



Research Article

Inter-Group Social Behavior, Contact Patterns and Risk for Pathogen Transmission in Cape Buffalo Populations

ELODIE WIELGUS ^{1,2} *Department of Natural Sciences, Manchester Metropolitan University, All Saints, Manchester M15 6BH, UK*
ALEXANDRE CARON,² *Faculdade de Veterinária, Universidade Eduardo Mondlane, Av. De Moçambique, CP 257, Maputo, Mozambique*
EMILY BENNITT, *Okavango Research Institute, University of Botswana, Shorobe Road, Maun, Botswana*
MICHEL DE GARINE-WICHATITSKY,² *Faculty of Veterinary Medicine, Kasetsart University, Pabolyothin Road Chatuchak, 10900 Bangkok, Thailand*
BRADLEY CAIN, *Department of Natural Sciences, Manchester Metropolitan University, All Saints, Manchester M15 6BH, UK*
HERVE FRITZ, *REHABS, CNRS - Université Lyon 1 - Nelson Mandela University, International Research Laboratory, George Campus, Madiba Drive, George, South Africa*
EVE MIGUEL,³ *Maladies Infectieuses et Vecteurs: Ecologie, Génétique, Evolution et Contrôle, Institut de Recherche pour le Développement, 911 Avenue Agropolis, 34394 Montpellier cedex 5, France*
DANIEL CORNÉLIS, *CIRAD, Forêts et Sociétés, F-34398 Montpellier, France; Forêts et Sociétés, Université de Montpellier, CIRAD, 34090 Montpellier, France*
SIMON CHAMAILLÉ-JAMMES ⁴, *CEFE, University of Montpellier, CNRS, EPHE, IRD, University Paul Valéry Montpellier 3, Montpellier, France*

ABSTRACT In social species, the transmission and maintenance of infectious diseases depends on the contact patterns between individuals within groups and on the interactions between groups. In southern Africa, the Cape buffalo (*Syncerus caffer caffer*) is a vector for many pathogens that can infect sympatric livestock. Although intra-group contact patterns of Cape buffalo have been relatively well described, how groups interact with each other and risks for pathogen transmission remain poorly understood. We identified and compared spatial behavior and contact patterns between neighboring groups of Cape buffalo under contrasting environments: within the seasonally flooded environment of the Okavango Delta in Botswana and the semi-arid environment of northern Kruger National Park in South Africa. We used telemetry data collected between 2007 and 2015 from 10 distinct groups. We estimated seasonal overlap and proximity between home ranges of pairwise neighboring groups, and we quantified seasonal contact patterns between these groups. We defined contact patterns within variable spatiotemporal windows compatible with the transmission of diseases carried by the Cape buffalo: bovine tuberculosis, brucellosis, and Rift Valley fever (mosquito-borne transmission). We examined the effects of habitat and distance to water on contact location. In both study populations, neighboring buffalo groups were highly spatially segregated in the dry and rainy seasons. Inter-group contact patterns were characterized by very few direct and short-term indirect (within 0–2 days) contacts, lasting on average 1 hour and 2 hours, respectively. Contact patterns were generally consistent across populations and seasons, suggesting species-specific behavior. In the drier study site, the probability of indirect and vector-borne contacts generally decreased during the dry season with increasing distance to water. In the seasonally flooded area, only the probability of vector-borne contact decreased with increasing distance to water. Our results highlight the importance of dry season water availability in influencing the dynamics of indirectly transmitted Cape buffalo pathogens but only in areas with low water availability. The results from this study have important implications for future modeling of pathogen dynamics in a single host, and the ecology and management of Cape buffalo at the landscape level. © 2021 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS contact patterns, disease transmission, dyadic interactions, home range, telemetry, seasonality, southern Africa, *Syncerus caffer caffer*.

Received: 13 November 2020; Accepted: 24 June 2021

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

¹E-mail: elodie.wielgus@orange.fr

²Additional affiliation: CIRAD, UMR ASTRE, F-34398 Montpellier, France; ASTRE, University of Montpellier, CIRAD, INRAE, Montpellier, France

³Additional affiliation: CREES Centre for Research on the Ecology and Evolution of Diseases Montpellier, France

⁴Additional affiliation: Department of Zoology & Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa

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, or when they are restricted to key limiting patches (e.g., waterholes in semi-arid areas; Redfern et al. 2003, Kolbe and Weckerly 2015). The simultaneous use of common space promotes the spread of pathogens transmitted directly (e.g., by aerosols) or indirectly via the environment (e.g., through contaminated materials such as feces; Altizer et al. 2003, Dougherty et al. 2018). Understanding how individuals share space and interact with conspecifics, either directly or indirectly, is essential for developing realistic epidemiological models and effective interventions to manage infectious diseases (Craft 2015, Reynolds et al. 2015).

Space-sharing between conspecifics is strongly influenced by social systems. Solitary animals generally avoid each other, apart from during breeding, during territorial conflicts, or randomly because of environmental constraints (e.g., in response to spatial heterogeneity in 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 long time periods or subject 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, Wielgus et al. 2020). At the landscape level, the spread of infectious diseases is also dependent on movements and interactions between social groups (Weber et al. 2013, Vanderwaal et al. 2016).

Many herbivore species do not defend territories and occupy home ranges that can vary seasonally with changes in resource abundance and distribution (Owen-Smith et al. 2010). Ungulate group spatial use varies according to species and ecological context, ranging from non-exclusive home ranges, but with possible temporal avoidance, such as mountain gazelle (*Gazella gazella*; Geffen et al. 1999), to exclusive home ranges that have little overlap between groups, such as impala (*Aepyceros melampus*; Murray 1982) and Roosevelt elk (*Cervus canadensis 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 between groups should also be taken into account. Interactions between groups can result in the maintenance of pathogens within populations even when group size is below the threshold for maintenance at group level (Weber et al. 2013, Vanderwaal et al. 2016, Sah et al. 2017).

The Cape buffalo (*Syncerus caffer caffer*) offers a unique opportunity to explore interactions between groups and implications for the spread of disease. Adult females,

subadults of both sexes, and juveniles live in groups that vary in size, ranging between 10 and >1,500 individuals according to geographic region (Sinclair 1977, Prins 1996, Hughes et al. 2017). In contrast, adult males move regularly between mixed-sex groups and smaller all-male bachelor groups (2–30 individuals up to 50) according to seasonal mating opportunities, forage availability, and predation avoidance (Sinclair 1977, Prins 1996, Halley and Mari 2004, Hughes et al. 2017). Mixed-sex groups occupy identifiable and stable home ranges with fixed membership and size, and within these large groups, subgroups of individuals regularly split and merge according to seasonality, group size, and predation pressure (fission-fusion dynamics; Sinclair 1977, Prins 1996, Ryan et al. 2006, Tambling et al. 2012, Wielgus et al. 2020). The relatively recent availability of telemetry data has enabled the examination of within-group contact patterns across several populations over long time periods (Wielgus et al. 2020). Wielgus et al. (2020) demonstrated that subgroups split and merge regularly for short periods (usually 1–3 days), with greater frequency during the wet season. Fission-fusion dynamics may indirectly promote the spread of pathogens at the landscape scale, but inter-group contact patterns and their effect on the spread of pathogens remain poorly understood (but see Bennitt et al. 2018 for a study on intergroup social behavior of Cape buffalo). Most studies investigating space sharing between neighboring groups have documented distinct and exclusive home ranges, with little overlap of Cape buffalo groups, such as in Lake Manyara National Park in Tanzania (Prins 1996), Chobe National Park in Botswana (Halley et al. 2002), Serengeti National Park in Tanzania (Sinclair 1977), and Klaserie Private Nature Reserve in South Africa (Ryan et al. 2006). However, strong spatial overlap between home ranges of neighboring groups has been reported in a Cape buffalo population from Sengwa Wildlife Research Area in Zimbabwe (Conybeare 1980). Cornélis et al. (2011) reported low direct contact rates (4 times over a season) between 2 neighboring groups of West African savanna buffalo (*S. c. brachyceros*), whereas Cape buffalo in the Okavango Delta (OD) in Botswana tended to come into contact more frequently with neighboring groups (Bennitt et al. 2018). Cape buffalo have become wildlife reservoirs for several pathogens of economic concern such as bovine tuberculosis and brucellosis and Rift Valley fever (Caron et al. 2013, Gorsich et al. 2015). Understanding the social behavior between Cape buffalo groups in relation to pathogen transmission windows can help us understand the spread of pathogens within the species.

In this study, we quantified and compared the spatial behavior and contact patterns between neighboring groups of Cape buffalo. Because buffalo movements are strongly constrained by water availability (Redfern et al. 2003, Valls-Fox et al. 2018), we studied 2 populations at similar population densities, living in contrasting environmental conditions (i.e., a semi-arid savanna environment and a seasonally flooded environment). We used location data from global positioning system (GPS)-collars on Cape

buffalo to explore the spatio-temporal dynamics of inter-group contact patterns using different spatiotemporal windows, defining direct and indirect contacts compatible with the intraspecific transmission of important pathogens. We tested the hypothesis that the neighboring groups in the seasonally flooded environment would be less likely to interact with each other compared to groups living in the semi-arid savanna environment because groups in the flooded environment would be less constrained by water availability. In the semi-arid savanna environment, the more limited and heterogeneously distributed resources would force buffalo groups to share areas with high resource abundance (Chaverri et al. 2007). We predicted that groups would be located closer to each other or have more overlapping home ranges during the dry season when water availability is lower, therefore leading to more interactions and potential infectious contacts. We also predicted that waterholes would be key areas for contacts in the dry season because limited water availability should force buffalo groups to share the same waterholes, thus facilitating potential transmission of pathogens.

STUDY AREA

We used data collected from 2 Cape buffalo populations inhabiting the northern Kruger National Park (KNP) in northeastern South Africa at the border between Zimbabwe and South Africa (18,959 km², 30°50'E, 22°25'S), and the southeastern area of the OD in northern Botswana (15,000 km², 22°00'E, 18°50'S). We monitored collared buffalo in the former study site in 2010–2015 and in the latter in 2007–2010. The 2 study sites are characterized by differences in climatic conditions and habitat structure but similar density of Cape buffalo, estimated at 0.9 buffalo/km² in KNP (based on the northern part of KNP, including our study area; Rodwell et al. 2001) and 0.94 buffalo/km² in OD (Chase 2011). Both study sites are inhabited by large carnivore species, such as spotted hyena (*Crocuta crocuta*), lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and wild dog (*Lycan pictus*).

The KNP study site is a semi-arid savanna primarily composed of woodland and bushland. The soils are shallow and calcareous, and the vegetation is dominated by mopane (*Colophospermum mopane*) shrubland and sandveld vegetation (Gertenbach 1983). Altitude ranges 200–300 m above sea level. Average annual rainfall is 450 mm, with 2 highly distinct seasons, which are the rainy (Nov–Mar) and dry seasons (Apr–Oct; Venter et al. 2003). The study area is surrounded by 2 rivers that cross the park from west to east: the Limpopo River in north, forming the border with Zimbabwe, and the Levhuvhu River in south. During the rainy 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, most natural pans dry up, and water is provided by 1 permanent river and some pools that persist in and along the seasonal Limpopo River (Gaylard et al. 2003; Fig. 1A). In addition to Cape buffalo, the most common herbivore species are impala, Burchell's zebra (*Equus quagga burchelli*),

greater kudu (*Tragelaphus strepsiceros*), elephant (*Loxodonta africana*), blue wildebeest (*Connochaetes taurinus*), and giraffe (*Giraffa camelopardalis*).

