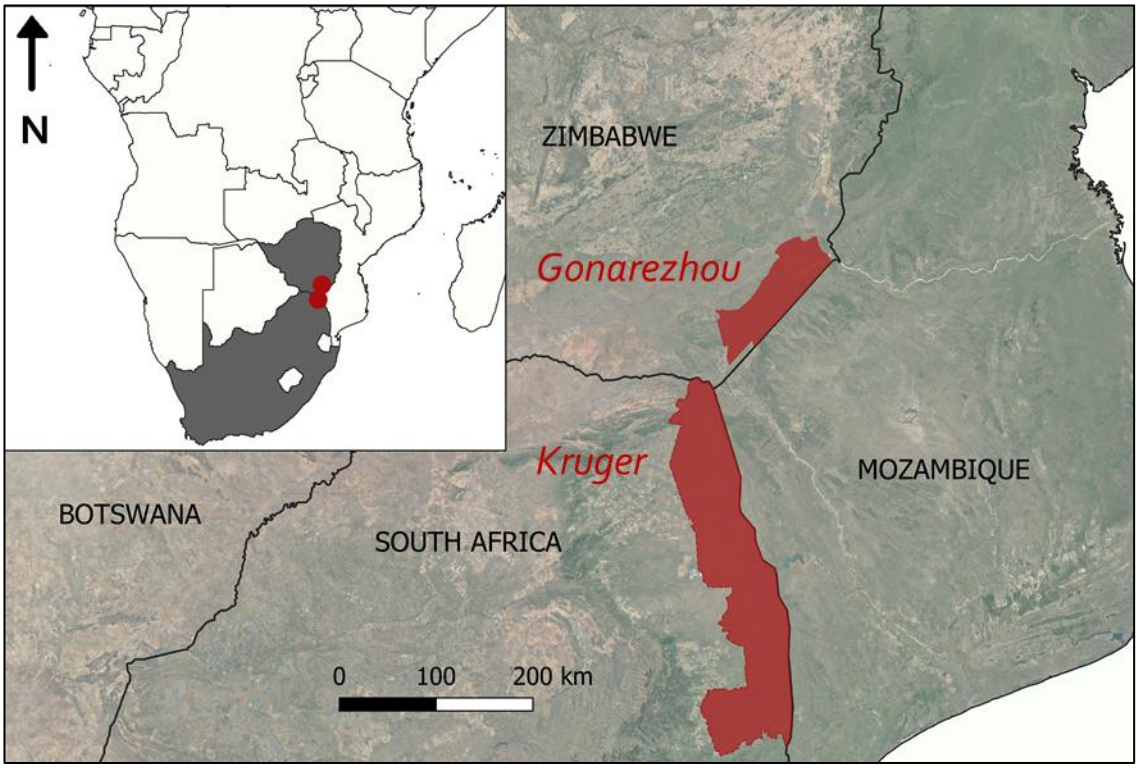


Figure 1. Location of the two study populations: Gonarezhou National Park in Zimbabwe and Kruger National Park in South Africa.

2.2 Collaring and GPS data collection

Between 2008 and 2015, a total of 59 GPS collars were deployed on female Cape buffalos (Gonarezhou: *n* = 18, Kruger: *n* = 41). As adult males can leave the group temporarily, I focused on cows to study the movements of mixed groups (Sinclair 1977, Prins 1996). Female buffalos were classified in two age classes: subadult (2.5 - 4.5 years old) and adult (> 4.5 years old). All animals were captured by authorized personnel using established techniques (la Grange 2006) and were observed returning to their groups after collaring operations. All field operations were conducted following the legal and permit requirements of the countries in which they were carried out.

The data acquisition periods extended from October 2008 to December 2012 in Gonarezhou and from June 2010 to July 2015 in Kruger and the duration of the tracking varied between 20 and 759 days (median = 409 days) across individuals. GPS loggers were scheduled to acquire locations at 1-hour intervals, although a GPS fix was not always acquired when scheduled. I computed fix success rate within each season for each individual and I retained data from 49 GPS collars for which the success rate was higher than 80% (corresponding to 39 different females given that some GPS collars were deployed on females already tracked the previous year). Of these 49 GPS collars, I used data from 38 collars in both wet and dry seasons (Gonarezhou: *n* = 15, Kruger: *n* = 23) and from 11 in a single season (Kruger: *n* = 11).

2.3 Defining group membership

Buffalo cows live in large groups whose members occupy an identifiable and stable home range (Ryan et al. 2006). To identify individuals in the same group, I considered seasonal home ranges as the 90% utilization distribution during the dry and wet seasons (Börger et al. 2006). Utilization Distributions (UD) were computed using the Movement-Based Kernel Density Estimation method (MKDE, Benhamou and Cornélis 2010) implemented in the 'adehabitatHR' package in R (Calenge 2007). I measured the overlaps in the seasonal home ranges between individuals using the Bhattacharyya's affinity index (Benhamou et al. 2014). The index accounts for variation in the intensity of home range use and varies from 0 (no overlap) to 1 (identical space use). Individuals with seasonal home range overlap ≥ 0.6 were considered *a priori* to belong to the same group (Chapters 3 & 4).

2.4 Empirical buffalo contact patterns

Since buffalo cows live in large groups that exhibit fission and fusion events, resulting in subgroups that regularly merge and divide, two given individuals alternate between events when they are said to be into 'contact' and events when they are not, called 'non-contact'.

To create contact networks with biologically meaningful group size (see section 2.5) and then assess the role of these contact networks in disease spread dynamics, I first quantified individual contact patterns (*i.e.* 'contact' or 'non-contact' periods) from empirical data. To do this, I calculated the distance between synchronous locations for every pair of individuals (*i.e.* dyad) belonging to the same group for a given season and a given year. I considered that two individuals were in contact when their hourly Euclidean distance based on GPS locations was ≤ 150 m. Some individuals left their group in which they were captured to be engaged in short- or long-distance movements such as dispersal or exploratory movements (n = 4 individuals, Chapter 5). For these individuals, I only considered GPS locations when they were in the group in which they were captured. A spatial window of 150 m was considered because (1) FMDV is most frequently transmitted by respiratory routes, therefore during close direct contacts (OIE 2009), (2) the buffalo tracked is part of a group, (3) the GPS precision is imperfect (i.e. precision range of 15 – 30 m from manufacturer data) and (4) the tracked individuals can move during the one hour between two recorded locations. To minimize the number of false contacts resulting from infrequent erroneous locations, some fluidity was allowed. If the distance between two individuals was ≥ 150 m for ≤ 2 h, I considered that they were still into contact. When one association value was missing between two known contact values (*i.e.* 'contact' or 'non-contact', *e.g.* the location of at least one of the two individuals had not been recorded), I substituted the missing value by the value of the previous hour (in other words, they were considered into contact only if they were in the previous hour). When two animals were in 'contact' or 'non-contact' for several consecutive intervals, the 1-h intervals were aggregated and were regarded as a single 'contact' or 'non-contact' event. For each dyad and each season, I calculated the probability of contact, as the total number of locations where the two individuals were in 'contact' divided by the total number of synchronous locations. I also calculated the duration of every 'contact' and 'non-contact' event for each dyad, but I excluded the events containing at least one missing timestamp. I quantified both the 'contact' and 'non-contact' events to be able to create networks at larger group size taking into account the temporal variation in contact patterns between two individuals due to group dynamics and the causality constraints between events.

I tested whether the duration of 'contact' and 'non-contact' events varied with the age of individuals, the season and the site using generalized linear mixed models with negative binomial distributions of errors. I used a separate model for contact and for non-contact events. Age of dyad (adult – adult, subadult – subadult, adult – subadult) was included as a fixed effect as well as the season, site and interaction between the latter two. The dyad identity was a random effect to account for dyad variation. I used the Akaike Information Criterion corrected for small sample size (AICc) to test whether a simpler model, nested in the full model, is more parsimonious (Burnham and Anderson 2002). The most

parsimonious model was the model with both a ΔAICc < 2 and the lowest number of explanatory variables (Arnold 2010).

2.5 Constructing contact networks on a larger group size

To explore how the dynamic nature of the host contact network affects the dynamics of pathogen spread, I considered a set of contact networks built on the explicit representation of the dynamic interactions between buffalo dyads (*i.e.* where the contact structure is dynamic over time and contacts are heterogeneous between dyads in their probability and duration), referred to as the "heterogeneous mixing" (HET) network against a benchmark network in which every individual has an equal probability of contacting other individuals at each time step, referring to as the "homogeneous mixing" (HOM) network (see below). To investigate pathogen spread in a buffalo group with a biologically meaningful group size, I used the empirical data on probability and duration of 'contact' and 'non-contact' event to create larger networks of 200 buffalos. I produced networks at the shortest available temporal resolution (1 hour) for each season (dry vs. wet) and for each site (Gonarezhou vs. Kruger). The networks consisted of nodes (individual buffalo) and undirected edges between two nodes, which represented potential infectious contacts between the two individuals at a given time step. As the duration of contact and non-contact events did not vary between age of the two individuals involved (see results), I did not consider heterogeneity in contact structure between age and did not assign age to node.

In the HET network, each pair of individuals was randomly assigned a pair of observed buffalos, which was described by a unique contact probability, a distribution of contact duration and a distribution of non-contact duration. At time step $t = 1$, each pair was defined as being in contact or not according to their probability of contact, then a corresponding event (*i.e.* 'contact' or 'non-contact') was drawn randomly in the time series of the corresponding observed pair of buffalo to calculate the duration for the remaining event (*i.e.* not the entire event). This method made it possible to capture a realistic contact structure at the start of the simulation, considering that individuals were potentially already in contact previously. Then, for each event in the networks (*i.e.* contact and non-contact), a time was assigned by sampling from the dyad-specific distribution of duration of contact and non-contact. The HET networks thus considered the empirical duration of contact and non-contact periods of the two individuals involved. The resulting network was a dynamic object that conserved heterogeneity in the duration of contact and non-contact between dyads and the causality constraints between contact events.

By contrast, the HOM network was constructed only from the observed probability of contact and without considering the observed duration of contact and non-contact periods. From the occurrence of contact and non-contact events between the observed

buffalo dyads, I calculated a unique probability of contact for each season and site, by aggregating the total number of locations where two buffalos were into contact divided by the total simultaneous locations between these two individuals. The resulted probability of contact did not consider the potential heterogeneity in contact structure between dyads. I constructed the HOM network by connecting individuals that came in contact according to the probability of contact corresponding to the season/site. The probability of contact was identical for all pairs and for all time steps. Therefore, the HOM network included information about contacts between dyads (who has met whom) but disregarded information about the heterogeneity in contact structure between individuals (no pair was more likely to be in contact than another) and the duration of contact and non-contact events (each time step is independent of the previous step).

