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Research Article

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

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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.

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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 (Conybear 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 (Lycaon 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 periods (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 (McCarty 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, Bennett et al. 2014).

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 season (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 (McCarty 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, Bennett 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, Bennett et al. 2014, Caron et al. 2016). We located buffalo groups from the air and randomly selected ≥1 adult females to be
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

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.
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 UDs from hourly GPS locations using the movement-based kernel density estimation method (MKDE; Benhamou and Cornélius 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
| Disease name (Pathogen) | Prevalence (%) in buffalo at each site [95% CI] | Mode of transmission | Spatial window | Time window | Contact name |
|-------------------------|-----------------------------------------------|---------------------|----------------|-------------|--------------|
| Bovine tuberculosis (bTB) | *Mycobacterium bovis* | KNP North: 1.5% [0.4–4.0] (n = 203)<sup>a</sup> <br> OD: 2.9% [0.8–9.8] (n = 70)<sup>b</sup> | Inhalation of aerosolized droplets <br> Ingestion or ingestion of infected materials (e.g., feces) | 150 m | 0 hr | Direct contact <br> Long-term indirect contact |
| Brucellosis | *Brucella abortus* | KNP North: 15.0% (n = 314)<sup>c</sup> <br> OD: 6% [3.0–9.0] (n = 247)<sup>d</sup> | Contact with or ingestion of infected fetus or other abortion products | 150 m | 0–2 days | Short-term indirect contact <br> Vector-borne contact |
| Rift Valley fever (RVF) | Rift Valley fever virus | KNP North: 3.6% (n = 196)<sup>e</sup> <br> OD: 9.7% [4.0–19.0] (n = 72)<sup>f</sup> | By the bite of a female mosquito | 2,500 m | 0–31 days | |

<sup>a</sup> Rodwell et al. (2001).  
<sup>b</sup> Jori et al. (2013).  
<sup>c</sup> Gorsich et al. (2015).  
<sup>d</sup> Alexander et al. (2012).  
<sup>e</sup> Beechler et al. (2015).  
<sup>f</sup> Jori et al. (2015).
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 (AICc; Burnham and Anderson 2002). We considered the most parsimonious model to be the model that had both an ΔAICc < 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 (Barton 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 (AICc) values of the best model (i.e., AICc < 2 and the lowest number of explanatory variables). Models are ordered from lowest to highest AICc, and the best model is indicated with an asterisk.

Model | df | Deva | ΔAICc | R2 marginal
--- | --- | --- | --- | ---
1. Home range overlap between dyads of neighboring groups (n = 19) | | | | |
Null† | 3 | 8 | 0.0 | 0.00
Site | 4 | 3 | 8 | 3.0 | 0.06
Season | 4 | 8 | 3 | 2.0 | 0.01
Site + season | 5 | 8 | 8 | 6.8 | 0.07
2. Distance between home ranges between dyads of neighboring groups (n = 19) | | | | |
Season † | 4 | 49 | 8 | 0.0 | 0.01
Site × season | 6 | 49 | 2 | 6.4 | 0.02
Site + season | 5 | 8 | 7 | 2.6 | 0.07
3. Contact rate between dyads of neighboring groups | | | | |
Direct contacts (only in dry season, n = 12) | | | | |
Null † | 3 | 25 | 0 | 0.0 | 0.00
Site | 4 | 25 | 4 | 7.0 | 0.00
Short-term indirect contacts (only in dry season, n = 24) | | | | |
Null † | 3 | 62 | 0 | 0.0 | 0.00
Site | 4 | 62 | 1 | 9.0 | 0.12
Long-term indirect contacts (n = 38) | | | | |
Season | 4 | 154 | 0 | 0.0 | 0.01
Null † | 3 | 158 | 0 | 1.8 | 0.00
Site + season | 5 | 153 | 2 | 0.0 | 0.08
Site | 4 | 157 | 0 | 3.5 | 0.07
Site × season | 6 | 153 | 4 | 7.0 | 0.09
Vector-borne contacts (n = 38) | | | | |
Null † | 3 | 149 | 0 | 0.0 | 0.00
Site | 4 | 148 | 1 | 0.0 | 0.11
Season | 4 | 148 | 1 | 2.0 | 0.02
Site + season | 5 | 146 | 2 | 5.0 | 0.13
Site × season | 6 | 144 | 3 | 5.0 | 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 | 0.00
Site | 4 | 73 | 1 | 8.0 | 0.03
Short-term indirect contacts (only in dry season, n = 126) | | | | |
Site | 4 | 458 | 0 | 0.0 | 0.01
Null † | 3 | 462 | 1 | 8.0 | 0.00
Long-term indirect contacts (n = 567) | | | | |
Site † | 4 | 2,571 | 0 | 0.0 | 0.01
Site + season | 5 | 2,570 | 0 | 9.0 | 0.01
Site × season | 6 | 2,570 | 0 | 3.0 | 0.01
Null | 3 | 2,579 | 6 | 2.0 | 0.00
Season | 4 | 2,579 | 8 | 0.0 | 0.00
Vector-borne contacts (n = 176) | | | | |
Null † | 3 | 1,586 | 0 | 0.0 | 0.00
Season | 4 | 1,585 | 0 | 0.9 | 0.00
Site | 4 | 1,586 | 2 | 1.0 | 0.00
Site + season | 5 | 1,585 | 3 | 0.0 | 0.00
Site × season | 6 | 1,585 | 5 | 0.0 | 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 | 0.00

Table 2. (Continued)

| Model | df | Deva | ΔAICc | R2 marginal
--- | --- | --- | --- | ---
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 + site + distance to water × vegetation type + vegetation type × site | 11 | 25,993 | 0.0 | 0.29
7. Probability of contact between dyads of neighboring groups according to distance to water and 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 = 215,935) | | | | |
Vegetation type × site | 7 | 93,422 | 0.0 | 0.14

a Degree of freedom.
b Deviance of the model, calculated as ~2 × loglikelihood.
c Difference in value between Akaike’s Information Criterion for small samples size (AICc) of the current model and the model with the lowest AICc.
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...
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),
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 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.
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. Chamaillé-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, Grear 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 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.
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.
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.