The OD is an alluvial zone, consisting of permanent swamps, temporary floodplains, riverine woodlands, and savannas that rarely flood on deep Kalahari sands (Ramberg et al. 2006). Dominant woody species are mopane, acacia (*Vachellia* spp. and *Senegalia* spp.), and lancepods (*Lonchocarpus* spp.); dominant grass species are couch grass (*Cynodon dactylon*), curly leaf grass (*Eragrostis rigidior*), and bushveld signal grass (*Urochloa trichopus*). Altitude ranges 900–1,000 m above sea level. The study site is bounded by a veterinary fence to the southeast erected to prevent the spread of disease from wildlife to livestock. As in KNP, rainfall is seasonal with an annual average of 490 mm falling mostly between November and March (McCarthy et al. 2000). Water is available year round throughout the flooded areas, but their extent varies seasonally; floodwaters rise from April to July and recede between August and November. Ephemeral pans are widespread across the landscape and provide water during the rainy season. Dominant herbivores include Cape buffalo, impala, red lechwe (*Kobus lechwe*), elephant, and Burchell's zebra (Ramberg et al. 2006, Chase 2011).

METHODS

Environmental Covariates

We adapted simplified vegetation maps from Bennitt et al. (2014) for OD and Pretorius and Pretorius (2015) for KNP. For comparative purposes, we defined 3 broad vegetation classes 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, scrubby, 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 (Google, Mountain View, CA, USA) at KNP using photographic captures taken at different times of the year (Fig. 1B–C).

In both sites, because of the presence of numerous natural pans, it was difficult to quantify water availability outside the core dry season. Because of this and to avoid transitional periods, we restricted our analyses to the core of the rainy (1 Jan–31 Mar; 90 days) and dry seasons (15 Aug–31 Oct; 78 days). We defined these periods based on similar rainfall patterns between the sites (McCarthy et al. 2000, Venter et al. 2003). We considered water as a non-limiting factor during the rainy season in both sites (Cornélis et al. 2011, Bennitt et al. 2014).

Collaring and Monitoring

We used GPS data from 31 adult female Cape buffalo obtained 2007–2015 (KNP: $n = 16$, OD: $n = 15$). Data were previously collected as part of epidemiological monitoring or space use studies (Miguel et al. 2013, Bennitt et al. 2014, Caron et al. 2016). We located buffalo groups from the air and randomly selected ≥ 1 adult females to be

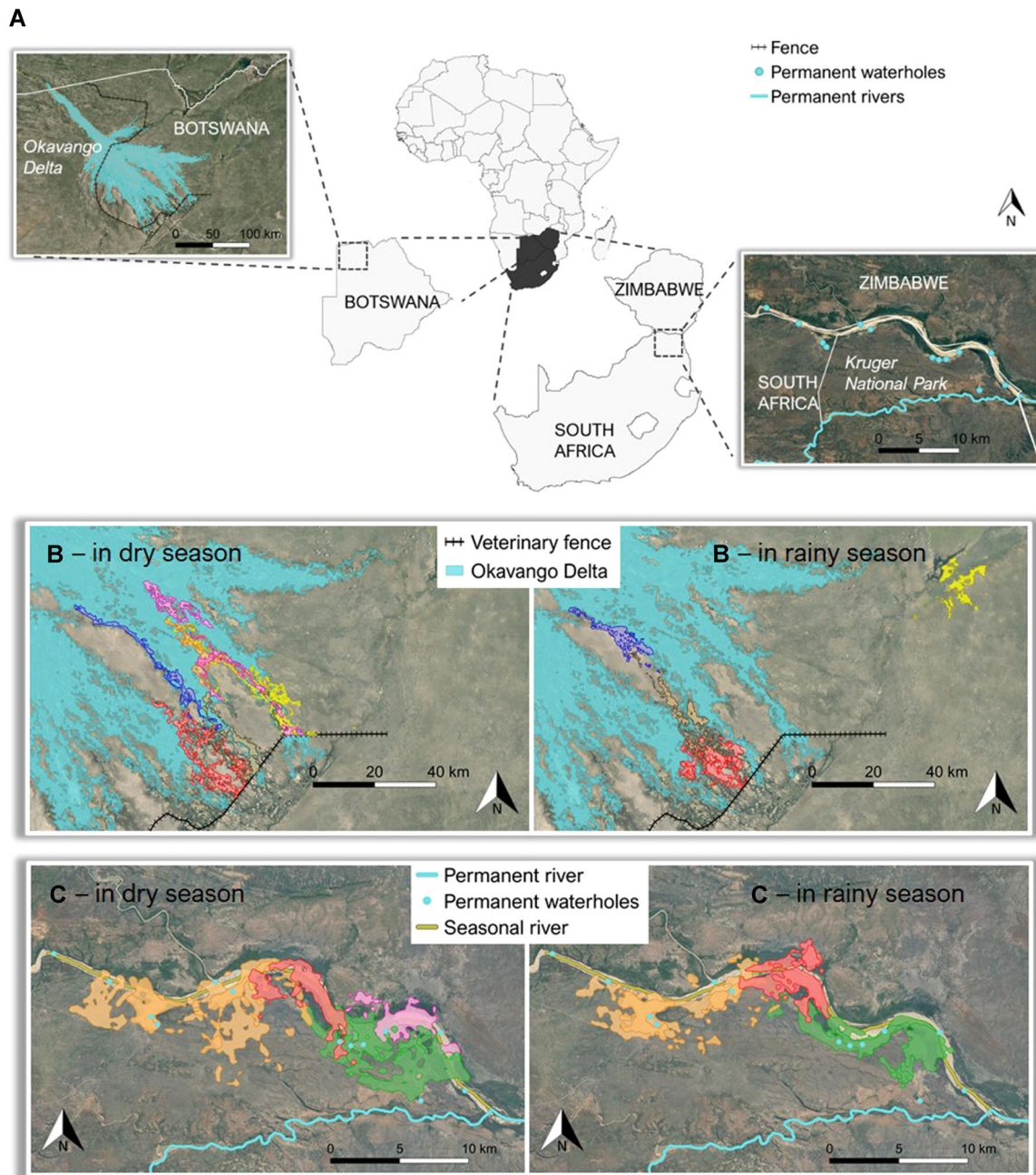


Figure 1. A) Location of the study areas in Kruger National Park (KNP), South Africa, and Okavango Delta (OD), Botswana; B) locations of seasonal home ranges of the 6 Cape buffalo study groups in OD tracked between 2007 and 2010; and C) the 4 Cape buffalo groups (from 6 individuals tracked at different years) in KNP followed between 2010 and 2015, during the dry (left) and rainy (right) seasons.

tele-anesthetized directly from the helicopter. Because adult males can leave the group temporarily, we focused on females to study the movements of groups (Sinclair 1977, Prins 1996). We fitted captured females with GPS-collars (KNP: Vectronic Aerospace, Berlin, Germany and Lotek Wireless, Newmarket, Ontario, Canada; OD: Followit, Lindenberg, Sweden). We made every effort to limit stress and immobilization time, and observed all animals returning to their subgroups after collaring operations. There were 3 capture sessions in KNP (Jun 2010, Jul 2011, and Oct 2013), and 4 in OD (Dec 2007, Oct 2008, Jun 2009, and Oct 2009). The research and handling procedures

conformed to legislation regarding wildlife and animal welfare of the American Society of Mammologists (Sikes et al. 2011) and were approved by the relevant authorities of respective countries (University of Bristol Ethics Committee [UB/08/034], Department of Wildlife and National Parks, Botswana [permits number: EWT 3/3/8 XXXVII 44 and EWT 8/36/4 IV 62], SANParks: South African National Parks).

We obtained GPS locations from Cape buffalo from June 2010 to July 2015 in KNP and from December 2007 to August 2010 in OD. Except for 1 collar that acquired locations for only a few hours after being deployed, the

duration of the tracking varied between 54 days and 1,013 days (median = 383) across individuals. We programmed the GPS loggers to record location data every hour at synchronous times between loggers (on the hour, 24 times/day), but a GPS fix was not always acquired when scheduled. We computed fix success rate within each season, within each year for each individual and we retained seasonal data from 23 individuals (KNP: $n = 15$, OD: $n = 8$) for which the success rate was $>80\%$.

Seasonal Home Range Proximity or Overlap of Neighboring Groups

We identified individuals belonging to the same group based upon high levels of home range overlap because Cape buffalo groups occupy identifiable and stable home ranges despite fission-fusion dynamics (Ryan et al. 2006, Wielgus et al. 2020). We considered seasonal home ranges as the 90% utilization distribution (UD) during the dry and rainy seasons for each year (Börger et al. 2006). We computed UD's from hourly GPS locations using the movement-based kernel density estimation method (MKDE; Benhamou and Cornélias 2010) implemented in the *adehabitatHR* package (Calenge 2007) in R version 3.6.0 (R Core Team 2019). We estimated home range overlap 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). We examined the distribution of seasonal home range overlap between dyads, seeking a breakpoint in distribution to indicate group membership. The distribution of seasonal home range overlap between dyads showed a set of pairs with a home range overlap <0.4 and a second set of pairs with a home range overlap >0.6 (Fig. S1, available online in Supporting Information). For this reason, we considered individuals with seasonal home range overlap ≥ 0.6 as belonging to the same group. We verified groupings based on field observations and capture location, by assuming that 2 individuals captured in the same subgroup should belong to the same group. We explored spatial behavior and contact patterns between 6 groups in OD and 4 groups in KNP. Because the number of individuals tracked per group differed between groups, we selected 1 individual per group (the individual with the most GPS data) for each season and year to be representative of the movement of the whole group.

To identify buffalo group dyads (i.e., pairs of radio-collared buffalo belonging to different groups) with adjacent home ranges, we computed the minimum distance between the contours of seasonal home ranges within a year, for each dyad. Because buffalos can cover distances up to 8–10 km in 24 hours (Sinclair 1977, Mloszewski 1983), we assumed that individuals whose home range limits were ≤ 10 km apart during the same season could have been in contact. We thus considered that 2 individuals for which we had simultaneous tracking data belonged to neighboring groups when their seasonal home ranges overlapped or when the minimal distance between their seasonal home ranges was ≤ 10 km during ≥ 1 season. We analyzed data from 13

individuals (KNP = 6, OD = 7) distributed in 6 and 7 dyads of neighboring groups tracked simultaneously in KNP and OD, respectively (Fig. 1B,C). Of these, we tracked 6 dyads in both rainy and dry seasons (KNP: $n = 3$, OD: $n = 3$) and 7 in only 1 season (KNP: $n = 3$, OD: $n = 4$).

