

ECOGRAPHY

Research

Where buffalo and cattle meet: modelling interspecific contact risk using cumulative resistant kernels

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Ecography

41: 1–11, 2018

doi: 10.1111/ecog.03039

Subject Editor: Timothy Keitt

Editor-in-Chief: Hanna Tuomisto

Accepted 28 November 2017

African buffalo the primary source of foot and mouth disease (FMD) infection for livestock in South Africa. Predicting the spatial drivers and patterns of buffalo–cattle contact risk is crucial for developing effective FMD mitigation strategies. Therefore, the goal of this study was to predict fine-scale, seasonal contact risk between cattle and buffaloes straying into communal lands adjacent to Kruger National Park. This study provides the first application of the cumulative resistant kernel method to calculate contact risk between two species. We built resistance surfaces from resource utilization models of buffalo and cattle and calculated the intersection of resistant kernels of the two species. This revealed that the contact risk is influenced by seasonality, water sources and fence strength, and the magnitude of contact risk is largely driven by buffalo and cattle dispersal abilities. The probability of contact was higher in the dry season, with hotspots along a main river and the weakest parts of the perimeter fence. In the wet season, contact risk was more diffuse and less concentrated along the main river and near settlements. The new approach of intersecting cumulative resistant kernels of two species can produce quantitative predictive maps of animals' contact risk and help identify potential hotspots of disease transmission.

Keywords: African buffalo, Kruger National Park, resistance surface, resistant kernel, landscape connectivity, interspecific interactions

Introduction

Foot-and-mouth disease (FMD) is endemic to Africa (Vosloo et al. 2002, Klein 2009) and causes high morbidity in cloven-hoofed animals and camelids (Thomson and Bastos 2004). Outbreaks of FMD have led to restrictions in meat export, which can impact the livestock industry in affected countries (Sutmoller et al. 2003). South Africa has obtained designated disease-free status without vaccination, by separating the endemic infected zone (Kruger National Park and neighbouring private and provincial nature reserves) from the disease-free zone by a buffer and inspection zones.



The buffer zone is a 10–20 km wide area directly adjacent to the infected zone, with strict control of cattle movement and intensive inspection to identify FMD infections, and FMD vaccination in defined areas. The inspection zone is a region beyond the buffer zone ranging from ~10–50 km wide, in which free movement of livestock is permitted and all livestock are regularly inspected to detect FMD (Modisane 2009, Jori et al. 2011).

African buffalo *Syncerus caffer* is the main reservoir of the FMD virus and the primary source of infection for susceptible livestock near Kruger National Park (KNP) and its adjoining reserves (Thomson 1996, Vosloo et al. 2006, van Schalkwyk et al. 2014). However, the ecological and anthropogenic factors controlling transmission are not fully understood. The climatic conditions in southern Africa are not conducive to long distance aerosol dissemination of the virus, suggesting that transmission primarily occurs through contact between infected buffaloes and livestock (Alexander et al. 2002, van Schalkwyk et al. 2014). Miguel et al. (2013) provided strong evidence that the contact rate between cattle and wild buffalo significantly influences FMD dynamics in Zimbabwe. Therefore, disease control efforts primarily focus on preventing contact between buffaloes and cattle.

In the 1960s an extensive network of game-proof fences was erected around KNP and the surrounding private game reserves to prevent contact between cattle and buffalo. Moreover, as an additional protection against infection, cattle are vaccinated twice a year in areas of the buffer zone immediately adjacent to protected lands (Brückner et al. 2002, Jori et al. 2009). However, vaccination is expensive, cannot include all areas at risk of FMD transmission, and its efficacy varies with the virus' serotype (Thomson et al. 2003). Additionally, the fence is not a perfect barrier, as it is frequently damaged by people, elephants, floods and erosion (Ferguson and Hanks 2010), with approximately 110 breakage incidents recorded in the study area between 2007–2012. As a result, buffaloes regularly escape into communal areas, with 30–120 events per year involving up to several hundred buffaloes annually (Jori et al. 2009, van Schalkwyk et al. 2014). These escapes are the primary source of the approximately 60 FMD outbreaks recorded since 1970 in the Mpumalanga and Limpopo provinces bordering with KNP, with the most recent outbreak in 2015 (Mpumalanga Veterinary Services census data).

African buffalo behavior has been extensively studied within African protected areas (Sinclair 1977, Mloszewski 1983, Prins 1996, Kaszta et al. 2016). Several authors reported that buffalo space use patterns differ seasonally (Funston et al. 1994, Ryan et al. 2006, Kaszta et al. 2016). However, according to our knowledge, only van Schalkwyk et al. (2014) in South Africa and Caron et al. (2016) in Zimbabwe provide some, but yet very limited, information on buffalo behavior once they stray into communal lands.

Cattle in most of the communal areas neighbouring KNP are traditionally managed and semi-free ranging (Dion et al. 2011, Kaszta et al. 2017). The animals are herded during

diurnal hours away from the village to graze, returning in the evening to their 'kraal' (a local term for a livestock enclosure located within a village). Moyo et al. (2013) found that cattle ranging patterns in Zimbabwe vary throughout the year and Kaszta et al. (2017) found very strong seasonal differences in cattle resource selection in the South African FMD protection zone. Specifically, Kaszta et al. (2017) found that cattle in the wet season behave like a non-selective bulk grazers, whereas in the dry season they select forage of higher quality and quantity.