2.6 Simulating pathogen spread in a dynamic contact network

The set of contact networks for HOM and HET in dry and wet seasons was used to simulate FMDV spread through a buffalo group. I used an individual-based and stochastic model to simulate FMDV transmission. A simple SEIR epidemic model was used, in which no births, deaths or introduction of new individuals occurred. S represents the number of susceptible individuals, E the number exposed (infected but not yet infectious), I the number of infectious and R the number recovered. Due to the lack of data on FMDV transmission in the Cape buffalo, the parameters used came from analysis of FMD outbreaks in domestic cattle (Bates et al. 2003, Thornley and France 2009). The simulation started with a single randomly chosen infectious individual, with the rest of the group being in the susceptible state. Susceptible individuals (S) could contract the pathogen in a time period of t (β_t) with a probability of infection given by: $\beta_{i,t} = 1 - \exp(\beta_0 C_{ji,t})$, where β_0 was the transmission coefficient (a constant equals 0.002 per hour, Thornley and France 2009) and $C_{i,t}$ represented the number of contacts of animal i with any infectious individuals in time t. Transmission to a susceptible occurred according to a binomial trial with the defined probability of infection $\beta_{i,t}$. When contracted the disease, a susceptible buffalo became exposed (E) but was not infectious during an incubation period of 4 days. After this period, the exposed individuals entered the infectious disease state (I) and could transmit the disease to the susceptible individuals during their infectious period, whose duration was equal to 4 days. The infectious individuals became recovered (R) at the end of the infectious period and acquired permanent immunity to the disease. I ran simulations over the length of the seasons, and I repeated simulations 100 times for each of the networks (HET and HOM) and each of the seasons and sites.

2.7 Analysis of the contact networks and the epidemiological simulation results

I compared the simulated contact networks by calculating the mean duration of contact and non-contact events, the mean degree of a node (defined as the number of connections an individual has in the network), the mean clustering coefficient (which describes the local cohesiveness and measures the tendency of individuals to form subgroups) and the average path length derived from 100 realizations of each of the two network models (HOM vs. HET networks) separately for each season and each site.

To explore the impact of the dynamic nature of the contact network on the dynamics of pathogen spread, I compared the epidemic outbreaks in the two types of networks by calculating the time taken for the pathogen to spread (defined as the time taken for half of the group to become exposed or infected), the maximum prevalence and its associated occurrence date. I also estimated the reproductive number R_0, which was the expected number of secondary infections from an initial infected individual in the susceptible buffalo group. I calculated the value of R_0 as the mean over all simulations of the number of secondary cases from the single initial randomly chosen infectious individual. I tested whether social metrics and epidemiological parameters were significantly different between seasons, sites and types of network using nonparametric Mann-Whitney U tests (pairwise comparisons: dry vs. wet, HOM vs. HET, Gonarezhou vs. Kruger). Statistical calculations were performed using R, v. 3.6.0 (R Development Core Team 2019).

3 Results

3.1 The season and site drive empirical contact patterns

The mean duration of both periods when individuals were in contact or in non-contact varied between 7.5 and 59 hours with large variations, meaning many contacts and non-contacts of short duration, a few contacts and non-contacts of long duration, and a broad tail, suggesting that no typical contact and non-contact durations could be defined (Figure 2). Non-contact and contact events were generally shorter in duration in Kruger than in Gonarezhou. Non-contact events usually lasted longer than the contact events in both seasons, but contacts in the wet season were generally shorter than in the dry season (Figure 2). These results were confirmed by using generalized mixed-effect models. The most parsimonious models for duration of contact and non-contact only included an interaction effect between site and season (contact: AICc = 35533.5, AICω = 0.80; non-contact: AICc = 39637.5, AICω = 0.70). The contact and non-contact events were longer in Gonarezhou than in Kruger and during the dry season than in wet season in both sites

(Table 1). Given these results, I built contact networks on a larger group size without distinction with age (see below).

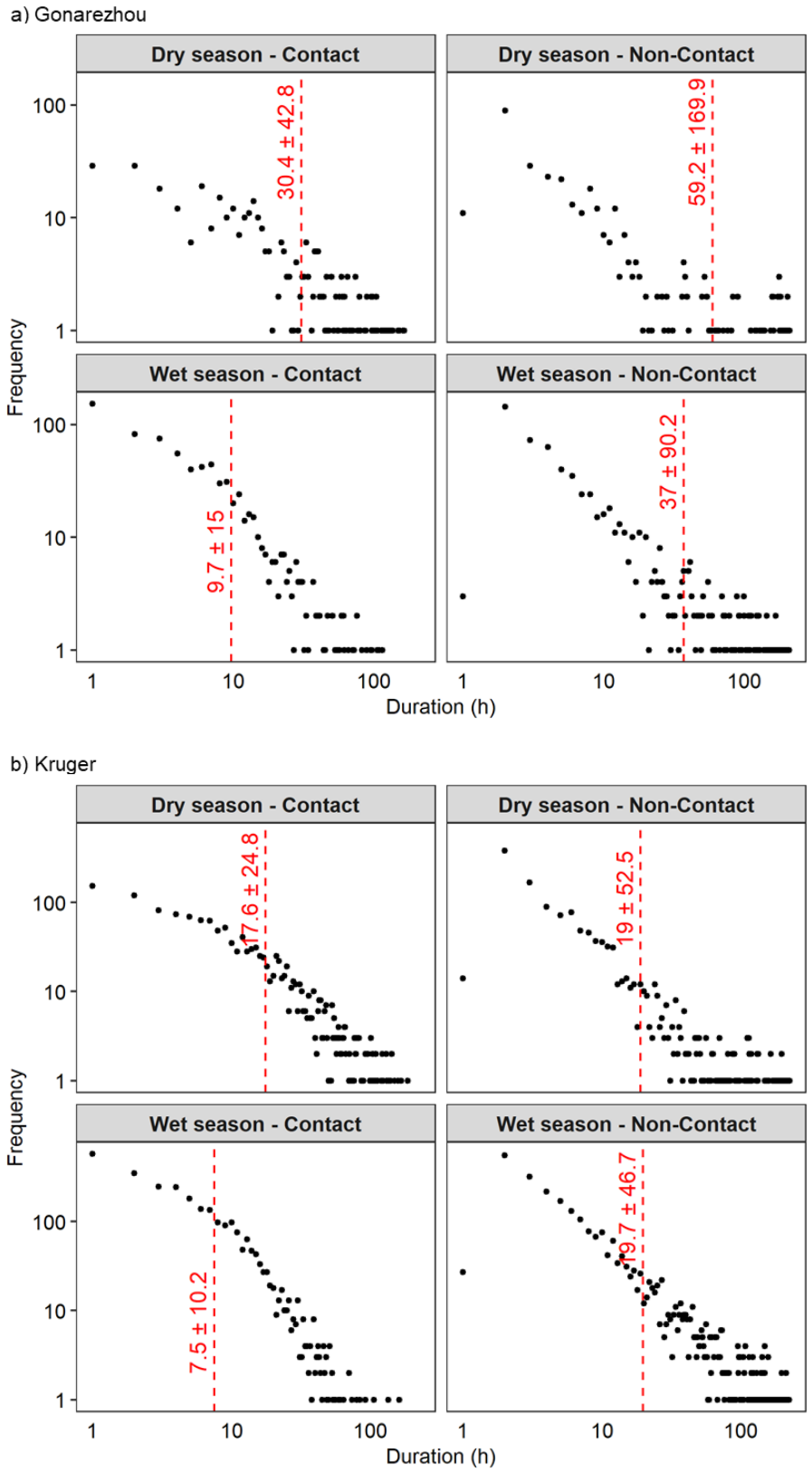


Figure 2. Observed distribution of the duration of 'contact' and 'non-contact' events between any two buffalos, for each season on a log-log scale for (a) Gonarezhou and (b) Kruger. The mean duration ± SD is given by the red dashed line.

Table 1. Results of the most parsimonious models explaining the duration of contact and non-contact events.

	Estimate	SE	Z	P	95% CI (lower, upper)
Duration of contact					
(Intercept)	3.41	0.09	37.17	<0.001	(3.23, 3.59)
Site [KNP > GNP]	-0.67	0.11	-6.37	<0.001	(-0.88, -0.47)
Season [Wet > Dry]	-1.15	0.07	-16.89	<0.001	(-1.28, -1.01)
Site [KNP > GNP]:Season [Wet > Dry]	0.39	0.08	5.02	< 0.001	(0.24, 0.55)
Duration of non-contact					
(Intercept)	4.19	0.13	32.75	<0.001	(3.95, 4.45)
Site [KNP > GNP]	-1.33	0.15	-8.96	<0.001	(-1.62, -1.04)
Season [Wet > Dry]	-0.58	0.09	-6.61	<0.001	(-0.75, -0.41)
Site [KNP > GNP]:Season [Wet > Dry]	0.62	0.10	6.04	< 0.001	(0.42, 0.82)

3.2 Buffalo simulated contact networks

HOM contact networks differed significantly from HET contact networks in each of the social metrics measured, within each season and each site (Figure 3). The duration of contact and non-contact events in the HET networks was significantly much larger than the values obtained for the HOM networks (Figures 3a-3b). Clustering coefficients were significantly higher for the HET networks, indicating that HET networks were more subdivided into subgroups than HOM networks (Figures 3d). The degree of a node was higher in the HET networks whilst the average path length was lower in those networks compared to the HOM networks, indicating that, within the HET networks, individuals had more direct connections and more indirect close connections (*i.e.* connections between individuals via other individuals) than in the HOM networks (Figures 3c-3e).

There were also significant differences in the structure of the networks across the sites and the seasons (Figure 3). During the wet season, individuals had generally fewer direct and indirect close connections with other individuals (*i.e.* lower degree of a node and higher average path length, respectively), had shorter contacts and were less likely to form subgroups (*i.e.* lower coefficient of clustering) than during the dry season in both the HOM and HET networks. According to the comparison of the HOM and HET networks between the sites, the most different metrics were the duration of the contact and non-contact events and the average degree of a node. In Kruger, contacts and non-contacts lasted less than in Gonarezhou, but individuals had more connections with different individuals.

