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The combined use of remote sensing and spatial modelling for animal movement - Application to the study of wildlife/livestock contacts and the risk of pathogen transmission in Southern Africa

Présentée par Florent RUMIANO

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**Sous la direction d'Annelise TRAN
et d'Alexandre CARON**

Devant le jury composé de

Présidente de jury

Emmanuelle GILOT-FROMONT, professeur, VetAgro SUP

Éric DAUDÉ, directeur de recherche, CNRS

Emmanuelle GILOT-FROMONT, professeur, VetAgro SUP

Annelise TRAN, directrice de recherche, CIRAD

Alexandre CARON, directeur de recherche, CIRAD

Eve MIGUEL, chargée de recherche, IRD

Edson GANDIWA, professeur, Zimbabwe Parks & Wildlife Management Authority

Jesse ABBATE, chargée de recherche, GEOMATYS

Nadine DESSAY, ingénieur de recherche, IRD

Rapporteur

Rapporteur

Directrice de thèse

Co-directeur de thèse

Encadrante de thèse

Membre du jury

Membre du jury

Membre du jury



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DE MONTPELLIER**

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« Ce n'est pas dans la science qu'est le bonheur, mais dans l'acquisition de la science »

Edgar Allan Poe

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Table of contents

“Remerciements”	i
Table of contents	ii
List of figures	ix
List of content	xiii
Acronyms	xiv
General abstract	xvii

Chapter 1: General introduction

1.1 The human/domestic animal/wildlife interface: places of interaction, places of emergence	2
1.1.1 Current trends (Anthropocene / Global changes) and wildlife-livestock interface	2
1.1.2 Ecological drivers of ungulates Wildlife-Livestock interactions in Africa	6
1.1.3 Anthropogenic drivers of Wildlife-Livestock interactions	8
1.1.4 The risk of pathogen transmission favored by the increase in contact between different animal species	10
1.2 Rural Zimbabwe, a land of contrasts and upheaval	12
1.2.1 History of biodiversity conservation and the relationship with wildlife in Zimbabwe (Pre-colonial and colonial periods)	12
1.2.2 Complex interactions between different actors in contemporary Zimbabwe. Social, economic, and political contexts (post-colonial period)	14
1.2.3 A changing climate that upset an already fragilized balance at the W/L interface	17
1.3 In a context of increased contact between wild and domestic animal species at interfaces: the choice of two focal species	19
1.3.1 The African buffalo (<i>Syncerus caffer</i>)	20
1.3.1.1 Intrinsic behaviors of one of the subspecies (<i>Syncerus caffer caffer</i>)	20
1.3.1.2 Direct links of the <i>Syncerus caffer caffer</i> with its immediate environment	23
1.3.2 Domesticated cattle (<i>Bos taurus</i> & <i>Bos indicus</i>)	25
1.3.2.1 Intrinsic behaviors of the species and its relations with the surrounding environments	25
1.3.2.3 A domestic animal species dependent on herders' decision rules	27
1.4 Research questions & objectives of the thesis	29
1.4.1 The origin of the thesis research's questions	29
1.4.2 Three main research questions	30
1.4.3 The structure of the manuscript	31

1.5 Chapter summary.....	33
---------------------------------	-----------

Chapter 2: Study sites and data used

2.0 Preamble.....	35
2.1 Three study sites, three W/L interfaces.....	35
2.1.1 The interface of Hwange/Dete.....	36
2.1.1.1 Geographical, climatic, vegetation and hydrology characteristics.....	36
2.1.1.2 Current ecological context.....	38
2.1.2 The interface of Gonarezhou/Malipati and Kruger/Pesvi.....	39
2.1.2.1 Geographical, climatic, vegetation and hydrology characteristics.....	39
2.1.2.2 Current ecological context.....	42
2.2 Data used in this thesis.....	43
2.2.1 Telemetry data.....	43
2.2.1.1 Capture of animals and installation of GPS collars.....	43
2.2.1.2 The utilization of pre-processed telemetry data.....	46
2.2.2 Remote sensing data.....	48
2.2.3 In-situ data and empirical knowledge.....	52
2.3 Chapter summary.....	53

Chapter 3: Literature review of the environmental drivers influencing the buffalo and cattle movements in space and time

3.0 Preamble.....	55
3.1 The article.....	56
3.1.1 Introduction.....	57
3.1.2 Review Article Methodology.....	58
3.1.3 Environmental Drivers Influencing the Movements of Buffalo and Cattle and the Satellite Remote Sensing Tools to Characterize them.....	60
3.1.4 Discussion.....	75
3.1.5 Conclusions.....	79
3.2 Chapter summary.....	96

Chapter 4: Characterization of the study sites' environmental variables via satellite remote sensing

4.0 Preamble.....	98
4.1 A three steps classification methodology.....	98
4.2 Characterizing the surface water.....	101
4.2.1 Methodological approach.....	101
4.2.2 Results and descriptions.....	103
4.3 Discriminating the agricultural areas.....	107
4.3.1 Methodological approach.....	107
4.3.2 Results and descriptions.....	108
4.4 Producing the final landcover maps.....	111
4.4.1 Methodological approach.....	111
4.4.2 Results and descriptions.....	112
4.5 Chapter summary.....	116

Chapter 5: A spatialized mechanistic animal movement model based on collective movements of self-propelled individuals

5.0 Preamble.....	118
5.1 Overview of the animal movement ecology.....	118
5.2 Mathematical models follow two paradigms.....	120
5.2.1 Statistical models.....	121
5.2.2 Mechanistic models.....	123
5.3 The choice of a mechanistic model based on collective movements of self-propelled individuals.....	124
5.3.1 The individual versus the collective.....	124
5.3.2 The synthesis of the two, when individuals influence the collective.....	126
5.4 Spatializing the model and combining it with SRS data.....	128
5.4.1 The notion of space in animal movement modelling.....	128
5.4.2 The language “Ocelet”.....	129

5.5 Chapter summary.....	131
---------------------------------	------------

Chapter 6: Combined use of remote sensing and spatial modelling: When surface water impacts buffalo (*Syncerus caffer caffer*) in savanna environments

6.0 Preamble.....	133
--------------------------	------------

6.1 The Article.....	134
-----------------------------	------------

6.1.1 Introduction.....	135
6.1.2 Material & method.....	135
6.1.3 Results.....	138
6.1.4 Discussion.....	139
6.1.5 Conclusion.....	140

6.2 Application of the buffalo movement model in two other W/L interfaces.....	143
---	------------

6.2.1 A movement model that also consider the landcover.....	143
6.2.2 Application in Gonarezhou/Malipati and Kruger/Pesvi.....	146

6.3 Chapter summary.....	149
---------------------------------	------------

Chapter 7: Spatial modelling of contacts between wildlife and livestock in Southern Africa

7.0 Preamble.....	152
--------------------------	------------

7.1 The article.....	152
-----------------------------	------------

7.1.1 Introduction.....	154
7.1.2 Method.....	155
7.1.3 Results.....	161
7.1.4 Discussion.....	164

7.2 Chapter summary.....	182
---------------------------------	------------

Chapter 8: General Discussions & perspectives

8.1 Summary of the objectives and findings.....	184
8.1.1 The global approach.....	184
8.1.2 From a thematical standpoint.....	185
8.1.3 From a methodological standpoint.....	186
8.2 Limits and recommendations.....	188
8.2.1 On the telemetry data used.....	188
8.2.2 On the remote sensing methodology to characterize the environmental data.....	189
8.2.3 On the mechanistic movement and contact model.....	191
8.2.4 On the movement and contact model ecological simulations.....	193
8.3 Future directions and perspectives.....	194
8.3.1 Combining methodologies and approaches to detect and characterize a wide array of environmental variables at multi-temporal and spatial scales.....	194
8.3.2 Improving the intrinsic robustness of the mechanistic movement and contact model.....	197
8.3.3 Enhancing the model's capacities to reproduce ecological processes.....	199
8.3.4 Adding an epidemiological compartment to the movement and contact model	201
8.3.5 Towards an "Eco Health" approach.....	202
8.4 A last word.....	205

Synthèse Générale de la thèse

9.1 Contexte général.....	208
9.2 Une thèse structurée en quatre temps.....	209
9.3 Approches méthodologiques.....	210
9.4 Principaux résultats.....	211
9.5 Éléments de discussion et perspectives.....	214

References.....	xix
List of poster, oral communications, publications, data produced and award.....	li

List of figures

Chapter 1

Figure 1.1 - This figure schematizes the wildlife-livestock-human interface and its different compartments (wildlife, peri-domestic wildlife, livestock, human societies) according to the transition from pristine natural ecosystem to highly human-modified landscape.....	5
Figure 1.2 - Figure summarizes the demographical, geographical and conservation states of Zimbabwe.....	17
Figure 1.3 - On the left, two buffalo (<i>Syncerus caffer caffer</i>) – photo taken by Ikiwaner. On the right, one nguni cattle (<i>Bos taurus</i>) specimen – photo taken by Bernhard Bekker.....	20
Figure 1.4 - Main taxonomy, physical, distribution and status, behavior, and ecology as well as reproduction and development characteristics of the buffalo.....	22
Figure 1.5 - Map representing the buffalo abundance across the African continent in 2010.....	23
Figure 1.6 - Main taxonomy, physical, distribution and status, behavior, and ecology as well as reproduction and development characteristics of the buffalo (<i>Bos taurus</i> & <i>Bos indicus</i>).....	26
Figure 1.7 - Map representing the cattle density in number of individuals across the African continent in 2010.....	27
Figure 1.8 - Diagrams showing the three main steps of the thesis.....	30

Chapter 2

Figure 2.1 - Location map of the three study sites (represented in red) and designated in relation to the proximity with their respective National Park.....	36
Figure 2.2 - Location map of the Hwange/Dete study site.....	38
Figure 2.3 - Location map of the Gonarezhou/Malipati study site.....	41
Figure 2.4 - Location map of the Kruger/Pesvi study site.....	41
Figure 2.5 - Spatialized localizations of the cattle and buffalo telemetry data for the entirety of their respective recorded periods at the three study areas.....	48
Figure 2.6 - Histograms representing the sum of annual precipitation and the maximum annual precipitation per year as well as the mean annual precipitation over the period 2000-2018 for all three study areas according to the TAMSAT V3.1 data.....	50

Chapter 3

Figure 3.1 - Environmental driver statistics of the step 1 bibliography.....	59
Figure 3.2 - Statistics and chronology of the article bibliography by topic category.....	60
Figure 3.3 - Illustrative examples of SRS-derived environmental drivers of buffalo and cattle movement in HNP, Zimbabwe.....	61
Figure 3.4 - Earth observation optical and radar satellites commissioning and time of service chronology.....	66
Figure 3.5 - Suitable SRS products for ecologists to characterize environmental drivers impacting animal movements in semi-arid savannas landscapes.....	78

Chapter 4

Figure 4.1 - Landcover classification general methodology.....	100
Figure 4.2 - Diagram describing the pre-classification, the classification and the post classification stages of the surface water supervised classification methodology.....	102
Figure 4.3 - Surface water classification results for the three study sites.....	104
Figure 4.4 - Temporal evolution of the monthly surface area of the surface water (in km ²) detected by the supervised classification for the three study sites.....	105
Figure 4.5 - Confusion matrices of supervised surface water classifications for the three study sites.....	106
Figure 4.6 - Diagram describing the pre-classification, the classification and the post classification stages of the agricultural area supervised classification methodology.....	108
Figure 4.7 - Maps of supervised water surface classification results for the three study sites.....	109
Figure 4.8 - Confusion matrices of supervised agricultural area classifications for the three study sites.....	110
Figure 4.9 - Diagram describing the pre-classification, the classification as well as the chosen vegetation typology of the vegetation unsupervised classification.....	112
Figure 4.10 - A) Maps of the three study sites landcover classifications. B) Percentage share of each landcover class relative to the total area of the landcover classification for each of the three study sites.....	113
Figure 4.11 - Confusion matrices of the unsupervised vegetation classifications for the three study sites.....	115

Chapter 5

Figure 5.1 - A) Diagram representing a general conceptual framework for movement ecology. B) Diagram representing the relationships the different compartments of the general conceptual framework for movement ecology.....	120
Figure 5.2 - Diagram representing the conceptual model in the simulation project life cycle.....	121
Figure 5.3 - Schematic diagram showing an practical example of different entities in interaction.....	130

Chapter 6

Figure 6.1 - Map of the study area and display of the data used in the study.....	136
Figure 6.2 - Flowchart combining remote sensing data with telemetry data to model the focal species movements.....	136
Figure 6.3 - Mean probabilities of the observed buffalo to be nearby surface water as a function of the time of the day, superimposed to the median speed of the observed buffalo, the median interdistance and the phi values.....	137
Figure 6.4 - Kappa index and overall accuracy (OA) of water classification along to the year for the two Sentinel-2 tiles.....	138
Figure 6.5 - Observed and simulated herd' centroids trajectories comparison for a period of one month.....	139
Figure 6.6 - A) Difference of density map between observed and simulated herd's centroids trajectories. B) Graph representing the distributions of pixel values in the simulated and observed median density raster.....	139
Figure 6.7 - A) Medium speed of buffalo in relation to the probability to be at proximity of the surface water depending on the hour of the day. B) Probability for buffalo to be on a specific landcover in regard to the entire duration of the telemetry data recording period for each of the study sites.....	144
Figure 6.8 - Evolution of the buffalo movement model. The later transitioned from a movement model considering surface water only with two behavioral phases to a movement model considering surface water as well as landcover with five behavioral phases.....	145
Figure 6.9 - A) Maps of the buffalo herd centroids observed and simulated trajectories at the Kruger/Pesvi study site, for one iteration (concerning the simulations) over a period of 15 days. B) Heat maps of density differences (simulated/observed).....	147

Chapter 7

Figure 7.1 - Location maps of the three study areas. Only the contact areas between buffalo and cattle are represented.....	155
Figure 7.2 - Classification general process.....	157
Figure 7.3 - Diagram representing the designed behavioral chronologies of the two focal species movement models as well as their respective landcover and surface water selection processes.....	160
Figure 7.4 - Maps representing the observed and simulated contact area spatial extensions in regard to the proximity of the communal area for the three study sites.....	162
Figure 7.5 - A) Line chart representing the monthly variations of the mean density for the observed contact area and the simulated contact areas. B) On the right, line chart representing the monthly variations of the sum density for the observed contact area and the simulated contact areas.....	163

Chapter 8

Figure 8.1 - Figure synthetizing the thesis's general approach.....	185
Figure 8.2 - Schematic of an idealized uncertainty and sensitivity analysis.....	197

Chapter 9

Figure 9.1 - Figure synthétisant l'approche générale de la thèse.....	210
--	-----

List of tables

Chapter 2

Table 2.1 - Details of the buffalo telemetry data used in this thesis.....	45
Table 2.2 - Details of the cattle telemetry data used in this thesis.....	46
Table 2.3 - Summary of the different Sentinel-2 tiles characteristics used in the thesis to produce the land use maps and the surface water classifications.....	51

Chapter 3

Table 3.1 - Small subset of Earth observation satellite systems allowing data acquisition that can potentially be used in the field of animal movement ecology.....	62
Table 3.2 - List of satellite remote sensing-based landcover products.....	64
Table 3.3 - Non-exhaustive list of spectral remote sensing indexes developed to discriminate vegetation and soil from optical satellite image analysis and that can be useful within the frame of animal movement studies in savanna environments.....	66
Table 3.4 - Non-exhaustive list of spectral remote sensing indexes developed to discriminate water surfaces from optical satellite image analysis and that can be useful within the frame of animal movement studies in savanna environments.....	68
Table 3.5 - Non-exhaustive list of remote sensing-based water products.....	70
Table 3.6 - Non-exhaustive list of satellite remote sensing-based fire products.....	71
Table 3.7 - Non-exhaustive list of spectral remote sensing indexes developed to discriminate fire from optical satellite image analysis and that can be useful within the frame of animal movement studies in savanna environments.....	72
Table 3.8 - Non-exhaustive list of available satellite-based precipitation products.....	74

Chapter 6

Table 6.1 - Model parameters estimated from telemetry data (*), expert knowledge (**), or calibration (***).....	138
Table 6.2 - Table that present the results of the Spearman correlation tests for the "water" and "water/ landcover" models.....	148

Chapter 7

Table 7.1 - Model parameters estimated from telemetry data (*), expert knowledge (**), or calibration (***).....	159
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Acronyms

ABMs	Agent-based models
ACP	African, Caribbean and Pacific
ANN	Artificial neural network
ANR	French National Research Agency
AVEDs	Animal-borne video and environmental data collection systems
CAMPFIRE	Communal Areas Management Program for Indigenous Resources
CART	Classification and regression tree
CIRAD	French Agricultural Research Centre for International Development
CL	Communal lands
DSL	Several domain specific languages
ESA	European Space Agency
EVI	Enhanced Vegetation Index
FAO	Food and Agriculture Organization of the United Nations
FMD	Foot-and-mouth disease
GAM	Generalized additive model
GDP	Gross Domestic Product
GIS	Geographic information systems
GL-TFCA	Great Limpopo TransFrontier Conservation Areas
GLM	Generalized linear model
GNP	Gonarezhou National Park
GPS	global positioning system
HMMs	Hidden Markov model
HNP	Hwange National Park
HWC	Human-wildlife conflicts
IBMs	Individual based models
IRD	French National Research Institute for Sustainable Development
IUCN	International Union for Conservation of Nature
KAZA-TFCA	KAvango – Zambezi TransFrontier Conservation Areas
KL	Kullback–Leibler
KNP	National Park
MCP	Maximum convex polygons

MNDWI Modified normalized difference water index
MODIS Moderate-Resolution Imaging Spectroradiometer
NASA National Aeronautics and Space Administration
NCAS National Centre for Atmospheric Science
NCEO National Centre for Earth Observation
NDVI Normalized Difference Vegetation Index
NDWI Normalized difference water index
NOAA National Oceanic Atmospheric Administration
NPWLMA National Parks and Wildlife Management Authority
OA Overall accuracy
ODD Overview, design concepts, and details
OSAVI Soil Adjusted Vegetation Index
PA Protected areas
RF Random Forest
RMSE Root mean square error
RP-PCP Research Platform – Production and Conservation in Partnership
RSF Resource selection function
RVF Rift Valley Fever
SACD Southern African Development Community
SAR Synthetic aperture radar
SARS-CoV-2 Severe acute respiratory syndrome coronavirus 2
SDEs Stochastic differential equations
SFA Sikumi Forest Area
SFR Sikumi forest reserve
SPP Self-propelled particle
SRS Satellite remote sensing
SSF Step selection function
SSM Step-space model
SWIR Short-wave Infrared
TAMSAT Tropical Applications of Meteorology using SATellite data and ground-based observations
TEMPO TELétection et Modélisation sPatiale pour la mObilité animale
TETIS Territoires, environnement, télédétection et information spatiale
TFCAs TransFrontier Conservation Areas

TIR Thermal Infrared
UAS Unmanned Aircraft System
UHF Ultra-high frequency
VNIR Visible Near Infrared
W/L Wildlife/livestock
WLI Wildlife-livestock interfaces

General abstract

In Southern Africa, human populations living in communal lands located at the edge of protected areas have significantly increased in recent years (Cleland and Machiyama, 2017; George Wittemyer et al., 2008). This burst in human population increases contacts between wildlife, people, and their livestock in areas where they have to coexist (Bengis et al., 2002; De Garine-Wichatitsky et al., 2013). As a result, interface areas face a growing number of human/wildlife coexistence related issues (J. Andersson et al., 2017) and among them, the risk of pathogen transmission between wild and domesticated species (Caron et al., 2013; Miguel et al., 2013; Olival et al., 2013). During the last decade or so, the number of emerging or re-emerging human diseases has significantly increased, and of these, 75% have a zoonotic origin. Ungulates have a particular proximity to humans and are considered as one of the main groups of species responsible for zoonotic diseases (Caron et al., 2013). Spatial proximity between populations has been clearly identified as one of the crucial risk factors in the transmission between species (Roche et al., 2012). However, the nature, frequency, and localization of these contacts between wild and domesticated ungulates remain largely unknown.