Several spatial models have been developed to predict FMD transmission in regions where this disease is not endemic, such as Australia, Europe and USA (Ferguson et al. 2001, Bates et al. 2003, Garner and Beckett 2005, Lawson and Zhou 2005). However, the mechanisms of FMD transmission in these regions are different from those in Africa. Apart from an agent-based model produced by Dion et al. (2011), models developed for Africa have not included the spatial dimension of FMD transmission (Sutmoller et al. 2000, Jori et al. 2009), which is necessary to identify areas of high potential risk of transmission. Although the mechanisms by which the disease spreads from buffalo to cattle in southern Africa are generally understood (Dawe et al. 1994, Miguel et al. 2013), there remains a strong need for rigorous spatially and temporally explicit models to delineate areas of high buffalo–cattle contact risk and to guide decision makers in targeting resources to locations most vulnerable to FMD transmission.

The development of robust spatially-explicit models of FMD transmission risk requires accurate predictions of cattle and buffalo movements, and estimation of contact probability across the landscape. Least-cost path analysis is a widely used way of modelling animals' movement routes (Adriaensen et al. 2003). However, the main disadvantage of this approach is that it assumes that dispersing animals have perfect knowledge of the landscape and make decisions to optimize movement to a certain a priori destination. This is not the case of buffalo or cattle movements, which would be better predicted as diffusive processes of cost-weighted random walks. It is also unrealistic to assume that animals will select a single pixel-wide optimum path. These limitations have been addressed with alternative approaches such as the circuit theory-based landscape connectivity (McRae and Beier 2007, McRae et al. 2008) and individual-based movement simulations (Hargrove et al. 2005, Dion et al. 2011). Their use, however, is limited by assumptions, data and computational requirements (Minor and Urban 2007). We therefore selected the cumulative resistant kernel approach (Compton et al. 2007) to model cattle dispersal and movement of buffaloes straying from protected areas into communal lands.

The advantage of the cumulative resistant kernel approach is that it does not assume a priori destination locations, but calculates an 'incidence function' of the expected relative density and frequency of movement through every pixel in the landscape. The resistant kernel

approach is also spatially synoptic, enabling the prediction of contact risk at every location (Cushman et al. 2014). It is explicitly driven by differential patterns of movement cost across the landscape, providing a high level of biological realism, and it takes into account both the distribution and density of the two target species and their dispersal abilities (Cushman and Landguth 2012). Lastly, resistant kernels are computationally more efficient than factorial least-cost path analysis (Cushman et al. 2013), agent-based modelling or circuit theoretic measures of current (McRae 2006), enabling fine-scale modelling across large geographic extents.

This study provides the first application of the cumulative resistant kernel method to calculate contact risk between two species. The approach estimates contact risk by intersecting the cumulative resistant kernel surfaces of buffaloes and cattle. This is a potentially powerful way of modelling probability of contact since it provides comprehensive information on the joint probability of both species occurring at the same place and time, as a function of their distribution, density, dispersal abilities and landscape resistance affecting movement.

The goal of this study was to improve knowledge of the FMD transmission risk by investigating seasonal differences and spatial pattern of buffalo–cattle contact risk. We hypothesised that the spatial patterns of contact risk will significantly differ between seasons as access to resources and their spatial patterns seasonally varies. Specifically, we hypothesised that in the dry season the contact risk between buffalo and cattle will be more intense and spatially concentrated, especially along the main river (southern part of the study area), which provides access to water and better quality fodder when resources are more limited. Furthermore, the fence along the main river is weak, and thus more permeable to movement of buffalo in this region of the study area.

Material and methods

Study area

The study area consists of approximately 256 km² and extends between 24.85–25.00°S and 31.35–31.52°E (corresponding to the scene of WorldView-2 image used for this study) in the low-lying savanna of north-eastern South Africa (Fig. 1). It encompasses three main land tenures: communal lands of Bushbuckridge (50% of the study area), the state-owned Kruger National Park (KNP; 14% of the study area) and the private Sabi Sands Wildtuin/Game Reserve (SSW; 36% of the study area). The protected areas are separated from neighbouring communal lands by a fence.

The topography is flat to gently undulating, with elevation ranging between 280 and 480 m a.s.l. Rains are confined to the summer (wet) season, from October to April (Venter et al. 2003). The total long-term annual average precipitation is 550 mm, and the mean annual temperature is 22°C. Kruger et al. (2002) found that the long-term rainfall and temperature average for Skukuza have remained fairly constant over the past 90 yr, but are characterized by high variability, with episodes of droughts and floods, which is typical to African savanna (Kruger et al. 2002).