### Table 3. Coefficient ($\beta$) ± 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 | $n$ | $\beta$ | SE  | 95% CI (lower, upper) |
|------------------|-----------|-----|---------|-----|-----------------------|
| Presence-absence of direct contacts | Intercept [grassland, OD] | 117,691 | -5.29 | 2.55 | (-10.28, -0.30) |
| | Distance to water | &nbsp; | 0.79 | 0.41 | (-0.02, 1.60) |
| | Site [KNP] | &nbsp; | -1.93 | 3.39 | (-8.57, 4.71) |
| | Vegetation [bushland] | &nbsp; | -0.04 | 0.72 | (-1.46, 1.37) |
| | Vegetation [woodland] | &nbsp; | -0.02 | 0.16 | (-0.34, 0.30) |
| | Distance to water: site [KNP] | &nbsp; | -3.06 | 0.47 | (-3.97, -2.14) |
| | Distance to water: vegetation [bushland] | &nbsp; | -2.44 | 1.58 | (-5.54, 0.67) |
| | Distance to water: vegetation [woodland] | &nbsp; | 1.55 | 0.40 | (0.78, 2.33) |
| Presence-absence of short-term indirect contact | Intercept [grassland, OD] | 148,882 | -3.80 | 0.16 | (-4.08, -3.44) |
| | Distance to water | &nbsp; | 0.82 | 0.23 | (0.38, 1.26) |
| | Site [KNP] | &nbsp; | 0.16 | 0.21 | (-0.26, 0.58) |
| | Vegetation [bushland] | &nbsp; | -9.84 | 890.53 | (-1,755.26, 1,735.57) |
| | Vegetation [woodland] | &nbsp; | 0.01 | 0.08 | (-0.15, 0.16) |
| | Distance to water: site [KNP] | &nbsp; | -1.37 | 0.23 | (-1.82, -0.91) |
| | Site [KNP]: vegetation [bushland] | &nbsp; | 10.31 | 890.53 | (-1,735.11, 1,755.72) |
| | Site [KNP]: vegetation [woodland] | &nbsp; | 1.24 | 0.14 | (0.97, 1.51) |
| | Distance to water: vegetation [bushland] | &nbsp; | -0.68 | 0.11 | (-0.90, -0.46) |
| | Distance to water: vegetation [woodland] | &nbsp; | -0.26 | 0.09 | (-0.44, -0.09) |
| Presence-absence of long-term indirect contact | Intercept [grassland, OD] | 136,271 | -3.24 | 1.54 | (-6.27, -0.21) |
| | Distance to water | &nbsp; | 0.15 | 0.12 | (-0.08, 0.38) |
| | Site [KNP] | &nbsp; | 1.72 | 1.89 | (2.00, 5.43) |
| | Vegetation [bushland] | &nbsp; | 1.62 | 0.35 | (0.94, 2.30) |
| | Vegetation [woodland] | &nbsp; | -0.51 | 0.05 | (-0.60, -0.42) |
| | Distance to water: site [KNP] | &nbsp; | -1.20 | 0.12 | (-1.43, -0.96) |
| | Distance to water: vegetation [bushland] | &nbsp; | -0.52 | 0.05 | (-0.62, -0.41) |
| | Distance to water: vegetation [woodland] | &nbsp; | 0.26 | 0.04 | (0.18, 0.35) |
| | Site [KNP]: vegetation [bushland] | &nbsp; | -1.49 | 0.35 | (-2.17, -0.81) |
| | Site [KNP]: vegetation [woodland] | &nbsp; | 0.38 | 0.07 | (0.24, 0.52) |
| Presence-absence of vector-borne contact | Intercept [grassland, OD] | 215,935 | -2.06 | 1.17 | (-4.36, 0.24) |
| | Distance to water | &nbsp; | -0.80 | 0.07 | (-0.92, -0.67) |
| | Site [KNP] | &nbsp; | 1.67 | 1.58 | (-1.42, 4.76) |
| | Vegetation [bushland] | &nbsp; | 2.54 | 0.12 | (2.30, 2.78) |
| | Vegetation [woodland] | &nbsp; | -0.18 | 0.03 | (-0.23, -0.13) |
| | Distance to water: site [KNP] | &nbsp; | 0.31 | 0.07 | (0.18, 0.44) |
| | Distance to water: vegetation [bushland] | &nbsp; | -0.37 | 0.02 | (-0.42, -0.33) |
| | Distance to water: vegetation [woodland] | &nbsp; | 0.18 | 0.02 | (0.14, 0.21) |
| | Site [KNP]: vegetation [bushland] | &nbsp; | -2.00 | 0.13 | (-2.25, -1.76) |
| | Site [KNP]: vegetation [woodland] | &nbsp; | 0.20 | 0.05 | (0.10, 0.30) |
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.

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