In this context, the present thesis, which is part of the TEMPO (TElédétection et Modélisation sPatiale pour la mObilité animale) project, aims to 1) Characterize the environmental variables, at a landscape scale, that potentially influence the movements of one wild ungulates species (the buffalo – *Syncerus caffer caffer*) and one domesticated ungulates species (the cattle – *Bos taurus* & *Bos indicus*) at three different interfaces located in Southern Africa (Hwange National park, Gonarezhou National Park, North Kruger National Park), 2) Develop a mechanistic model to simulate the movements of the two focal species, at the individual and herd scales, in relation with the surface water seasonality and the type of landcover representative of their respective environments, 3) Determine the nature, frequency and localization of the contacts between the two focal species and the role played by environmental variables and herder behaviours, in this instance, by combining the developed mechanistic movement models to apprehend the risks of pathogen transmission.

The environmental variables have been characterized at the landscape scale using supervised and non-supervised classifications on a temporal series of Sentinel-2 satellite images to produce monthly surface water maps and one landcover map with a 7 elements typology at 10 meters spatial resolution for each of the three study sites. These environmental variables have then been

integrated into a spatialized mechanistic movement model based on a collective motion of self-propelled individuals (Grégoire & Chaté, 2004) to simulate buffalo and cattle movements and contacts in response to the surface water seasonality and the type of landcover. To spatialize the movements and contacts models, the domain specific language Ocelet has been used (Degenne & Lo Seen, 2016b). Telemetry data collected at the three study areas in previous studies (Miguel, 2012; Valls Fox, 2015) have been used as reference data to design, calibrate and validate the movement and contact models.

Sentinel-2 classification results highlighted strong space and time variabilities of water availability in the three study areas. The landcover classified maps accurately reproduced the specificities in landscape compositions of the three study areas, thus reinforcing the relevance of a comparative analysis of the developed site's specific movements and contacts models. By only taking surface water into account, the mechanistic movement models showed a positive and significant correlation between observations/simulations movements and space-use of buffalo's and cattle herds despite overestimating the presence of buffalo individuals at proximity of the surface water. Contacts patterns and their accuracies differed according to the study area. The quantity and quality of available environmental data (i.e., surface water and landcover), especially the anthropogenic water sources located in communal areas, strongly impacted the models' ability to accurately reproduce the contacts observed through the collected telemetry data.

It is clear, however, that combining remote sensing and spatial modelling offers possibilities to develop simple models to simulate animal movements and contacts in direct relation with the environment with only few parameters to be efficient. These models can integrate heterogeneous spatial data while being scalable, making dynamic observations at different spatiotemporal scales possible and reproducible in other ecological contexts with different focal species. The potential for the integration of an epidemiological model into a spatialized animal movement model in direct relation with the environmental variables to understand the risk of pathogen transmission is there. However, it needs to be further developed, tested, and studied to be fully operational and potentially be used and integrated into an "EcoHealth" approach (Charron, 2012).

Chapter 1

General introduction

Table of content

1.1 The human/domestic animal/wildlife interface: places of interaction, places of emergence

- 1.1.1 Current trends (Anthropocene / Global changes) and wildlife-livestock interface
- 1.1.2 Ecological drivers of ungulates Wildlife-Livestock interactions in Africa
- 1.1.3 Anthropogenic drivers of Wildlife-livestock interactions
- 1.1.4 The risk of pathogen transmission favored by the increase in contact between different animal species

1.2 Rural Zimbabwe, a land of contrasts and upheaval

- 1.2.1 History of biodiversity conservation and the relationship with wildlife in Zimbabwe (Pre-colonial and colonial periods)
- 1.2.2 Complex interactions between different actors in contemporary Zimbabwe. Social, economic, and political contexts (post-colonial period)
- 1.2.3 A changing climate that upset an already fragilized balance at the W/L interface

1.3 In a context of increased contact between wild and domesticated animal species at interfaces: the choice of two focal species

- 1.3.1 The African buffalo (*Syncerus caffer*)
 - 1.3.1.1 *Intrinsic behaviors of one of the subspecies (Syncerus caffer caffer)*
 - 1.3.1.2 *Direct links of the Syncerus caffer caffer with its immediate environment*
- 1.3.2 Domesticated cattle (*Bos taurus* & *Bos indicus*)
 - 1.3.2.1 *Intrinsic behaviors of the species and its relations with the surrounding environments*
 - 1.3.2.2 *A domestic animal species dependent on herders' decision rules*

1.4 Research questions & objectives of the thesis

- 1.4.1 The origin of the thesis research's questions
- 1.4.2 Three main research questions compose this thesis
- 1.4.3 The structure of the manuscript

1.5 Chapter summary

1.1 The human/domestic animal/wildlife interface: places of interaction, places of emergence

1.1.1 Current trends (Anthropocene / Global changes) and wildlife-livestock interface

The world's population has grown steadily since the appearance of *Homo sapiens* and which, despite some irregularities over the ages, now exceeds seven and a half billion people (UN - World Population Prospects 2019). Population growth was particularly rapid during the 20th and the 21st centuries, even if the global rate of population growth is starting to decline. As a result, human activities engendered an exponential expansion of human settlements and associated activities that have drastically altered wild habitats, threatened biodiversity and provoked profound modifications to interfaces among animals and humans (Vicente et al., 2021). 1000 years ago, less than 4% of the world's ice-free and non-barren land area was used for farming (E. C. Ellis et al., 2010). Today, in comparison, half of what is considered habitable area (70% of the global land area) is used for agriculture and livestock farming purposes (FAO, 2021).

The removal of primary vegetation, as concomitant consequence of land transformation by human activities (anthropization), impacted wildlife abundance, distribution, and behavior. In parallel and since pre-industrial times, the number of livestock husbandry practices have been increasing and have directly determined wildlife-livestock interface organizations and structuration (Ottichilo et al., 2000). Currently, wildlife is becoming less abundant, and populations are more fragmented and isolated (Kaplan et al., 2009). For most large mammals, the cumulative impact of human activities on the environment has driven most species into severe declines and regional extinctions, a trend that is currently undergoing for many of the planet's animal species (Ripple et al., 2015).

Globalization has resulted in the multiplication of trade in livestock, other animals and their associated products (e.g., ivory for the use of traditional medicine), the relocation of farming centers, industrialization and uniformization of farming process, and unprecedented speed, volume, and reach of global exchanges of goods, knowledge and people (Vicente et al., 2021). The so-called “Livestock Revolution” initiated in the 1970s, in response to world population increase, urbanization, higher incomes, and demand for animal products expanded rapidly to

developing countries. The world's meat production nearly doubled from 1980 to 2004 (FAO 2006). This revolution implied a progressive replacement of traditional farming systems by intensive ones. In these intensive farming systems, large numbers of genotypically similar animals are bred under concentrated confinement with rapid population turnover (Pearson, 2005), which raises environmental concerns due to the large amount of waste, gas emissions, elevated need for feed (e.g., soy) and biodiversity loss (both vegetal and animal). In low-income country rural areas, the proximity of increasingly concentrated smallholder farming communities to intensified, industrial farming systems is growing as their respective land is degrading in quality (e.g., fertility) and in quantity (e.g., surface area) (Barbier & Hochard, 2018). Today, diverse types of production farming, ranging from free-range to outdoor paddocks and finally, intensive farming, are ecologically and epidemiologically connected (Vicente et al., 2021). As human societies need to adapt continuously to the changing environmental, climatic, social, economic, market and trade conditions, farmers expand cultivated areas, encroach natural areas, intensify production and close integration of crops and livestock (C. A. Jones & Sands, 2013), often in proximity to wildlife. In Africa for example, the pressures induced by human activities such as progressive intensification of agriculture and the concomitant ecological fragmentation of natural habitats, the hunting and the consumption of bush meat, the capture of wildlife that is shipped to live animal markets (e.g., wet markets), and the farming of game animals in proximity to traditional livestock and humans, have had important consequences on the pattern of contacts between wild and domestic species at the landscape scale (e.g., the link between deforestation and Ebola outbreaks that has been observed in West and Central Africa (Rulli et al., 2017). Agricultural intensification and ecological fragmentation also have a negative effect on biodiversity, modifying the diversity of interactions between organisms (e.g., Lyme disease) (Wood & Lafferty, 2013). Moreover, these changes have been implicated as drivers of some recent emerging disease events that had important impacts on human livelihoods and health at global, regional and local scales (Allen et al., 2017; K. E. Jones et al., 2008).

The subsequent alteration in habitats, changes in host communities, diversity, and functional interactions are increasing the potentiality of contact rates and, as a result, the susceptibility, and/or exposure of pathogens. Adding these trends to the effects of the globalization (i.e., growing worldwide human population, global trade, and ease of travel) and the need to assess the complex and constantly evolving mechanisms of wildlife, livestock, and humans' interactions at different spatial and temporal scales has never been so vital. Wildlife/livestock (W/L) interfaces concentrate many challenges in coherent spaces that also operate on much larger scales. In this instance, W/L interfaces are in the "front line" and give the tempo of the

global changes that are currently taking place everywhere on the globe with different frequency and intensity.

The W/L interface concerns areas of smaller spatial and more fragmented scales which, when considered as a whole, potentially covers vast territories. Indeed, W/L interfaces have evolved in terms of spatial extent and complexity, shifting from a few centers of domestication amongst pristine natural habitats to a world dominated by humans and their domestic species pressuring the remaining patches of natural habitats (Caron et al., 2021). Currently, the W/L interface is considered as the physical space in which wild and livestock species overlap in range and potentially interact (Huyvaert et al., 2018). In turn, W/L interfaces are reciprocally structured and shaped by interactions and contacts occurring within their delineations. Contacts and interactions can be continuous or discontinuous in time and direct or indirect in space. For example, indirect contacts can occur through the exposure of aerosols, feces, urine, saliva or nasal discharge as well as through natural reservoirs such as soil, water or forage. The W/L interface spatial and temporal organizations are subject to changes, changes that are closely related and function of landscape structuration and composition, climate variables (e.g., precipitation, temperature) as well as human interventions (Jori et al., 2019). Indeed, the W/L interface is the result of complex interactions between natural ecosystems within which livestock production takes place (Ostrom, 2009). It cannot be envisioned and apprehended without considering the human socioeconomic systems and their relative influences on natural ecosystems. Therefore, the W/L interface should be thought of as the wildlife-livestock-human interface because the focus is on the interaction between “natural” and “human-influenced” sub-systems (Caron et al., 2021). The W/L interface concept implies to step away from a conventional line of thought in which conservation and human activities are represented by separate, competing sectors of society. The W/L interface concept supposes integrated approaches at the landscape scale (Sayer et al., 2013) with local citizens empowered to benefit from wildlife and livestock together while enhancing the resilience and virtue of entire social-ecological systems (Biggs et al., 2012; Ostrom, 2009).

The W/L interface is constituted of four main component compartments of the biosphere ([Figure 1.1](#)): wildlife and peri-domestic wildlife, livestock, human societies that are all localized in the anthropized area of interfaces. All these compartments are in constant interaction with each other within a fluctuating environmental gradient that strongly influences the ecological and epidemiological dynamics of these interfaces. Four indicative gradients can be considered when taking into account the human interactions perspective: i) “pristine” ecosystems with human incursion to harvest wildlife and other resources; ii) ecotones and fragmentation of natural ecosystems (farming edges, human incursion to harvest natural resources, i.e., wood);

iii) evolving landscapes characterized by rapid intensification of agriculture and livestock, alongside extensive and backyard farming; and iv) managed landscapes that consist of islands of intensive farming, highly regulated, and farmland converted to recreational and conservancy uses (C. A. Jones & Sands, 2013).

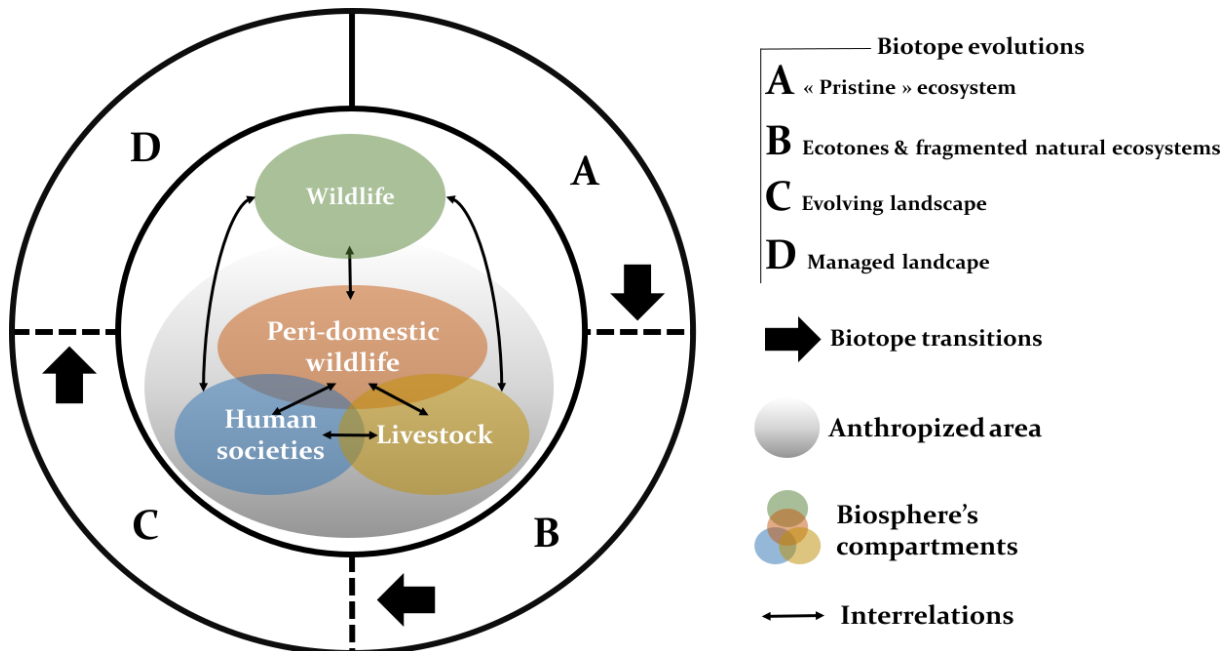


Figure 1.1: This figure schematizes the wildlife-livestock-human interface and its different compartments (wildlife, peri-domestic wildlife, livestock, human societies) according to the transition from pristine natural ecosystem to highly human-modified landscape (based on Jones et al. 2013).

Due to the constant interactions of these different compartments, the W/L interface has a proper ecosystem that can potentially impact multiple sectors and levels of a given territory (Vercauteren et al., 2021). For instance, when located at boundaries between land uses with different management objectives, W/L interactions can impact every land use management and compromise their development objectives. Here lies potential conflict between protected areas managers who aim to conserve biodiversity and its ecological functions and communal areas stakeholders dedicated to agricultural activities to produce food and economic benefits (Caron et al., 2021). Such conflicts can take many forms: for example in Africa, crop raiding by elephants or predation of livestock by wild carnivores (Kuiper et al., 2015a; Lamarque et al., 2009), illegal use of natural resources and/or mismanagement of plant successions and soil fertility in grazing ecosystems (P. Lindsey et al., 2015) or disease transmission (Caron, Miguel, Gomo, Makaya, Pfukenyi, Foggin, Hove, & de Garine-Wichatitsky, 2013). These conflicts possibly stimulate human intervention as local people living in interaction with wildlife have different positive and negative representations of wild animals, associated with their cultural and individual experience (Guerbois et al., 2012). This interplay of ecological and human factors (socioeconomic and anthropogenic), reinforced by livestock and wildlife share and/or

competition for natural resources (e.g., water, forage, cover), increase opportunities for pathogen transmission (Vicente & VerCauteren, 2019). Even if consequences of W/L interactions depend on the composition and structuration of ecological communities at the W/L interface, cascading effects on community composition, trophic relationships, and pathogen dynamics are increasingly recognized (Becker et al., 2015; De Vos et al., 2016; Ostfeld, 2009). These issues are directly impacting wildlife, livestock, and human health, requesting a better understanding of the holistic functioning of these W/L interfaces. It is particularly true for the ungulates Wildlife-Livestock interactions in Africa.

1.1.2 Ecological drivers of ungulates Wildlife-Livestock interactions in Africa

The African continent needs to reconcile the exponential growth of its human populations and the preservation of its conservation areas in the years to come (Chape et al., 2005; Wittemyer et al., 2008a). Sub-Saharan Africa's population was 1.14 billion in 2020 (World Bank) and could reach 2.12 billion by 2050 (Ezeh et al., 2020). Africa is a continent where more than 4 million km² of land is protected (Chape et al., 2005) and where a wide diversity of large herbivores and large carnivores still exist (Fritz, De Garine-Wichatitsky, et al., 1996; Fritz & Loison, 2006). It is also a continent where competition for space is frequently accompanied by habitat fragmentation. Indeed, the strong growth of cultivated areas, the intensification of livestock activities and the expansion of urban areas are exacerbating pressures on W/L interfaces located at the periphery of protected areas (Craigie et al., 2010). Combined with the consequences of climate change, which are projected to intensify in the years to come (WMO, 2020), this anthropogenic pressure poses a significant threat to the sustainability of African ecosystems and particularly at the W/L interfaces (Vicente et al., 2021).