The vegetation of the study area is largely influenced by the geological substrate (Venter et al. 2003). The ‘granite lowveld’ covers approximately half of the study area and is characterized by nutrient-poor soils with dense tickets and woody communities dominated by *Combretaceae* (Venter et al. 2003), with unpalatable and sparse grasses (Mucina and Rutherford 2006). In contrast, ‘gabbro grassy bushveld’, covering 20% of the study area (northern part), constitutes an open savanna characterized by fertile dark soils. Vegetation in those areas consists mainly of a dense cover of nutritious grasses, scattered shrubs and trees, primarily *Mimosaceae* (Mucina and Rutherford 2006). A comparison of land cover

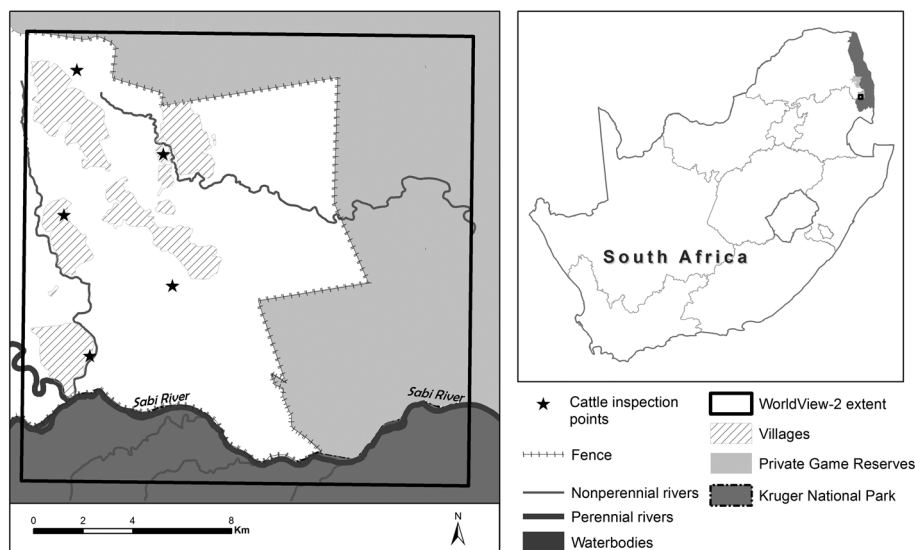


Figure 1. Study area adjacent to Kruger National Park and Sabi Sands Wildtuin, in northeast South Africa.

composition in communal lands and protected areas within the study area is presented in Supplementary material Appendix 1 Table A2 and Table A3.

Data and methods

Data analyses were conducted in five steps. First, we combined seasonal landscape resistance maps derived from buffalo resource utilization models (Kaszta et al. 2016) with a model predicting fence permeability (Kaszta et al. 2014). Second, to account for poor knowledge of buffalo behaviour outside protected areas, we considered two scenarios of buffalo dispersal: one assuming similar behaviours inside and outside the KNP and SSW, and another in which buffaloes change behaviour when entering communal lands. Third, we used landscape resistance maps based on cattle resource utilization models for the wet and dry seasons (Kaszta et al. 2017) to generate seasonal cumulative resistance maps of cattle dispersal in communal lands. Fourth, to minimize the effect of cost values on model performance, we incorporated three different scenarios of maximal resistance cost, and ran resistant kernel models to produce spatial incidence functions for cattle and buffaloes under each scenario (Table 1). Fifth, we intersected the final buffalo and cattle cumulative resistance kernel surfaces across all scenarios to predict the probability of interspecific contact between buffalo and cattle in wet and dry seasons.

Fence permeability model

To assess the cost of movement through the fence separating protected areas from communal lands we incorporated the model developed by Kaszta et al. (2014), who used a

generalized linear model (GLM), with logit link function, to predict probability of fence breakage. The predictor covariates included fence quality (electrified or not), presence of river crossings, and human pressure. We rescaled per-meter cost of movement to 7000 for the least permeable parts of the fence. This made the least permeable parts of the fence a complete barrier for a moving buffalo, while weaker parts of the fence functioned as partial barriers, with resistance inversely proportional to fence strength.

Buffalo resistance surface

We compared two scenarios of buffalo behaviour once they enter communal lands: 1) buffaloes behave in the same way outside and inside the protected areas, 2) buffaloes outside KNP and SSW changed behaviour as per the study undertaken by van Schalkwyk et al. (2014).

Scenario with consistent buffalo behaviour – to generate the surface of buffalo movement cost we used a buffalo resource utilization mixed-effect model developed by Kaszta et al. (2016), based on buffalo GPS locations in the southern part of KNP, about 40 km east from our study site. We modified this model to improve its robustness given model uncertainty. Kaszta et al. (2016) used buffalo kernel density generated by the plug-in method (Gitzen et al. 2006) as the response variable and N content of vegetation, vegetation biomass, type of vegetation as predictor variables (all derived from 5 m resolution layers, see Supplementary material Appendix 2 for data sources). We modified this model by including all possible interactions between continuous variables and linear and quadratic terms for N, biomass and altitude. We then used the ‘dredge’ function of the ‘MuMIn’

Table 1. List of the analysed contact risk scenarios.