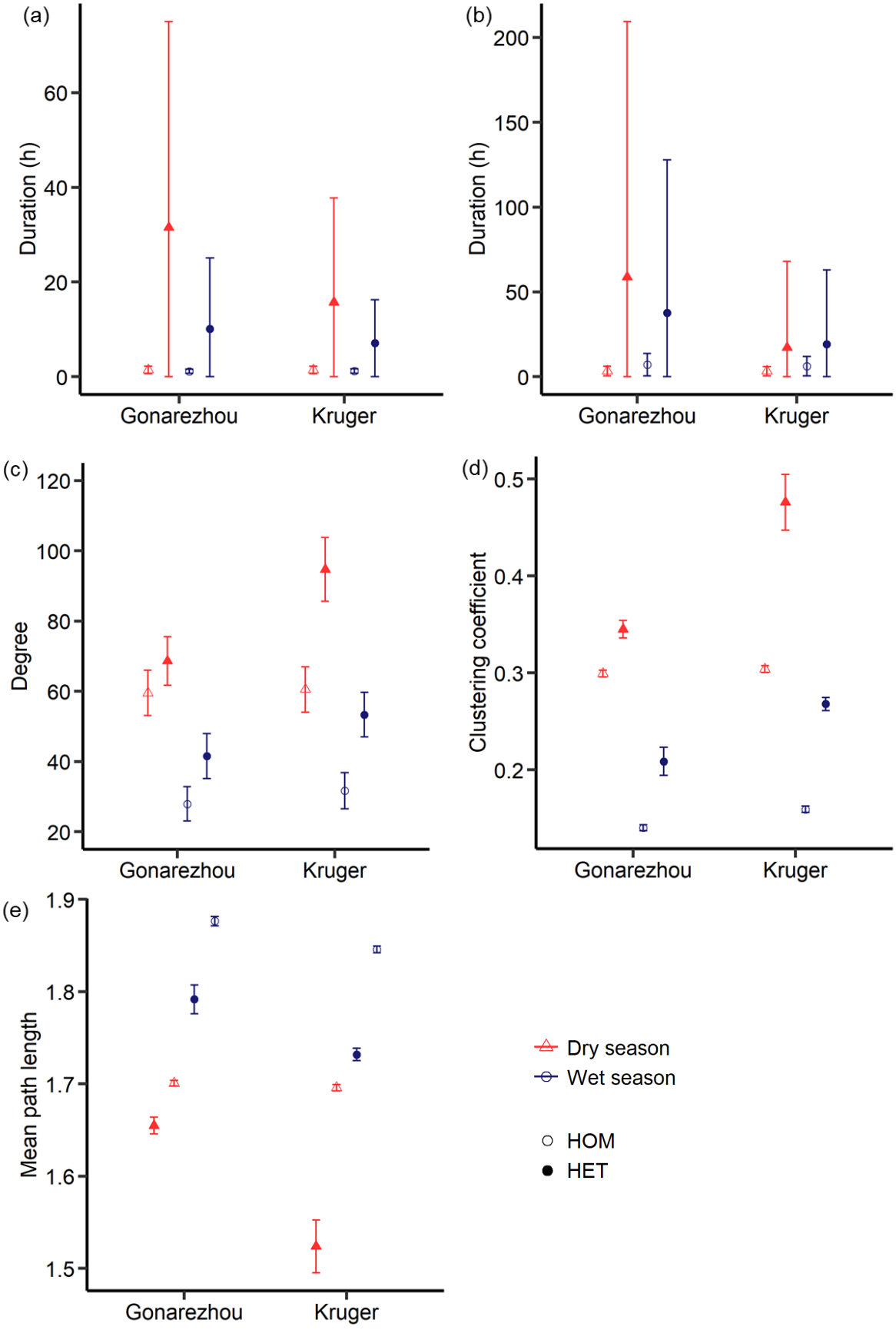


Figure 3. Comparison of social network metrics between HOM and HET networks during wet and dry seasons in Gonarezhou and Kruger: (a) duration of contact events, (b) duration of non-contact events, (c) degree of a node, (d) clustering coefficient, and (e) path length. All relevant pairwise comparisons (across seasons, sites or types of network) were significantly different ($p < 0.001$). See table Appendix 1 for raw values of mean ± SD.

3.3 *Buffalo pathogen spread*

The time series of mean number of individuals in each state for the HOM and HET networks for each site and each season are presented in Figure 4. The influence of season, site and type of network on the characteristics of pathogen transmission, namely the maximum prevalence, its associated occurrence date, time taken for the pathogen to spread (T_s), and basic reproduction number (R_0) are plotted in Figure 5. The distribution of R_0 for each condition (HOM vs. HET, site, season) is also plotted in Appendix 2.

The majority of the simulations resulted in the local extinction of the pathogen as all individuals of the group were infected once before being recovered, whatever the season, site or type of network. Most of the disease characteristics were significantly different between the HET and HOM networks (Figure 5, Table 2). The R_0 was significantly higher in the HET networks than in the HOM networks, but only in Kruger in both seasons. In the HET networks, T_s was significantly higher, meaning that the pathogen took longer to infect half of the group, but the epidemic peak was reached more quickly in comparison to HOM networks; the exception was for the dry season in Gonarezhou, where both parameters (T_s and occurrence date of maximum prevalence) did not significantly differ (Table 2). Additionally, the number of individuals infected at the epidemic peak in the HET networks was greater than in the HOM networks (Figure 5). Overall, the differences between networks were generally small with high variability. Despite the significant differences, the values were generally highly variable, and some differences were quite small (Figure 5).

Significant differences between sites were also observed (Table 3); most parameters were higher in Kruger, except for T_s (Figure 5). Nevertheless, there was no difference in the parameters between the two sites for HOM networks in the dry season (Table 3). The most substantial differences in the characteristics of pathogen transmission were noticed between seasons (Table 4). During the wet season, the values of time taken for the disease to spread (T_s) and maximum prevalence occurrence date were higher than in the dry season whilst maximum prevalence and R_0 were lower, in both sites and for both HOM and HET networks (Figure 5). Overall, these seasonal differences combined with temporal evolution of number of individuals in each state (Figure 4) indicated that, during the dry season, the pathogen spread faster and reached a greater number of individuals in the same time step compared to the wet season.

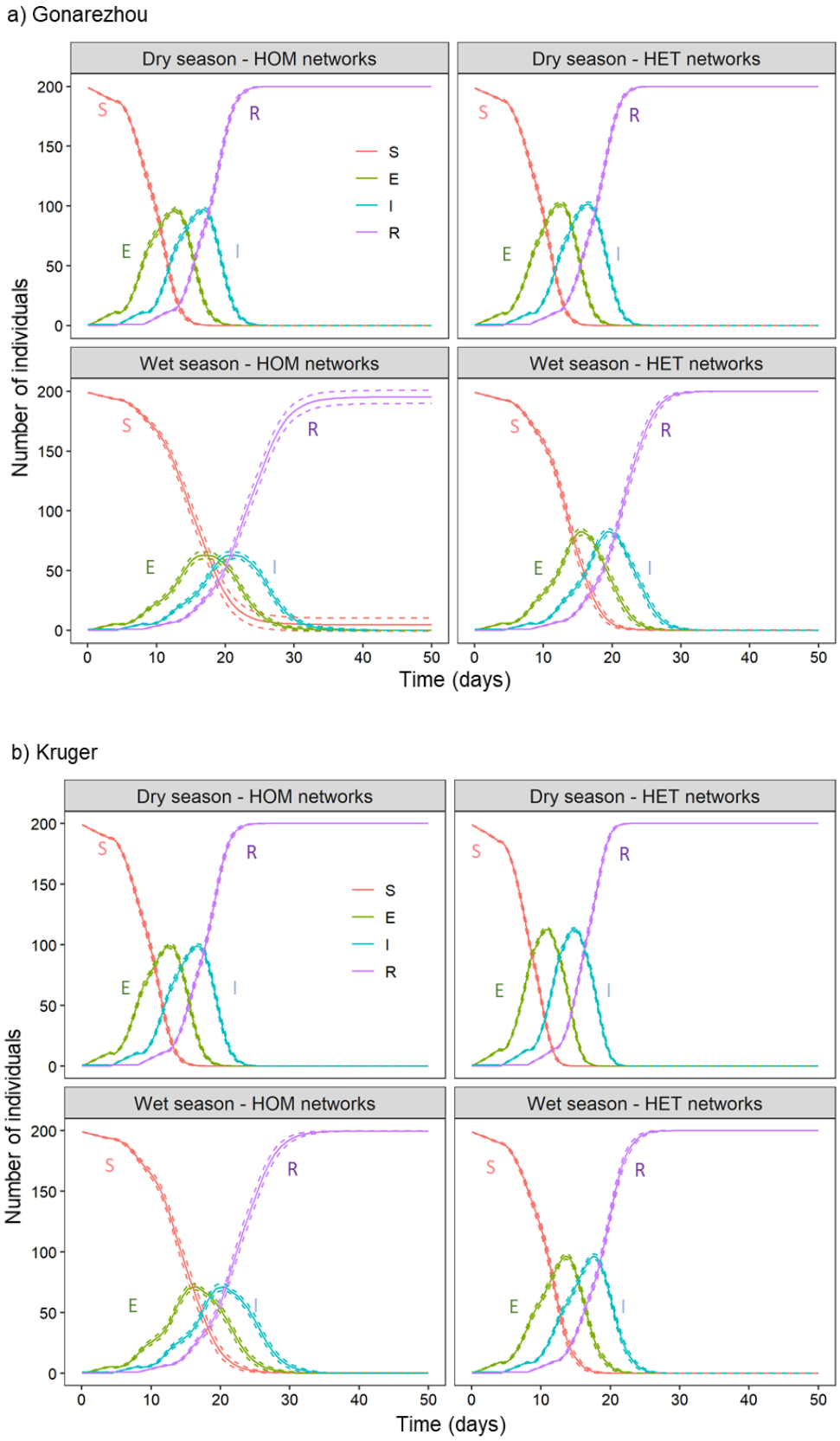


Figure 4. Temporal evolution of the number of susceptible (S), exposed (E), infectious (I) and recovered (R) individuals for the homogeneous (HOM) and heterogeneous (HET) networks for each season and each site: (a) Gonarezhou; (b) Kruger. Solid lines represent the mean values, and dashed lines represent the fifth and ninety-fifth percentiles of the number of individuals in each state.