Many interfaces, interactions occur in the context of anthropized resources (e.g., plantations ecosystems), natural resources (e.g., wildlife) and a mix between natural and anthropized resources. In African W/L interfaces, natural resource preference can be considered as one of the key predictors of W/L interactions. Domestic and wild herbivores, for example, have a phylogenetic proximity that induced similar resource requirements and thus, potential resource competition. Even if dietary niche partitioning can condition resource competition between animal species, large herbivores consume several shared forage resources. Indeed, most of the literature provides evidence for potential competition via dietary overlap (Breebaart et al., 2002) and emphasizes that dietary overlap is greater for animal species with similar body size (e.g., gut

capacity, bite size, food intake rate, and feeding site selection) (Kartzinel et al., 2015). Domestic animal species such as cattle, for instance, are more likely to compete with similar size ruminant grazers such as African buffalo than browsers (e.g., kudu), non-ruminant grazers (e.g., wildebeest), very large herbivores (e.g., elephant), or small herbivores (e.g., duikers). However, empirical studies on foraging between herbivores of different body sizes, and the nature of the interspecific interactions between these herbivores does not always match theoretical expectations (Stears & Shrader, 2020). Larger grazers can compete with smaller grazers by reducing food availability, especially during the dry season in tropical areas (Arsenault & Owen-Smith, 2002), or through more long-term negative effects via habitat modification (Prins, 2000). Conversely, small herbivores can potentially outcompete larger herbivores by reducing the availability of high-quality forage in areas where resources can be scarce according to season (Illius & Gordon, 1987). If competition influences W/L interactions, facilitation can also play a role in mechanisms that may increase or decrease the likelihood of direct or indirect interactions. Some wildlife species such as the wildebeest can select areas grazed by livestock contrary to the buffalo that tend to avoid such areas (Tyrrell et al., 2017a). Facilitation may lead animal species to share forage patches and use these patches successively to allow post-grazing regeneration (Odadi et al., 2011a) or high-quality grass regrowth thus positively easing forage accessibility for smaller grazers (Western & Gichohi, 1993).

When natural resources (e.g., pasture, surface water) are abundant and widely distributed, free ranging wild animals tend to avoid areas frequented by livestock due to direct competition, as described above, or simply because of fear of humans (Connolly et al., 2021; Riginos et al., 2012). However, the behavioral response by wildlife to the proximity of strongly anthropized areas differs according to animal species and locations. In savanna W/L interfaces found in Zimbabwe for instance, African buffalo completely avoid communal areas whereas elephants sometimes enter these territories for crop raiding (Guerbois et al., 2012). These differences in behavior imply a diversity in frequency, temporality, and location of interactions between wildlife and livestock. On the contrary, when natural resources are limited, localized areas where resources can be found become potentially favorable to the aggregation of many animal species. In arid and semi-arid areas, animal species spatial distribution is constraint by the location and availability of this natural resource (Ogutu, Reid, et al., 2014). Seasonal variability encourages resource-driven patterns and intensify potential interactions when the resource becomes scarce due to the limited distance that animal species can travel and therefore, their ability to reach other resource points potentially still available (Valls-Fox et al., 2018). However, this analysis must be nuanced. When natural resources are sparsely distributed, animal species or group of animal species that have a limited movement radius around their core home range can use different resource points that are too far apart for them to interact (Borchering et al., 2017).

Furthermore, as natural resource density potentially increases, animal species can adopt flexible behavior and decide to avoid interactions.

Predation also potentially impacts animal species interactions at W/L interfaces as it is likely to affect habitat use of certain species, notably herbivores (Valeix et al., 2009), as well as the benefit/risk for livestock owners to conduct their herd in areas considered frequented by wild carnivores (Kuiper et al., 2015b). It has been demonstrated that in some areas, certain animal species attract predators in territories frequented by livestock, creating a de-facto spatiotemporal avoidance between species in relation with carnivores' activities and their favored prey type (Miguel, Grosbois, Fritz, Caron, de Garine-Wichatitsky, et al., 2017). The level of predation dictates livestock herder strategies at the W/L interfaces, thus influencing the use of protected areas by the livestock when the constraints in communal areas allow it (e.g., availability of crop residue for the cattle).

Ultimately, interspecific interactions between animal species at W/L interfaces depend on animal species density (Bhola et al., 2012), season (Odadi et al., 2011a), predation (Valeix et al., 2009), the biology of the interacting species (Økland et al., 2009) and animal community composition (Landi et al., 2018). As wildlife continues to experience increased pressure from livestock (Ottichilo et al., 2000), understanding the nature and processes that rule interspecific interactions between different animal species at the W/L interface scale can ensure a potential virtuous management and coexistence of mixed wildlife and livestock as well as the mitigation of disease transmission risk and conflicts in these complex ecosystems.

1.1.3 Anthropogenic drivers of Wildlife-Livestock interactions

W/L interactions are dependent on the management of wildlife populations inside and outside protected areas for recreational and associated economic activities by human societies. Livestock, when not released alone in the wild, is entirely tied to farmers who adjust their management practices to constantly evolving demographic, economic, local knowledge, and socio-cultural parameters. These adjustments in livestock management practices are not without direct and indirect consequences for W/L interactions. They have evolved in contrasted ways and at different paces between industrialized and developing countries in recent decades (J. A. Andersson et al., 2013) with one general trend however, a recognition of the importance of integrated cross-sectoral management of animal health and an inclusion of environmental and wildlife conservation agencies in decisions (Binot et al., 2015).

The emergence of the conservation paradigm at the end of the nineteenth and the beginning of the twentieth century (Olival et al., 2013) have led to the creation of reserves and national parks that in turn, generated land use boundaries around the protected “natural landscape”, and human rights’ abuse, social and environmental inequities in regards to citizens who have been excluded from their land after decades, centuries and sometimes millennia of presence (Lankester & Davis, 2016b). These land use boundaries produced virtual W/L interfaces that would evolve according to the socio-ecological context, resulting in different regulations being applied on each side of the boundary. On the protected side, the control of human activities (e.g., tourism, limited natural resource collection, cattle grazing) and environment alterations through the creation of infrastructures (e.g., water holes, roads, camps) durably modified the wildlife-livestock-human interactions at local, regional, and continental scales. For example, logging roads in Central African forests played an important role on increasing wildlife trade in Central African forests (Burivalova et al., 2014). In Southern Africa, African buffalo populations have been negatively impacted by the human footprint within protected areas (Naidoo, Preez, et al., 2012). To try to mitigate human-wildlife conflicts at the W/L interface scale, other types of protected areas (e.g., controlled hunting zones, forest reserves) have been put in place around the core of national parks. These controlled and monitored territories are expected to act as buffer to partially absorb human activities and conversely decrease human-wildlife conflicts inside national parks that negatively affect surrounding rural areas. To complement this approach, a newer model has been envisioned, first in Southern Africa and now progressively expanding in East Africa, the creation of “TransFrontier Conservation Areas” (TFCAs). TFCAs interconnect protected areas (under different land uses) and rural landscapes with the intention to integrate biodiversity conservation and local rural development in the heart of their respective functions (Cumming et al., 2013). TFCAs promote wildlife population connectivity while encouraging the development of a more socio-ecosystemic centric approach to landscape management. However, health issues in these interconnect areas have already been highlighted as potential threats (Gariné-Wichatitsky et al., 2013; Osofsky & Cleaveland, 2005) despite potential positive ecological, social, and economic outcomes in the long term. Even if strict land policies on animal movement controls (e.g., fencing) have sometimes locally solved the problem when they have been strictly applied (Thomson, 1995), the lack of sustainability of these control options and the indirect costs they induce have raised concerns for decades among conservationists (e.g., Taylor and Martin, 1987). TFCAs remain a viable option nevertheless, as it has been proven that the best maintained fences cannot restrain the movements of all wild animals anyways (Dion et al., 2011).

Traditional livestock systems and rangelands can’t cope with the increase in human populations in general and demands from a more and more urbanized population across the world. Land

grabbing for crop agriculture (Borras & Franco, 2013), irrigation schemes (Houdret, 2012), conservation (Balehegn, 2015), and hydroelectric or extractive industries (Martinez-Alier, 2014), largely promoted by State and private actors are drastically affecting rural communities dependent of agricultural and pastoral activities (Davis et al., 2014). As a result, less and less land are available for livestock and many negative impacts (e.g., drought, crop failure) driving the socioeconomic decline of rural communities potentially increase pressures on wildlife. Pastoralists often have no choice but to diversify livelihoods and practices while expanding their sphere of influence in preserved areas, and inevitably settle down, if not permanently, at least on a more frequent basis by shifting to agro-pastoralism or mixed livestock and cropping land use when possible. More sedentary livestock and associated land degradation, which was uncommon in nomadic systems, further reinforce the vulnerability of these ecosystems. With a fundamental shift from traditional livestock, not only will there be more pathogens circulating but more virulent variants will undoubtedly emerge (De Garine-Wichatitsky et al., 2021). This will lead to economic loss and increased costs for control for human societies, and more impacts of pathogens on wildlife.

1.1.4 The risk of pathogen transmission favored by the increase in contact between different animal species

Direct and indirect interactions between different animal species potentially result in the transmission of pathogens from wildlife to livestock, and from livestock to wildlife in space and time (Nugent, 2011). Most pathogen transmission events remain undetected at the W/L interface and when they are detected, it is difficult to assess when and where exactly they have happened accurately (Voyles et al., 2015).

In pathogen transmission event, wildlife can act as maintenance hosts for diseases, exacerbating the circulation of pathogens and their circulation within W/L interfaces (Bengis, Kock, & Fischer, 2002). Livestock can be directly impacted through increased mortality and reduced productivity that, in turn, can affect human societies via economic losses associated with cost of control, loss of trade, decreased market values and food insecurity (Dehove et al., 2012). Animal species respective roles and relative importance are extremely difficult to quantify and disentangle in a system associating wildlife and livestock (Lefevre et al., 2010). This diversity of species included in host communities implies complex and dynamic mechanisms of W/L interactions who are dependent on seasonal dynamics, strains circulations, virulence according

to the inter-specific contacts, intra and inter-specific contact rates and frequency of contacts (Miguel, 2012a).

On the other end, pathogen transmissions have the capacity to directly impact wildlife by disturbing whole species' health, affecting biodiversity, engendering changes in animal behaviors and population compositions or, in the most extreme cases, causing community collapse with multiple extinctions (Williams et al., 2002). Inventory of known livestock pathogens revealed that 77% are capable of infecting multiple host species, including wildlife (Cleaveland et al., 2001). This potential of pathogen transmission from livestock to wildlife can be amplified as we know that W/L interfaces are dynamic and bidirectional with pathogens circulating freely within and between wildlife and livestock species (Bengis, Kock, & Fischer, 2002). Indeed, most wild animal species are sympatric using shared resources (e.g., pasture, surface water), are in direct interaction with similar vectors and are exposed to human negative effects on their habitats (e.g., shifts in farming practices, land use changes, deforestation, encroachment into pristine habitats) (Perry et al., 2013).

Successive pathogen transmission events between sympatric hosts can as well occur over time (de Garine-Wichatitsky et al., 2013) via large scale movements (i.e., regional, continental, and intercontinental movements). For instance, in the Great Limpopo TFCA, pathogen and subsequent disease transmission risks across this W/L interface exist and can occur both ways threatening cattle and wildlife population (Caron et al., 2016). These patterns of pathogen circulation reinforce the risk of potential transmissions to humans as a great number of these circulating pathogens are zoonoses (Jones et al., 2008). Humans have evolved in proximity of animals for a long time, especially with domestic animals with whom they exchange pathogens frequently through diverse transmission modes (e.g., contact via animal husbandry activities, animal consumption) (Cleaveland et al., 2001). Of course, direct, and indirect interactions between humans and wildlife are less common but exist. Wildlife represents a direct source of pathogens which can lead to pathogen jumps and result in disease developments within the host. For these phenomena to occur, livestock species can perfectly play the role of “bridge” between humans and wildlife (Caron et al., 2015).

The consequences of pathogen transmission favored by W/L livestock interactions for the currently globalized human societies can be terrible for humans (in terms of health, political, social, and economic aspects), as the on-going severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) pandemic is demonstrating us (at the time of writing this manuscript), but also for the animal well-being in the case of some pathogens. Until recently, wildlife wasn't considered as impacted by pathogens and researchers, managers as well as the general public

were not as aware and equipped to apprehend and to measure such risks (de Garine-Wichatitsky et al., 2014). Therefore, our ability to model W/L interactions and the associated potential disease transmissions at the W/L interface is crucial in order to better apprehend the functioning of these complex ecosystems, thus improving our capacities to counter the constant increase of these phenomena more efficiently (Gibb et al., 2020).

1.2 Rural Zimbabwe, a land of contrasts and upheaval

Access to, the use of, and the global apprehension of natural resources have changed over the years in Zimbabwe, thus shaping the structures and organizations of its contemporary W/L interfaces. Three representative periods of natural resource conservation and utilization can be identified in that regard, namely the precolonial period, the colonial period, and the post-independence period (Muboko & Murindagomo, 2014).

1.2.1 History of biodiversity conservation and the relationship with wildlife in Zimbabwe (Pre-colonial and colonial periods)

In Precolonial Zimbabwe (before 1890), societies, large and small, were mainly farming communities practicing agriculture and pastoralism in a subsistence-oriented economy that included trades. Several multi-ethnic empires succeeded one another according to periods of expansion and isolation. In this period of time, access to natural resources was mostly governed by traditional beliefs, taboos, and customs (Chenje et al., 1998; Kwashirai, 2007). Specific areas were believed to be hosts to some spiritual forces and thus were considered as sacred sites where visiting, hunting, collecting fruits, extracting firewood, and any other natural products were prohibited activities (Chemhuru & Masaka, 2010). While the sacredness of some sites is difficult to establish and formally prove, the fact that such myths helped protect natural environments, as some areas remained intact, is clear. Traditional societies enforced wildlife conservation by discouraging indiscriminate killing of animals, as such acts were punishable by the spirits conveyed through control mechanisms of traditional taboos, totems, and customs (Kwashirai, 2007). Historically in Zimbabwe, intensive cattle productions were clustered along the edges of the Matabeleland plateau close from the line of maximum possible extension of the tsetse fly (*genus Glossina*), vector of human and animal trypanosomiasis (Garlake, 1978). This settlement

configuration allowed herding extension in additional areas during the time of the year when the fly was not dangerous for humans and livestock. Seasonal transhumance was necessary in order to extend the grazing range and supposedly to alleviate pressures such as lack of political control of the plateau, demands on the land by population or cereal agriculture, exhausting of grazing areas condensed on the plateau by intensive herding practices, and seasonal loss of nutrition of the plateau grasses (Garlake, 1978). In the 19th century, the population densities were far less than what they are today (37 inhabitants per km² in 2018, source: The World Bank), the human habitats were more fragmented across the land, and land-tenure system functioned as a mechanism of social control (Cousins et al., 1992).

During the colonial period (from 1890 to 1980), colonialism gradually disrupted the traditional structuration of societies by introducing Christianity, mercantilism, and capitalism, thus favorizing the emergence of new identities, new commodities, new languages, new ideologies, new political and economic outlooks, and new relationship to the environment. The British colonial administration progressively introduced protective and command type natural resource and wildlife conservation legislations to preserve a once plentiful wildlife population which had been severely endangered by the great rinderpest epidemic of 1896-1897 (Onselen, 1972) as well as by intensive exploitation by slave traders, hunter explorers, prospectors, and adventurers (Child, 2008). In 1929, the Game and Fish Preservation Act gave the governor of colonial Zimbabwe the ability to control the exploitation of wildlife and resulted in the creation of several natural reserves that correspond, for some of them, as the current National Parks (e.g., Hwange National Park) (Bond & Cumming, 2006). Wildlife populations increased drastically as a result of such law and began, at the same, to threaten human settlements and commercial cattle ranching by competing for grazing and harboring pests and diseases (G. Child, 2008). In 1930, the Land Apportionment Act (Jennings, 1935) divided the entirety of the land into European settler's areas and African native reserves. The application of this act gradually led to the emergence of a landholding structure where only 4,800 large-scale "European-colonial" commercial farmers occupied 11.2 million hectares of land amongst the most fertile while one million communal-area families occupied only 16.3 million hectares located in marginal agricultural areas (Chenje et al., 1998). In 1975, the Parks and Wildlife Act gave responsibility for wildlife to the private landowner (Murombedzi, 2010). The purpose was to protect wildlife populations within protected areas due to the deterioration of migration routes, to reduce wildlife management costs, and to reinforce the colonial government authorities in involving the private sector to the wildlife management to avoid personal interests (Duffy, 2000). The Parks and Wildlife Act was not extended to communal areas and local populations but to designated administrative authorities responsible to manage communal lands. This uneven system resulted in disastrous disequilibrium. Natural resources in the "European-colonial"-

owned areas were largely underutilized contrary to those in communal areas, where high poverty levels and taxation resulted in overexploitation of natural resources despite imposed use restrictions (Chigonda, 2018).

Rural population lost access to wildlands as protected areas were established and as a result, have been deprived legal access to wildlife on their own land. The appropriation by the central government of natural resources facilitated the emergence of individual entrepreneurship, suppressing all collective sense of proprietorship (Murphree, and Cumming, 1990). These restrictive and uneven laws, as well as the development and multiplication of land conversions for agriculture, mining, and human settlement set the foundation for the increasing of W/L interfaces and the associated socioeconomic and ecological challenges currently occurring in Zimbabwe.

1.2.2 Complex interactions between different actors in contemporary Zimbabwe. Social, economic, and political contexts (post-colonial period)

Independent Zimbabwe attempted to maintain the principle of state of control of the wildlife estate. Indeed, private wildlife ranching has been established during the 1970s but started to really flourish after independence in the 1980s up to the late 1990s. The Lancaster House Agreement signed in 1979 set the necessary conditions for the management of wildlife by farms in the large-scale commercial farming sector, even if it failed to establish a successful wildlife industry at the country scale (Bond & Cumming, 2006). However, the growth in live game sales and tourism in the 1990s have resulted in an increase in allocating resources to the management of wildlife by large farms (Wolmer et al., 2004). This trend was further encouraged by the decline in commercial meat prices, severe droughts in the early 1990s, the collapse of the Zimbabwean dollar and a broader shift towards export-oriented agriculture (Lindsey et al., 2009). As a result, significant changes in land use occurred, ranchers destocked cattle in favor of wildlife and livestock production systems became the formation of wildlife conservancies. Prior to 2000, there were 669 game farms and conservancies registered with a combined area of 2.5 million hectares and constituting at least 20% of the country's commercial farmland (about 5% of the country) (Feresu et al., 2010). Consequently to the wildlife ranches and conservancies paradigm, the National Parks and their management became irrelevant to the local development effort to prevent threats on animal species and the isolation of their respective habitats (e.g., fencing of National Parks). Adding factors such as population growth, poverty, corruption, weak enforcement, and a lack of representation and viable local market economies have contributed

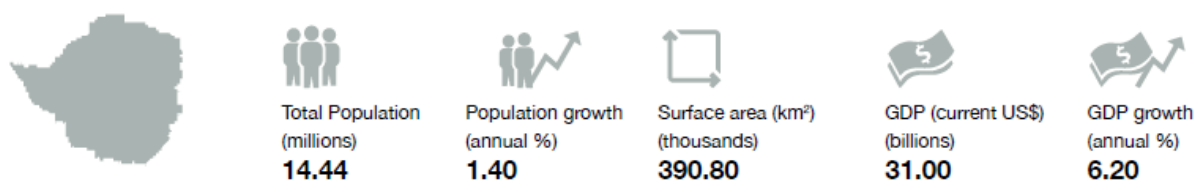
to the fragmentation of ecosystems around protected areas (Metcalf, 2013). In 1992, the Land Acquisition Act was put in place, enabling the government to acquire any land for resettlement (Wels, 2003). This law enforcement severely hampered the wildlife ranches and conservancies paradigm as it was considered by the government as a menace to food security. Indeed, wildlife ranches and conservancies were developing in areas suitable for both commercial and subsistence crop production (Duffy, 2000) and were perceived as perpetuating a racially unequal distribution of land and resources (Chigonda, 2018). Resulting from the application of the Land acquisition Act, a radical switch to wildlife farming took place, reorganizing the land use, the wildlife conservation and the livelihood of communities bordering protected areas.