	No.	Scenario	Acronym
Null models	1	Null model without fence in dry season	N-NF-D
	2	Null model without fence in wet season	N-NF-W
	3	Null model with fence in dry season	N-F-D
	4	Null model with fence in wet season	N-F-W
	5	Same buffalo behaviour, max resistance 50 dry season	SB-50-D
Same behaviour	6	Same buffalo behaviour, max resistance 50 wet season	SB-50-W
	7	Same buffalo behaviour, max resistance 100 dry season	SB-100-D
	8	Same buffalo behaviour, max resistance 100 wet season	SB-100-W
	9	Same buffalo behaviour, max resistance 200 dry season	SB-200-D
	10	Same buffalo behaviour, max resistance 200 wet season	SB-200-W
Different behaviour	11	Different buffalo behaviour, max resistance 50 dry season	DB-50-D
	12	Different buffalo behaviour, max resistance 50 wet season	DB-50-W
	13	Different buffalo behaviour, max resistance 100 dry season	DB-100-D
	14	Different buffalo behaviour, max resistance 100 wet season	DB-100-W
	15	Different buffalo behaviour, max resistance 200 dry season	DB-200-D
	16	Different buffalo behaviour, max resistance 200 wet season	DB-200-W

package of R (R Development Core Team) to compute possible models and compute model averaged coefficients based on corrected Akaike information criterion (AICc; Burnham and Anderson 2002, Zuur et al. 2009, Grueber et al. 2011). These changes improved AICc from 5989 in the Kaszta et al. (2016) model to AICc of 5871 in the modified model used in this paper, from which we produced the map of predicted buffalo utilization distribution in the study area.

To produce the cost surface of buffalo movement we inverted and rescaled this map, assigning high movement cost to pixels of lower utilization distribution, considering three scenarios of maximum resistance value (50, 100 or 200). The minimum cost was always equal 1.

There is no information in the literature about the effect of roads and settlements on African buffalo behaviour. Rost and Bailey (1979) have shown that elk *Cervus canadensis* and mule deer *Odocoileus hemionus* in Colorado, USA, prefer areas at least 200 m away from roads and Dyer et al. (2001) found out that the influence of roads on caribou *Rangifer tarandus* in open coniferous wetland in Canada waned at a distance of 250–500 m from main roads. Montgomery et al. (2012) also argued that not only the distance from a road is important but also the visibility from the road. Our studied landscape is dominated by rather open savanna, we specified a resistance due to roads that decreases linearly from the main roads to no additional effect at 500 m in ArcGIS 10.x (ESRI 2012).

Due to lack of information on how settlements affect buffalo behaviour, we adapted results from Cushman et al. (2010), who found that African elephants *Loxodonta africana* strongly avoided small settlements at distances of up to 1 km and larger villages up to 5 km. We modelled the buffalo resistance due to distance from settlements as a linearly decreasing function to a maximum of 2 km, given the expectation that buffalo may be somewhat more risk averse than elephants. The roads and settlement resistance layers were then rescaled between 1 and 50, 100 or 200, depending on the resistance surface scenario. We then summed the resistance surfaces generated from the resource utilization model and the settlements and roads cost distance layers, giving each of the latter two layers a weight of 0.25 – assuming that their influence on buffalo movement is less than their impact on resource utilization, following Mateo-Sánchez et al. 2015a, b. The final resistance surface was then rescaled between 1 and 50, 100 or 200.

Scenario with different buffalo behaviour in the communal lands – in this scenario we applied the final resistance layers generated in the previous section only to the protected areas. For the communal areas we produced a resistance surface based on the frequency of land cover classes where stray buffaloes were detected in communal lands (van Schalkwyk et al. 2014). Using compositional analyses (Aebischer et al. 1993), we produced an index of buffalo selection for each cover type and assessed the cost of buffalo movement for each class and each season, creating resistance surfaces with the maximum cost equal to 50, 100 and 200 respectively (Supplementary material Appendix 1 Table A1 and Table A8).

Cattle resistance surface

At the time of this study there were approximately 6100 head of cattle and 410 cattle owners in the study area (Mpumalanga Veterinary Services census data of 2013). The resistance surface for cattle movement was generated based on two cattle resource utilization mixed-effect models (for wet and dry season), developed by Kaszta et al. (2017). To enhance the robustness of the model we also included interactions between variables and quadratic terms. The final models (with lowest AICc value) included land cover type, vegetation N content, vegetation biomass, Euclidean distance to water and Euclidean distance to settlements as explanatory variables (all data were derived from 5 m resolution layers, see Supplementary material Appendix 1 Table A1 for data sources).

Null models

To compare differences between resistance scenarios and uniform patterns of landscape resistance we generated two null resistance surfaces. In the first null model, all pixels were assigned a resistance value 1; in the second null model, pixels representing fence had the resistance value predicted by the fence permeability model and all the remaining cells had resistance equal to 1.