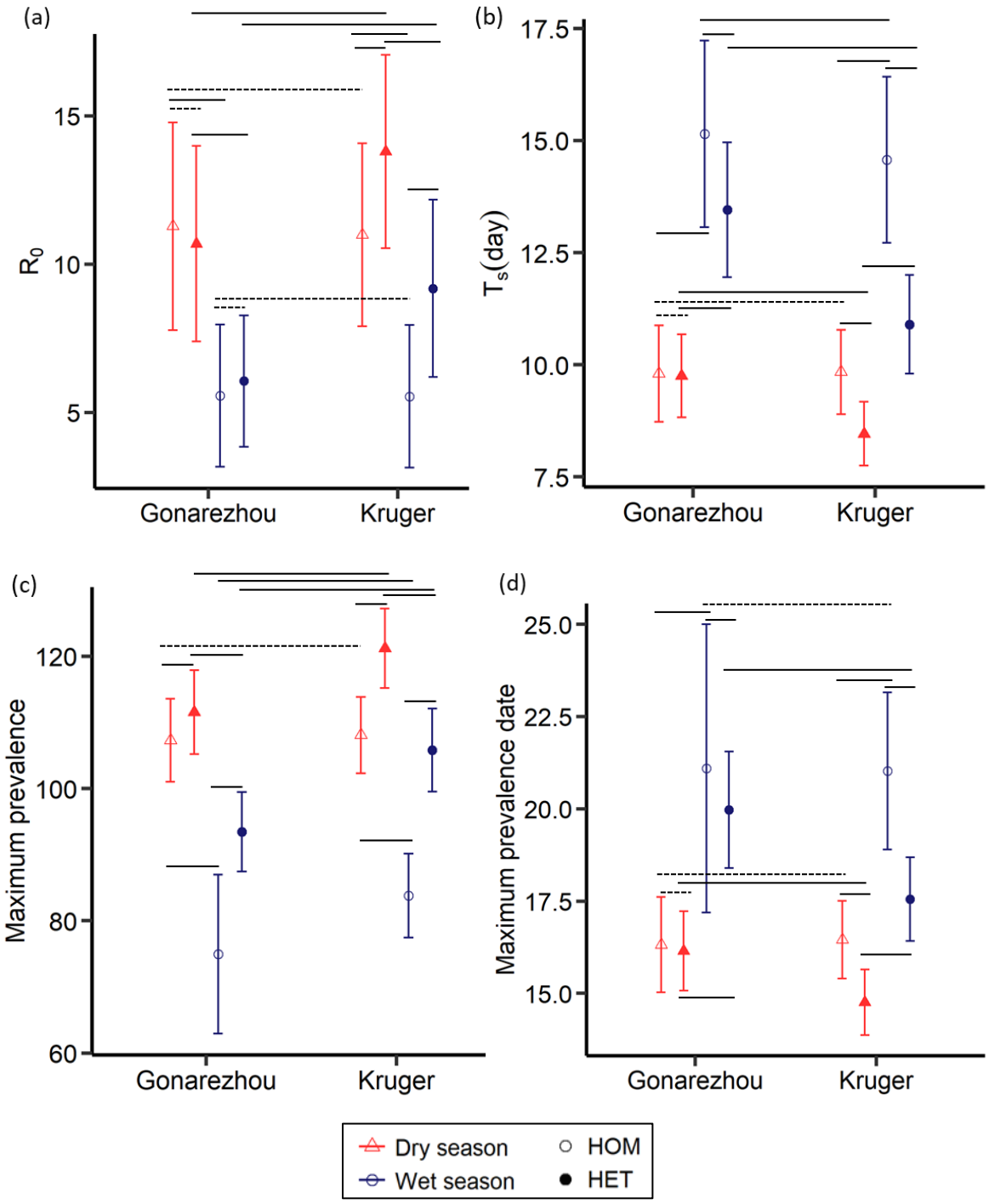


Figure 5. Comparisons of (a) the reproductive ratio, R_0, (b) the time taken for the disease to spread into 50% of the group, T_s, (c) the maximum prevalence and (d) its occurrence date in HOM and HET networks during wet and dry seasons in Gonarezhou and Kruger. The symbols denote means and the error bars indicate standard deviation over 100 simulations. Solid horizontal lines indicate significant pairwise differences ($p < 0.05$) whilst dashed lines indicate non-significant difference in the pairwise comparison. See table Appendix 3 for raw values of means ± SD and Tables 2-4 for the results of Mann-Whitney U tests.

Table 2. Summary of results for Mann-Whitney U tests comparing epidemiological parameters from SEIR model between HOM and HET networks within each site and each season.

Variable			Comparison	*W*	*p value*
R_0	Gonarezhou	Dry	HOM vs. HET	5491	0.23
	Gonarezhou	Wet		4256	0.07
	Kruger	Dry		2559	< 0.001
	Kruger	Wet		1690	< 0.001
T_s	Gonarezhou	Dry	HOM vs. HET	5055	0.89
	Gonarezhou	Wet		7633	< 0.001
	Kruger	Dry		8766	< 0.001
	Kruger	Wet		9732	< 0.001
Max prevalence	Gonarezhou	Dry	HOM vs. HET	3224	< 0.001
	Gonarezhou	Wet		226	< 0.001
	Kruger	Dry		542	< 0.001
	Kruger	Wet		63	< 0.001
Max day	Gonarezhou	Dry	HOM vs. HET	5419	0.31
	Gonarezhou	Wet		7050	< 0.001
	Kruger	Dry		8894	< 0.001
	Kruger	Wet		9552	< 0.001

Table 3. Summary of results for Mann-Whitney U tests comparing epidemiological parameters from SEIR model between Gonarezhou and Kruger within each season and each type of network.

Variable			Comparison	W	*p value*
R_0	HOM	Dry	Gonarezhou vs. Kruger	5193	0.64
	HOM	Wet		4964	0.93
	HET	Dry		2450	< 0.001
	HET	Wet		2016	< 0.001
T_s	HOM	Dry	Gonarezhou vs. Kruger	4829	0.68
	HOM	Wet		5799	0.03
	HET	Dry		8657	< 0.001
	HET	Wet		9378	< 0.001
Max prevalence	HOM	Dry	Gonarezhou vs. Kruger	4626	0.36
	HOM	Wet		1936	< 0.001
	HET	Dry		1376	< 0.001
	HET	Wet		815	< 0.001
Max day	HOM	Dry	Gonarezhou vs. Kruger	4704	0.47
	HOM	Wet		5569	0.16
	HET	Dry		8427	< 0.001
	HET	Wet		9235	< 0.001

Table 4. Summary of results for Mann-Whitney U tests comparing epidemiological parameters from SEIR model between dry and wet season within each site and each type of network.

Variable			Comparison	*W*	*p value*
R_0	Gonarezhou	HOM	Dry vs. Wet	9197	< 0.001
	Gonarezhou	HET		8812	< 0.001
	Kruger	HOM		9219	< 0.001
	Kruger	HET		8626	< 0.001
T_s	Gonarezhou	HOM	Dry vs. Wet	13	< 0.001
	Gonarezhou	HET		45	< 0.001
	Kruger	HOM		15	< 0.001
	Kruger	HET		227	< 0.001
Max prevalence	Gonarezhou	HOM	Dry vs. Wet	9999	< 0.001
	Gonarezhou	HET		9888	< 0.001
	Kruger	HOM		9987	< 0.001
	Kruger	HET		9701	< 0.001
Max day	Gonarezhou	HOM	Dry vs. Wet	303	< 0.001
	Gonarezhou	HET		56	< 0.001
	Kruger	HOM		24	< 0.001
	Kruger	HET		254	< 0.001

4 Discussion

It is now widely recognized that the impact of infectious disease on a population depends on contact structure between individuals rather than group size (Smieszek 2009, Craft 2015, Nunn et al. 2015, Sah et al. 2017, White et al. 2017). In this study, I built dynamic network models using empirically derived buffalo contact data within groups to simulate pathogen spread through a buffalo group in two distinct populations. In order to explore the influence of the intragroup structure on the dynamics of the pathogen, I compared the spread of pathogen between heterogenous dynamic contact networks (HET, considering heterogeneity in contact structure between dyads and the causality constraints between contact events) and homogeneous dynamic contact networks (HOM, the heterogeneity in contact structure between dyads and temporal series of contacts were ignored). Empirical contacts between dyads were influenced by season (dry vs. wet) and site (Gonarezhou vs. Kruger). The simulated contact networks indicated a difference in structure between HOM and HET networks. In the latter, individuals formed tighter social subgroups (higher clustering coefficient), had more frequent (higher degree of a node) and longer direct contacts. Both HOM and HET networks varied with the season, and more slightly with the site. Using known FMDV parameters for this case study, the speed of pathogen spread within a group depended more on the season of pathogen introduction than the topology of

the contact network. FMDV tended to spread faster and reached a larger number of individuals in a given time step when FMDV was introduced during the dry season. The spread of FMDV across the HET networks was slightly higher to that across the traditional HOM networks. Even though this study was based on the characteristics of FMDV, it is important to mention that the contact networks built here can be applied to any pathogen with a direct mode of transmission. This might be modelled in extensions of this study.

It is important to note that the simulations of contact networks and pathogen spread were based on GPS data collected over different years between the populations (2008-2012 in Gonarezhou and 2010-2015 in Kruger). This may be responsible for the small observed differences in contact patterns between the populations. In addition, I used fixed dates to define seasons, but small differences in resource availability within seasons among years (*e.g.* drought year) may lead to changes in spatial behaviour and thus contact patterns in Cape buffalos between the years. However, the markedly different contact patterns between seasons suggest that this difference in the period of data collection does not affect the results. Another limitation of this study is the lack of data on buffalo males. For a full understanding of pathogen dynamics in buffalo groups, and this is also true at the population level, it is important to consider the behaviour of not only grouping females, but also adult and subadult males that come into contact with females, at least part of the year (Halley and Mari 2004). Males tend to break the GPS collar within a few months of deployment, either intentionally or by accident during fights (Halley and Mari 2004, Caron et al. 2016), but it is essential in the coming years to successfully deploy monitoring devices on these animals (*e.g.* GPS ear tags). This chapter only focused on within-group pathogen transmission, while in natural conditions pathogens can spread between Cape buffalo groups and between species (Bastos et al. 2000, Michel 2002, Miguel et al. 2013, Caron et al. 2016 and Chapter 4). For a complete understanding of pathogen dynamics, it would be beneficial to consider contact networks between all individuals, *i.e.* from the same species or not, living in the same study area. However, this would require a large amount of data collected over relatively long periods of time. Such extensive databases are rare, but recent studies on the social structure and contact rates between buffalo and other species at seasonal scale (Miguel et al. 2013, Kiffner et al. 2014, Meise et al. 2019) and the new information of contact rate and duration between Cape buffalo groups (Chapter 4) should help to create contact networks at the regional scale and therefore to better understand pathogen spatial spread.

As with all modelling approaches, there are a few simplifications that I needed to be made in the simulation model and two assumptions are worth discussing. First, I assumed that the infection status did not change the social behaviour of individuals. This implicit assumption is not inappropriate here, since the aim of this study was to demonstrate the role of heterogeneous and dynamic contact patterns on pathogen dynamics (*i.e.*

comparison between the observed network and traditional network). In fact, there are few studies on the impact of infectious status on the social behaviour of the Cape buffalo, but loss of body condition due to chronic infections (Caron et al. 2003) may force infected individuals to increase their sleep and rest, making them thus less social. Therefore, the presence of some parasites may alter social interactions and contact patterns. Second, I considered that group composition and size were stable throughout the simulation (*i.e.* 200 females) without the demographic processes of birth and death, and even dispersion. Yet births allow the recruitment of susceptible individuals and can prevent the local extinction of pathogens by providing new individuals that can be infected and to transmit the pathogen (see below). Females can also disperse (Halley et al. 2002, Caron et al. 2016, Spaan et al. 2019), and this process can alter contact network properties by the arrival or departure of individuals. Despite these limitations, the results of this study indicate that fine-scale contact data appear to be irrelevant to predict the number of individuals infected with FMDV, but seasonal differences in resource availability and distribution alter the contact network properties, which in turn affect the pathogen spread.

4.1. The impact of network topology on predicted FMDV spread

I found that considering the duration of contacts and non-contacts and the heterogeneity of contact structure between individuals alter the observed pattern of contact networks. Not surprisingly, I showed that the distributions of contact and non-contact duration reported in HET networks were more consistent with those observed from empirical data than the values from the HOM networks. In HET networks and observed data, contact events lasted on average 7-31 hours and non-contact events 19-59 hours depending on the season and the site, compared to an average duration of one hour for contacts and from 3 and 7 hours for non-contacts depending on the site or the season in HOM networks. Few studies on contact networks in buffalo are available in the literature for comparison with my HET networks and when they existed, the distance threshold used to define a contact was different (Bennitt et al. 2018). However, the consistency between the HET networks and the empirical data suggests a good representativeness of this model compared to what occurs in natural conditions. Homogeneous models assume that contact patterns within a population or a group shape a regular random network with no individual variability (Bansal et al. 2007). However, in agreement with previous observations made in other buffalo populations (Bennitt et al. 2018), I showed that the distributions of contact and non-contact durations varied with both time and individual. This suggests that non-regular dynamic networks characterize the intra-group buffalo contact network better than a regular dynamic network. Previous studies have either considered the importance of individual heterogeneity in static networks (Christley et al. 2005, Lloyd-Smith et al. 2005) or temporal changes in the

contact network (Blonder et al. 2012) but a broad understanding of the role of these two factors simultaneously is usually lacking (Stehlé et al. 2011 in a human system).