The Communal Areas Management Program for Indigenous Resources (CAMPFIRE), that have been initiated in the early 1980s in areas not suitable for arable agriculture, illustrates the attempt of the government to initiate institutional changes by delegating some authorities to local communities in communal areas (Murombedzi, 2010). The CAMPFIRE program aimed at deriving revenues from wildlife through the taxation of safari operators and hunting concessions. The revenues received by district councils and wildlife producer wards (i.e., municipal districts) were expected to provide the financial incentive for individuals, households, natural resource cooperatives and village companies to participate in the common management of wildlife at the local scale (Gandiwa et al., 2013). From 1989 to 2001, the program earned a total of US\$ 20.3 million, increasing from US\$ 350 000 in 1989 to US\$ 2 million in 2001 (Child et al., 2003). However, even if few wards with low human population densities and endowed with higher wildlife populations produced annual household cash dividends (although merely supplementing crop and livestock production revenues) (Mutandwa & Gadzirayi, 2007), the CAMPFIRE program reconciled parks and local communities within a wider regional plan. The local communities, their respective authorities (councils), and the Ministry of Environment (parks, forests, and natural resources agencies) had finally a common framework for joint actions via the CAMPFIRE program. This framework made holistic management of natural resources possible in communal lands and offered opportunities to educate communities on the importance of the natural processes of the ecosystem by empowering them with responsibility for its costs and rents (Metcalf, 2013). The softening of the "hard edge" (i.e., fencing surrounding National Parks) between communal lands and National Parks by the CAMPFIRE program had always been an underlying objective, but relationships between people and parks remained asymmetrical most of the time and could not be considered as a genuine meeting of land users and authorities.

Today, Zimbabwe has 232 protected areas covering 106,838 km² (UNEPWCMC & IUCN, 2019) where strict conservation and preservation are implemented in some areas and sustainable use

is established in others ([Figure 1.2](#)). Zimbabwe includes parts of seven transboundary conservation areas, namely Chimanimani TFCA, Great Limpopo Transfrontier Park and Conservation Area, Greater Mapungubwe TFCA, Kavango-Zambezi TFCA, Lower Zambezi-Mana Pools TFCA, Mosi-oa-Tunya Victoria Falls Transboundary World Heritage Site and ZIMOZA TFCA. Zimbabwe is part of the Biodiversity and Protected Areas Management (BIOPAMA) program that aims to improve the long-term conservation and sustainable use of natural resources in African, Caribbean and Pacific (ACP) countries, in protected areas and surrounding communities.

These large-scale sharing initiatives should eventually enable the reestablishment of a true spirit of stewardship by local communities via the process of institution-building for wildlife and natural-resource management. This may prove to be all the more valuable as the balance between the inherent needs of already weakened human societies and the preservation of an increasingly pressured wildlife is changing with the consequences of climate change. Even if the CAMPFIRE program has not worked since 2000 due to the Zimbabwe's economic and political situations, the will to relaunch it by adapting it is however present.



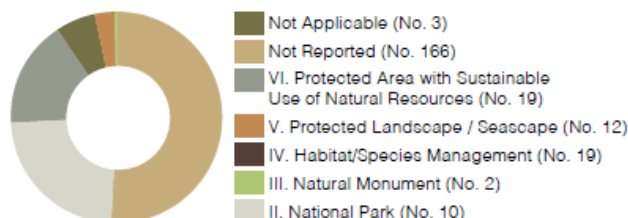
Source: The World Bank Group, 2018.

Area Protected:

232
protected
areas covering
106 838 km²
of land

Source: UNEP-WCMC & IUCN, (2019y)

Protected and conserved areas in Zimbabwe in IUCN Management Categories



Source: UNEP-WCMC & IUCN (2019y).



Coverage of protected areas in Zimbabwe

Type of protected area	Area protected or conserved*	Area protected or conserved**
Terrestrial and inland water	27.21%	28.00%

* WDPA dataset

** From National Report on Biodiversity

Source: Republic of Zimbabwe (2016); UNEP-WCMC & IUCN (2019y).

Protected and conserved areas designated as global sites of importance in Zimbabwe

Global designation	No. of sites
UNESCO Man and Biosphere Reserves	1
UNESCO World Heritage Sites (Natural or Mixed)	2
Wetlands of International Importance (Ramsar sites)	7

National designations of protected and conserved areas in Zimbabwe

National designation	No.	Area (km ²)
Sanctuary	11	6 660
National Park	11	26 896
Recreation Park	9	3 642
National Monument	1	7
Wildlife Management Area	104	39 376
Botanical Reserve	14	16
Nature Reserve	1	17
Recreational Park	3	129
Botanical Garden	3	6
Safari Area	16	18 988
State Forest	43	9 341
Protected Forest	6	608

Figure 1.2: Figure extracted from the “State of protected and conserved areas in Eastern and Southern Africa” (IUCN ESARO, 2020). It summarizes the demographical, geographical and conservation states of Zimbabwe.

1.2.3 A changing climate that upset an already fragilized balance at the W/L interface

Zimbabwe already experiences a changing climate. The country lies in a semi-arid region where rainfalls are limited as well as spatially and temporally variable. The temperatures fluctuate via altitudinal and seasonal gradients and are particularly prone to variations. At the country scale,

climate change increases the frequency and intensity of heavy rainfall events while exacerbating drought effects in space, time, and amplitude. The increase of intensity of mid-season dry-spells illustrates this phenomenon (Unganai, 2009). According to the Zimbabwe Meteorological Service, daily minimum temperatures have risen by approximately 2.6°C over the last century, while daily maximum temperatures have risen by 2°C during the same period of time (Brown, 2012). These occurring changes in rainfall and temperatures are not without consequences as shown by declining water resources, fall in agricultural productivity, biodiversity loss, geographical spread of pathogens and volatile weather and climatic disasters (e.g., flood and drought) at the country scale (Brazier, 2015).

In Zimbabwe, more than 70% of crop farming practice is rain fed (Zimbabwe Human Development Report, 2017), making agriculture, food security, and nutrition highly sensitive to changes in rainfall and temperatures associated with climate change. Currently, we can already observe shifts in agricultural farming regions, with consequential loss in productivity (Chikodzi et al., 2013; Mugandani et al., 2012). The expansion of more arid environments makes it difficult for most food and cash crops to grow, especially for highly sensitive crops such as maize (a staple crop), tobacco (the major cash crop), wheat, corn and soya beans that are cultivated in Zimbabwe. The areas suitable for maize production are projected to decrease by 2080, while spatial suitability of crops such as cotton and wheat is expected to increase in some areas (Zimbabwe National Climate Change Response Strategy, 2015). This agricultural reconfiguration will potentially produce socio-economic turmoil and migration of consequent populations in a country already affected by endemic poverty and shortages in necessary goods. As a result, W/L interfaces composition and sustainability will evolve all the more so as climate change heavily impacts livestock and wildlife through the decline of plant productivity associated with arid environment and through surface water scarcity. In the short and medium term, this shortage in natural resources will likely directly and indirectly affect animal species home range, interactions, adaptation efforts and exposure to pathogens within their respective environments. For example, the drought experienced in 2014/2015 and 2015/2016 seasons have forced cattle herds to move over larger areas in search of water and forage in six of the Zimbabwe's ten provinces, thus aggravating the spread of foot-and-mouth disease (FMD) through an increase rate of contacts with wild and domestic animal species (Chanza & Gundu-Jakarasi, 2020). Even if climate change is not uniformly experienced across all of Zimbabwe, small-scale subsistence farmers, whose operations are not covered by irrigation schemes, national parks and peripheral communal land located in semi-arid regions of Zimbabwe (agro-ecological regions IV and V) are more likely to be negatively affected, making them more vulnerable than they already are (Jiri et al., 2017). Currently, where communities used to easily access water through shallow wells, they now need to dig deeper to tap up available water (Chanza, 2018).

Facing already fragmented and degraded landscapes, as well as new barriers consisting of urban settlements, agriculture, and inhospitable land, wildlife will have very little room to maneuver in order to adapt to the drastic changes that are taking place in every level of the ecosystems (i.e., biotic, and abiotic). If some animal species will be able to survive and even thrive, others, such as large mammals, will likely experience more difficulties to adapt. In this context, W/L interfaces will have an important role to play as they display interaction dynamics that can favor scientists, amongst others, in understanding the responses of certain animal species to these changes. By focusing analysis and observations on these W/L interfaces, the characterization of human societies actions and influences on the evolution of the functioning of these particular ecosystems in a context of climate change and increased anthropisation can bring potential capacities of assessment and projection. These assets can be a definite advantage in preserving and/or enhancing the resilience of these ecosystems.

1.3 In a context of increased contact between wild and domestic animal species at interfaces: the choice of two focal species

The African buffalo (*Syncerus caffer*) and cattle (*Bos taurus* & *Bos indicus*) ([Figure 1.3](#)) are keystone species for conservation and production systems in W/L interfaces in Zimbabwe. The African buffalo is one of the “Big Five” (P. H. Williams et al., 2000) and is an important member of the ungulate guild who shapes habitat heterogeneity in and outside protected areas where the human presence is low (Estes, 2012). Cattle, in subsistence farming communities, provide draught power, source of protein, cash incomes, safety net and social status (Baudron et al., 2012). Buffalo and cattle are both grazer ungulates, close phylogenetically, sharing common resources (i.e., forage and water) (Hoffmann, 2002), and are thus likely to overlap in range and compete for resources, particularly in environments where natural resources are spatially segregated (e.g., savannas) (Odadi et al., 2011). Both species rely on their behavior and the management of the land use by humans to cope with constrained access to natural resources (e.g., access to artificial water, forage intake by the herder) (Kaszta et al., 2018). Their shared use of space increases the likelihood of direct and indirect interactions which, in turn, promotes the risk of pathogen transmission (Caron et al., 2013), a threat to farmers and biodiversity conservation (Caron et al., 2013). In the context of this thesis, we have decided to focus on those two particular species in order to deploy our methodology and follow up on several previous studies (Miguel, 2012; Perrotton, 2015; Valls Fox, 2015) that have focused on these two animal species and the different problematics associated with their interactions.



Figure 1.3: On the left, two buffalo (*Syncerus caffer caffer*) – photo taken by [Ikiwaner](#). On the right, one nguni cattle (*Bos taurus*) specimen – photo taken by Bernhard Bekker

1.3.1 The African buffalo (*Syncerus caffer*)

“The scientific name Syncerus caffer is derived as follows: Sun (Greek) together; keras (Greek) the horn of an animal: a reference to the closely abutting bases (or boss) of the horns in adult male Cape buffalo. Cafer (Latin) means “of Caffraria/Kaffraria”, the country of the Kaffirs (Africa).” – Brent Huffman

1.3.1.1 Intrinsic behaviors of one of the subspecies (*Syncerus caffer caffer*)

The African buffalo (*Syncerus caffer*) is a ruminant mammal belonging to the Bovidae family ([Figure 1.4](#)) and is the existing largest and most massive of the African bovids. The African buffalo is currently considered as a single species despite displaying important morphological variations such as body size, weight, fur color, horn shape, and length according to geographical locations. Four subspecies form the entire African buffalo population: Cape buffalo (*Syncerus caffer caffer*), forest buffalo (*Syncerus caffer nanus*), West African savanna buffalo (*Syncerus*

caffer brachyceros) and Central African savanna buffalo (*Syncerus caffer aequinoctialis*) (East, 1999). The population density of these subspecies is unevenly distributed throughout the African continent. The highest population densities are found along the African Rift, in East Africa ([Figure 1.5](#)).

In this thesis, we are focusing our interest on the Cape buffalo as this specific subspecies is the only representative of the *Syncerus caffer* species in southern Africa, and more particularly in Zimbabwe, our defined study area. The social structure of the Cape buffalo has been closely studied, even if most of the studies are often descriptive (Prins, 1996; Ryan et al., 2006; Sinclair, 1977). Cape buffalo live in large herds containing 50 to 500 animals (Cornélis et al., 2014) and a number of smaller social groups made up of several females and their most recent offspring (up to two years of age). The herd structure tends to maintain cohesion in order to provide protection for weakened individuals even if complex fusion-fission dynamics exist within herds (Wielgus, 2020). Bachelor groups containing as many as a dozen or so males, along with groups of similarly aged juveniles are also found within the herd substructure. Adult males either associate with a female group or distance themselves apart from the herd in a small unit of similar older males. In some instances, old males can be solitary, living away from the herd from which they originate (Grzimek, 1990). Where and when large and rich pastures are present, temporary aggregations of 2,000 to 3,000 buffalo can potentially form from several smaller herds (Kingdon, 2015). However, contrary to the smaller herds, these large groups lack social cohesion and occur occasionally. Cape buffalo tend to be non-migratory, usually inhabiting an exclusive home range that can vary in size ([Figure 1.4](#)) and are specific to one herd (Nowak & Walker, 1999). In southern and eastern Africa though, Cape buffalo herds can periodically subdivide due to fission (splitting) - fusion (merging) dynamics but within the herd's usual home-range (Prins, 1996; Ryan et al., 2006).



 	<h3>Taxonomy</h3> <p>Kingdom: Animalia Phylum: Chordata Class: Mammalia - mammals Order: Artiodactyla - even-toed hoofed animals Family: Bovidae Genus: <i>Syncerus</i> Species: <i>Syncerus caffer</i> - African buffalo, Cape buffalo</p>
<h3>Physical characteristics</h3> <p>Weight: 300-900 kg Head-body length: 170-340 cm Shoulder height: 100-170 cm Tail length: 70-110 cm Pelage: Black or nuances of brown</p>	<h3>Distribution & status</h3> <p>Distribution: throughout most of Africa south of the Sahara Habitat: savannas interspersed with patches of forest, reeds, or scrub Home-range: 126 to 1075 km² IUCN status: Red List of Threatened Species Population in wild: >513,000 individuals across the continent (Cornélis <i>et al.</i>, 2014)</p>
<h3>Behavior & ecology</h3> <p>Locomotion: walk and run for burst of speed Activity cycle: active throughout the day, spending 18 hours per day moving and foraging. Feeding is most frequent in the late afternoon and evening. Drinking usually occurs in the morning and at dusk Social groups: herds of 50-500 animals, comprised of smaller subgroups of bachelor males, females and their young, or juveniles. Old males may be solitary Diet: grasses, herbs, swamp vegetation, and occasionally browsing on leaves – (ruminants) Predators: Lions, spotted hyenas, crocodiles, humans</p>	<h3>Reproduction & development</h3> <p>Sexual Maturity: 3.5-5 years Gestation: 340 days Litter size: 1, rarely 2 Interbirth interval: around 2 yers Birth weight: 40-53 kg (88-117 lb) Age at weaning: Around 6 months Life span: 18-20 years, up to 29 years in captivity</p>

Figure 1.4: Main taxonomy, physical, distribution and status, behavior, and ecology as well as reproduction and development characteristics of the buffalo (*Syncerus caffer caffer*).

Cape buffalo are usually active throughout the day, spending 18 hours per day moving and foraging (Nowak & Walker, 1999). Grazing occurs as the herds move through their home range on a circuitous route and is most frequent in the late afternoon and during the evening (Nowak & Walker, 1999). Drinking usually occurs during the early morning and at dusk (Nowak & Walker, 1999) and at least once every 24 hours when surface water is available (Cornélis *et al.*, 2011a). During the hottest time of the day, Cape buffalo tend to rest and ruminate, although in areas with high human disturbance such as the W/L interfaces, Cape buffalo can switch from continuous grazing to night-time foraging to avoid other wild and domesticated species (Kingdon, 2015). The average speed of travel is 5.4 km per hour, although Cape buffalo can run up to 57 km per hour for short distances (Nowak & Walker, 1999).