To explore how neighboring groups shared space across seasons, we examined overlap in seasonal home ranges between individuals from neighboring groups using the Bhattacharyya's affinity index (Benhamou et al. 2014; see above). We also explored seasonal variations in minimum distance between home range contours of dyads when home ranges did not overlap.

Contact Analysis

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 (e.g., individual moves during the 1-hour period between 2 recorded locations). Traditionally, studies that attempt to estimate contact between animals with 1-hour GPS data use a relatively large spatial window to define contacts (Miguel et al. 2013, Podgorski et al. 2018). We addressed this problem and reduced the risk of underestimating 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 and London 2018). From these models, we predicted the locations of individuals every 5 minutes, and estimated contacts from the interpolated data.

We 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 and vector-borne contact, within a larger temporal window). To explore contact patterns between groups, we used various spatiotemporal windows defining direct, indirect, and vector-borne contacts compatible with the transmission modes of 3 important pathogens in buffalo: *Mycobacterium bovis* causing bovine tuberculosis (bTB), *Brucella* spp. causing brucellosis, and the phlebovirus causing Rift Valley fever (RVF), which are present in our 2 study areas (Table 1).

Mycobacterium bovis is most frequently transmitted by respiratory routes (i.e., during direct close contacts; Bengis et al. 1996). The pathogen can also spread by indirect contacts because mycobacteria can survive in feces for up to 1 month in natural conditions in southern Africa (Tanner and Michel 1999). *Brucella* spp. (e.g., *Brucella abortus*) is mainly transmitted by direct or mucosal contact with a contaminated fetus, placenta, or birthing fluids (Kiros et al. 2016). Because the bacteria can persist in a bovine fetus for several weeks, or even months in temperate regions (Aune et al. 2011), we assumed that the most limiting factor for transmission would be the persistence of a contaminated fetus in the environment before being eaten by scavengers. To estimate this variable, in November 2010 de Garine-Wichatitsky (Kasetsart University, unpublished data) placed

Table 1. Characteristics of selected pathogens transmitted between Cape buffalos and corresponding spatiotemporal windows chosen to define contacts. We also report the prevalence of each pathogen in our 2 study populations from Kruger National Park (KNP), South Africa, and Okavango Delta (OD), Botswana. The spatial windows consider the mode of transmission of the pathogen (i.e., close 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.

Disease name	Pathogen	Prevalence (%) in buffalo at each site [95% CI] (n = number of buffalo sampled)	Mode of transmission	Spatial window	Time window	Contact name
Bovine tuberculosis (bTB)	<i>Mycobacterium bovis</i>	KNP _{north} : 1.5% [0.4–4.0] (n = 203) ^a OD: 2.9% [0.8–9.8] (n = 70) ^b	Inhalation of aerosolized droplets Inhalation or ingestion of infected materials (e.g., feces)	150 m 150 m	0 hr 0–31 days	Direct contact Long-term indirect contact
Brucellosis	<i>Brucella abortus</i>	KNP _{north} : 15.0% (n = 314) ^c OD: 6% [3.0–9.0] (n = 247) ^d	Contact with or ingestion of infected fetus or other abortion products	150 m	0–2 days	Short-term indirect contact
Rift Valley fever (RVF)	Rift Valley fever virus	KNP _{north} : 3.6% (n = 196) ^e OD: 9.7% [4.0–19.0] (n = 72) ^f	By the bite of a female mosquito	2,500 m	0–31 days	Vector-borne contact

^a Rodwell et al. (2001).

^b Jori et al. (2013).

^c Gorsich et al. (2015).

^d Alexander et al. (2012).

^e Beechler et al. (2015).

^f Jori et al. (2015).

10 mixed offal-meat bags (mimicking fetuses) inside Gonarezhou National Park in Zimbabwe and in open areas in Malipati Communal Land. The bait bags persisted for 43 hours on average (range = 6–71 hr). The RVF virus is transmitted between animals through the bite of a female mosquito (usually *Aedes* and *Culex* spp.; Bengis et al. 2002). The main factors limiting the transmission of the virus from mosquito to buffalos are the lifespan of mosquitoes and their ability to disperse. 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, like other ruminants (Manore and Beechler 2015), we assumed that a buffalo may be able to transmit the virus responsible for RVF within 1 month of infection. Mosquitoes can fly from a few hundred meters up to 2,500 m (Shannon and Davis 1930, Wolfensohn and Galun 1953, Ba et al. 2006). For each pathogen, we defined a relevant spatiotemporal window 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 1).

For each buffalo dyad of neighboring groups and each spatiotemporal window, we identified the time and place of contacts. We defined the location of an individual of a given dyad as a pathogen-specific contact location when, during the previous period defined by the temporal window, ≥ 1 GPS location of the other buffalo in the dyad was within a distance shorter than the spatial window. For instance, for *Brucella* spp., we considered the location of a buffalo to be a contact location when ≥ 1 GPS location of the other buffalo was located ≤ 150 m within the 2 days preceding the time of that GPS location. If several successive locations were defined as contacts, we considered these locations as a single contact and calculated its duration because the duration of contacts is likely to be an important factor in pathogen transmission (Smieszek 2009). We used contact occurrence to calculate the number of contacts per dyad per month (i.e., contact rate) as the number of contact events divided by the number of months of simultaneous tracking.

Statistical Analyses

For all subsequent analyses, we used hierarchical (i.e., mixed) models with dyad identity as a random intercept because dyads were not independent (i.e., some individuals, each representing a group, can belong to several dyads of neighboring groups). For example, individual A from group 1 could contact individuals B from group 2 and C from group 3. We first investigated variation in home range overlap and the distance between home ranges of neighboring groups using 2 generalized linear mixed models (GLMMs). In both models, we used a negative binomial distribution of errors to account for overdispersion and the explanatory variables were site, season, and their interaction.

We tested the effects of site and season on contact rate and duration between neighboring groups. We built 1 GLMM for each spatiotemporal window (Table 1) for the number and duration of contacts (i.e., 4 models each). To account for overdispersion and excess zeros in the contact rate data, we

used a negative binomial distribution of errors. We explored the duration of each contact (in hours) using a Gamma error structure because all values were positive but not normally distributed. The relatively small sample size for dyads displaying direct and short-term indirect contacts during the rainy season in both sites did not allow for testing of the influence of season or site during the rainy season on rate and duration of these contacts. We therefore tested 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 and vector-borne contacts, explanatory variables included site, season, and their interaction.

Finally, we explored the probability of contact between 2 neighboring groups in relation to distance from permanent water sources (only in the dry season) and vegetation type (in both seasons). We extracted distance to nearest permanent water source and vegetation type for every predicted buffalo GPS location. For each buffalo dyad of neighboring groups, we classified the locations of each of the 2 individuals as a contact or not, depending on the different spatiotemporal windows. To determine whether distance to water and vegetation type affected the probability of contact, we ran 4 GLMMs for the dry season GPS locations (i.e., 1 corresponding to each spatiotemporal window), with a binomial distribution of errors. In each model, the binary response variable was the presence or absence of contact (i.e., whether the individual location was a contact [scored 1] or not [scored 0]), and the explanatory variables included distance to water, associated vegetation type, site, and the interactions between site and distance to water, site and vegetation type, and distance to water and vegetation type. The GLMMs for the rainy season locations were similar, but distance to water was not included as an explanatory variable, and we built the GLMMs for long-term indirect and vector-borne contacts because of the low number of direct and short-term indirect contacts in the rainy season. We also tested whether Cape buffalo distribution changed as a function of site and distance to permanent water during the dry season to ensure that the conclusions of the previous analyses in the dry season (i.e., the relationship between distance to water and probability of contact) were not simply due to the variation in water availability between sites. We performed a GLMM with distance to water at every hourly buffalo dry season location as the response variable to ensure independence of data, and site as the explanatory variable. We used a negative binomial distribution of errors to account for overdispersion. In this model, the random effect was buffalo identity to account for variable number of locations from each individual.

For each analysis, we 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 (AIC_c; Burnham and Anderson 2002). We considered the most parsimonious model to be the model that had both an $\Delta AIC_c < 2$ and the lowest number of explanatory variables (Arnold 2010). We quantified goodness of fit of the models, defined as the variance explained by the fixed effects, with marginal theoretical, lognormal, and delta

coefficient of determination R^2 (Nakagawa et al. 2017) for GLMMs with a binomial, negative binomial, and Gamma distribution of errors, respectively, using the MuMIn (Bartoń 2019) and piecewiseSEM R packages (Lefcheck 2016). We performed all spatial and statistical analyses in R version 3.6.0 (R Core Team 2019) and we used the lme4 (Bates et al. 2015) and glmmTMB (Brooks et al. 2017) R packages for statistical models. The data that support the findings of this study are available from Manchester Metropolitan University's repository at <https://doi.org/10.23634/MMUDR.00628120>.

RESULTS

Spatial Behavior Between Neighboring Groups

The most parsimonious model of home range overlap variation did not include the effects of site or season (Table 2, analysis 1; see Table S1, available in Supporting Information, for full set of models). Estimated home range overlap between neighboring groups was 0.07 (95% CI = 0.01–0.36, $n = 19$; Fig. 2A). Although groups only seemed to be farther apart in OD during the rainy season (Fig. 2B), model selection indicated no effect of site on distance between neighboring groups, but there was a seasonal effect (Table 2, analysis 2). Regardless of site, groups were farther apart during the rainy season (predicted distance between home ranges = 1.96 km, 95% CI = 0.21–18.41 km, $n = 7$) compared to the dry season (0.17 km, 95% CI = 0.02–1.60 km, $n = 12$; Fig. 2B).

Contact Characteristics

We recorded 32 direct contacts between dyads of neighboring groups, with 12 in KNP and 20 in OD (Fig. 3A). Indirect contacts were more frequent, ranging from 177 for short-term indirect contact (KNP: $n = 121$, OD: $n = 56$; Fig. 3B), to 567 for long-term indirect contact (KNP: $n = 326$, OD: $n = 241$; Fig. 3C), and 176 for vector-borne contacts (KNP: $n = 135$, OD: $n = 41$; Fig. 3D).

The most parsimonious models explaining inter-site variation of direct and short-term indirect contact rates during the dry season and long-term indirect and vector-borne contacts during both seasons were the null models (Table 2, analysis 3). Estimated contact rates were 0.02 (0.00–3.89, $n = 12$) and 0.01 (0.00–0.07, $n = 24$) during the dry season for direct and short-term indirect contacts, respectively, and 0.39 (0.03–5.25, $n = 38$) and 1.32 (0.55–3.19, $n = 38$) during both seasons for long-term indirect and vector-borne contacts, respectively (Fig. 3).