I found significant differences in epidemiolocal parameters between the HOM and HET networks. In HET networks, pathogen appeared to spread quicker and reached a larger number of individuals in a given time step than in HOM networks. However, the differences were quite small and values of parameters highly variable. The small effect of the heterogeneity in contact networks observed can be due to low stability in dyadic contact patterns, which compensates the clustering in subgroups by high mobility among subgroups. Therefore, dynamic changes in social structure by fission-fusion in the Cape buffalo may only slightly affect pathogen dynamics. This indicates that the fine-grained structure of Cape buffalo network has little impact on predicted transmission patterns for FMDV. Consequently, for the simulation of pathogen spread such as that considered in this study, information on contact probability at a seasonal resolution within dynamic contact network might be enough for correctly characterizing pathogen transmission patterns in a buffalo group, and consideration of heterogeneity in the contact structure between individuals might not be necessary. Nevertheless, it might be worth exploring other modes of transmission (*e.g.* environmental, vector-borne, water- or food-borne), whose transmission properties could lead to substantial differences between homogeneous and heterogeneous networks.

4.2. The impact of seasonality on contact patterns and predicted FMDV spread

This study highlights a strong seasonal dynamic in the structure of contact networks. During the wet season, individuals generally had fewer contacts with other individuals, had shorter contacts and were less likely to form subgroups than during the dry season. Irrespective of subgroup size, these results suggest that, during the wet season, subgroups are more fluid, and individuals are less close to each other resulting in more scattered subgroups. Conversely, in the dry season, subgroups may be more stable. It seems likely that changes in resource availability *(e.g.* mainly water and grazing) between the seasons or in predation pressure are responsible for the observed changes in contact network properties (Zvidzai et al. 2013, Murwira et al. 2014, Zengeya et al. 2015). During the wet season, Cape buffalo subgroups may prefer to be more fluid by splitting more often and form scattered subgroups to exploit available habitat more efficiently. These findings are consistent with what was observed in a population of Cape buffalo in Chobe National Park (Botswana, Halley et al. 2002) and in a population of forest buffalo (*Syncerus caffer nanus*) in Dzanga-Ndoki National Park (Central African Republic, Melletti et al. 2007b), where individuals formed larger subgroups during the dry season when resources are more limited. The opposite

was, however, reported in Serengeti National Park (Tanzania, Sinclair 1977) and Klaserie Private Nature Reserve (South Africa, Ryan et al. 2006).

FMDV is maintained in buffalo populations in Africa and can threaten sympatric cattle populations living in the same ecosystems and, therefore, livestock economies (Hargreaves et al. 2004, Caron et al. 2013, van Schalkwyk et al. 2016, Guerrini et al. 2019). Here, I found that seasonal contact patterns strongly influence FMDV spread in my two study populations. How buffalos interact with each other during the dry season facilitates the more rapid spread of FMDV through the group. This is consistent with observations made by Miguel et al. (2013), showing that incidence of FMDV in a buffalo-cattle system was the highest during the hot-dry season. Most buffalo populations maintain FMDV and therefore the introduction-spread event modelled in this study is not realistic. However, the results indicate that FMDV spreads faster when FMDV is introduced in the dry season than if introduced in the wet season. In the simulation, I did not consider young buffalos, whereas the influx of young buffalos into the group during the wet season, corresponding to the breeding season during which most female buffalos calve synchronously (Ryan et al. 2007), may alter the spread of FMDV. Infection with FMDV can occur in calves when they lose their maternally acquired immunity around the age of 4-6 months (Condy et al. 1985, Bengis et al. 1986, Bastos et al. 2000). Calves are then susceptible and are subsequently infected almost rapidly during the next dry season, which can accelerate the transmission of the FMDV within the group and could cause small group 'epidemics' (Bengis et al. 1986). Even though I have already found a strong seasonal dynamic in FMDV spread, determining the contact patterns by integrating young calves and how the pathogen is transmitted would be an interesting avenue for future investigations. However, one could assume that a calf's contact pattern would be very similar to that of its mother.

5 Conclusions

The results of this study have implications for the risk of pathogen spillover at the wildlife/livestock interface and the management of these interfaces. In the case of FMDV, the spread of FMDV between African buffalo and adjacent cattle populations (and vice versa) has been studied (Vosloo et al. 2002) and the geographical and seasonal patterns of outbreaks have been scrutinised (Kock et al. 2014, Guerrini et al. 2019): the type of interface, resource availability (*e.g.* due to seasonal changes), the population dynamics of buffalo calves and the efficiency of wild animal movement control measures (*e.g.* antelope jumping over fences after being infected through contact with buffalos) have been identified as potential drivers of pathogen spillover (Bengis et al. 1986, Sutmoller et al. 2000, Kock 2005, Jori et al. 2009, Miguel et al. 2013). Here, the structure of contact patterns within

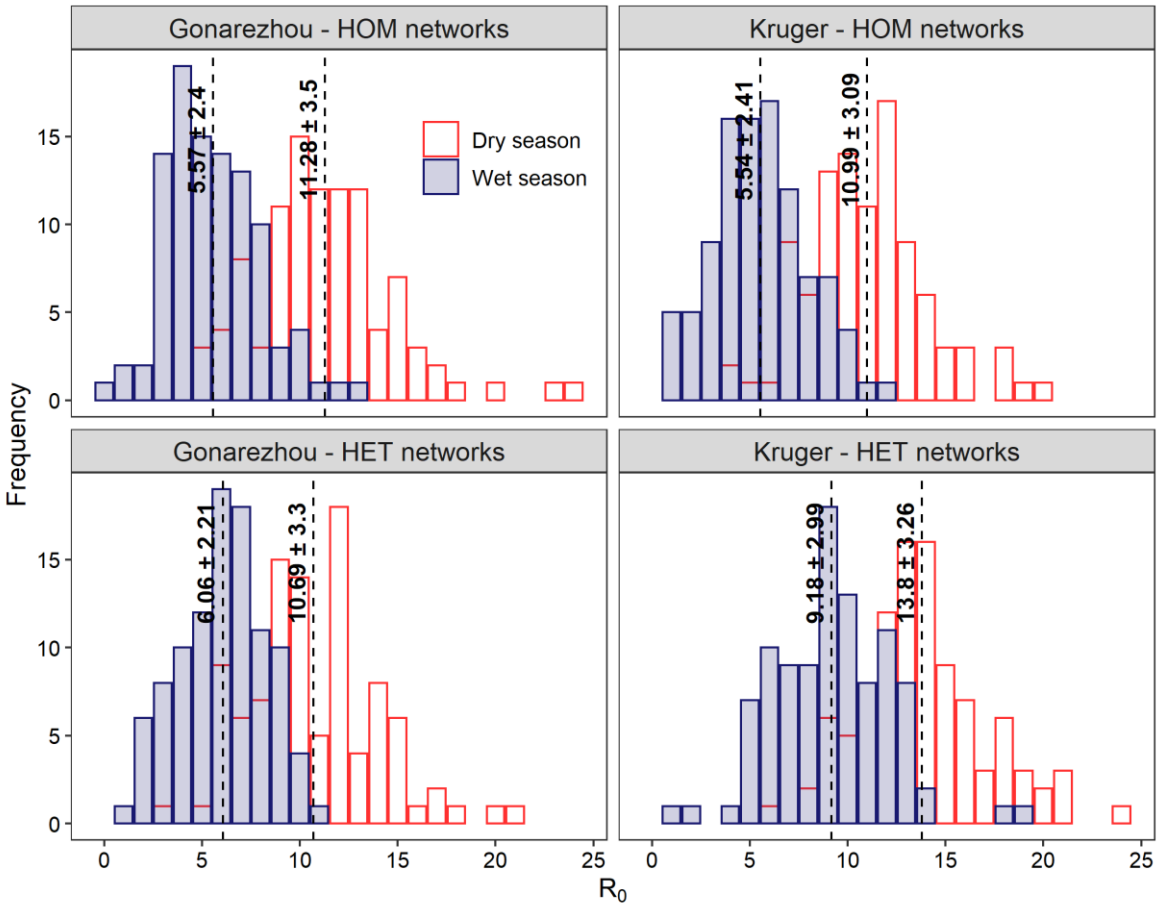
buffalo groups during the dry season is presented as a new potential driver through an increased FMDV circulation within buffalo populations, with an increased risk of spillover to in-contact species such as cattle.

6 Appendices

Appendix 1. Mean ± SD of social network metrics from the 8 simulated networks (HOM and HET networks for each season and each site). ± values indicated standard deviation from 100 simulations.

Condition	Gonarezhou		Kruger	
	HOM	HET	HOM	HET
In dry season				
Duration of contact	1.43 ± 0.78	31.50 ± 43.50	1.44 ± 0.79	15.7 ± 22.1
Duration of non-contact	3.34 ± 2.79	58.8 ± 151.0	3.28 ± 2.74	17.3 ± 50.7
Average path length	1.70 ± 0.003	1.65 ± 0.01	1.70 ± 0.003	1.52 ± 0.03
Mean clustering coefficient	0.30 ± 0.003	0.35 ± 0.01	0.30 ± 0.003	0.48 ± 0.03
Mean degree of a node	59.6 ± 6.46	68.70 ± 6.92	60.5 ± 6.49	94.70 ± 9.05
In wet season				
Duration of contact	1.16 ± 0.44	10.10 ± 15.0	1.19 ± 0.48	7.09 ± 9.19
Duration of non-contact	7.11 ± 6.59	37.7 ± 90.1	6.26 ± 5.74	19.2 ± 43.8
Average path length	1.88 ± 0.005	1.79 ± 0.02	1.85 ± 0.003	1.73 ± 0.007
Mean clustering coefficient	0.14 ± 0.002	0.21 ± 0.01	0.16 ± 0.003	0.27 ± 0.006
Mean degree of a node	27.9 ± 4.90	41.50 ± 6.37	31.7 ± 5.16	53.3 ± 6.35

Appendix 2. Distribution of R_0 (number of secondary cases) for the homogenous (HOM) and heterogenous (HET) networks for each season (dry vs. wet) and each site (Gonarezhou vs. Kruger). The mean duration ± SD is given by the black dashed line.



Appendix 3. Mean ± SD of epidemiological parameters from the 8 simulated networks (HOM and HET networks for each season and each site). ± values indicated standard deviation from 100 simulations. T_s, time taken for the disease to spread; Max prevalence, maximum prevalence; Max day, maximum prevalence occurrence date; R_0, basic reproduction number.