Cumulative resistant kernel models

We selected buffalo and cattle source locations for resistant kernel analysis generated cattle source locations randomly within each of the five villages in the study area, at the density reported by the Mpumalanga Veterinary Services (number of cattle herds per village in the dry season 2012 and wet season 2013; Supplementary material Appendix 1 Table A4). We considered that the portion of KNP and SSW within the study area can host approximately three buffalo herds (L. van Schalkwyk pers. comm.) roaming across a wide area. Therefore, to represent the spatial pattern of buffalo use we generated 150 buffalo source points, located probabilistically with density and distribution reflecting the pattern of habitat suitability from the resource utilization function (Kaszta et al. 2016). Once cumulative resistant kernels were computed, we divided the predicted buffalo density values by 50 to represent the kernel density of three buffalo herds.

We used UNICOR (Landguth et al. 2012) with Gaussian distance decay function to compute the cumulative resistant kernel (Compton et al. 2007) maps separately for buffalo and cattle in each scenario representing different dispersal abilities and seasonality (high, middle, low resistance, across wet and dry seasons, Table 1). We calculated the resistant kernels for each source point with the maximum cost distance of 300 000. The values in the resulting surfaces, after summing the resistant kernels, represent the spatial incidence function reflecting expected density of buffalo and cattle, respectively at each pixel at any given moment in time. An example of cumulative resistant kernel surfaces for buffalo and cattle in one of the scenarios is presented in Fig. 2a, b.

To generate the final buffalo–cattle contact risk surfaces we multiplied the cumulative resistant kernel surfaces for buffalo and cattle to provide the synoptic likelihood of cattle

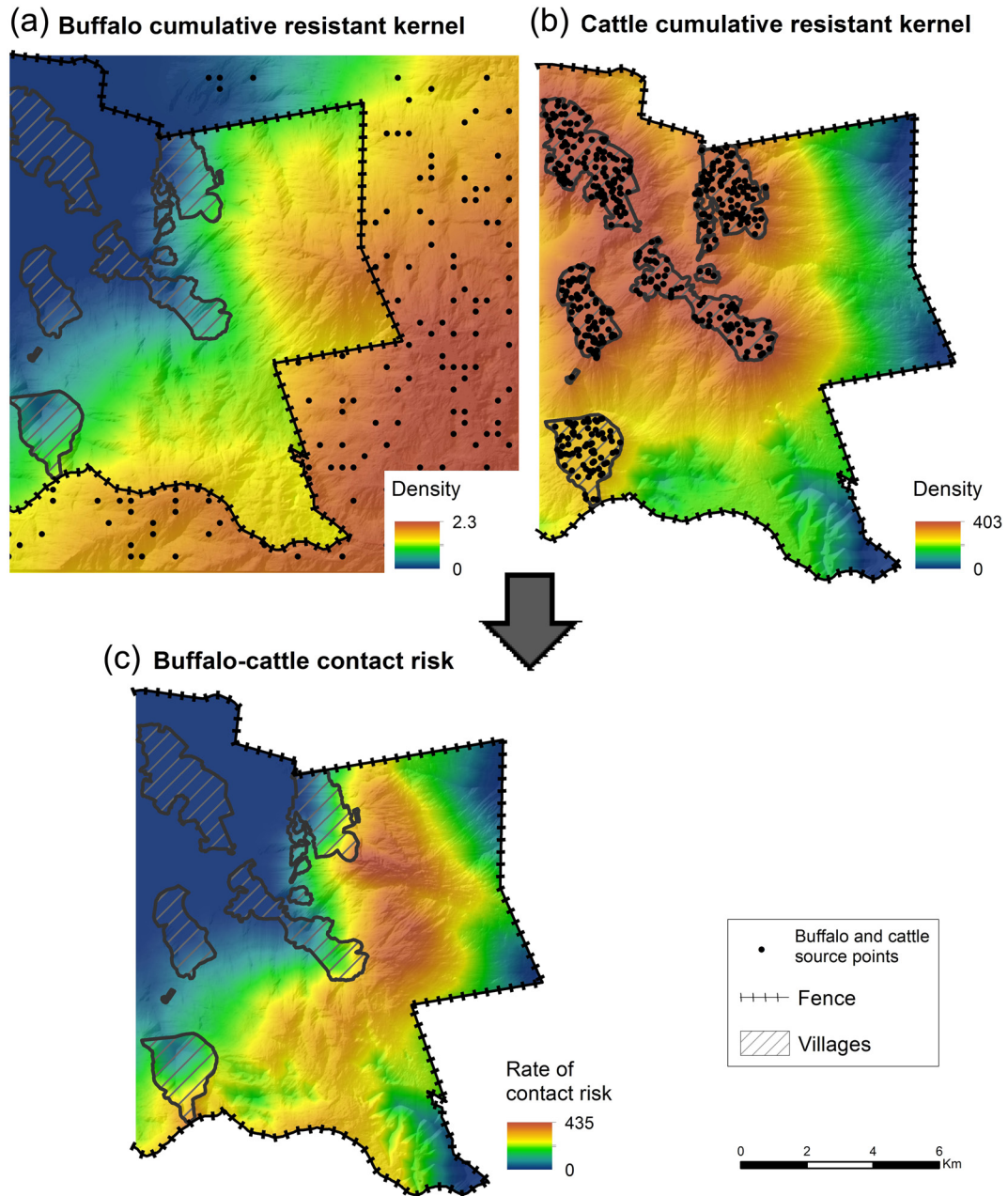


Figure 2. Example of buffalo–cattle contact risk map for the scenario with consistent buffalo behaviour inside and outside protected areas, maximum resistance of 100 and during wet season.