Model selection suggested that the duration of contacts was generally consistent across seasons or sites (the seasonal effect was only tested for the duration of long-term indirect and vector-borne contacts; Table 2, analysis 4; Fig. 4). The only exception was for the duration of long-term indirect contacts, where the most parsimonious model included the effect of site (Table 2, analysis 4) with slightly shorter contacts in OD (2.38 hr, 95% CI = 2.05–2.84, $n = 241$) than in KNP (4.68 hr, 95% CI = 4.04–5.55, $n = 326$), irrespective of season (Fig. 4). Estimated contact duration was 1.20 hours (0.89–1.83, $n = 30$) and 2.28 hours (1.88–2.91,

Table 2. Summary of candidate models fitted for each analysis in a study of Cape buffalo inter-group contact patterns for potential disease transmission in Kruger National Park (KNP), South Africa, and Okavango Delta (OD), Botswana, study sites during dry and rainy seasons, 2007–2015. We modeled response variables, calculated at the level of dyads of neighboring groups, as a function of different combinations between site (KNP or OD), season (dry or rainy season), distance to water, and vegetation type (grassland, bushland, woodland). We included dyad identity as a random intercept. The exception is in analysis 5, which we computed at the individual level with the individual identity as the random effect. We statistically explored only direct and short-term indirect contacts during the dry season because of the quasi-absence of these contacts during the rainy season. We report models within 10 corrected Akaike's Information Criterion (AIC_c) values of the best model (i.e., $\Delta AIC_c < 2$ and the lowest number of explanatory variables). Models are ordered from lowest to highest ΔAIC_c and the best model is indicated with an asterisk.

Model	df ^a	Dev ^b	ΔAIC_c ^c	R^2 ^{marginal} ^a
1. Home range overlap between dyads of neighboring groups ($n = 19$)				
Null*	3	8	0.0	0.00
Site	4	8	3.0	0.06
Season	4	8	3.2	0.01
Site + season	5	8	6.8	0.07
2. Distance between home ranges between dyads of neighboring groups ($n = 19$)				
Season*	4	89	0.0	0.16
Site × season	6	83	2.4	0.24
Site + season	5	87	2.6	0.27
3. Contact rate between dyads of neighboring groups				
Direct contacts (only in dry season, $n = 12$)				
Null*	3	25	0.0	0.00
Site	4	25	4.7	0.00
Short-term indirect contacts (only in dry season, $n = 24$)				
Null*	3	63	0.0	0.00
Site	4	62	1.9	0.12
Long-term indirect contacts ($n = 38$)				
Season	4	154	0.0	0.01
Null*	3	158	1.8	0.00
Site + season	5	153	2.0	0.08
Site	4	157	3.5	0.07
Site × season	6	153	4.7	0.09
Vector-borne contacts ($n = 38$)				
Null*	3	149	0.0	0.00
Site	4	147	1.0	0.11
Season	4	148	1.2	0.02
Site + season	5	146	2.5	0.13
Site × season	6	144	3.5	0.22
4. Duration of contacts between dyads of neighboring groups				
Direct contacts (only in dry season, $n = 30$)				
Null*	3	73	0.0	0.00
Site	4	73	1.8	0.03
Short-term indirect contacts (only in dry season, $n = 126$)				
Site	4	458	0.0	0.01
Null*	3	462	1.8	0.00
Long-term indirect contacts ($n = 567$)				
Site*	4	2,571	0.0	0.01
Site + season	5	2,570	0.9	0.01
Site × season	6	2,570	3.0	0.01
Null	3	2,579	6.2	0.00
Season	4	2,579	8.0	0.00
Vector-borne contacts ($n = 176$)				
Null*	3	1,586	0.0	0.00
Season	4	1,585	0.9	0.00
Site	4	1,586	2.1	0.00
Site + season	5	1,585	3.0	0.00
Site × season	6	1,585	5.0	0.00
5. Distance of buffalo location to the nearest permanent water during the dry season ($n = 17,241$)				
Site*	4	233,866	0.0	0.80

(Continued)

Table 2. (Continued)

Model	df ^a	Dev ^b	ΔAIC_c ^c	R^2 ^{marginal} ^a
6. Probability of contact between dyads of neighboring groups according to distance to water and vegetation type in dry season				
Direct contacts ($n = 117,691$)				
Distance to water × site + distance to water × vegetation type*	9	4,619	0.0	0.63
Distance to water × site + distance to water × vegetation type + vegetation type × site	11	4,618	3.2	0.62
Short-term indirect contacts ($n = 148,882$)				
Distance to water × site + distance to water × vegetation type + vegetation type × site*	11	25,993	0.0	0.29
Long-term indirect contacts ($n = 136,271$)				
Distance to water × site + distance to water × vegetation type + vegetation type × site*	11	76,606	0.0	0.14
Vector-borne contacts ($n = 215,935$)				
Distance to water × site + distance to water × vegetation type + vegetation type × site*	11	142,098	0.0	0.06
7. Probability of contact between dyads of neighboring groups according to vegetation type in rainy season				
Long-term indirect contacts ($n = 86,156$)				
Vegetation type × site*	7	32,723	0.0	0.05
Vector-borne contacts ($n = 86,156$)				
Vegetation type × site*	7	93,422	0.0	0.14

^a Degree of freedom.

^b Deviance of the model, calculated as $-2 \times \log$ likelihood.

^c Difference in value between Akaike's Information Criterion for small samples size (AIC_c) of the current model and the model with the lowest AIC_c.

^d Variance explained by fixed factors of the model, calculated according to Nakagawa et al. (2017). Higher values indicate better model fit.

$n = 126$) during the dry season for direct and short-term indirect contacts, respectively, and 30.54 hours (20.53–59.60, $n = 176$) during both seasons for vector-borne contacts (Fig. 4).

Location of Contacts

During the dry season, the probability of contact varied by site, vegetation type, and distance to water for each type of contact (Fig. 5A–D; Table 2, analysis 6). In KNP, contacts (i.e., direct, short- and long-term indirect, and vector-borne) were more likely when closer to water, regardless of vegetation type (Fig. 5A–D; Table 3). In OD, only vector-borne contacts were more likely to occur with decreasing distance to water, especially in bushlands (Fig. 5D; Table 3). Cape buffalo in OD were observed closer to water (distance to water = 209.08 m, 95% CI = 136.97–319.16, $n = 10,033$) than those in KNP (1,801.80 m, 95% CI = 1,181.12–2,748.63 $n = 7,208$; Table 2, analysis 5). In general, we did not identify any vegetation types where contacts

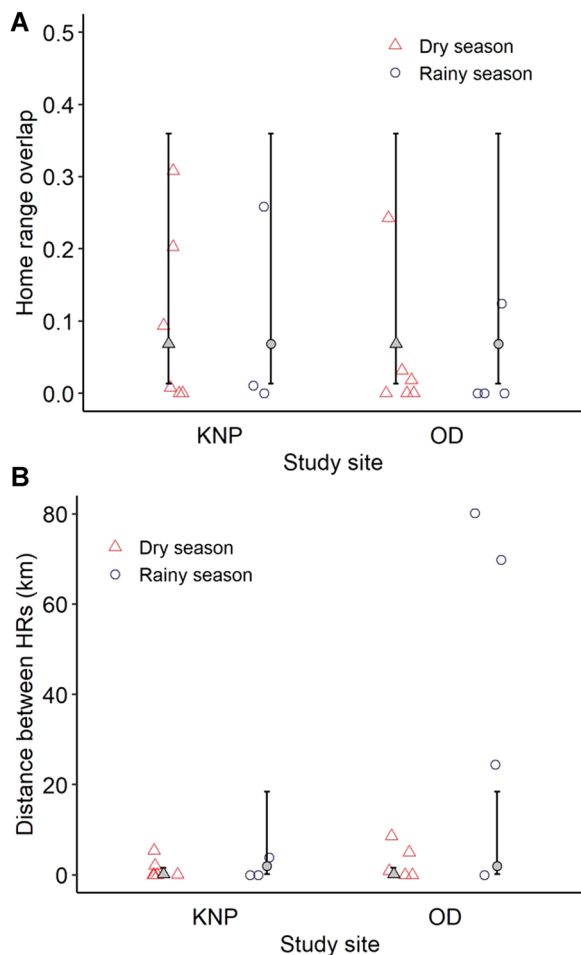


Figure 2. A) Home range overlap and B) minimum distance between home ranges (HRs) of 4 Cape buffalo groups in Kruger National Park (KNP), South Africa, 2010–2015, distributed in 6 dyads of neighboring groups, and 6 Cape buffalo groups in Okavango Delta (OD), Botswana, 2007–2010, distributed in 7 dyads of neighboring groups, during the dry season (in red) and rainy season (in blue). Error bars indicate 95% confidence intervals around the estimate of the most parsimonious models. The observed values are given by the open symbols for information. Each data point represents 2 individuals (i.e., a dyad of neighboring groups).

in both sites were more likely to occur because of the low difference in contact probability between vegetation types (Fig. 5A–D; Table 3). The exception was for short-term indirect contacts in KNP, which were more likely to occur in woodlands than in bushlands and grasslands, regardless of distance to water (Fig. 5B). The R^2 values for analyses on the indirect and vector-borne contacts were low (Table 2, analysis 6), suggesting that a very large variability remained after accounting for distance to water and vegetation type.

During the rainy season, the most parsimonious models explaining the probability of long-term indirect and vector-borne contacts included an interaction effect between vegetation type and site (Table 2, analysis 7). In KNP, vector-borne contacts were more likely to occur in woodlands than in bushlands and grasslands (Fig. 5F; Table 4). The R^2 of the models were small (Table 2, analysis 7), indicating that, within sites, vegetation had only minor effects on the probability of contact (Fig. 5E,F; Table 4).

DISCUSSION

We used GPS data to assess spatial behavior and contact patterns between Cape buffalo groups from 2 populations living in contrasting environmental conditions. Using bTB, brucellosis, and RVF as models to define contacts, we demonstrate that neighboring groups are spatially segregated and direct contacts between different groups are very rare; contact rates and durations between buffalo groups are generally similar between seasons and sites, suggesting a potential species-specific pattern; and surface water distribution may be a key factor moderating buffalo inter-group contacts in semi-arid savannas (KNP), where water sources are scarce and patchily distributed.

Wielgus et al. (2020) reported that direct contact rates between individuals in the same group ranged from 2.7–17/month in the Cape buffalo population in KNP. In this study and for the same population, we found that direct contacts between individuals from neighboring groups were much rarer, on average 0.2 and 0.6 contacts/month in the rainy and dry season, respectively (0 and 1.3 contacts/month in OD in the rainy and dry season, respectively). The quasi-absence of contacts between neighboring groups is consistent with previous work on West African savanna buffalo (Cornélis et al. 2011). Differentiation in direct contact rates between and within Cape buffalo groups suggests that directly transmitted pathogens could spread much more rapidly within groups than between groups. Additionally, most observed direct contacts between groups may not result in pathogen transmission, as any transmission requires an infected host to be excreting the pathogen at the time of contact with a susceptible animal. Effects of differentiation in direct contact structure that occur between and within groups on disease dynamics are, however, likely to depend on group characteristics (e.g., size) and fission-fusion dynamics of Cape buffalo groups (Prins 1996, Wielgus et al. 2020).