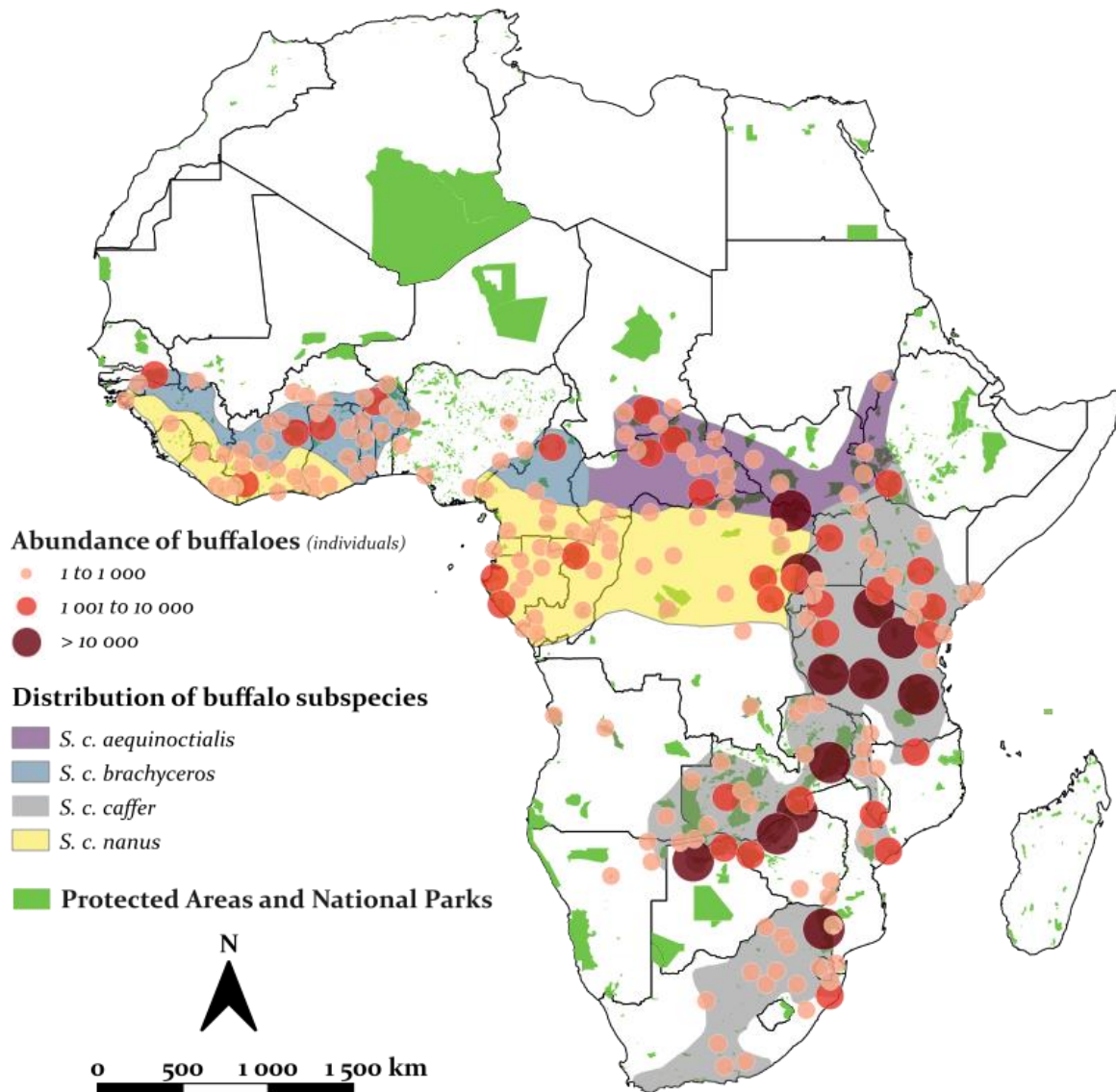


Figure 1.5: Map representing the buffalo abundance across the African continent in 2010 (dots represented in shades of red and fluctuating sizes) in relation with the National Park locations (represented in green) and the distribution of buffalo subspecies (represented in purple, blue, gray, and yellow) – Source: IUCN ; East, 1999

1.3.1.2 Direct links of the *Syncerus caffer caffer* with its immediate environment

Geographical distribution and population sizes of the Cape buffalo have greatly decreased since the nineteenth century as a result of habitat loss, poaching, disease outbreaks and climatic events (Cornélis et al., 2014). The majority of buffalo populations are now confined to protected areas and managed hunting areas (East, 1999) with population densities that approximate 0.45 individuals per km² in some areas in Zimbabwe (Chamaille-Jammes et al., 2009). The species is

currently specified as “near threatened” by the International Union for Conservation of Nature (IUCN) (IUCN 2019). Cape buffalo is considered as a key species with high economic value. It attracts hunters as animal trophy (Munag’andu et al., 2006) and local inhabitants as preferred species to produce income and to supplement the diet with protein (Alexander et al., 2012). More recently, Cape buffalo has also gained in value for eco-tourism and is a popular wildlife species for tourists participating in safaris (Merwe et al., 2004).

Cape buffalo inhabits a wide range of habitats across Africa (Megaze et al., 2013; Melletti et al., 2007). They are mostly found in Eastern and Southern African savanna and woodland mosaics, seeking areas with rapid and easy access to grass, water, and dense cover, such as thickets, reeds, or forest (Kingdon, 2015). They tend to prefer frequenting glades where possible but can stay out in the open without shade for extended periods of time (Kingdon, 2015). Cape buffalo is a grazer that feeds on grasses, herbs, and occasionally browses on leaves when the competition for the resource with other animal species is high and/or when the availability of grasses is sparse during the dry season (Grzimek, 1990; Nowak & Walker, 1999). Preferred grass species reported by Kingdon, 2015 include *Cynodon*, *Sporobolus*, *Digitaria*, *Panicum*, *Heteropogon*, and *Cenchrus* species. As Cape buffalo eats large quantity of vegetations as a bulk grazer and moves en masse, the species facilitates the opening up of habitats, which benefits more selective species or short-grass grazers (Eby et al., 2014).

However, despite positive ecological impacts on ecosystems, Cape buffalo carries many pathogens such as FMD, bovine tuberculosis, brucellosis, and tick-borne diseases, that can be potentially transmitted from one animal species to another (Caron, Miguel, Gomo, Makaya, Pfukenyi, Foggin, Hove, & de Garine-Wichatitsky, 2013; Dion et al., 2011; Garine-Wichatitsky et al., 2013). Domesticated species, such as cattle that are taxonomically close from Cape buffalo, are also concerned by these pathogen transmission risks (Bengis, Kock, & Fischer, 2002; R. Kock et al., 2014). Buffalo and cattle have similar ecological niches and tend to utilize the same type of resources (*i.e.*, forage and water) (Odadi et al., 2011a; Valls-Fox et al., 2018). The competition between these two animal species in areas where they live sympatrically (*e.g.*, W/L interfaces) can potentially lead to direct and/or indirect interactions, facilitating pathogen transmissions (Miguel, Grosbois, Caron, Boulinier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & de Garine-Wichatitsky, 2013). Even if Cape buffalo usually avoids cattle, seasonal patterns of interactions between buffalo and cattle are observed (Miguel, 2012a). Interactions are usually more frequent during the dry season when both water and forage resources are depleted or when cattle range further into protected areas in search of food and water (Kock, 2005; Valls-Fox et al., 2018; Zengeya et al., 2015).

1.3.2 Domesticated cattle (*Bos taurus* & *Bos indicus*)

*“Nguni cattle derive their name from the black tribes of Africa, collectively known as the Nguni people. Nguni cattle descend from both *Bos taurus* and *Bos indicus* cattle and entered Africa around 8000 years ago. As the tribes migrated south into Africa, they took their cattle along. Through natural selection and environmental interaction, the cattle evolved into the hardy breed we know today as the Nguni. As the tribes settled in different areas, distinctive cattle ecotypes developed, but are essentially still Ngunis.”* (The cattle site - www.thecattlesite.com)

1.3.2.1 Intrinsic behaviors of the species and its relations with the surrounding environments

Cattle (*Bos taurus* or *Bos indicus*) are ruminant mammals belonging to the *Bovidae* family ([Figure 1.6](#)) and domesticated by human societies. They are considered escaped or released domestic animals because if not well contained by adequate fences or herder's directives, cattle tend to form feral herds and wander into native vegetation wherever suitable food is available (Findley, 1976). A cattle's herd is structured according to a dominance hierarchy where each individual yield to those above in the hierarchy. The hierarchy's status is hereditary and as a result, calves adopt their mother's status. Females protect their respective calves by chasing anything that threatens them and is not reluctant to share parental care within the ensemble of the herd. Dominant males maintain this status until defeated by younger males in challenges. (Patent & Munoz, 1993). Cattle's herd home-ranges vary greatly ([Figure 1.6](#)) according to geographical locations and their respective socio-ecological organizations and seasonal climate fluctuations (Moyo et al., 2013). In some W/L interfaces, where restrictions of access due to seasonal crop productions apply, cattle can be encouraged by the herder to range away from communal land into natural reserves or National Parks despite not having an official granted access (Valls-Fox et al., 2018).

Cattle usually feed on grasses, stems, and other herbaceous plant material present in pastures not maintained by humans or in open agricultural fields and consume about 70kg of grass in an 8-hour day in average (Ng, 2001). Cattle can modify native vegetation by browsing, crushing, and trampling, and in areas with high human density, they can severely impact natural systems, causing erosion, introduction of non-native grasses and herbaceous plants, destruction of

riparian habitats, as well as overgrazing (Moyo et al., 2013). In addition to their grazing activities, cattle need to drink every day, and in some instances, are totally dependent on the water resources made available by humans (e.g., borehole, dip tank) in areas where the availability of surface water is spatially and seasonally sparse.


		Taxonomy Kingdom: Metazoa Phylum: Chordata Class: Mammalia - mammals Order: Artiodactyla - even-toed hoofed animals Family: Bovidae Genus: <i>Bos</i> Species: <i>Bos taurus</i> - domestic cattle
Physical characteristics Weight: 147-1363 kg Head-body length: 245 cm (average) Shoulder height: 130-140 cm Tail length: - Pelage: White with nuances of brown and black		Distribution & status Distribution: currently found throughout much of the world. native to northern Africa, Europe, and southern Asia Habitat: Born and raised on rangelands. Desert, savanna, grassland, chaparral, forest, scrub forest, agricultural areas Home-range: 3.09 ha in average (Moyo et al., 2013) IUCN status: No special status Population in wild: Estimated at around 5,5 million in Zimbabwe (Chanza and Gundu-Jakarasi, 2020)
Behavior & ecology Locomotion: walk and run for burst of speed Activity cycle: Cattle activity and their watering and feeding areas depend on the decisions of the herders. Cattle are grouped together at night in kraals, protected from predators Social groups: Cattle herds are structured according to a dominance hierarchy. Females also share parental care within the group. Dominant males maintain this status until defeated by younger males in challenges Diet: grasses, stems, and other herbaceous plant material – (ruminants) Predators: Lions, humans		Reproduction & development Sexual Maturity: at 1 year Gestation: 9 months Litter size: 1 to 2 Interbirth interval: around 2 years Birth weight: - Age at weaning: Around 6 months Life span: around 20 years

Figure 1.6: Main taxonomy, physical, distribution and status, behavior, and ecology as well as reproduction and development characteristics of the buffalo (*Bos taurus* & *Bos indicus*).

Across Africa, cattle abundance is spatially unevenly distributed with a strong presence in the Sahelian strip, in Ethiopia and around Lake Victoria (Figure 1.7). The increase in cattle population in a wide array of African W/L interfaces (Ogotu et al., 2016) multiplies the likelihood of interactions with nearby wildlife at the W/L interfaces, thus facilitating the risk of pathogen circulation among animal species (Jori et al., 2009; Miguel, Grosbois, Caron, Boulinier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & de Garine-Wichatitsky, 2013).

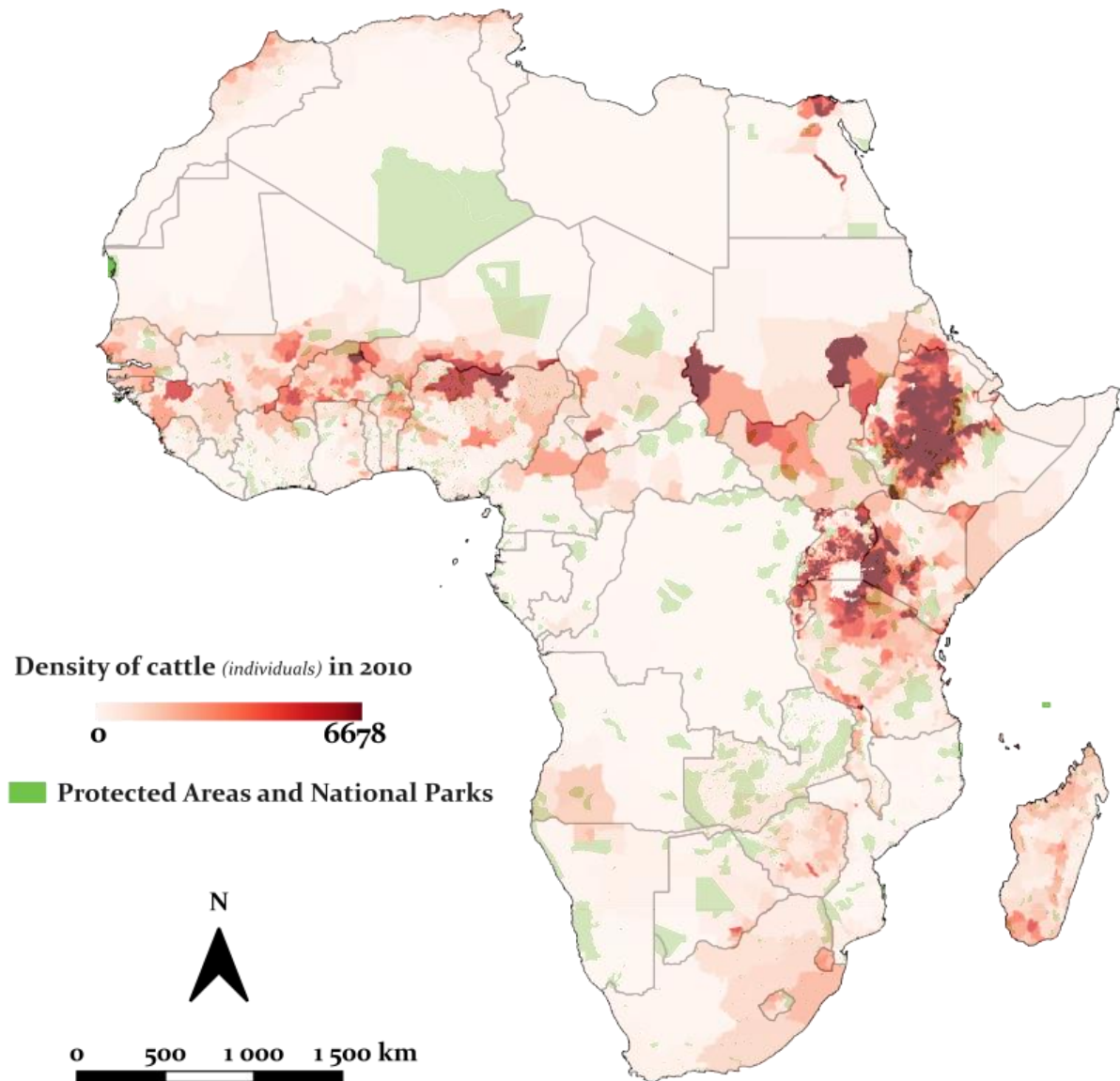


Figure 1.7: Map representing the cattle density in number of individuals per country district across the African continent in 2010 (represented in shades of red) in relation with the National Park locations (represented in green) – Source: Robinson *et al.*, 2014

1.3.2.3 A domestic animal species dependent on herders' decision rules

In Southern Africa, many of the region's economies are dependent on agriculture, which was contributing to about 38% of its Gross Domestic Product (GDP) in 2015 (DZAMA, 2016). The livestock sector is an important component of the agricultural economies of the region, as over 60% of the region's total land area is non-arable (DZAMA, 2016). The countries that form part of the Southern African Development Community (SADC) have an estimated populations of 64 million cattle as of 2015 and most of them are kept under smallholder traditional farming

systems where women and children are the major caretakers (Dzama, 2016). Domesticated cattle are widely used by smallholder farmers and pastoralists for the production of dairy products (e.g., milk, cheese) and meat. Cattle are therefore central to agricultural production, and draft animals are often borrowed or sometimes rented, strengthening social cohesion amongst neighbors as there are the main form of capitalization for rural populations (Ndengu et al., 2017). Beyond their agricultural value, cattle also have a social and cultural dimension through the definition of the social status of men and the payment of the bride price (Perrotton et al., 2017) and are considered, in some areas, as a form of currency (Patent & Munoz, 1993). Furthermore, cattle are essential for diversifying income sources, investment, and risk management, providing manure/fertilizer, draught power, and transportation (Baudron et al., 2012).

Ecological and physical environmental factors influence adaptation patterns employed by herders to cope with seasonal variations in forage (Kauffman et al., 1983). Indeed, the season will affect forage quantity and quality as the rainfall fluctuate (Sal et al., 1991). For a species like Cattle that preferentially graze plant communities of high nutritive value (Roath & Krueger, 1982; Ueckert et al., 1980), this variation in forage quality and quantity may potentially have an important impact on their respective foraging strategies (Putman et al., 1987). However, cattle's foraging strategies are also likely to differ according to the communities in which they are kept as well as the adopted livestock management system (e.g., kraaling, meaning keeping cattle at night close to the homestead in corals). Although the forage resource is a crucial driver of cattle herding practices, cattle herding calendars in mixed used smallholder farming systems are largely determined by agricultural practices (Perrotton, 2015; Valls Fox, 2015a). The agricultural calendar depends on weather patterns both on a large and a fine scales as plowing strategies are revised almost daily by local farmers. In the Dete communal area, close to Hwange National Park (Zimbabwe), the 32% of homesteads that own cattle with an average of 5.5 cattle per herd (Perrotton et al., 2017) adapt their herding practices in three distinguish phases: 1) the cropping season (November–May) when herders maintain cattle away from agricultural fields to minimize incursions and crop damages, 2) out of the harvest time when cattle are no longer herded to forage and can roam freely within the agricultural fields, feeding on grass and crop residues and when cattle are taken daily to communal dams or to boreholes to drink, 3) toward the beginning of the hot and dry season (end of August) when cattle start going unguarded outside the communal area limits in search of available fodder that became too scarce within the communal area. It is important to note however that these are general patterns for the majority of the cattle herds. At an individual level, cattle-herding strategies are complex mechanisms failing under personal histories of owners and herders, consideration of environmental parameters, proximity

of homesteads to the outskirts of the communal area, as well as neighbors' strategies (Perrotton et al., 2017).

1.4 Research questions & objectives of the thesis

1.4.1 The origin of the thesis research's questions

As mentioned in [section 1.1](#), W/L interfaces play a preponderant role in the emergence of pathogens (Despommier et al., 2006) due to important interactions between humans, domesticated species and wildlife in space and time (Haydon et al., 2002). These pathogen transmissions are naturally bidirectional between the reservoir and susceptible populations (wild -> domestic vs. domestic -> wild) and can thus be potentially spatialized around “hot spots” of wild/domestic species interactions. Spatial proximity between populations has been clearly identified as one of the crucial risk factors in the transmission between species (Roche et al., 2012). However, the nature, frequency, and localization of these contacts between wild and domesticated animals remain largely unknown despite their importance in explaining how ecosystems operate a different spatial scale.

The development and the democratization of recent technologies such as telemetry and satellite remote sensing (SRS) technologies, currently allow to characterize domestic and wild animal species interactions in time and space at the W/L interface (Triguero-Ocaña et al., 2021). These technologies bring additional tools to characterize animal species movements and interactions in space and time and participate to multidisciplinary approaches that already combine different fields of studies (e.g., behavioral studies of wild and domestic species, social science methodologies) (Caron et al., 2021). Amongst these methodologies, spatial modelling of animal movement, contacts and interactions taking into account biotic and abiotic ecological features as well as behavioral mechanisms have been developed in recent years (Moorcroft, 2012; Rastetter et al., 2003a; Westley et al., 2018). Yet, there is a need to further develop these animal movement, contact and interaction models to integrate independent and validated environmental SRS data. This could enable potential landscape scale analysis of inter-species contact and interactions. Such models could benefit from the integration of specially characterized environmental SRS data while extending their application capacities to different environmental and ecological contexts (Neumann et al., 2015). This is particularly true in the

current context where the number of SRS sensors is expanding (Paganini et al., 2018) and the wide variety of already existing SRS methodologies and applications extend the analytical capacities of ecologists specialized in animal movement and behavior (Pettorelli, Laurance, et al., 2014).