and buffalo being at the same locations in the landscape at the same time (Fig. 2c). We calculated average absolute difference between contact risk surfaces, and computed the correlation between the pixel values among contact risk surfaces. We then used simple and partial Mantel tests to determine what factor (season, dispersal ability, behaviour) had the largest influence on contact risk, based on the idea that factors having the largest relationship with contact risk would have significant Mantel correlations with difference between and correlation of contact risk surfaces, partialing out other factors.

Results

The resource utilization model indicated that buffalo select Tshokwane-Hlane Basalt Lowveld vegetation, with grasses of high nitrogen content, and avoid areas located far from water sources and with high vegetation biomass, primarily avoiding high tree and shrub cover (Supplementary material Appendix 1 Table A5). In contrast, the cattle resource utilization model found that cattle select vegetation of high biomass and quality only in the dry season (Supplementary material Appendix 1 Table A6 and Table A7). In both seasons, cattle prefer areas

covered by grass and trees, and close to water sources, avoiding recently burnt or shrubby patches.

While comparing the differences between contact risk scenarios, we found that there was a large difference in the magnitude of contact risk between null models and all other scenarios (Supplementary material Appendix 1 Table A8 and Supplementary material Appendix 2 Fig. A6), with null models predicting uniformly much higher contact risk across the study area. Furthermore, the difference in contact risk was also high between models with maximum resistance 50 and those with maximum resistance greater than 100. The difference however was low between models of consistent buffalo behaviour and models of different buffalo behaviour when maximum resistance is ≥ 100 . This indicates that dispersal ability (proxied by maximum resistance) has greater influence than other factors influencing contact risk, such as season and behaviour.

Null models including fence had high correlation with each other across seasons (Supplementary material Appendix 1 Table A8 and Supplementary material Appendix 2 Fig. A6). Correlations between null models with fence and null models without fence effect were substantially lower, showing effect of fence is substantial in the null models. Correlation between null models and other models was generally low, with many negative correlations, particularly for correlations between null models and dry season models with large maximum resistance. Among non-null models, all three factors of maximum resistance, behaviour and season affected the strength of the correlations. Correlations decreased when dispersal abilities were different between scenarios, and also were higher when models had the same season and same behaviour parameterization.

For difference between contact risk surfaces, the Mantel tests indicated that dispersal ability (proxied by maximum resistance value) was the most influential factor, and affected contact risk significantly and independently of both seasonality and behavioural parameterization (Table 2). In contrast, neither seasonality nor behaviour were significantly related to the difference between contact risk surfaces, and were not independent of dispersal ability. However, seasonality was the primary factor affecting the correlation between contact risk scenarios, with significant effects that were independent of both behaviour and dispersal ability.

Figure 3 presents a visual comparison of four scenarios for the wet and dry seasons: null models without the fence effect and models with different buffalo behaviour in and outside of protected areas accounting for medium dispersal (maximum landscape resistance of 100). These scenarios were chosen since they represent the central set of parameterization; all scenarios are presented in supplementary material (Supplementary material Appendix 2). The spatial pattern of contact risk in the null models did not differ substantially across seasons (see also Supplementary material Appendix 2 Fig. A1), or between the fence/no-fence null models (Supplementary material Appendix 2 Fig. A6). However, comparison of the null models with the scenarios of different buffalo behaviour and medium dispersal reveals important seasonal differences.

Table 2. Results of simple and partial Mantel test for correlation and differences between scenarios. Partial Mantel tests are indicated by variable 1 | variable 2, with the correlation with variable 2 partialled out of the correlation between variable 1 and contact risk.

Factor	Difference		Correlation	
	R	p-value	R	p-value
Season	0.10	0.28	0.43	0.008
Behaviour	0.07	0.47	0.03	0.71
Dispersal	-0.44	0.001	0.12	0.21
Season behaviour	0.11	0.22	0.44	0.006
Season dispersal	0.04	0.66	0.46	0.008
Behaviour season	0.08	0.42	0.09	0.34
Behaviour dispersal	0.004	0.97	0.05	0.59
Dispersal season	-0.43	0.001	0.21	0.05
Dispersal behaviour	-0.43	0.002	0.13	0.22

In the latter models, contact risk was substantially higher in dry season and mainly concentrated in the south, along the Sabi River, which is the only major river in the study area. In the wet season, however, the risk of contact was more widespread, but highest along the Sabi River and close to settlements. This seasonal pattern of contact risk is also visible in the prediction maps of all other scenarios (Supplementary material Appendix 2 Fig. A2–A5).