Most of the contacts between groups occurred within 1 month and only occasionally within a 2-day window. In this context, we can expect rapid population-wide transmission of pathogens that persist in the environment or are vector-borne for long time periods (e.g., bTB and RVF viruses). This can also be the case with foot-and-mouth disease (FMD) virus, which can survive in the environment for up to 15 days (Miguel et al. 2013). The quasi-absence of direct contacts between Cape buffalo groups suggests that bTB transmission opportunities could be much more frequent through an indirect route (i.e., through inhalation or ingestion of contaminated materials) than a direct route. Yet the slow spread of bTB from buffalo populations in southern KNP to those in the north between 1960–2005, and then among populations in Zimbabwe in 2009, may suggest limited indirect between-group transmission of pathogens, despite the high levels of indirect contacts between groups that we observed. In accordance with this result, Omondi et al. (2020) reported genetically distinct variants of FMD virus between neighboring groups of Cape buffalo in Kenya. How intergroup contacts affect pathogen dynamics may depend on other factors, such as population dynamics (e.g., density),

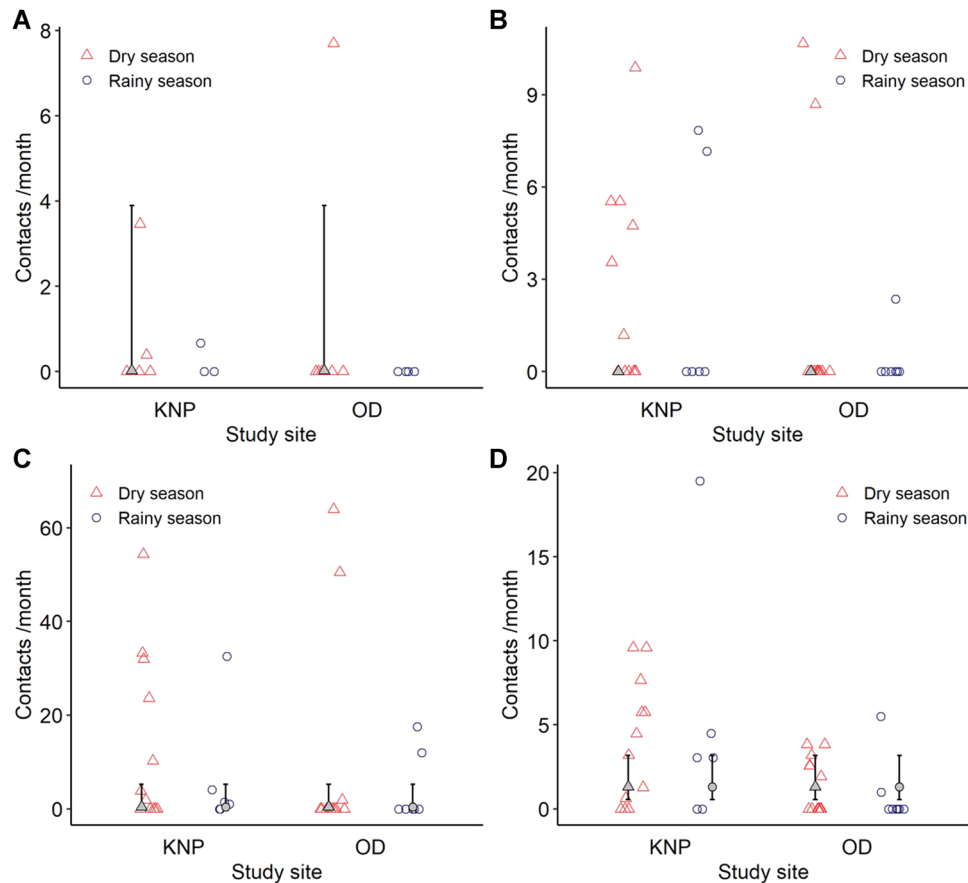


Figure 3. The predicted contact rates between 4 Cape buffalo groups in Kruger National Park (KNP), South Africa, 2010–2015, distributed in 6 dyads of neighboring groups, and 6 Cape buffalo groups in Okavango Delta (OD), Botswana, 2007–2010, distributed in 7 dyads of neighboring groups for each type of contact: A) direct contacts, B) short-term indirect contacts, C) long-term indirect contacts, and D) vector-borne contacts during the dry season (in red) and rainy season (in blue). Error bars indicate 95% confidence intervals around the estimate of the most parsimonious models. The observed values, where each data point represents a dyad, are given by the open symbols for information. Note different y-axis scales.

geographic features (e.g., barriers), pathogen maintenance ability (e.g., through group size), and pathogen characteristics (e.g., infectiousness, incubation period, host diversity). The involvement of a vector (i.e., mosquito in case of RVF) can add factors that can influence the transmission such as vector capacity and density, and susceptible hosts (Chitnis et al. 2013, Manore and Beechler 2015).

We hypothesized that the higher abundance and wider distribution of water and productive forage across the landscape in OD would lead to lower levels of contacts between groups than in KNP. We found no difference in the rate or duration of contacts or in home range overlap between sites. The only exception was for long-term indirect contacts compatible with bTB transmission that lasted significantly longer in KNP than in OD (estimate = 4.68 hr vs. 2.38 hr, respectively), but the magnitude of this site effect was small. The absence of significant inter-site differentiation in contact patterns between groups may simply suggest that contact structure between groups in the Cape buffalo is specific to the species. Alternatively, the lack of differences may be a result of small sample sizes and low statistical power. Our previous work on intra-group contacts with larger sample sizes revealed similar patterns between 3 different populations (Wielgus et al. 2020), so

the absence of inter-site variation in this study may be possible.

We did not identify any vegetation types in OD where contacts are more likely to occur, but our data indicated that some indirect contacts are more likely to occur in woodlands in KNP, depending on the season. Additionally, our data supported that contacts are more likely closer to waterholes in KNP where water is more of a limiting factor. In KNP, water is very scarce during the dry season with only 1 permanent river and permanent pools remaining in a dry riverbed (Fig. 1). Dry-season water availability constrains water-dependent buffalos to aggregate within a few kilometers from available water and may increase inter-group contacts (Miguel et al. 2013). In contrast, in the OD, the wetland system progressively dries up as the dry season progresses, but water remains available over a large area. These analyses are based on large datasets compared to previous analyses and non-independent location data (interpolated every 5 min). But the effect sizes of site, distance to water, and vegetation type on the probability of contact are not qualitatively different when estimated from models based on subsampled datasets (i.e., every hr, 6 and 12 hr). Based on these findings, we tentatively suggest that surface water creates hotspots for

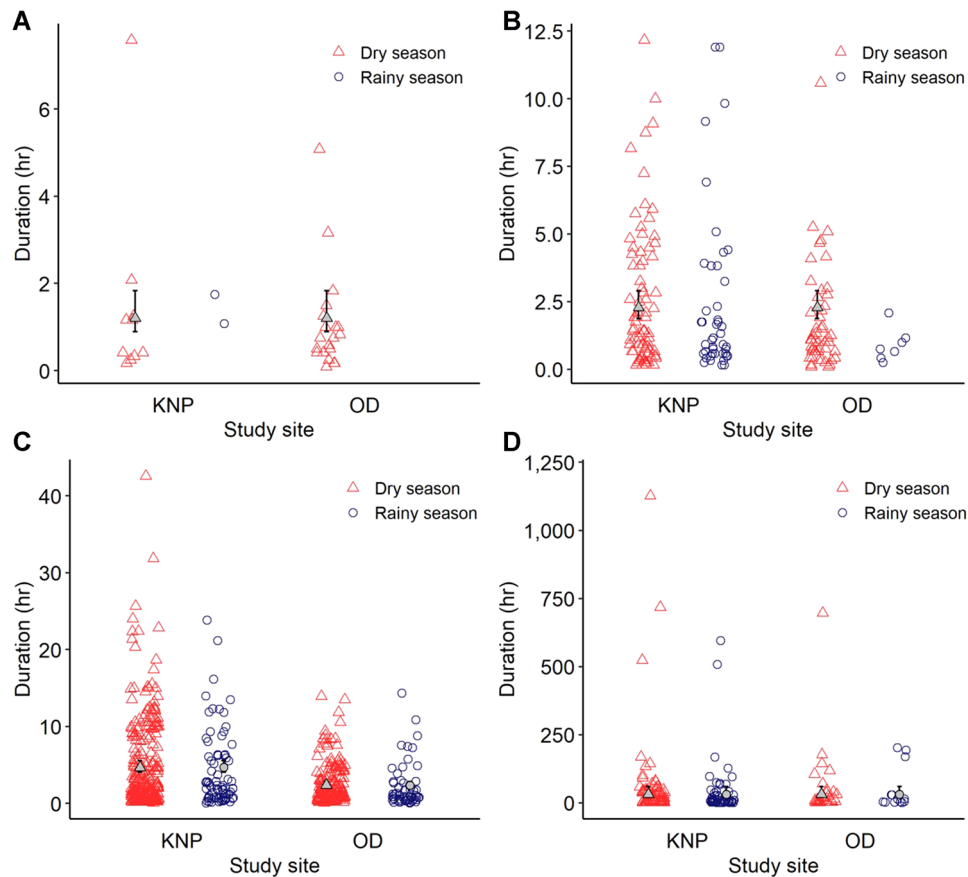


Figure 4. The predicted contact duration in hours between 4 Cape buffalo groups in Kruger National Park (KNP), South Africa, 2010–2015, distributed in 6 dyads of neighboring groups, and 6 Cape buffalo groups in Okavango Delta (OD), Botswana, 2007–2010, distributed in 7 dyads of neighboring groups for each type of contact: A) direct contacts, B) short-term indirect contacts, C) long-term indirect contacts, and D) vector-borne contacts during the dry season (in red) and rainy season (in blue). Error bars indicate 95% confidence intervals around the estimate of the most parsimonious models. The open symbols are the observed values, where each data point represents a dyad. Note different y-axis scales.

contact between Cape buffalo groups, and associated pathogen spread, but only during the dry season in areas where water availability is low.

A potential limitation of our study is that the data were not collected during the same period in both populations (from Dec 2007 to Aug 2010 in OD and from Jun 2010 to Jul 2015 in KNP). We used fixed dates for defining seasons, but differences in resource availability within seasons among years (e.g., drought year) could influence potential differences in observed spatial behavior and affect interpretation. Our study took advantage of the gregarious habits of buffalo that move in cohesive groups and occupy similar home ranges (Sinclair 1977, Ryan et al. 2006) to capture the movements of the groups and to examine the factors moderating contact patterns. Our data likely underestimate contact rates because 1) a buffalo from 1 group may have come into contact with several individuals from another group; 2) groups could have encountered small bachelor groups that could transmit pathogens between different mixed groups (Sinclair 1977, Prins 1996); 3) buffalo groups are subject to fission-fusion dynamics in which there are no permanent social bonds except between females and their young (Wielgus et al. 2020); 4) groups can be widely dispersed, for instance over several hundred meters when a buffalo group arrives at a waterhole (S. Chamaille-Jammes, Centre d'Ecologie Fonctionnelle

et Evolutive, unpublished data), allowing for contacts between neighboring groups that were not detected because they involved non-collared animals; 5) not all buffalo groups in the study sites were monitored; and 6) males regularly switch from 1 mixed group to another (Halley and Mari 2004, Turner et al. 2005), and can therefore serve as key individuals in pathogen transmission between groups. Although our results are based on limited data sets and may be biased low, this study quantifies and compares potentially infectious contacts between Cape buffalo groups in multiple populations.