Within the framework of this thesis, we positioned ourselves at the interface between a wild compartment (protected area) and an anthropic compartment (communal areas) at three different study areas in Zimbabwe (described in [section 2.1](#)) to apprehend buffalo and cattle interactions in space and time using a multidisciplinary approach that combines, ecology, SRS and spatial modelling ([Figure 1.8](#)). We are particularly interested in the relationship between interspecies interactions and how environmental factors (e.g., surface water, landcover, human infrastructures) can influence these interactions at the landscape scale. The data as well as an important part of the empirical knowledges used in this thesis have been collected and developed during previous thesis (Guerbois, 2012; Miguel, 2012; Valls Fox, 2015; Wielgus, 2020).

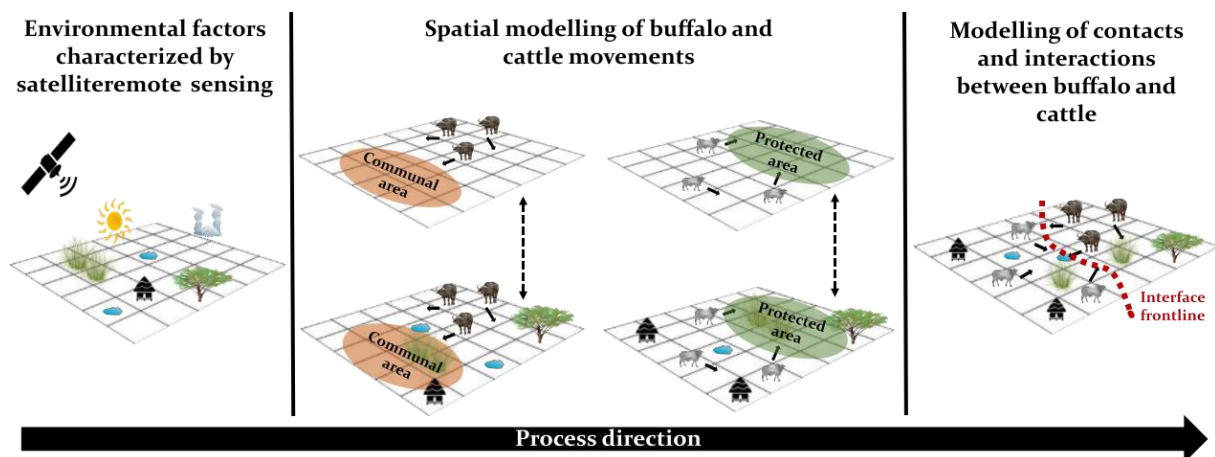


Figure 1.8: Diagrams showing the three main steps of the thesis. 1) characterization of environmental factors influencing the buffalo and cattle movements by SRS, 2) spatial modeling of buffalo and cattle movements in relation with the previously characterized environmental factors, 3) linking these movement patterns to model buffalo/cattle contacts in space and time

1.4.2 Three main research questions

Question 1: How to characterize the environmental indicators that impact the movements of buffalo and cattle in time and space at the landscape scale with the support of remote sensing?

Objectives: The main objective is to develop a classification methodology that allows to characterize environmental factors, such as surface water and landcover, at the landscape scale

(i.e., 10 meters of spatial resolution) and with pertinent temporal resolutions (i.e., intra-annual and inter-annual). The methodology has to be effective on three different locations with different geographical and physical characteristics, reproducible, as well as easy to apprehend. The use of open-access SRS data as well as open-access software are favored.

Question 2: How can we model the movements of buffalo and cattle, at the individual and herd levels, while considering the spatial and temporal variations of environmental indicators?

Objectives: The main objective is to develop a mechanistic model that enable the simulation of buffalo and cattle movements in space and time while considering the individual and collective dynamics of the focal species. The model also needs to take into account the environmental factors previously characterize by SRS as it aims to spatialize the focal species movements in relation with their direct environment.

Question 3: Is it possible to model contacts between buffalo and cattle while determining the contribution of environmental indicators in order to characterize the risk of pathogen transmission between these two species?

Objectives: The main objective is to assess the nature, frequency, locations of buffalo and cattle contacts and interactions by combining the two spatialized models previously developed in three different W/L interfaces that present different ecological and geographical configurations.

1.4.3 The structure of the manuscript

The manuscript is divided in eight main chapters (including the general introduction) that answer the three main questions in the order that they have been presented in the previous section. In addition, an extra chapter which succinctly summarizes the thesis key components in French is present at the end of this manuscript. The one question one chapter is not in play here. We've preferred to subdivide a main question into several chapters for a better readability and comprehension. It is important to note that some chapters include already published articles. They, however, are implemented in a way that does not disrupt the reading flow.

Just after the general introduction, the second chapter presents the three study sites in details and describe the different data used in the thesis to facilitate the comprehension of the analysis further developed within the manuscript.

The third and fourth chapters address the research question 1. The third chapter focuses on the use of remote sensing in the context of animal movement ecology. It consists of a published article in 2020 which is entitled “Remote Sensing of Environmental Drivers Influencing the Movement Ecology of Sympatric Wild and Domestic Ungulates in Semi-Arid Savannas, a Review.” The fourth chapter describes the SRS classification methodologies that have been developed and presents the obtained results of the three study sites.

The fifth and sixth chapters address the research question 2. The fifth chapter details a state of the art in modelling and animal movement modelling in particular, as well as a presentation of the concept of spatial modelling and the platform used to program the model developed within the framework of this thesis. The fifth chapter consists of a published article in 2021 which is entitled “Combined use of remote sensing and spatial modelling, when surface water impacts buffalo movements in savanna environments” and focuses on Hwange/Dete study site. In addition to the article, a section details the application of the buffalo movement model in the two other W/L interfaces of the study.

The seventh chapter address the question 3. It presents, in the form of an unpublished article, the spatialized mechanistic model developed to simulate the contacts between buffalo and cattle at the three W/L interfaces.

The eighth chapter presents the general discussion of the thesis by first focusing on the summary of the main objectives and the different results obtained. Then, the inherent limitations of the developed methodology by giving some thoughts and recommendations are detailed. To conclude the chapter, the perspectives on how to improve the robustness of the developed model and implement an epidemiological compartment to the latter with the underlying objective of a use of the model in an “EcoHealth” approach are highlighted.

1.5 Chapter summary

- The growing demography on a global scale, more particularly in the southern countries, as well as the expansion behaviors of human societies multiply the interfaces and contact areas between highly anthropized territories and territories still relatively preserved by human activity.
- The combination of these interdependent effects multiplies and promotes interface spaces where wild and domesticated animal populations come into contact with contrasted frequencies in space and time.
- The increase in contacts between wild and domesticated animal species is not without consequences both for the animal populations themselves and for the human societies that live in their vicinity. We could mention in particular the increased risk of transmission and circulation of pathogens with, in the process, zoonoses that could eventually cause pandemics on a global scale, or a general degradation of plant and animal biodiversity.
- Zimbabwe, a land of contrasts, is fully concerned by the extension of interface areas where wild and domestic animal populations interact. This country is particularly vulnerable because of the political, economic, and social crisis that has been going on for several decades and because the already tangible effects of climate change are reducing the country's capacity to deal with the potential consequences of the increase in interactions between wild and domesticated animals year after year.
- Buffalo (*Syncerus caffer caffer*) and cattle (*Bos taurus* and *Bos indicus*) are keystone animal species for conservation and production systems in southern African wildlife livestock interfaces. They have been chosen to illustrate the interactions between wild and domesticated animal species within the frame of this thesis.
- This work focuses on the relationship between interspecies interactions (i.e., between buffalo and cattle) and how environmental factors (e.g., surface water, landcover, human infrastructures) can influence these interactions at the landscape scale within three wildlife and domesticated interfaces located in Zimbabwe. To tackle these thematical questions, this thesis aims to develop an innovative methodology by combining remote sensing and spatial modeling.

Chapter 2

Study sites and data used

Table of content

2.0 Preamble

2.1 Three study sites, three W/L interfaces

2.1.1 The W/L interface of Hwange/Dete

2.1.1.1 Geographical, climatic, vegetation and hydrologic characteristics

2.1.1.2 Current ecological context

2.1.2 The W/L interfaces of Gonarezhou/Malipati and Kruger/Pesvi

2.1.2.1 Geographical, climatic, vegetation and hydrologic characteristics

2.1.2.2 Current ecological context

2.2 The Data used in this thesis

2.2.1 The telemetry data

2.2.1.1 Capture of animals and installation of GPS collars

2.2.1.2 Pre-processing of the telemetry data

2.2.2 Remote sensing data

2.2.3 In-situ environmental data and empirical knowledge

2.3 Chapter summary

2.0 Preamble

The objective of this chapter is to detail the three study sites that each represent an interface between wild and domesticated animal species in Zimbabwe, as well as to give an overview of the telemetry, satellite imagery and spatialized environmental datasets used to design, calibrate, and validate the methodology developed in this thesis. It is important to underline that the developed methodology requires a spatialization of the information at the landscape scale and takes into consideration data of heterogeneous order on the spatial level certainly but also on the temporal level. The use of data (as far as satellite images are concerned) and open-source software to process the data spatially are privileged in order to facilitate the reproducibility of the method to the greatest number.

2.1 Three study sites, three W/L interfaces

The three chosen study sites ([Figure 2.1](#)) are located on the periphery of protected areas in Zimbabwe (i.e., Hwange National Park (HNP), Gonarezhou National Park (GNP) and Kruger National Park (KNP)). These three study sites are part of a new trend in conservation and management of protected areas, which has been concretized almost twenty years ago (International Treaty signed by the Heads of States for Mozambique, South Africa, and Zimbabwe at Xai-Xai, Mozambique in December 2002) by the creation of two TFCA: (1) KAvango - ZAmbezi- (KAZA-TFCA) for Hwange National Park and (2) Great Limpopo (GL-TFCA) for Gonarezhou and Kruger National Parks. These sites are located in areas where boundaries between protected areas and communal areas are often permeable (i.e., river, railroad, or road) and without barriers, where movements occur in both directions and where the number of conflicts between human communities as well as humans and wildlife are increasing (Baudron et al., 2011; Guerbois et al., 2012). Domestic and wild animal movements between the three study sites' natural and anthropogenic compartments are frequently observed in both directions (de Garine-Wichatitsky et al., 2013). Both in the Sengwe communal land in the Chiredzi district, the "Gonarezhou/Malipati" site (main village studied: Malipati), and the

“Kruger/Pesvi” site (main village studied Pesvi) present the same geographical, climatic, hydrologic, and ecologic characteristics due to their geographical proximity. As such, they are described within the same section.

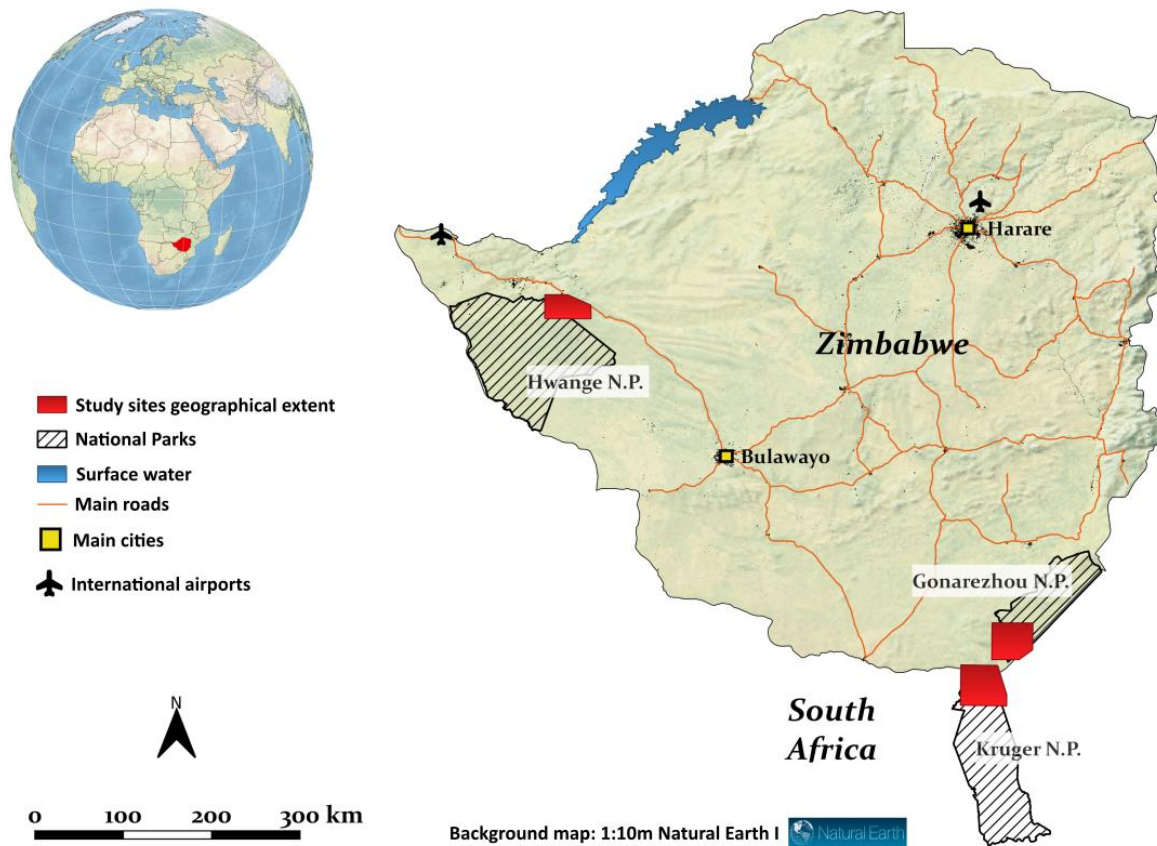


Figure 2.1: Location map of the three study sites (represented in red) and designated in relation to the proximity with their respective National Park.

2.1.1 The interface of Hwange/Dete

2.1.1.1 Geographical, climatic, vegetation and hydrology characteristics

The Hwange/Dete study site (area of 1192 km², this area have been determined to encompass the full spatial extent of the observed telemetry data available) is located at proximity of the Dete village in the Hwange district and close to two types of protected areas ([Figure 2.2](#)) in the Matabeleland North Province of Zimbabwe: the HNP (area of 14,651 km²) and the Sikumi forest reserve (SFR) (around 11,000 km²), a wildlife conservation and timber production area separated from the villages only by a tarred road. The study area is located in a semi-arid climate (Beck et

al., 2018) at an altitude of around 1090 meters above sea level and annual mean temperatures of 22°C and characterized by three seasons: a cold and dry season from May to August, a hot and dry season from September to October, and a rainy season from November to April, although the start of the rainy season varies greatly among years (Perrotton, 2015). Mean annual precipitation ranges between 450 and 650 mm per year and is spatially highly heterogeneous (Chamaillé-Jammes, Fritz, et al., 2007). Droughts as well as “dry spells” can occur during the rainy season (Matarira & Jury, 1992). The vegetation is typical of a highly heterogeneous dystrophic wooded savanna (Arraut, Loveridge, Chamaillé-Jammes, et al., 2018). The woody cover increases with distance from water pans (Chamaillé-Jammes et al., 2009) and the open grassland is located along drainage lines. Several vegetation species dominate within the landscape, among them we can find *Baikiaea plurijuga* woodlands, *Colophospermum mopane* bushland or woodlands, mixed bushland community dominated by *Combretum* species, *Terminalia sericea* and *Acacia* groves (Rogers, 1993). Open grasslands can also be found along drainage lines. The surface water is mainly composed of natural pans of different sizes (ranging from approximately 10 meters of diameter to 1 kilometer of diameter) widely distributed across the area with the addition of artificial pans fed by underground water pumping stations (present both in the communal area but also within the HNP). During the wet season, surface water content is high and water is widely distributed across the landscape. On the contrary, during the dry season only artificial pumped waterholes provide water for humans as well as for domestic and wild animals (Chamaillé-Jammes, Fritz, et al., 2007).