Discussion

Our findings demonstrate that, as hypothesized, there is a large seasonal difference in the risk of buffalo–cattle contact, with 41% higher average contact risk in the dry season across scenarios. Although we found that the magnitude of contact risk is highly affected by the dispersal abilities of buffalo and cattle, the spatial pattern of the contact risk is driven by seasonal differences in the animals' distributions and landscape resistance. Similarly, seasonal patterns of buffalo–cattle contact risk were also reported by Miguel et al. (2013) in Zimbabwe, suggesting that the distribution of contact risk is determined by resource availability.

Our results showed that high contact risk was localized along the main river (especially in the dry season) and the weakest parts of the perimeter fence. This pattern is likely driven by buffalo and cattle concentrating near permanent water sources in the dry season and by the attraction of crops. During the wet season our models revealed that the risk of contact is relatively greater near settlements than in the dry season, as there are no water limitations and the forage is generally of better quality, allowing buffaloes to disperse farther from the fence.

The southern part of the study area, near the Sabi River and directly neighbouring the Kruger National Park, showed the highest contact risk in both seasons, as it provides water

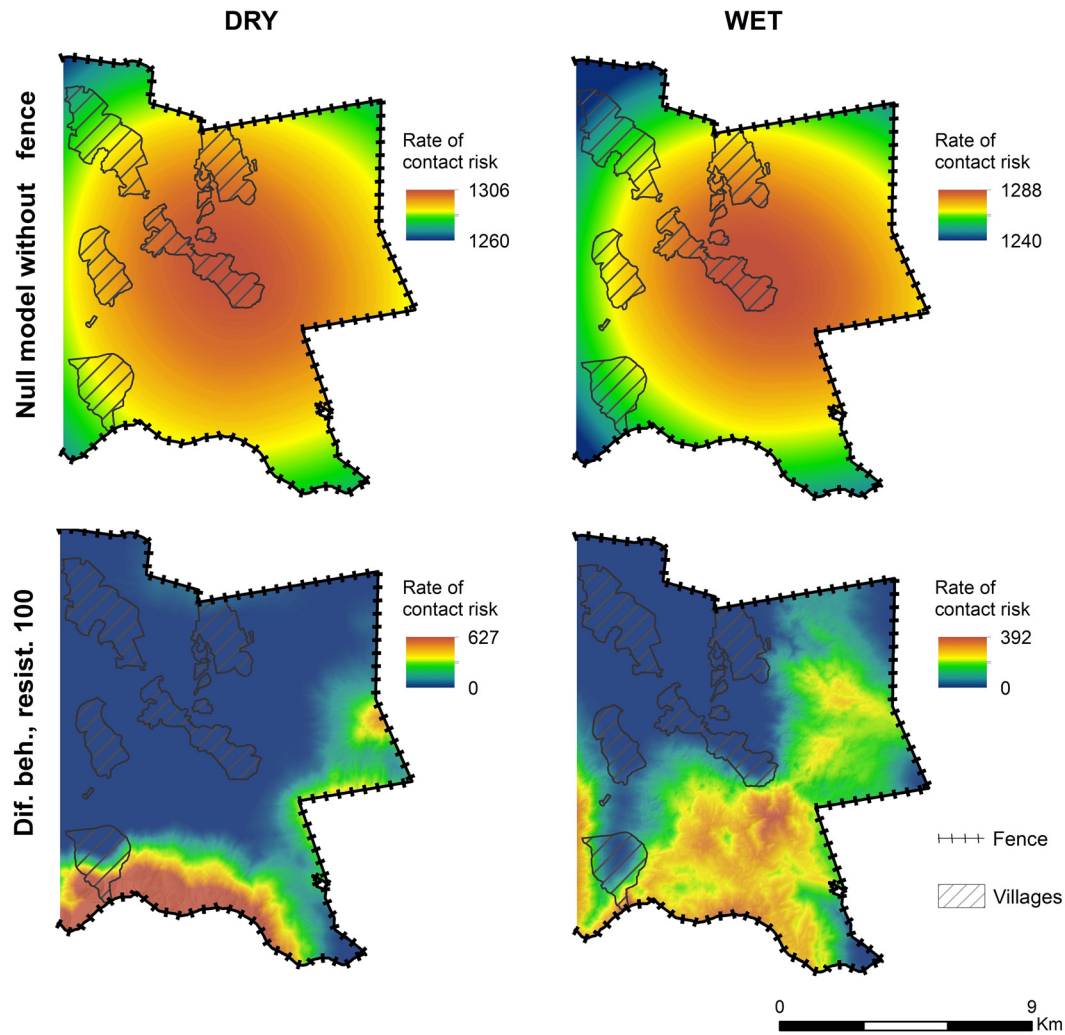


Figure 3. Comparison of four scenarios of buffalo–cattle contact risk representing the null models without the fence and models with central set of parameterization for the wet and dry seasons.

and high quality and quantity of forage for herbivores, as well as the weakest part of the fence. This pattern is also reflected in the map of buffalo–cattle contact risk for South Africa by Dion et al. (2011). However, contrary to our findings, Dion et al. (2011) predicted substantial risk of contact north of the settlements, where the fence is the strongest and vegetation overgrazed. This might be due to the differences in fence data used in both models. The Dion et al. (2011) model was based on fence breakage events from only one year (2007), whereas our fence permeability model incorporated an updated and more comprehensive dataset on fence quality and breakages collected over 7 yr. Furthermore, in contrast to the Dion et al. (2011) model, our model is based on high frequency buffalo GPS locations linked to fine-scale data on vegetation quality and quantity, which may provide more reliable prediction of buffalo distribution and movement patterns.