Condition	Gonarezhou		Kruger	
	HOM	HET	HOM	HET
In dry season				
T_s (days)	9.80 ± 1.07	9.75 ± 0.93	9.84 ± 0.94	8.46 ± 0.71
Max prevalence	107.00 ± 6.29	112.00 ± 6.31	108.00 ± 5.78	121.00 ± 6.01
Max day	16.30 ± 1.29	16.20 ± 1.08	16.50 ± 1.05	14.80 ± 0.89
R_0	11.28 ± 3.50	10.69 ± 3.30	10.99 ± 3.09	13.80 ± 3.26
In wet season				
T_s (days)	15.10 ± 2.08	13.50 ± 1.50	14.60 ± 1.85	10.90 ± 1.10
Max prevalence	75.00 ± 12.00	93.50 ± 6.02	83.80 ± 6.35	106.00 ± 6.27
Max day	21.10 ± 3.90	20.00 ± 1.58	21.00 ± 2.13	17.60 ± 1.13
R_0	5.57 ± 2.40	6.06 ± 2.21	5.54 ± 2.41	9.18 ± 2.99

CHAPTER 7

DISCUSSION, GENERAL CONCLUSIONS, AND FUTURE WORK

1 Summary of objectives and findings

This thesis aimed to investigate the social dynamics of the Cape buffalo across several populations in southern Africa and the implications in terms of pathogen transmission. In Chapter 3, the objectives were (i) to quantify the dynamics of fission and fusion events by estimating the frequency and duration of events between dyads belonging to the same group in 3 populations, (ii) to determine when fission and fusion events of dyads occurred in a day and (iii) examine the influence of seasonality, inter-population variance and indirectly, the spatial distribution of resources on these dynamics. Chapter 4 aimed to (i) quantify the spatial relationships (*i.e.* home range overlap) and the patterns of direct and indirect contact between dyads from neighbouring groups in 2 populations, via the estimation of the frequency and duration of contact, (ii) examine the influence of seasonality, inter-population variance and indirectly, the spatial distribution of resources on these contact patterns and (iii) to consider the implications of the results for the spread of multiple pathogens. Chapter 5 aimed to examine whether dispersal in the Cape buffalo was sex-biased at 2 organizational levels: among populations and among groups within local populations. Finally, the objectives of Chapter 6 were to use a dynamic network approach to (i) determine whether the structure of contact network within a buffalo group influenced the pathogen spread, (ii) to compare the results of predicted pathogen spread between the populations and seasons to assess the impact of the environmental context and seasonal environmental changes on the threat of disease and (iii) to consider the implications of the results for the spread of pathogens that are transmitted directly. In addition to improving our fundamental knowledge of the social structure of the Cape buffalo, these results aim to better understand the transmission of diseases within buffalo populations, and ultimately towards cattle populations and humans at the interfaces between protected areas and communal lands.

The results of this thesis revealed that the spatiotemporal dynamics in the Cape buffalo differed with the organizational level, but the intragroup and intergroup dynamics were generally consistent among the study populations (Chapters 3 & 4). In Chapter 4, at the population scale, Cape buffalos form relatively distinct groups occupying unique and separated home ranges, with minimal overlap. The neighbouring groups studied in Kruger NP and Okavango Delta (and two groups in Gonarezhou NP) showed very little direct contacts, consistently with previous results of forest buffalo (Cornélis et al. 2011). The groups tended to avoid areas previously used by another group in the previous two days during both the dry and wet seasons. The indirect contacts between the neighbouring groups occurring within one month were more frequent than direct contacts, which can have serious implications for indirectly transmitted pathogen (*e.g.* vector-, water-, food-borne) in the population (Chapter 4). Despite temporal avoidance and the low spatial overlap between

the home ranges of the neighbouring groups, the results of Chapter 5 revealed that Cape buffalo groups were interconnected by dispersal events. Similarly, the examination of the dispersion among 10 populations suggested a high rate of dispersion among populations, especially among the closest populations given the isolation-by-distance pattern of genetic variation observed. However, I found that dispersal would be female-biased when happening among populations, but probably not at a smaller organizational level (among groups, Figure 1). Note that the results of this chapter should be taken with caution as alternative explanations of the observed results are also possible.

Within groups, the results of Chapter 3 showed that two buffalos can spend very little time together (only 10%), contrary to what may be thought for a group (*i.e.* a cohesive group of individuals that spend most of their time together), although some pairs of buffalo still spend most of their time together (up to 90%). Individuals form very unstable dyadic associations with fission patterns lasting 1 to 3 days before individuals merge again for an equivalent average duration (Chapter 3). The degree of fission-fusion dynamics varied seasonally with a higher frequency of fusion event during the wet season, but fission and fusion events between dyads were not more likely to occur at specific times during the day. These results reveal high intragroup dynamics, which has never been observed before. However, the results of Chapter 6 on the comparison of the pathogen spread within a network representative of the observed intragroup social dynamics (based on the populations of Gonarezhou and Kruger) with a hypothetical network of random mixing indicated that the way individuals interact with each other only slightly affects the transmission of a directly transmitted pathogen within group. The strong intragroup social dynamics observed could ultimately generate such mixture that a pathogen would be transmitted as easily, or even slightly easier, than in a group where individuals mix randomly. In contrast, I found that seasonal variation in intragroup social structure affected the speed of pathogen spread within a group. The pathogen tended to spread faster and reached a larger number of individuals when introduced during the dry season due to the more clustered social structure with longer contacts. This seasonal variation in the intragroup social structure is probably due to the seasonal changes in resource availability and distribution, forcing buffalo to be closer when resources are rare. Overall, these findings suggest a two-speed diffusion of pathogens within buffalo populations, characterized by rapid spread within groups, but a lower spreading capacity among groups. The implications for disease ecology in buffalo populations will be discussed in more detail later. Together, these different results contribute to our understanding of the social dynamics of the Cape buffalo (Figure 1).

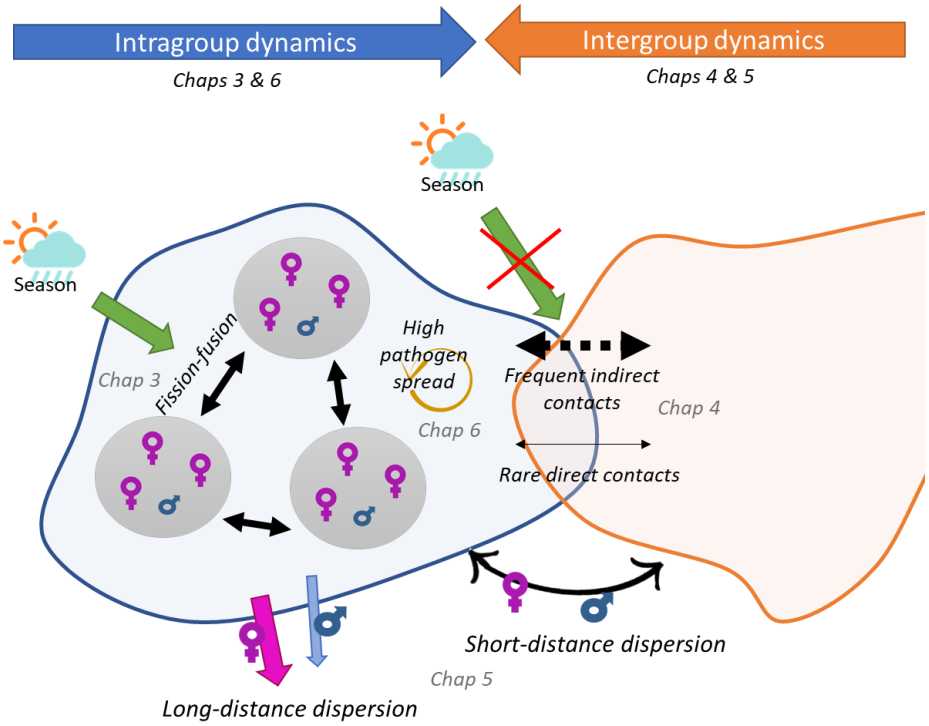


Figure 1. Schematic representation of the main results of this thesis to explain the social dynamics of the Cape buffalo. Although I did not explore the movement of males (see below), the literature indicates that they are sometimes in groups with females.

2 Limitations and recommendations

2.1 *Social behaviour of males*

Although this thesis contributes to our understanding of the social dynamics of the Cape buffalo, it is important to mention the lack of movement data for males, both subadults and adults, in this thesis project. Mixed groups are the basic structural unit of this species and the presence of adult males is generally temporary as they can live alone or in all-male 'bachelor' groups (Eltringham and Woodford 1973, Sinclair 1977, Prins 1996). The pattern of group affiliation of adult males is related to mating opportunities, forage availability and predation pressure (Prins 1996, Halley and Mari 2004, Turner et al. 2005). Conversely, subadult males remain in their native group until their adulthood. Their movement is, therefore, similar to the rest of the group, *i.e.* mainly females. For my thesis project, focusing on the movement of adult females was the optimal compromise between the largest sample size to represent the social structure and the deployment costs of the GPS collars. Nevertheless, males could be important vectors of pathogens at the population scale due to their group affiliation behaviour between groups of females and groups of bachelors. Future research should now focus on understanding

the movements of adult males to improve the socioecological model of the species and their impact on pathogen transmission. Collecting movement data for this age-sex class is challenging since males tend to break their collar within a few months of deployment, either intentionally or by accident during fights (Halley and Mari 2004). During this study in Kruger NP, two adult males were collared but they lost their collars within two months of deployment. The development of GPS ear tags might provide new insights when tracking this sex-age group, as already used for investigating the social structure of wild boars *Sus scrofa* (Podgórski et al. 2014).

2.2 *Sampled populations*

This study is the first to quantify and compare the fission-fusion dynamics and intergroup dynamics of the Cape buffalo across several populations using a common methodology. However, the studied populations represent a small proportion of the historic and current geographical range of the species. The conclusions drawn from this study could, therefore, not be generalized to other ecosystems, especially since the comparison of the fission-fusion dynamics observed between these three studied populations and that in the Okavango Delta highlighted substantial differences (see Chapter 3). Movement data from 33 Cape buffalo living in the Niassa National Reserve, northern Mozambique, were also available but the low resolution of location acquisition (every 4 hour) did not allow investigation of social dynamics. By contrast, the three populations in which I examined fission-fusion dynamics were previously chosen based on their close location to human populations (Miguel et al. 2013). In these interfaces among humans, cattle and buffalo, the questions linked to pathogen transmission between buffalo and cattle are crucial for local livelihoods, livestock trade and some zoonoses. Therefore, even if the results cannot be generalized to the whole species, they provide new insights on what is happening in terms of the sociality of the Cape buffalo at the human-wildlife interfaces, which can be critical to understanding pathogen transmission with cattle. In any case, it would be worth to continue exploring the fission-fusion dynamics (and even the intergroup dynamics) in other Cape buffalo populations under various environmental conditions to learn more about the variation in social behaviour of this species within its geographical range, especially in the current context of anthropological environmental changes.

2.3 *The use of GPS technology*

Technological tracking developments, such as GPS loggers used in this study, allow continuous data collection and provide new data to examine the social behaviour (Kays et al. 2015, Mejía-Salazar et al. 2017). However, the constraints associated with this

technology (*e.g.* costs) have limited the number of individuals to be monitored simultaneously within the same group. Given the gregarious behaviour of the Cape buffalo, one might wonder whether the tracking of a few individuals within a group is enough to describe the movement and the spatial distribution of all individuals of the group. This study provides evidence for high fission-fusion dynamics, it is thus very likely that some fission-fusion events have not been recorded because they involved non-collared animals. The same is true when I examined the dynamics of the intergroup encounters. However, it is unlikely that the behaviour of collared animals was highly different from the other buffalos within the study areas and that biases related to sample size have been heterogeneous between sites and seasons. Consequently, the trends observed across sites and seasons should remain appropriate. Also note that the deployment costs limit the detection of infrequent events, such as dispersal events undertaken by buffalos.