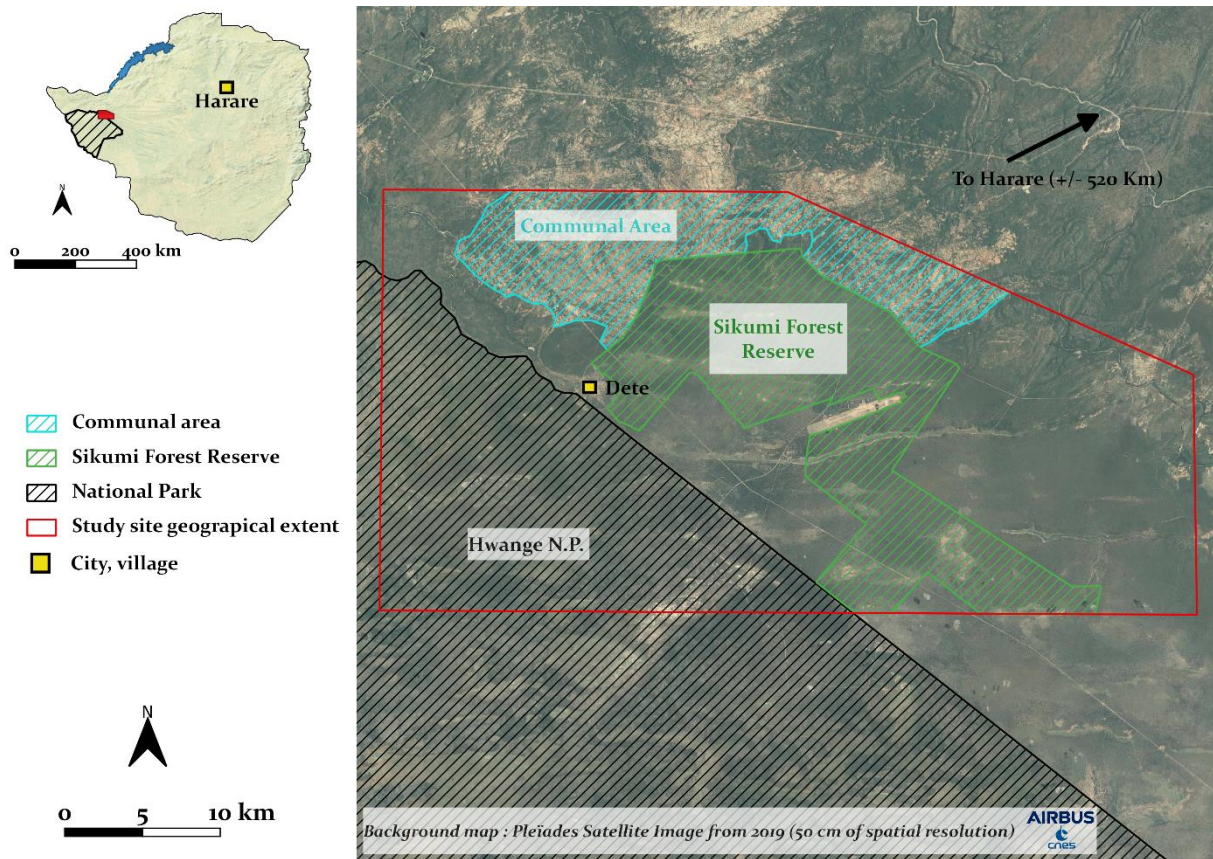


Figure 2.2: Location map of the Hwange/Dete study site

2.1.1.2 Current ecological context

The communal area of Dete is an area dedicated to human settlements with lands allocated by traditional leaders (Guerbois et al., 2013), while HNP is managed by the National Parks and Wildlife Management Authority (NPWLMA) and the SFR is under the supervision of the Forestry Commission, which are both governmental authorities. At the interface between HNP, SFR and communal land tensions exist between local stakeholders. These tensions concern human-wildlife conflicts (Metcalf, 2008), poaching (Muboko & Murindagomo, 2014), illegal wood harvesting, livestock predation by wild carnivores and crop raiding (Guerbois et al., 2012), and disease transmission between domestic livestock and wildlife (de Garine-Wichatitsky et al., 2013; Miguel, Grosbois, Caron, Boulinier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & Garine-Wichatitsky, 2013). Human settlement's locations in the area take their roots in colonial and post-independence policies (Ncube, 2004; Raftopoulos & Mlambo, 2009). Another factor of the human presence in the area is the proximity of protected areas, which attract people hoping to find abundant natural resources for the establishment of traditional subsistence farming and animal husbandry activities (Guerbois et al., 2013). Currently, local communities have no right

of access for any use/extraction of natural resources from HNP, except for occasional grass harvesting for thatching, under close supervision of rangers. The management of the SFR, on the other end, includes a direct use of natural resources as a result of established collaboration between traditional leaders and the forestry commission authority (Perrotton, 2015). Since the droughts that occurred in the area in the early 1990's (Maphosa, 1994), the Forestry Commission and traditional leaders negotiated complementary rights of access in the SFR for neighboring communities. Among those complementary rights, herders obtained the right to graze their cattle within the SFR, although the official authorized distance of incursion remains unclear (2 to 3 km according to the forestry commission and up to 7 km according to local herders) (Guerbois et al., 2013). Indeed, the SFR is essential to local herders as it provides high-quality forage and water for their livestock, both resources that are being scarce in communal land where subsistence mixed farm systems (i.e., seasonal subsistence agriculture and traditional subsistence pastoralism) are the dominant economic activities. The use of the SF also represents a form of land claiming on a territory that was formerly used by the villagers a few decades ago (Perrotton, 2015). Today, contentions between local communities and governmental authorities on the use of the SFR's natural resources still exist and are difficult to resolve. From one end, an extended authorized distance of incursion into the forest is asked while on the other end, a fear of overgrazing to the detriment of wildlife and of an increase of illegal activities such as wood harvesting and poaching is argued. The balance between the different parties living by and for this W/L interface is more precarious than ever.

2.1.2 The interface of Gonarezhou/Malipati and Kruger/Pesvi

2.1.2.1 Geographical, climatic, vegetation and hydrology characteristics

The first study area (1696 km², this area have been determined to encompass the full spatial extent of the observed telemetry data available) presented in this section, the Gonarezhou/Malipati study site, is located in the Southeast Lowveld of Zimbabwe in the Chiredzi district at an altitude ranging between 300 m and 600 m above sea level (Chenje et al., 1998) and at the periphery of the GNP ([Figure 2.3](#)). The second study area presented in this section (2043 km², this area have been determined to encompass the full spatial extent of the observed telemetry data available), the Kruger/Pesvi Study site, is adjacent to the KNP (separated by the international boundary) and, as the Gonarezhou/Malipati study site from

which it is separated by about 32 km following a straight line, is part of the Malipati communal land ([Figure 2.4](#)). The climate of Gonarezhou/Malipati and Kruger/Pesvi study sites is considered as semi-arid (Beck et al., 2018) and is characterized by mean annual temperatures ranging from 25°C to 27°C. The mean annual precipitation is 300 mm–600 mm and is characterized by high inter-annual variability (coefficient of variation \approx 40-45%) (Chenje et al., 1998). The seasons are relatively similar to the ones observed in the Hwange/Dete study site. The rainy season occurs from December to March followed by a cold dry season between April and July and a hot dry season from August to November.

The natural vegetation of the study sites is predominantly Mopane woodlands (*Colophospermum mopane*) found in association with *Kirkia acuminata*, *Dalbergia melanoxylon*, *Adansonia digitata*, as well as diverse species of *Combretum*, *Acacia* and *Commiphora*. In addition, perennial grasses such as *Urochloa mosambicensis* and *Aristida congesta* can be found in the area, usually close from surface water and along dewatered drainage lines. The Mwenezi River, a river with an intermittent flow (generally from November to April with a hydrological peak between December and February), runs north to south through the study area close to the GNP seasonally supporting both wildlife and livestock in water supply before flowing to the Limpopo River. The Limpopo River runs eastwards through the study area close to the KNP and marks the frontier between Zimbabwe and South Africa as well as with the KNP. Contrary to the Mwenezi River, the Limpopo River stays in water all year round despite strong seasonal variabilities of its hydrological regime (Purdon & van Aarde, 2017). During the dry season, water in the Mwenezi River is only available in a few pools that remain in water inside and at close proximity of the main riverbed (Zvidzai et al., 2013).

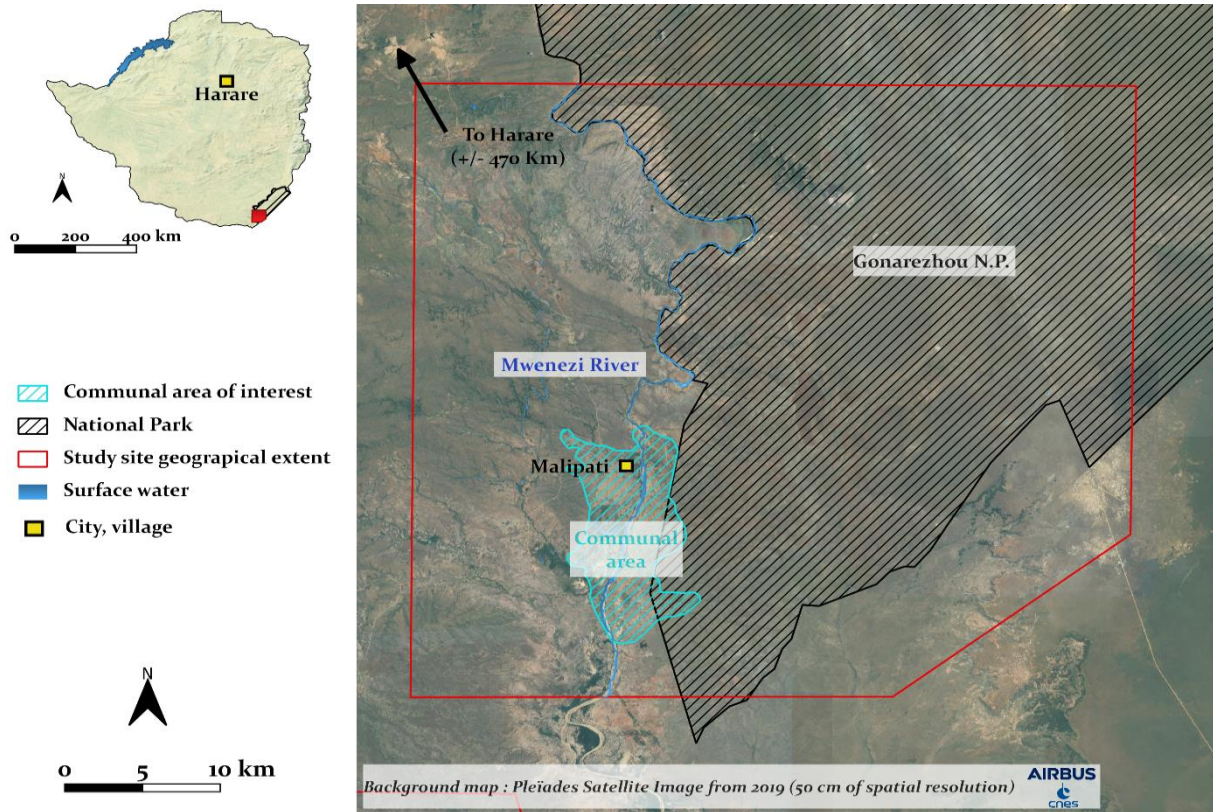


Figure 2.3: Location map of the Gonarezhou/Malipati study site

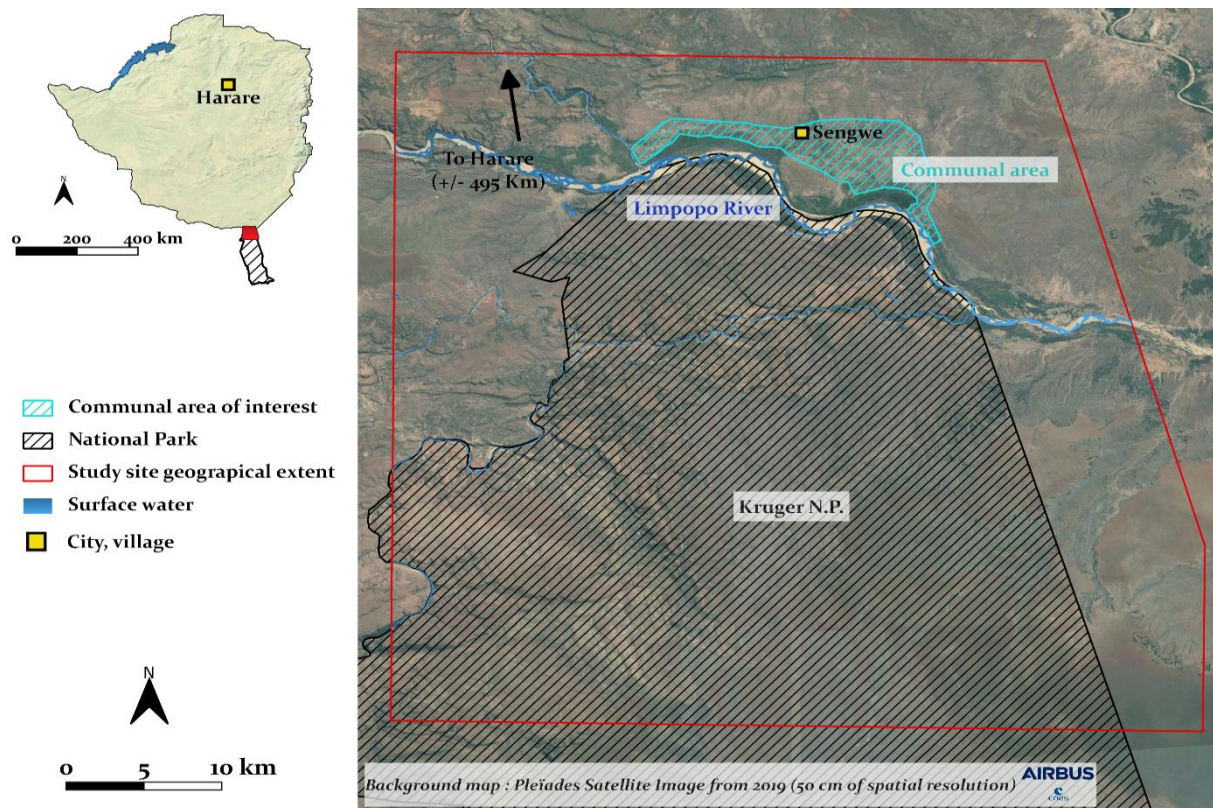


Figure 2.4: Location map of the Kruger/Pesvi study site

2.1.2.2 *Current ecological context*

Two main land use types compose the Gonarezhou/Malipati and Kruger/Pesvi study sites' landscape: a mixed land-use for agriculture and livestock grazing comprised within the communal lands and conservation areas composed of the GNP and less anthropized areas composed of the KNP. Communal lands are characterized by collective and/or community land ownership (Murwira & Skidmore, 2005) and the major land use activities include livestock production, irrigated cropping, as well as rainfed cropping (Harris et al., 2001). The GNP and the KNP are both part of the Great Limpopo TFCA that contains a great diversity of wildlife species, hosting the full spectrum of African savanna mammal diversity, mostly in high abundance (except for rhinos).

The GNP is under the jurisdiction of Zimbabwean governmental authorities for conservation management of the national Park's fauna and flora as well as the hunting and tourism activities supervision and management. In the GNP study area, part of the conservation area adjacent to the communal land is at times used for supplementary grazing by cattle (de Garine-Wichatitsky et al., 2013). This is made possible by a highly porous fenced boundary (damaged by both elephants and humans) between the conservation area and surrounding communal lands. The broken boundary increases the intensity and frequency of interactions between wildlife and livestock (de Garine-Wichatitsky et al., 2013) making this W/L interface particularly prone to potential human-wildlife conflicts such as pathogen transmission (Miguel, Grosbois, Caron, Boulinier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & Garine-Wichatitsky, 2013).

The KNP study site, on the other end, is in an intricate geographical situation as the Limpopo River ([Figure 2.4](#)) acts as a natural border and separates Zimbabwe and South Africa. KNP is dependent of South African National Parks (SANParks) regulations since the creation of the Great Limpopo TFCA in 2002. Even if wildlife cannot roam completely freely between the GNP and the KNP through the Sengwe communal land, regular incursions of wildlife into communal areas has been observed, making interactions and their inherent effects between wild and domesticated animal species at this particular W/L interface possible (Caron et al., 2016).

2.2 Data used in this thesis

2.2.1 Telemetry data

Satellite telemetry using global positioning system (GPS) has the ability to determine temporal and spatial positions of animals in a given area with high precision, temporal accuracy, and position updates available in rapid frequency 24 hours a day (Cagnacci et al., 2010). This breakthrough in technology enabled new insights (e.g., patterns of biodiversity, ecological characteristics of individual species and ecosystem function) into the ecology of animal movements (Kays et al., 2015). Data describing the entire lifetime of movement by individual animals, and species-wide sampling from multiple populations, are now becoming available and offer new opportunities to measure and estimate contacts (Flack et al., 2015). However, few studies on large herbivores occupying African savanna environments using these technologies have been conducted so far (Owen-Smith et al., 2020) and the data used in this thesis and collected in previous works (Miguel, 2012; Valls Fox, 2015) are as valuable as they are scarce.

2.2.1.1 *Capture of animals and installation of GPS collars*

The telemetry dataset used in this thesis has been collected by the CIRAD and its partners (including CNRS, IGF, SANParks, FAO) in several research projects such as the EU-PARSEL project founded by the Food and Agriculture Organization of the United Nations (FAO) and the CIRAD between 2008 and 2011 (Caron, 2011), the Eve Miguel's PhD in 2009-2012 (Miguel, 2012) and the Hugo Valls-Fox's PhD in 2012-2015 conducted within the frame of the ANR SAVARID project (Valls Fox, 2015). Ultra-high frequency (UHF) GPS collars (such as the UHF GPG collars manufactured by African Wildlife Tracking) have been used to monitor buffalo and cattle movements. Alexandre Caron and colleagues collected buffalo and cattle data in Gonarezhou/Malipati study site, Eve Miguel and colleagues collected buffalo and cattle telemetry data in the three study sites and Hugo Valls-Fox and colleagues collected cattle telemetry data in the Hwange/Dete study site. For the three projects, the GPS collars systems were scheduled to acquire locations with a frequency of one hour 24 hours a day. Data were acquired during several periods of recording ([Table 2.1](#) and [Table 2.2](#)). One collar was fitted per herd for the cattle and 2 to 4 per group of buffalo. For the cattle data collected, the dominant

female, according to their owner's perception, was equipped with a collar in order to track the movements of each cattle herd in agreement with cattle owners, traditional authorities, and local veterinary services.

Contrary to the cattle that are relatively easy to access, buffalo required the application of different methods of capture, depending on the site, the capture team's composition, the available material, and the experience. Buffalo groups were sighted from above by helicopter then, one or more buffalo were selected given the protocol requirements (*e.g.*, adult females) to be tele-anesthetized (de Garine-Wichatitsky et al., 2010). The helicopter then landed close to the one or more buffalos and, with or without the support of a ground team, proceeded to sampling (*e.g.*, blood sample, a small piece of tissue (ear) and/or hair) and collaring, before waking-up the animal using chemical antidote. The other method consisted of using a funnel-type boma with a diameter of approximately 400 m. After the installation of the boma, buffalo groups were oriented inside the structure using a helicopter as an instrument to prevent any escape. After an observed lull in buffalo activity, a group team entered the boma to dart selected individuals and proceeded to sampling and collaring. All animals were observed returning to their group after the darting operation. All field operations conformed to the permits and legal requirements of the countries in which they were carried out.