Although assessing inter-group 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 (Cross et al. 2004, Blanchong et al. 2007, Gear et al. 2010). Although males were previously thought to be the main disperser, long-range dispersal of subadult Cape buffalo females could also be important in the spread of disease between groups and among distant populations (Caron et al. 2016). Most pathogens infecting buffalo can be transmitted to multiple sympatric host species in southern Africa, such as domestic cattle, wildebeest, and

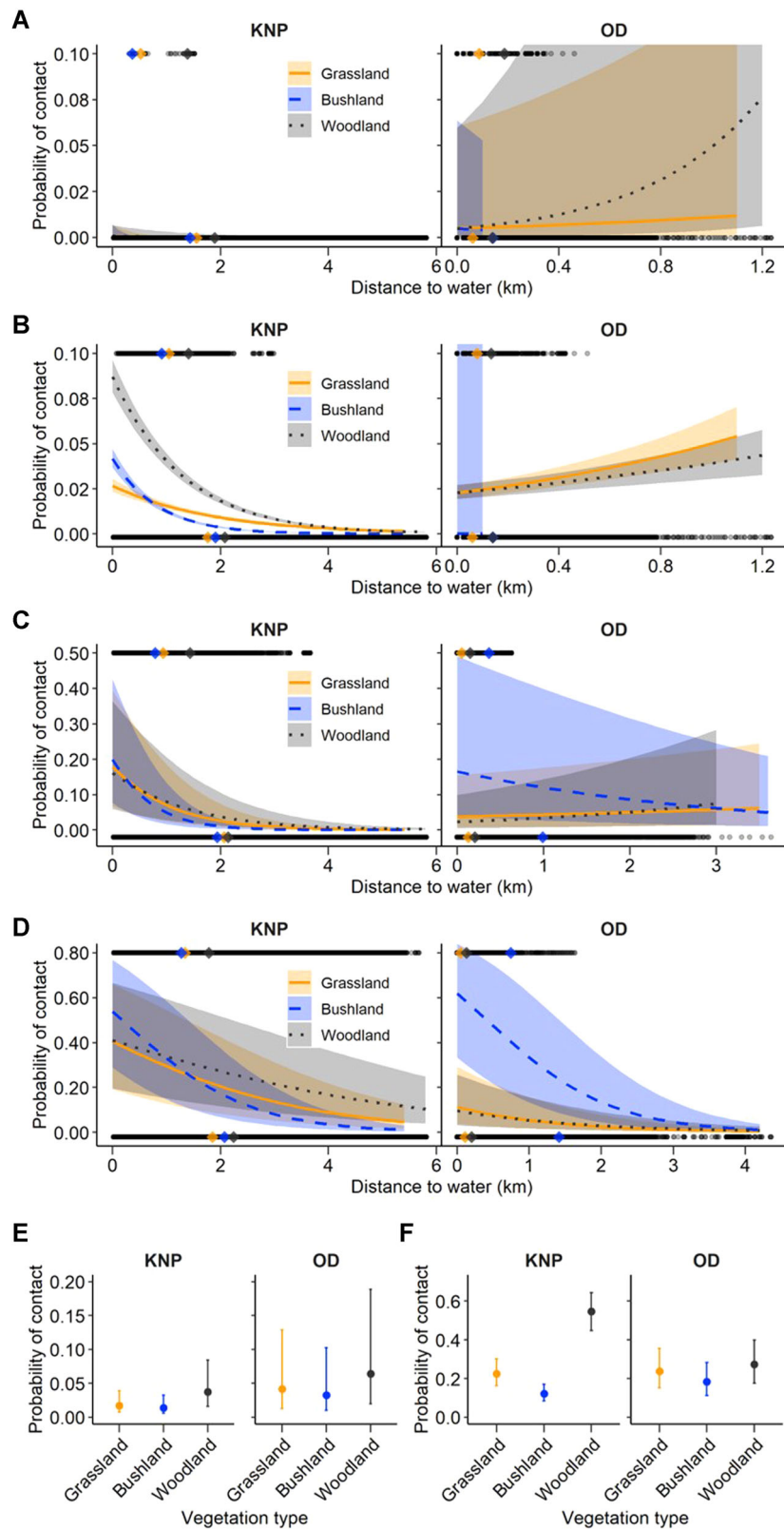


Figure 5. The predicted probability of contact between Cape buffalo groups according to season, site, distance to permanent water, and vegetation type during the dry season for each type of contact: A) direct, B) short-term indirect, C) long-term indirect, and D) vector-borne contacts and according to site and vegetation type during the rainy season for E) long-term indirect and F) vector-borne contacts. We obtained data from 13 dyads of neighboring groups of Cape buffalo from populations in Kruger National Park (KNP), South Africa, 2010–2015, and Okavango Delta (OD), Botswana, 2007–2010, during dry and rainy seasons. Shaded areas and error bars represent 95% confidence intervals around the estimate of the most parsimonious models. Distance to water during the dry season at the observed locations are plotted by tick marks, with marks on bottom corresponding to the non-contact locations and marks at top to the contact locations between dyads of neighboring groups. Note different y-axis and x-axis scales.

Table 3. Coefficient (β) \pm standard error (SE) and 95% confidence intervals (95% CI) of variables included in the most parsimonious models explaining variation in probability of contact between neighboring groups of Cape buffalo in populations from Kruger National Park (KNP), South Africa, 2010–2015, and Okavango Delta (OD), Botswana, 2007–2010, during the dry season. We built 4 separate models for each type of contact (i.e., direct, short- and long-term indirect, and vector-borne contacts) among 13 dyads of neighboring groups. We fit response variables with binomial generalized linear mixed models with identity of dyads as random factor. The binary response variable was the presence or absence of contact (i.e., whether the individual location was a contact [scored 1] or not [scored 0] with the other individual of the dyad). Candidate explanatory variables included distance to nearest permanent water (continuous variable), vegetation type (grassland, bushland, woodland), and site (KNP or OD). The reference category for vegetation type was grassland and reference category for site was OD.

Response variable	Parameter	<i>n</i>	β	SE	95% CI (lower, upper)
Presence-absence of direct contacts		117,691			
	Intercept [grassland, OD]		-5.29	2.55	(-10.28, -0.30)
	Distance to water		0.79	0.41	(-0.02, 1.60)
	Site [KNP]		-1.93	3.39	(-8.57, 4.71)
	Vegetation [bushland]		-0.04	0.72	(-1.46, 1.37)
	Vegetation [woodland]		-0.02	0.16	(-0.34, 0.30)
	Distance to water: site [KNP]		-3.06	0.47	(-3.97, -2.14)
	Distance to water: vegetation [bushland]		-2.44	1.58	(-5.54, 0.67)
Presence-absence of short-term indirect contact		148,882			
	Intercept [grassland, OD]		-3.80	0.16	(-4.08, -3.44)
	Distance to water		0.82	0.23	(0.38, 1.26)
	Site [KNP]		0.16	0.21	(-0.26, 0.58)
	Vegetation [bushland]		-9.84	890.53	(-1,755.26, 1,735.57)
	Vegetation [woodland]		0.01	0.08	(-0.15, 0.16)
	Distance to water: site [KNP]		-1.37	0.23	(-1.82, -0.91)
	Site [KNP]: vegetation [bushland]		10.31	890.53	(-1,735.11, 1,755.72)
Presence-absence of long-term indirect contact		136,271			
	Intercept [grassland, OD]		-3.24	1.54	(-6.27, -0.21)
	Distance to water		0.15	0.12	(-0.08, 0.38)
	Site [KNP]		1.72	1.89	(2.00, 5.43)
	Vegetation [bushland]		1.62	0.35	(0.94, 2.30)
	Vegetation [woodland]		-0.51	0.05	(-0.60, -0.42)
	Distance to water: site [KNP]		-1.20	0.12	(-1.43, -0.96)
	Distance to water: vegetation [bushland]		-0.52	0.05	(-0.62, -0.41)
Presence-absence of vector-borne contact		215,935			
	Intercept [grassland, OD]		-2.06	1.17	(-4.36, 0.24)
	Distance to water		-0.80	0.07	(-0.92, -0.67)
	Site [KNP]		1.67	1.58	(-1.42, 4.76)
	Vegetation [bushland]		2.54	0.12	(2.30, 2.78)
	Vegetation [woodland]		-0.18	0.03	(-0.23, -0.13)
	Distance to water: site [KNP]		0.31	0.07	(0.18, 0.44)
	Distance to water: vegetation [bushland]		-0.37	0.02	(-0.42, -0.33)
	Distance to water: vegetation [woodland]		0.18	0.02	(0.14, 0.21)
	Site [KNP]: vegetation [bushland]		-2.00	0.13	(-2.25, -1.76)
	Site [KNP]: vegetation [woodland]		0.20	0.05	(0.10, 0.30)

kudu (Bengis et al. 2004, Miguel et al. 2013). Inter-specific transmission could therefore enhance or sustain disease spread within buffalo populations independently of inter-group contacts in the species.

How Cape buffalo groups interact with each other and how site and season influence contact patterns and space use also have implications for the socio-spatial organization of the species. We provide evidence for spatial segregation and short-term behavioral avoidance between neighboring buffalo groups in 2 populations. Home ranges of buffalos from neighboring groups had little to no overlap, with direct and short-term indirect contacts rare and short in duration. The tendency to use exclusive home ranges has already been observed in several Cape buffalo populations by Sinclair

(1977), Prins (1996), Halley et al. (2002), and Ryan et al. (2006). Cornélis et al. (2011) reported similar results in West African savanna buffalo (between <2% and 7% of spatial overlap between neighboring groups), and reported low contact rate (4 contacts within 500 m for <1 hr over a season) between 2 neighboring groups despite relatively high overlap of their home ranges (21%). The low overlap and few direct contact rates we observed during the dry season are surprising and do not support our hypothesis that low water availability during this season could force buffalo groups to contract their home ranges around the same water sources (Ryan et al. 2006, Cornélis et al. 2011). We acknowledge that these results are based on small sample sizes and further studies are required to confirm this trend. Our

Table 4. Coefficient (β) \pm standard error (SE) and 95% confidence intervals (95% CI) of variables included in the most parsimonious models explaining variation in probability of contact between neighboring groups of Cape buffalo in populations from Kruger National Park (KNP), South Africa, 2010–2015, and Okavango Delta (OD), Botswana, 2007–2010, during the rainy season. We built 2 separate models for each type of contact (i.e., long-term indirect and vector-borne contacts, among 13 dyads of neighboring groups). We fit response variables with binomial generalized linear mixed models with identity of dyads as random factor. The binary response variable was the presence or absence of contact (i.e., whether the individual location was a contact [scored 1] or not [scored 0] with the other individual of the dyad). Candidate explanatory variables included vegetation type (grassland, bushland, woodland), and site (KNP or OD). The reference category for vegetation type was grassland and reference category for site was OD.