Another limitation that can be identified for the use of this technology is the scheduled temporal resolution. In this thesis, locations were acquired every hour. When examining the fission-fusion dynamics, given the gregarious behaviour of the species, it was unlikely that the fission and fusion events last less than one hour. However, this temporal resolution does not allow to identify when exactly buffalo groups became aware of each other and decided whether to approach and merge, preventing to determine the potential mechanisms underlying fission-fusion dynamics. The temporal resolution raised questions when I investigated the interactions between groups, which were hypothesized to be rarer and shorter (Cornélis et al. 2011). To overcome this potential limitation, I modelled the individual path to best estimate the start of contact, but the short duration of direct contacts between neighbouring groups observed (average 1-1.5h) underlines the importance of higher temporal resolution. Finally, this methodology does not allow to discriminate the type of social interactions between individuals, especially in the case of short fusion or contact (*e.g.* affiliative, agonistic) while they could be important to understand the mechanims, especially for the rare intergroup encounters.

Hourly GPS fixes should be enough when examining the intragroup social structure of social species, but the use of proximity loggers could provide better data. Indeed, proximity loggers directly record synchronous contacts between two individuals, and their lower cost compared to GPS technology makes it possible to simultaneously monitor a larger number of individuals (Ji et al. 2005, Prange et al. 2006, Böhm et al. 2009, Walrath et al. 2011, Robert et al. 2012). However, they would not be appropriate in the investigation of intergroup dynamics because they record only the direct contacts (*i.e.* at the same time, in the same place) while buffalo groups mainly interact with each other indirectly (Chapter 4). Use of GPS collars with higher temporal resolution combined with direct field observations may help to understand why buffalo groups avoid each other. After all, my thesis suggests that a study design can only answer a limited set of questions and it is of

utmost importance to define the research questions before the deployment of tracking devices.

2.4 Combination of genetic and GPS analyses

In this project, the combination of GPS and genetic data has not addressed the relationship between kinship (mother, sisters and daughters) and patterns of fission and fusion events. In some ungulate species, females preferentially associate with their close relatives, which means that during the fission of their group, females remain with their closest relatives (Archie et al. 2006, Bercovitch and Berry 2012, Godde et al. 2015). The same could be true for the Cape buffalo, thus constituting the family unit, which could thus represent a limitation to the fluidity observed in buffalo groups in this thesis. I have tried to provide some answers by correlating a relatedness index (Queller and Goodnight 1989) to the time that two individuals spent together (< 1000 m, Figure 2). The result does not seem to reveal any influence of relatedness on association strength, but in fact, very few individuals had been both monitored and genotyped (some genetic samples had been degraded preventing genotyping). Further studies should now explore to what extent genetic relatedness (if possible, by determining mothers and their calves, and sisters) predicts the patterns of fission and fusion to identify the smallest stable unit in the Cape buffalo. This would require tracking a lot of individuals within the same group to increase the likelihood of tracking genetically related individuals and collecting blood and/or hair samples of these individuals. Once again, proximity collars provide a useful tool, allowing tracking of a large number of individuals while determining contact rates and fission and fusion patterns (Ji et al. 2005).

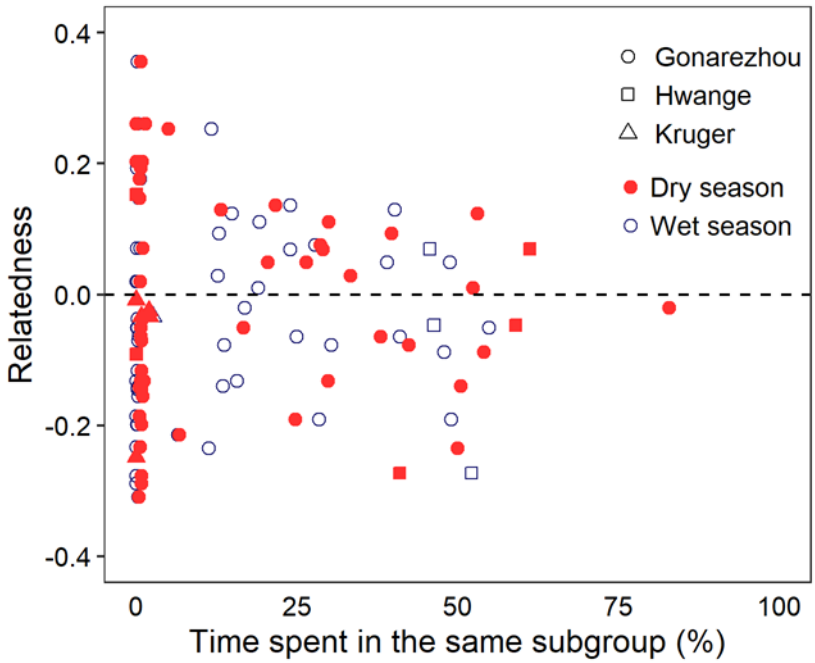


Figure 2. Relationship between estimates of relatedness (Queller and Goodnight 1989) and time spent together (< 1000 m) among pairs of 28 Cape buffalos in Hwange and Gonarezhou National Parks, Zimbabwe, and Kruger National Park, South Africa. Queller and Goodnight's index is an unbiased estimate of relatedness, ranging from -1 and 1 based on the population allele frequencies. A positive value indicates that the pair is more related while a negative value indicates that the pair is less related than average. Colours represent associations during each season: red = dry season, blue = wet season.

3 Implications for socioecology and disease spread

3.1 Drivers underlying fission-fusion dynamics

This study, along with previous research, revealed a higher level of sociality between dyads with high levels of spatial overlap (Chaverri et al. 2007, Bennitt et al. 2018). The cause and effect of this relationship can, however, be hard to distinguish: animals may be attracted to each other (*e.g.* because they are related or because they have the same nutritional needs), leading them to share space; or they may be attracted to the same space (*e.g.* where the resources or fewer pathogens are, de garine-Wichatitsky et al. 1999), leading to higher contact rates (Best et al. 2014). Habitat structure tends to affect the social behaviour of herbivores by modifying the strategies adopted by individuals to avoid predation. Herbivores usually live in larger groups in open habitats, where visibility is high, allowing individuals to detect predators more efficiently (Jarman 1974, Hirth 1977, Molvar and Bowyer 1994, Isvaran 2007, Fortin and Fortin 2009, Bercovitch and Berry 2010). In such habitats, individuals can perceive themselves easily and can, therefore, tend to attract each other because of their gregarious behaviour, leading to a fusion event followed by a fusion period (Pays et al. 2007). In the current study, I showed that fusion periods were not dependent on the vegetation type (Chapter 3). This result suggests that buffalos associate to interact

socially regardless of the environment and, therefore, independently of resource distribution. Fission could occur at any time when key individuals differ in their decisions regarding the next activity or the next foraging location and were joined by regular followers, leading to a split of the subgroup (Ramos-Fernández and Morales 2014). Due to the high degree of fission-fusion dynamics observed in Chapter 3, conflict resolution might not be important in Cape buffalo groups. The group can simply split when conflicts arise. As all buffalos were not collared in my study areas, the information on whether collared individuals leaving a dyad initiated the fission, or were followers instead, is not available. Overall, the results found in this thesis suggest that fission-fusion dynamics between Cape buffalo dyads may be driven by resource availability at the seasonal scale, while at a finer temporal scale, *i.e.* within seasons, conflicts of interest and social attraction may be responsible for fission and fusion events.

Factors such as predation pressure and group size have already been mentioned as potential drivers of intragroup dynamics in the African buffalo (Prins 1996, Tambling et al. 2012). Tambling and collaborators (2012) have found that, after the reintroduction of lions in the Addo Elephant National Park (South Africa), buffalos tended to congregate into larger groups, but over the long-term (*i.e.* not responsible for fusion or fission events). In the European roe deer, Pays et al. (2007) reported that some fusion and fission events were not caused by spontaneous attraction or splitting-up, but by external disturbances related to human activities (disturbances or hunting). African buffalos usually respond to the scent of lions with panic and flight behaviours (A. Caron, pers. comm.). Therefore, it is very likely that the presence of lions creates confusion among buffalos within a group, leading to the splitting into subgroups. This factor deserves to be further investigated, for example, by combining GPS data for both buffalos and lions (Miguel et al. 2017). This study was not designed to identify the impact of the human presence on grouping patterns and social decisions of buffalos. In the study areas, the only data available were the geographic locations of villages and roads. Movement data for buffalo were also available in the Niassa National Reserve (Prin 2014), where human populations live inside the reserve. Unfortunately, the way the GPS data was collected (*e.g.* low temporal resolution, few collared individuals in the same group, collars placed over several years) did not allow the examination of movements and social decisions of buffalo at a fine temporal scale. In future, it would be of interest to investigate how buffalos adapt their intragroup dynamics in Niassa National Reserve where encounters and disturbances linked to human activities are much more important than in the populations studied in this thesis.

The group size around the collared individuals could not be followed during my project. Group size monitoring is often done at snapshot times rather than continuously, hence, information about the duration of fission and fusion periods is often not accessible. Same is true for understanding where fission and fusion events occur. This thesis thus

focused on, and estimated, the extent to which two individuals of a group spend time together, irrespectively of whether they occur in large or small, consistent or not, subgroups. However, variation in fission-fusion dynamics observed in the three studied populations may be due to variation in group size. Ideally, such a study would require both behavioural data (*e.g.* size and composition of subgroups) and movement data, which can identify the precise moment when the events take place. Direct observations are generally very time-consuming, but the use of drones or camera traps can provide valuable alternative approaches to regularly monitor size and composition of groups containing collared individuals (McCarthy et al. 2018, Vink et al. 2020). Recently, camera traps have been used to study the social structure of western chimpanzees, *Pan troglodytes verus* (McCarthy et al. 2019) and social dynamics of striped hyaenas, *Hyaena hyaena* (Mandal 2019). This method may be applied to the Cape buffalo to estimate group size, but also to characterize social relationships (*e.g.* agonistic) among individuals.

3.2 Consequences for disease transmission within buffalo populations and at buffalo/cattle interfaces

In social species, it is not surprising that the risk of pathogen transmission is greater within social groups, due to higher contact rates (Altizer et al. 2003), and the results of my thesis support this statement. I identified a significant social structure of contacts in Cape buffalo populations (Chapters 3 & 4). Contacts were mainly contained within groups, whilst most of the between-group contacts were indirect, occurring within one month. The social and spatial constraints on buffalo direct contacts may reduce the rate of spread of directly transmitted pathogens in the population but may promote rapid spread within groups. In agreement with the first assumption, Omondi et al. (2020) have found genetically distinct variants of FMDV (mainly transmitted by direct contact in semi-arid habitats) between neighbouring groups of buffalos (in Ol Pejeta Conservancy, Kenya). Conversely, the ease of propagation of a direct-transmitted pathogen within a group (Chapter 6) emphasizes the importance of preventing pathogen transmission from being introduced into a susceptible buffalo group. It is, however, important to note that the social structure of the Cape buffalo would promote the spread of a directly transmitted disease, unlike random group patterns usually assumed in modelling studies (Chapter 6). Further studies should be undertaken to consider other pathogens with different modes of transmission. These results have important implications for developing strategies for managing diseases in Cape buffalo populations. In particular, management measures that reduce social and spatial constraints of buffalo contact rates among groups, such as intensive hunting if they enhance movement rates, may increase the rate of pathogen spread and should be avoided to mitigate epidemiological risks. In that way, many studies have refuted the effectiveness of culling to

control the disease spread and may even demonstrate a contrary effect to the one expected, by promoting disease spread (Miguel et al. 2020). For example, badger culling in the UK appeared to decrease bovine tuberculosis spread at local scale but increased transmission to adjacent areas, probably through enhanced dispersal rates (Donnelly et al. 2006, Carter et al. 2007, Woodroffe et al. 2009).