This study highlights the utility of resistant kernel modelling to evaluate interspecific interactions such as contact

risk. Intersecting cumulative resistant kernels of cattle and buffalo produced a spatially explicit and synoptic surface of contact risk, which is biologically appealing compared to the ‘salt and pepper’ patterns produced by agent-based models (Dion et al. 2011). Similarly, Cushman et al. (2014) found that resistant kernel modelling performed better than factorial least cost paths when predicting the locations of animals crossing highways, producing predictions with higher stability and robustness. The resistant kernel method has a number of additional advantages in the context of quantifying contact risk across the landscape, as opposed to predicting the locations of particular events, such as crossing of a highway. A least cost path analysis approach will predict the single lowest cost route among a priori defined sources and destinations (Cushman et al. 2009), whereas in the current analysis there are no meaningful destinations given that buffalo flow out of the park is a diffusive process governed by local landscape resistance. In addition, reliable quantification of contact risk requires assessment of the intersection of movement prob-

ability for all locations in the landscape (e.g. synoptic spatial incidence functions), not just the single least-cost routes between sources and destinations. The resistant kernel is an attractive approach for this task, given that it predicts the frequency or density of movement synoptically across the landscape as a function of cost-weighted flow from source locations, without the constraint of a priori destinations. It also provides a rigorous means to assess contact risk as the product of the density surfaces for each species.

The resistant kernel is also a simpler approach than complex multi-agent simulation, which relies on many dependencies and assumptions. For example, Dion et al. (2011) parameterised their model based on expert opinion on buffalo behaviour, whereas our resistance surfaces were developed through empirical analyses of fence permeability, and buffalo and cattle space use patterns across multiple seasons. It has been pointed out by several authors that the quality of input data has the biggest influence on the prediction of animal movement, and models relying on expert opinions may not accurately explain landscape effects on actual movement, as they reflect human rather than animal perception of habitat (Seoane et al. 2005, Theobald 2006, Beier et al. 2008, Shirk et al. 2010, Cushman et al. 2014). Furthermore, our approach enabled us to incorporate and evaluate the effect of uncertainty in dispersal abilities of both species. Given that dispersal ability and movement distances were not well resolved for either species, it was essential to evaluate the effect of different dispersal distances (Cushman et al. 2012, Riordan et al. 2016).

The absence of validation of the results of the modelling using independent field data on actual locations of buffalo–cattle contact is a limitation of this paper. Therefore, future work should focus on collecting extensive data on locations where buffalo and cattle come into close proximity, which would provide an independent data set to validate our predictions. We did not validate our models due to lack of reliable data on the initial location of FMD outbreaks or stray buffalo events in our study area. It is difficult to establish primary source locations of FMD outbreaks, and data on stray buffalo locations in communal lands are often not reliable, as buffaloes are usually chased by people, and the final location recorded by veterinary services does not correspond to the overall behaviour of the animal. Therefore, development of appropriate protocols to collect relevant field data on buffalo–cattle contact sightings, and/or FMD incidences in cattle herds should be prioritized.

An additional extension of this study could be a comparison of the results of buffalo–cattle contact risk in the study area generated by different modelling approaches, such as resistant kernels, least-cost-paths, circuit theory. An analysis such as this was done for American black bear *Ursus americanus* probability of crossing highways by Cushman et al. (2014) and quantified the relative performance of these methods. Conducting a multi-model evaluation of contact risk for buffalo and cattle would reveal the specific strengths and weaknesses of each modelling method, which in turn would clarify the interpretation of the predicted contact risk.

The maps produced by intersecting resistant kernels of two species provide spatially explicit and quantitative predictions of relative contact risk across the study area, which is the most important information needed to guide management actions and to provide explanations for complex interspecific relationships. In our study, the maps provide information which should prove useful in allocating resources for FMD mitigation efforts in the region (e.g. vaccination, fence maintenance, increasing people's awareness, more frequent patrolling and cattle inspection). For example, our results showed large seasonal differences in buffalo–cattle contact risk, which should be accounted for in future interventions. On the other hand, the southern part of the study area seems to be a permanent high contact risk zone, highlighting the importance of fence maintenance in this particular section.

Acknowledgements – This paper benefited from the comments and suggestions of Louis Van Schalkwyk and Ben Du Plessis. The authors also wish to thank South African National Parks, especially Sandra MacFadyen, Rheinhardt Scholtz and Izak Smith for the logistical support.

Funding – The authors wish to thank The Philippe Wiener – Maurice Anspach Foundation, the Belgian Science Policy (BELSPO) and A European and South African Partnership on Heritage and PastErasmus Mundus Programme for funding the study.

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Supplementary material (Appendix ECOG-03039 at <www.ecography.org/appendix/ecog-03039>). Appendix 1–2.