Response variable	Parameter	<i>n</i>	β	SE	95% CI (lower, upper)
Presence-absence of long-term indirect contact	Intercept [grassland, OD]	86,156	-3.13	1.22	(-5.52, -0.74)
	Vegetation [bushland]		-0.26	0.07	(-0.40, -0.12)
	Vegetation [woodland]		0.45	0.06	(0.34, 0.56)
	Site [KNP]		-0.94	1.50	(-3.87, 2.00)
	Vegetation [bushland]: site [KNP]		0.06	0.10	(-0.14, 0.26)
	Vegetation [woodland]: site [KNP]		0.36	0.08	(0.21, 0.52)
Presence-absence of vector-borne contact	Intercept [grassland, OD]	86,156	-1.16	0.57	(-2.27, -0.05)
	Vegetation [bushland]		-0.33	0.03	(-0.40, -0.27)
	Vegetation [woodland]		0.19	0.03	(0.13, 0.24)
	Site [KNP]		-0.08	0.69	(-1.44, 1.28)
	Vegetation [bushland]: site [KNP]		-0.41	0.05	(-0.50, -0.31)
	Vegetation [woodland]: site [KNP]		1.24	0.04	(1.17, 1.32)

results did not suggest seasonal variation in home range overlap between dyads from neighboring groups, but the distance between home ranges of neighboring groups did vary seasonally. Model selection did not show a site effect, but home ranges of neighboring groups in OD tended to be farther apart during the rainy than the dry season. This is probably because, unlike KNP, the OD's environment provides abundant and well-distributed resources to allow some groups to disperse and use more of the available habitat (Bennitt et al. 2016). Buffalo groups in KNP could be much more limited in their movements, especially because of communal lands to the north and fences around KNP to the west (Naidoo et al. 2012, Caron 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 neighboring groups during this season. Although the spatial segregation observed in our 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 (e.g., scent markings facilitated by feces), vocalizations emitted by individuals to maintain group cohesion and order (Mloszewski 1983), or passive avoidance of patches used by other groups through spatial memory (Riotte-Lambert et al. 2015). To understand the mechanisms underlying behavioral avoidance, spatio-temporal windows could be used to assess direct (i.e., visual) and indirect (e.g., feces, marking) contacts between groups, but there is currently a lack of empirical data to estimate these windows. It is unclear why neighboring groups did not use the same areas at the same time or within a short time interval, but this may be to limit competition for resources (Benhamou and Riotte-Lambert 2012). Cape buffalo groups may also avoid each other to prevent pathogen transmission, but to date there is no evidence of a

relationship between home range overlap and level of pathogen infection in Cape buffalo groups. Further studies are required to understand the causal factors underlying behavioral avoidance between Cape buffalo groups.

MANAGEMENT IMPLICATIONS

We suggest that the evidence that buffalo groups do not have greatly overlapping home ranges, even in 2 populations with different climatic conditions, could be used in models of disease spread in Cape buffalo populations. Values of inter-group contact rates and durations from this study can be used in contact networks of Cape buffalo populations and be linked to epidemiological models to simulate pathogen spread at the landscape scale. Because contact rates and durations are similar between our 2 populations, it would not be wrong to consider epidemiological models at the level of the species. The study presented here shows that contacts between groups are much rarer than within groups, so we recommend that epidemiological models consider differential transmission risks to account for within- and between-group contact rates. In addition, because contacts are more likely to occur closer to water in semi-arid savanna environments, managers could try to manipulate the landscape in such a way so that each group can access key resource patches without having to share with another group. We recommend monitoring the waterholes (e.g., counting visits) to ensure that the higher probability of contact near water is not a response to the removal of water sources in KNP in the 1990s, which could have increased the sharing of same waterholes and therefore the spread of pathogens.

ACKNOWLEDGMENTS

We thank the South African National Parks for permission to conduct our research in KNP, the Ministry of Environment, Wildlife and Tourism of Botswana to operate around OD, the Department of Wildlife and National

Parks of Botswana, the Veterinary Services of both countries and Zimbabwe for efficient field support, and everyone involved in fieldwork. The project was implemented under the framework of the Research Platform “Production and Conservation in Partnership” (RP-PCP) and within the framework of the AHEAD initiative. This research was funded by CIRAD, South African National Parks, Veterinary Services in South Africa's Department of Agriculture, the Ministère Français des Affaires Étrangères through the French Embassy in Zimbabwe, the François Sommer Foundation (Paris), J. and M. Bennett, the Dulverton Trust, H. Ferguson, I. Fuhr, R. Fuhr, D. Hawk, Idea Wild, the North of England Zoological Society, the Roberts Fund, and Wilderness Safaris Wildlife Trust.

LITERATURE CITED

- Alexander, K. A., J. K. Blackburn, M. E. Vandewalle, R. Pesapane, E. K. Baipoleli, and P. H. Elzer. 2012. Buffalo, bush meat, and the zoonotic threat of brucellosis in Botswana. *PLoS ONE* 7:e32842.
- Altizer, S., C. L. Nunn, P. H. Thrall, J. L. Gittleman, J. Antonovics, A. A. Cunningham, A. P. Dobson, V. Ezenwa, K. E. Jones, A. B. Pedersen, M. Poss, and J. R. C. Pulliam. 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics* 34:517–547.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178.
- Aune, K., J. C. Rhyan, R. Russell, T. J. Roffe, and B. Corso. 2011. Environmental persistence of *Brucella abortus* in the Greater Yellowstone Area. *Journal of Wildlife Management* 76:253–261.
- Aureli, F., C. M. Schaffner, C. Boesch, S. K. Bearder, J. Call, C. A. Chapman, R. Connor, A. Di Fiore, R. I. M. Dunbar, S. P. Henzi, et al. 2008. Fission-fusion dynamics: new research frameworks. *Current Anthropology* 49:627–654.
- Ba, Y., D. Diallo, C. M. F. Kebe, I. Dia, and M. Diallo. 2006. Aspects of bioecology of two Rift Valley fever virus vectors in Senegal (West Africa): *Aedes vexans* and *Culex poicilipes* (Diptera: Culicidae). *Journal of Medical Entomology* 42:739–750.
- Bartoń, K. 2019. MuMIn: multi-model inference. R package version 1.43.6. <https://CRAN.R-project.org/package=MuMIn>
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Beechler, B. R., R. Bengis, R. Swanepoel, J. T. Paweska, A. Kemp, P. J. van Vuren, J. Joubert, V. O. Ezenwa, and A. E. Jolles. 2015. Rift Valley fever in Kruger National Park: do buffalo play a role in the inter-epidemic circulation of virus? *Transboundary and Emerging Diseases* 62:24–32.
- Bengis, R. G., R. A. Kock, and J. Fischer. 2002. Infectious animal diseases: the wildlife/livestock interface. *Revue Scientifique et Technique (International Office of Epizootics)* 21:53–65.
- Bengis, R. G., N. P. Kriek, D. F. Keet, J. P. Raath, V. de Vos, and H. F. Huchzermeyer. 1996. An outbreak of bovine tuberculosis in a free-living African buffalo (*Syncerus caffer*-Sparrman) population in the Kruger National Park: a preliminary report. *Onderstepoort Journal of Veterinary Research* 63:15–18.
- Bengis, R. G., F. A. Leighton, J. R. Fischer, M. Artois, T. Möerner, and C. M. Tate. 2004. The role of wildlife in emerging and re-emerging zoonoses. *OIE Revue Scientifique et Technique* 23:497–511.
- Benhamou, S., and D. Cornélis. 2010. Incorporating movement behavior and barriers to improve kernel home range space use estimates. *Journal of Wildlife Management* 74:1353–1360.
- Benhamou, S., and L. Riottte-Lambert. 2012. Beyond the utilization distribution: identifying home range areas that are intensively exploited or repeatedly visited. *Ecological Modelling* 227:112–116.
- Benhamou, S., M. Valeix, S. Chamaillé-Jammes, D. W. Macdonald, and A. J. Loveridge. 2014. Movement-based analysis of interactions in African lions. *Animal Behaviour* 90:171–180.
- Bennett, E., M. C. Bonyongo, and S. Harris. 2014. Habitat selection by African buffalo (*Syncerus caffer*) in response to landscape-level fluctuations in water availability on two temporal scales. *PLoS ONE* 9:e101346.
- Bennett, E., M. C. Bonyongo, and S. Harris. 2015. Behaviour-related scalar habitat use by Cape buffalo (*Syncerus caffer caffer*). *PLoS ONE* 10:e0145145.
- Bennett, E., M. C. Bonyongo, and S. Harris. 2016. Effects of divergent migratory strategies on access to resources for Cape buffalo (*Syncerus caffer caffer*). *Journal of Mammalogy* 97:1682–1698.
- Bennett, E., M. C. Bonyongo, and S. Harris. 2018. Cape buffalo (*Syncerus caffer caffer*) social dynamics in a flood-pulsed environment. *Behavioral Ecology* 29:93–105.
- Blanchong, J. A., K. T. Scribner, A. N. Kravchenko, and S. R. Winterstein. 2007. TB-infected deer are more closely related than non-infected deer. *Biology Letters* 3:104–106.
- Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75:1393–1405.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9:378–400.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer Verlag, New York, New York, USA.
- Calenge, C. 2007. Exploring habitat selection by wildlife with adehabitat. *Journal of Statistical Software* 22:1–19.
- Caron, A., D. Cornelis, C. Foggini, M. Hofmeyr, and M. de Garine-Wichatitsky. 2016. African buffalo movement and zoonotic disease risk across transfrontier conservation areas, southern Africa. *Emerging Infectious Diseases* 22:277–280.
- Caron, A., E. Miguel, C. Gomo, P. Makaya, D. M. Pfukenyi, C. Foggini, T. Hove, and M. De Garine-Wichatitsky. 2013. Relationship between burden of infection in ungulate populations and wildlife/livestock interfaces. *Epidemiology and Infection* 141:1522–1535.
- Chase, M. 2011. Dry season aerial survey of elephants and wildlife in Northern Botswana. *Elephants Without Borders*, Kasane, Botswana.
- Chaverri, G., M. Gamba-Rios, and T. H. Kunz. 2007. Range overlap and association patterns in the tent-making bat *Artibeus watsoni*. *Animal Behaviour* 73:157–164.
- Chitnis, N., J. M. Hyman, and C. A. Manore. 2013. Modelling vertical transmission in vector-borne diseases with applications to Rift Valley fever. *Journal of Biological Dynamics* 7:11–40.
- Conybeare, A. 1980. Buffalo numbers, home range and daily movement in the Sengwa Wildlife Research Area, Zimbabwe. *South African Journal of Wildlife Research* 10:89–93.
- Cornélis, D., S. Benhamou, G. Janeau, N. Morellet, M. Ouedraogo, and M.-N. de Visscher. 2011. Spatiotemporal dynamics of forage and water resources shape space use of West African savanna buffaloes. *Journal of Mammalogy* 92:1287–1297.
- Craft, M. E. 2015. Infectious disease transmission and contact networks in wildlife and livestock. *Philosophical Transactions of the Royal Society B* 370:20140107.
- Cross, P. C., J. O. Lloyd-Smith, J. A. Bowers, C. T. Hay, M. Hofmeyr, and W. M. Getz. 2004. Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. *Annales Zoologici Fennici* 41:879–892.
- Dougherty, E. R., D. P. Seidel, C. J. Carlson, O. Spiegel, and W. M. Getz. 2018. Going through the motions: incorporating movement analyses into disease research. *Ecology Letters* 21:588–604.
- Elbroch, L. M., and H. Quigley. 2017. Social interactions in a solitary carnivore. *Current Zoology* 63:357–362.
- Gaylard, A., N. Owen-Smith, and J. Redfern. 2003. Surface water availability: implications for heterogeneity and ecosystem processes. Pages 171–188 in J. T. du Toit, K. H. Rogers, and H. C. Biggs, editors. *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington, D.C., USA.
- Geffen, H., A. Perevolotsky, E. Geffen, and Y. Yom-Tov. 1999. Use of space and social organization of female mountain gazelles (*Gazella gazella gazella*) in Ramat HaNadiv, Israel. *Journal of Zoology* 247:113–119.
- Gertenbach, W. P. D. 1983. Landscapes of the Kruger National Park. *Koedoe* 26:a591.