In the Cape buffalo, pathogens with indirect transmission modes (*e.g.* by the air, water, soil, vector) may spread easily within the whole population because of the higher indirect contact rates between neighbouring groups (Chapter 4). Moreover, even though indirect contacts within groups were not examined within this thesis, pathogens that can survive in the environment for several days, and even for several months, should spread at least as easily as directly transmitted pathogens. The high immigration rate observed in Cape buffalo in Chapter 5 may also accelerate the spatial spread of infectious diseases, as it is suggested for the bTB spread from Kruger NP to Gonarezhou NP (Caron et al. 2016). Infectious diseases are thought to influence dispersal behaviour, through either direct impact on animal behaviour or indirectly by affecting body condition (Armsworth 2009, Debeffe et al. 2012, 2014). A recent study on the Cape buffalo has found that the infectious diseases, including brucellosis and bovine tuberculosis, did not directly affect dispersal decision in adult females (Spaan et al. 2019). By contrast, they found that individuals in poor body condition were more likely to disperse. Therefore, infectious diseases that negatively affect body condition (Caron et al. 2003, Gorsich et al. 2015), could indirectly influence dispersal and promote the spread of disease. Other factors such as resource availability, competition or position in the group can decrease an individual's body condition, and explain the greater propensity of these individuals to disperse, independently of their infectious status (Sinclair 1977, Mloszewski 1983). The results of this study raise questions about the effect of dispersal on disease transmission among Cape buffalo populations.

The Cape buffalo is considered an important reservoir host for many pathogens, such as foot-and-mouth disease virus (FMDV), *Theileria* sp., *Trypanosoma* sp., *Mycobacterium bovis* (bTB), and *Brucella* sp. (Bengis et al. 2002, Kock et al. 2014). For the majority of these pathogens, there are few if any impacts on their populations since buffalos are highly tolerant. In contrast, buffalos can be sensitive to introduced pathogens from cattle, such as the rinderpest virus imported from Europe through cattle, which had dramatic consequences on buffalo populations (Kock et al. 1999). Buffalo populations can also represent a risk for cattle infection, mainly with bTB, FMDV and theileriosis (Caron et al. 2013). At buffalo-cattle interfaces, the type of interface, resource availability (*e.g.* due to seasonal changes), population dynamics of buffalo calves and efficiency of wild animals movement control measures (*e.g.* antelope jumping over fences infected due to contact with buffalos) have been identified as potential drivers of pathogen spillover between buffalo and cattle (Bengis et al. 1986, Sutmoller et al. 2000, Kock 2005, Jori et al. 2009, Dube et al.

2010, Caron et al. 2013, Miguel et al. 2013, Kock et al. 2014). Results in Chapter 6 suggest that the risk of spread within a group of Cape buffalo may be higher when the pathogen establishes during the dry season due to changes in contact structure. The seasonal variation in intragroup contact structure of Cape buffalo is a new potential driver to increase the risk of spillover to cattle. During the dry season, risk of contact between the two species is generally higher due to the limitation of resources (forage and water, Kock 2005, Valls-Fox et al. 2018). Therefore, the ease of pathogen spread within buffalo groups increases the risk of transmission through contact with cattle, and pathogen transmission in buffalo groups by cattle may spread very quickly within the groups. Although manipulation of available resources for buffalo may reduce the temporal constraints of resource availability on buffalo contact structure (*e.g.* resource limitation during the dry season), this is usually challenging, and it is easier to limit the interactions between buffalo and cattle, mainly during the dry season. Cattle-buffalo interactions may be reduced by removing artificial waterholes maintained for wildlife that are located at the edge of protected areas and closer to communal lands where cattle populations are hosted. Alternatively, one could try to reduce the practice of herding (or letting) cattle to pasture inside protected areas (Miguel et al. 2013, 2017) or use waterholes inside or at the edge of protected areas, notably by increasing access to boreholes in communal lands.

3.3 Impact of climate change

In tropical environments, seasonality and interannual variation in forage and water availability are largely driven by rainfall patterns (Bucini and Hanan 2007). However, around 80% of climate projections indicate that southern Africa will have increased temperatures, reduced precipitation, and later onset of rains (James and Washington 2013). The results of this thesis suggest that social dynamics of the Cape buffalo may change due to anthropogenic climate change and surface water availability. I found that intragroup dynamics varied according to the season: during the dry season, individuals formed tighter subgroups, split less often, and remained in contact for longer (Chapters 3 & 6). Consequently, the drier conditions that will be experienced in semi-arid ecosystems of southern Africa in the coming years could reduce intragroup dynamics, with more stable groups than those currently observed. Buffalo population dynamics could be affected given the relationship between social organization, *i.e.* group size, composition and stability, and demographic parameters, such as survival, reproduction and dispersal abilities (Baird and Whitehead 2000). Such changes in the social structure of the Cape buffalo because of climate warming will have consequences for disease transmission processes within buffalo populations, but also at the buffalo-cattle interfaces. The drier conditions we will experience in the coming decades may accelerate the spread of pathogens within buffalo groups.

Combined with the expected increasing competition for resources between buffalo and cattle, this ease of spread within buffalo groups could further increase the risk of transmission to cattle. The reverse is also true; if pathogens are transmitted more easily within buffalo groups, then it will be more important to limit the interactions between the two species for conservation issues. The results of this thesis tentatively suggest that water sources might act as hotspots for intra- and intergroup contacts during the dry season, but only in areas with low water availability (Chapters 3 & 4). The expected decrease in water availability due to global warming could intensify the role of water points in these areas, thus promoting transmission processes in buffalo and with cattle.

4 Future directions

4.1 Decision-making during fission event

To maintain group cohesion, individuals of a group must move synchronously and in the same direction (Petit and Bon 2010). Before leaving an area, individuals must decide about the direction and/or time of departure (Bourjade and Sueur 2010). Group members can show their motivation to move by increasing their activity or producing more vocalizations, such as in Verreaux's sifakas, *Propithecus verreauxi,* or in mountain gorilla, *Gorilla gorilla berengei* (Stewart and Harcourt 1994, Trillmich et al. 2004). In Tonkean macaque, *Macaca tonkeana*, 'voting behaviours' have been observed where individuals turn their bodies in a specific direction to indicate their choice for the upcoming move (Sueur and Petit 2008, Sueur et al. 2010a, King and Sueur 2011). In the African buffalo, females would urinate and defecate more before a collective movement, indicating their motivation to move (Prins 1996). They also have a particular stance position looking in one direction and with the head higher than the normal resting position. Group fission may occur when a first subgroup decides to move in one direction while the second one decides either to stay in the current area or to move in another direction (Kerth et al. 2006, Ramos-Fernández et al. 2006). Mechanisms underlying collective movements, *i.e.* the decisions of each individual to join one of the two subgroups, are increasingly studied, but they are still unknown in the Cape buffalo. The probability to follow one of the two subgroups can depend on the number of individuals already involved in the movement, whatever their identities, the social or affiliative relationships with individuals already moving or still resting, or on their needs at that time (Okamoto and Matsumura 2001, Kerth et al. 2006, Sueur et al. 2010b, 2011b, Jacobs et al. 2011). It would be interesting to examine the decision-making during group fission in the Cape buffalo to measure the weight of social influence, compared with that of ecological influence (often examined), on group stability. This could be done by direct behavioural observations, through the collection of departure latencies of each individual,

the order of individuals during departure, *i.e.* who is following whom, and the complete progression order. In addition, data on age, kinship and affiliative relationships would allow an understanding of how these factors affect social decisions.

4.2 Mechanisms underlying intergroup segregation

Chapter 4 demonstrates that groups of buffalo tend to avoid each other spatially and temporally, but the underlying mechanisms are unknown. Many social species defend their territories to have exclusive access to resources and different patterns of territory marking are adopted (Miura 1984, Grant et al. 1992, Sillero-Zubiri and Macdonald 1998, Lazaro-Perea 2001). Animals can defend their territories through fighting (Sillero-Zubiri and Macdonald 1998), but the quasi-absence of direct contacts observed in my study suggests that buffalo groups do not actively defend their home ranges. Buffalo may thus adopt indirect strategies to inform ownership to intruders and therefore avoid conspecifics, such as scent-marking or vocalizations already observed in many species (Waser 1975, Sillero-Zubiri and Macdonald 1998). Buffalos use different types of vocalization for maintaining group cohesion (Mloszewski 1983), it is, therefore, possible that neighbouring groups interact with each other through vocalizations to inform on their location. In some African mammals, including the elephant (Langbauer et al. 1991) and several species of rhinoceros (von Muggenthaler et al. 1993), infrasounds have been shown to play an important role in long-distance communication. Further research is needed to better understand the population structure and how a change in the environment (introduction of a group of buffalo, scarcity of resources due to climate change) could impact the space use by buffalo groups. This could be done by measuring the response of group members to playback of recorded vocalizations or by studying the response to faeces materials from neighbouring or unknown groups (*e.g.* from another population).

4.3 Measuring the causal factors underlying sex-biased dispersal

The causes responsible for the dispersal of individuals usually include temporal and spatial heterogeneities of the environment, inbreeding avoidance and local competition (Cockburn et al. 1985, Lebigre et al. 2010). In mammals, dispersal is generally male-biased (Cockburn et al. 1985, Harris et al. 2009), mainly to avoid the strong local mate competition that characterises the female-defence mating system, but counter-examples exist (*e.g.* Favre et al. 1997, Hammond et al. 2006, Zhan et al. 2007). Causes of dispersal are likely to differ depending on whether dispersal is undertaken over long distances, occurring among populations, or over short distances, occurring among groups within a local population. Inbreeding might be avoided by short moves, whilst avoiding poor environmental conditions

or colonizing new territories require greater movements. Distance dispersal may differ among sexes (Fontanillas et al. 2004). For example, in the brushtail possum, Ji et al. (2001) have shown that movements among occupied territories were male-biased, whereas both sexes disperse when the aim was to colonize empty sites. In this thesis, I found that Cape buffalos disperse with high immigration rates that involve both females and males at two organizational levels (*i.e.* among populations and among groups). Nevertheless, it seemed that females dispersed more than males when it came to among population movements. Dispersal of the Cape buffalo has been described in the literature, but the ecological and social drivers are poorly understood, especially for females. Recently, using tracking devices, Spaan et al. (2019) have explored the influence of the environmental conditions, the characteristics and health of adult female buffalos, and the location of the group, on the propensity to disperse. Because this study was only based on adult females (Spaan et al. 2019), further studies are required to understand the main factors affecting the dispersal in buffalos, both in females and males, and both in subadults and adults. Tracking devices seem to be the best tools for such questions, providing complete picture of the movements of individuals, even at long distance (unlike to Capture-Mark-Recapture method). To increase the chances of monitoring individuals that will disperse, many GPS collars must be fitted, possible on a single group at the start. A strong temporal resolution for the collection of data is not needed because it is not required to know the exact time of the start of the dispersal event. This choice would increase the battery life. Knowing not only the age, the sex and the condition of each animal (*e.g.* health status) but also the social (*e.g.* group size) and ecological (*e.g.* resource availability) conditions in which they live would enable us to examine how these different factors affect the likelihood to disperse.

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