- Gorsich, E. E., V. O. Ezenwa, P. C. Cross, R. G. Bengis, and A. E. Jolles. 2015. Context-dependent survival, fecundity and predicted population-level consequences of brucellosis in African buffalo. *Journal of Animal Ecology* 84:999–1009.
- Grear, D. A., M. D. Samuel, K. T. Scribner, B. V. Weckworth, and J. A. Langenberg. 2010. Influence of genetic relatedness and spatial proximity on chronic wasting disease infection among female white-tailed deer. *Journal of Applied Ecology* 47:532–540.
- Halley, D. J., and M. Mari. 2004. Dry season social affiliation of African buffalo bulls at the Chobe riverfront, Botswana. *South African Journal of Wildlife Research* 34:105–111.
- Halley, D. J., M. E. Vandewalle, M. Mari, and C. Taolo. 2002. Herd-switching and long-distance dispersal in female African buffalo *Syncerus caffer*. *African Journal of Ecology* 40:97–99.
- Hughes, K., G. T. Fosgate, C. M. Budke, M. P. Ward, R. Kerry, and B. Ingram. 2017. Modeling the spatial distribution of African buffalo (*Syncerus caffer*) in the Kruger National Park, South Africa. *PLoS ONE* 12:1–18.
- Johnson, D. S., and J. M. London. 2018. crawl: an R package for fitting continuous-time correlated random walk models to animal movement data. Zenodo. <https://doi.org/10.5281/zenodo.596464>
- Johnson, D. S., J. M. London, M.-A. Lea, and J. W. Durban. 2008. Continuous-time correlated random walk model for animal telemetry data. *Ecology* 89:1208–1215.
- Jori, F., K. A. Alexander, M. Mokopasetso, S. Munstermann, K. Moagabo, and J. T. Paweska. 2015. Serological evidence of Rift Valley fever virus circulation in domestic cattle and African buffalo in northern Botswana (2010–2011). *Frontiers in Veterinary Science* 2:1–7.
- Jori, F., M. Mokopasetso, E. Etter, S. Munstermann, S. H. Newman, and A. Michel. 2013. Preliminary assessment of bovine tuberculosis at the livestock/wildlife interface in two protected areas of northern Botswana. *Transboundary and Emerging Diseases* 60:28–36.
- Kiros, A., H. Asgedom, and R. Duguma. 2016. A review on bovine brucellosis: epidemiology, diagnosis and control options. *ARC Journal of Animal and Veterinary Sciences* 2:8–21.
- Kolbe, N. R., and F. W. Weckerly. 2015. Home-range overlap of Roosevelt elk herds in the Bald Hills of Redwood National Park. *California Fish and Game* 101:208–217.
- Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution* 7:573–579.
- Manore, C. A., and B. R. Beechler. 2015. Inter-epidemic and between-season persistence of Rift Valley fever: vertical transmission or cryptic cycling? *Transboundary and Emerging Diseases* 62:13–23.
- Mattisson, J., P. Segerström, J. Persson, M. Aronsson, G. R. Rauset, G. Samelius, and H. Andrén. 2013. Lethal male-male interactions in Eurasian lynx. *Mammalian Biology* 78:304–308.
- McCarthy, T. S., G. R. J. Cooper, P. D. Tyson, and W. N. Ellery. 2000. Seasonal flooding in the Okavango Delta, Botswana—Recent history and future prospects. *South African Journal of Science* 96:25–33.
- Miguel, E., V. Grosbois, A. Caron, T. Boulinier, H. Fritz, D. Cornélis, C. Foggini, P. V. Makaya, P. T. Tshabalala, and M. de Garine-Wichatitsky. 2013. Contacts and foot and mouth disease transmission from wild to domestic bovines in Africa. *Ecosphere* 4:art51.
- Mloszewski, M. J. 1983. The behavior and ecology of the African buffalo. Cambridge University Press, Cambridge, United Kingdom.
- Murray, M. G. 1982. Home range, dispersal and the clan system of impala. *African Journal of Ecology* 20:253–269.
- Naidoo, R., P. Du Preez, G. Stuart-Hill, M. Jago, and M. Wegmann. 2012. Home on the range: factors explaining partial migration of African buffalo in a tropical environment. *PLoS ONE* 7:e36527.
- Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of The Royal Society Interface* 14:20170213.
- Omondi, G. P., F. Gakuya, J. Arzt, A. Sangula, E. Hartwig, S. Pauszek, G. Smoliga, B. Brito, A. Perez, V. Obanda, and K. VanderWaal. 2020. The role of African buffalo in the epidemiology of foot-and-mouth disease in sympatric cattle and buffalo populations in Kenya. *Transboundary and Emerging Diseases* 67:2206–2221.
- Owen-Smith, N., J. M. Fryxell, and E. H. Merrill. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2267–2278.
- Podgorski, T., M. Apollonio, and O. Keuling. 2018. Contact rates in wild boar populations: implications for disease transmission. *Journal of Wildlife Management* 82:1210–1218.
- Pretorius, E., and R. Pretorius. 2015. Improving the potential of pixel-based supervised classification in the absence of quality ground truth data. *South African Journal of Geomatics* 4:250.
- Prins, H. H. T. 1996. Ecology and behaviour of the African buffalo: social inequality and decision-making. Chapman and Hall, London, United Kingdom.
- R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramberg, L., P. Hancock, M. Lindholm, T. Meyer, S. Ringrose, J. Sliva, J. Van As, and C. VanderPost. 2006. Species diversity of the Okavango Delta, Botswana. *Aquatic Sciences* 68:310–337.
- Redfern, J. V., R. Grant, H. Biggs, and W. M. Getz. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84:2092–2107.
- Reynolds, J. J. H., B. T. Hirsch, S. D. Gehrt, and M. E. Craft. 2015. Raccoon contact networks predict seasonal susceptibility to rabies outbreaks and limitations of vaccination. *Journal of Animal Ecology* 84:1720–1731.
- Riotte-Lambert, L., S. Benhamou, and S. Chamaillé-Jammes. 2015. How memory-based movement leads to nonterritorial spatial segregation. *American Naturalist* 185:E103–E116.
- Rodhain, F. 1996. Ecology of *Aedes aegypti* in Africa and Asia. *Bulletin de la Société de Pathologie Exotique* (1990) 89:103–106.
- Rodwell, T. C., N. P. Kriek, R. G. Bengis, I. J. Whyte, P. C. Viljoen, V. de Vos, and W. M. Boyce. 2001. Prevalence of bovine tuberculosis in African buffalo at Kruger National Park. *Journal of Wildlife Diseases* 37:258–64.
- Ryan, S. J., C. U. Knechtel, and W. M. Getz. 2006. Range and habitat selection of African buffalo in South Africa. *Journal of Wildlife Management* 70:764–776.
- Sah, P., S. T. Leu, P. C. Cross, P. J. Hudson, and S. Bansal. 2017. Unraveling the disease consequences and mechanisms of modular structure in animal social networks. *Proceedings of the National Academy of Sciences* 114:4165–4170.
- Shannon, R. C., and N. C. Davis. 1930. The flight of *Stegomyia aegypti* (L.). *The American Journal of Tropical Medicine and Hygiene* s1-10:151–156.
- Sikes, R. S., W. L. Gannon, and The Animal Care and use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- Sinclair, A. R. E. 1977. The African buffalo: a study of resource limitation of populations. University of Chicago Press, Chicago, Illinois, USA.
- Smieszek, T. 2009. A mechanistic model of infection: why duration and intensity of contacts should be included in models of disease spread. *Theoretical Biology and Medical Modelling* 6:25.
- Tambling, C. J., D. J. Druce, M. W. Hayward, J. G. Castley, J. Adendorff, and G. I. H. Kerley. 2012. Spatial and temporal changes in group dynamics and range use enable anti-predator responses in African buffalo. *Ecology* 93:1297–1304.
- Tanner, M., and A. L. Michel. 1999. Investigation of the viability of *M. bovis* under different environmental conditions in the Kruger National Park. *Onderstepoort Journal of Veterinary Research* 66:185–190.
- Turner, W. C., A. E. Jolles, and N. Owen-Smith. 2005. Alternating sexual segregation during the mating season by male African buffalo (*Syncerus caffer*). *Journal of Zoology* 267:291.
- Valls-Fox, H., S. Chamaillé-Jammes, M. de Garine-Wichatitsky, A. Perrotton, N. Courbin, E. Miguel, C. Guerbois, A. Caron, A. Loveridge, B. Stapelkamp, M. Muzamba, and H. Fritz. 2018. Water and cattle shape habitat selection by wild herbivores at the edge of a protected area. *Animal Conservation* 21:365–375.
- Vanderwaal, K. L., V. Obanda, G. P. Omondi, B. McCowan, H. Wang, H. Fushing, and L. A. Isbell. 2016. The strength of weak ties and helminth parasitism in giraffe social networks. *Behavioral Ecology* 27:1190–1197.
- Venter, F. J., R. J. Scholes, and H. C. Eckhardt. 2003. The abiotic template and its associated vegetation pattern. Pages 83–129 in J. T. Du Toit, K. H. Rogers, and H. C. Biggs, editors. *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington, D.C., USA.

Weber, N., S. P. Carter, S. R. X. Dall, R. J. Delahay, J. L. McDonald, S. Bearhop, and R. A. McDonald. 2013. Badger social networks correlate with tuberculosis infection. *Current Biology* 23:R915–R916.

White, L. A., J. D. Forester, and M. E. Craft. 2017. Using contact networks to explore mechanisms of parasite transmission in wildlife. *Biological Reviews* 92:389–409.

Wielgus, E., D. Cornélis, M. de Garine-Wichatitsky, B. Cain, H. Fritz, E. Miguel, H. Valls-Fox, A. Caron, and S. Chamaillé-Jammes. 2020. Are fission–fusion dynamics consistent among populations? A large-scale study with Cape buffalo. *Ecology and Evolution* 10:9240–9256.

Wolfensohn, M., and E. Galun. 1953. A method for determining the flight range of *Aedes aegypti* (Linn.). *Bulletin of the Research Council of Israel* 2:433–436.

Associate Editor: Kathryn Schoenecker.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.