BUFFALO

Study site	Group s	Number of individuals	Individual id	Period of recording	Utilizations
Hwange/Dete	Gp 1	3	AU287/AU291 /AU297	20/04/2010 to 18/08/2011	Calibration/ validation
	Gp 2	4	SAT524/SAT526 /11456/11472	14/11/2012 to 28/09/2013	Calibration/ validation
	Gp 3	4	SAT526/11456 /11472/11473	03/12/2013 to 15/04/2014	Calibration/ validation
Gonarezhou/Malipati	Gp 1	3	B80/B83/B85	13/10/2008 to 03/03/2011	validation
	Gp 2	4	B80/B83/B84/ B85	14/10/2008 to 19/11/2019	validation
Kruger/Pesvi	Gp 1	7	B31810/B34559 / B34564/B34567/ B34571/B34572 /B34575	31/10/2013 to 25/01/2015	validation
	Gp 2	7	B31805/B31810 / B31811/B31813/ B31817/ B31818/ B31820	25/07/2011 to 15/09/2011	validation
	Gp 3	5	B34562/B34563/ B34566/B34574/ B34576	20/12/2013 to 12/02/2014	validation
	Gp 4	4	B34562/B34566/ B34574/B34576	31/10/2013 to 06/02/2015	validation
	Gp 5	2	B1130/B8526	04/06/2010 to 24/12/2011	validation
	Gp 6	3	B1130/B8526/ B31808	25/07/2011 to 14/04/2012	validation

Table 2.1: Details of the buffalo telemetry data used in this thesis

CATTLE

Study site	Number of individuals	Individual id	Period of recording	Utilizations
Hwange/Dete	10	AU387	15/12/2010 to 15/08/2011	calibration/ validation
		AU388/AU389 AU390/AU392	20/04/2010 to 15/08/2011	
		U4	28/11/2012 to 22/11/2014	
		U6	30/11/2012 to 27/06/2014	
		U7	29/11/2012 to 23/01/2014	
		U8	29/11/2012 to 04/12/2014	
		U9	29/11/2012 to 21/11/2014	
Gonarezhou/Malipati	4	382/384/386	26/11/2009 to 16/05/2011	validation
		383	26/11/2009 to 21/10/2010	
Kruger/Pesvi	4	681/682 684/685	16/06/2010 to 25/07/2011	validation

Table 2.2: Details of the cattle telemetry data used in this thesis

2.2.1.2 The utilization of pre-processed telemetry data

The GPS telemetry used in this thesis have been pre-processed by Elodie Wielgus during her PhD (Wielgus, 2020). GPS locations have originally been acquired in decimal degrees with the WGS84 datum. In order to project the data and calculate metrics variables such as distances and speed, all the telemetry data have been projected under the civilian UTM grid reference system (Stott, 1977). Within the civilian UTM grid reference system, horizontal lines are designated by their distance from the equator in meters and vertical lines are measured from a separate point for each zone, namely an imaginary line lying 500 000 meters west of the zone's central meridian. The UTM grid cells corresponding to the study sites were: WGS84 UTM 35S for the

Hwange/Dete study site and WGS84 UTM 36S for the Gonarezhou/Malipati and Kruger/Pesvi study sites. The established technique by Bjørneraas *et al.*, 2010 has then been applied to identify GPS locations where movement patterns was unrealistic, using thresholds for distance, speed and turning angles between two recorded locations (criteria used: $\Delta = 100,000$ m; $\mu = 10,000$ m; $\alpha = 3,000$ m/h; $\theta = -0.95$) (Wielgus, 2020). Some of the GPS locations were presenting time delays after the collecting sessions. In the case when the GPS location has been taken within 5-min interval from programmed acquisition time, the GPS location has been conserved and the corresponding time attribute recessed at the top of the hour. In the other case, the GPS location has been recalculated for the programmed acquisition time by linear interpolation (Wielgus, 2020).

Having spatialized the pre-processed telemetry data to visually and qualitatively (e.g., observation of the attribute data such as IDs and dates of recording) the buffalo and cattle telemetry data have been grouped by locations and time of recording for each of the three study sites ([Table 2.1](#) and [Table 2.2](#)). All the individuals of each of the two species that had the same location at the same time have been considered as a herd entity (group) in order to derivate herd's metrics (herd metrics will be detailed in chapter 5). The same individual could be considered as part of several groups ([Table 2.1](#) and [Table 2.2](#)). Also, from all the telemetry data available, only individuals that geographically overlapped with the other focal species have been considered for each of the three study sites ([Figure 2.5](#)), thus respecting a generic selection protocol. Combining the three study sites, a total of 18 cattle and 33 buffalo individuals have been used within this thesis ([Figure 2.5](#)).

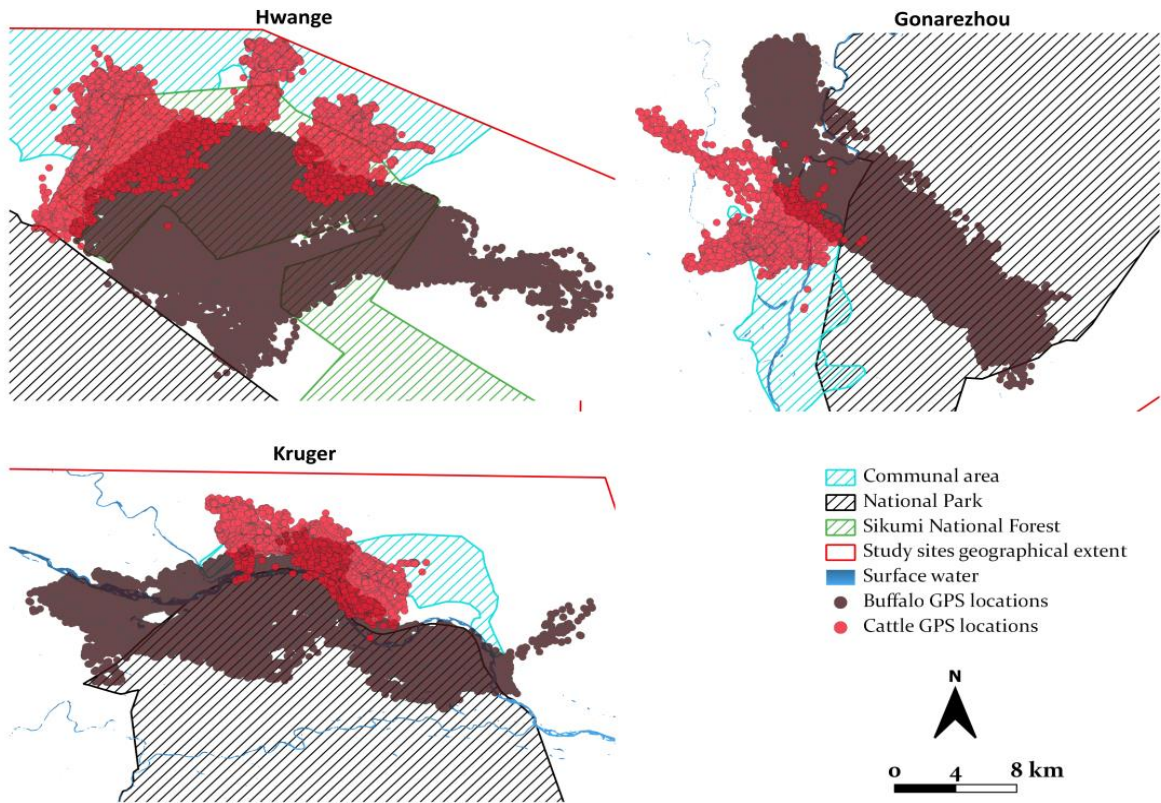


Figure 2.5: Spatialized localizations of the cattle (represented in red dots) and buffalo (represented in brown dots) telemetry data for the entirety of their respective recorded periods at the three study areas. In Hwange/Dete, 10 cattle individuals and 8 buffalo individuals complete the dataset. In Gonarezhou/Malipati, 4 cattle individuals and 4 buffalo individuals complete the dataset. In Kruger/Pesvi, 4 cattle individuals and 21 buffalo individuals complete the dataset.

2.2.2 Remote sensing data

The use of SRS in ecology regarding environment monitoring in general and animal conservation and movement in particular is well known and well disseminated through current scientific information channels (Pettorelli, Laurance, et al., 2014; Rose et al., 2015). The last few years have seen the emergence of a multitude of new optical and radar sensors, thus multiplying the possible applications for the scientific community (Zhu et al., 2017). In this particular context, we opted to use SRS imagery to characterize the environmental drivers that influence the movements of the two focal species in space and time and use them in combination with the already collected telemetry data at our disposal.

Within the frame of this thesis, we have chosen to use satellite images produced by the Sentinel-2 satellite constellation that comprises two polar-orbiting satellites placed in the same sun-synchronous orbit and phased at 180° to each other (Drusch et al., 2012). These two optical

satellites provide images with wide swath width (290 km), a high revisit time (10 days at the equator with one satellite and 5 days with 2 satellites, which results in 2-3 days at mid-latitudes), a medium spatial resolution of 10 meters, 20 meters and 60 meters, and 13 spectral bands in the visible, near infrared, and short wave infrared part of the spectrum (Drusch et al., 2012). The first satellite has been launched in June 2015 while the second one has been launched in March 2017. The Sentinel-2 constellation is part of the Copernicus program that has been initiated by the European Commission in partnership with the European Space Agency (ESA) in 1998. Currently, access to the database of satellite images produced by the Sentinel-2 satellite constellation is opened to everyone and completely free of charge. Sentinel-2 satellite images' spatial resolution allows landscape scale analysis (Ramoelo et al., 2014) as well as landcover classification (Pelletier et al., 2019) while the included 13 spectral bands offer the possibilities to derive spectral indices that can be used to efficiently characterize different elements of the environment such as surface water (Bie et al., 2020) and different types of vegetation (Frampton et al., 2013). Sentinel-2 SRS images also offers a large orbital swath which limits the number of tiles to be downloaded to cover large areas and have a sufficient revisit time period to monitor the temporal variation of surface water for instance. For all these reasons, we have favored the use of Sentinel-2 SRS images over other medium spatial resolution SRS images such as Landsat that are produced and made available by the National Aeronautics and Space Administration (NASA) since 1972. These images certainly offer greater temporal coverage than Sentinel-2 satellite images but at a lower spatial resolution (30 meters), with a more limited orbital swath capacity (185 km compared to 290 km for the Sentinel-2) as well as with a lower time revisit frequency (16 days and 8 days with Landsat 7 and 8 combination). All these elements combined can be considered too restrictive for the analysis of animal movements at the landscape scale and the combine use with our telemetry dataset.

As no Sentinel-2 satellite images were produced at the time of the telemetry data acquisition ([Table 2.1](#) and [Table 2.2](#)), satellite images from 2018 have been selected. 2018 was the most recent year of SRS data acquisition at the beginning of the thesis and was a representative year regarding the annual precipitation measured in the three study areas according to the Tropical Applications of Meteorology using SATellite data and ground-based observations (TAMSAT) ([Figure 2.6](#)). The TAMSAT V3.1 data that have been used is among the best open-source precipitation data in terms of precipitation event detection over the African continent at a spatial resolution of 0.0375° (approx. 4 km) (Dinku et al., 2018). The TAMSAT data have been developed by the University of Reading in collaborations with the Climate Division of the National Centre for Atmospheric Science (NCAS) and the National Centre for Earth Observation (NCEO) (Maidment et al., 2014, 2017; Tarnavsky et al., 2014). TAMSAT cumulative rainfall datasets and the derived daily estimates can be considered temporally consistent, which is

important in both assessing climatic risks and for seasonal rainfall monitoring (Thiemig et al., 2012; Toté et al., 2015).

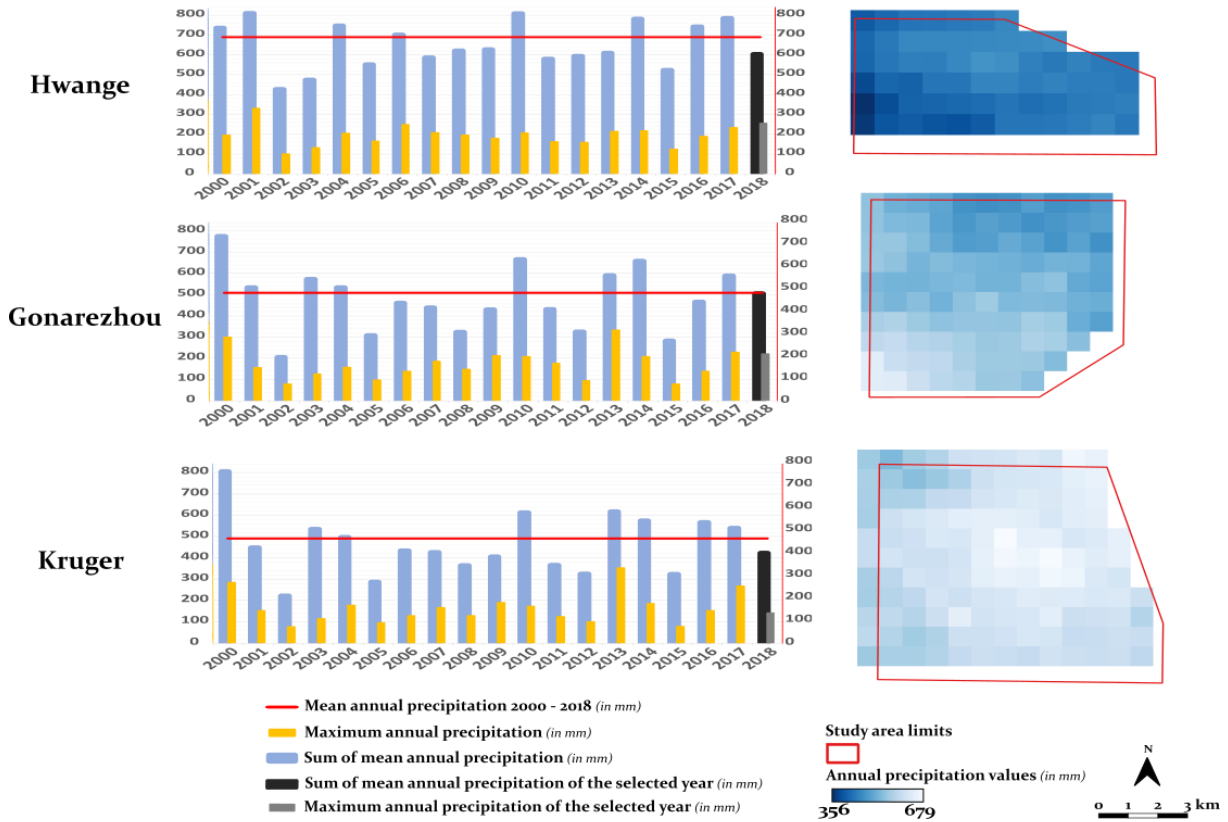


Figure 2.6: Histograms representing the sum of annual precipitation (blue bars) and the maximum annual precipitation per year (yellow bars) as well as the mean annual precipitation (red line) over the period 2000-2018 for all three study areas according to the TAMSAT V3.1 data (Maidment et al., 2017; Maidment et al., 2014; Tarnavsky et al., 2014). The year 2018 used as reference for the download of the Sentinel-2 images is represented in black (sum of annual precipitation) and gray (maximum annual precipitation). The 2018 annual precipitation are slightly under average in Hwange/Dete (610 mm < 695 mm) and Kruger/Pesvi (420 mm < 490 mm) but remain in the same orders of magnitude and are right on average in Gonarezhou/Malipati (at around 510 mm). The maps of the specialized mean annual precipitations for the period 2000-2018 are also represented on the right side of the figure. These maps show a spatial homogeneity of precipitation across the three study areas.

Therefore, to characterize the landcover and the surface water (more details in chapter 4), 72 Sentinel-2 satellite images have been downloaded in level 1C which provides Top of Atmosphere reflectance and orthorectified images (Table 2.3). The Sen2Cor v2.8 application (Sen2Cor, ESA, <http://step.esa.int/main/third-party-plugins-2/sen2cor/>) (Louis et al., 2016) has been used to apply the atmospheric corrections, thus transforming L1C images to level L2A (Top of Canopy) images. 6 tiles (one tile corresponding to the spatial extent of one of the spatial division grid cells) were necessary to cover the entire study zone spatial extent (Table 2.3). The dates of the image selected represent days with less than 10% of cloud cover for the entire year 2018 with

one image per month for each tile. For the month of February however, no images were cloud free in 2018. As a result, Sentinel-2 satellite images from February 2019 have been selected instead ([Table 2.3](#)).

Characteristics	Values
Spatial and spectral resolutions	10 x 10 m B2 (490 nm), B3 (560 nm), B4 (665 nm), B8 (842 nm) 20 x 20 m B5 (705 nm), B6 (740 nm), B7 (783 nm), B8a (865 nm), B11 (1610nm), B12 (2190 nm)
Temporal resolution	5 days
Swath width	290 km
Tile size	100 x 100 km
References of selected tiles	T35KNV – T35KNU – T35KMOV – T35KMU – T35KLV – T35KLU
Dates of the downloaded tiles	T35KNV (2018-01-05 / 2019-02-24 / 2018-03-16 / 2018-04-20 / 2018-05-05 / 2018-06-04 / 2018-07-04 / 2018-08-18 / 2018-09-12 / 2018-10-12 / 2018-11-16 / 2018-12-21) T35KNU (2018-01-05 / 2019-02-24 / 2018-03-16 / 2018-04-25 / 2018-05-10 / 2018-06-14 / 2018-07-04 / 2018-08-18 / 2018-09-12 / 2018-10-12 / 2018-11-11 / 2018-12-11) T35KMOV (2018-01-08 / 2019-02-22 / 2018-03-14 / 2018-04-23 / 2018-05-03 / 2018-06-12 / 2018-07-02 / 2018-08-16 / 2018-09-15 / 2018-10-10 / 2018-11-19 / 2018-12-14) T35KMU (2018-01-13 / 2019-02-22 / 2018-03-14 / 2018-04-23 / 2018-05-03 / 2018-06-12 / 2018-07-02 / 2018-08-16 / 2018-09-15 / 2018-10-10 / 2018-11-14 / 2018-12-14) T35KLV (2018-01-08 / 2019-02-22 / 2018-03-14 / 2018-04-23 / 2018-05-03 / 2018-06-12 / 2018-07-02 / 2018-08-16 / 2018-09-15 / 2018-10-10 / 2018-11-14 / 2018-12-14) T35KLU (2018-01-08 / 2019-02-22 / 2018-03-14 / 2018-04-23 / 2018-05-03 / 2018-06-12 / 2018-07-02 / 2018-08-16 / 2018-09-15 / 2018-10-10 / 2018-11-14 / 2018-12-14)

Table 2.3: Summary of the different Sentinel-2 tiles characteristics used in the thesis to produce the land use maps and the surface water classifications

2.2.3 In-situ data and empirical knowledge

A dataset of GPS coordinates locating surface water (both artificial and natural) through field exploration has been used to assess the accuracy of the developed surface water classification (more details in chapter 4). These data have been collected during previous studies in the three different study areas and correspond to projected vector points (Guerbois, 2012; Miguel, Grosbois, Caron, Boulinier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & Garine-Wichatitsky, 2013; Valls Fox, 2015). In The Hwange/Dete study site, 38 boreholes (artificial surface water supplies by solar pumping station) have been identified in the communal area. Within the SRF, 57 vector points constitute the first dataset of boreholes while the second dataset is composed of 86 vector points. Regarding these two datasets, some of the points are located in direct proximity of the surface water while others are located on a road passing by. Their precision and the recording protocol differ greatly. In the Gonarezhou/Malipati study site, 16 boreholes have been identified within the communal area. In the Kruger/Pesvi study site, the borehole dataset is composed of 126 referenced vector points but the majority of them are located within the national park. Only two of them are located within the geographical extent of the study site recorded buffalo telemetry data.

Also, it is important to note that empirical knowledge gathered during previous studies in the three study sites has been extensively and continuously transmitted through a variety of contact with scientists involved or still exercising in the field (most of the thesis supervising team) and various local stakeholders (farmers, veterinarians, park rangers, Zimbabwean students, and village leaders). Indeed, a short field trip of 10 days has been organized in the Hwange/Dete region in June 2019 to probe the field reality and give an overview of the issues that this thesis aims to address. This valuable knowledge positively influenced the current work by limiting potential cognitive bias as well as by reinforcing the apprehension of the study area geography, landscape composition, socio-economic situation, and ecological context.

2.3 Chapter summary

- The three wildlife livestock interfaces chosen as study sites have very contrasting ecological, geographic, and hydrological profiles.
- The three study sites have relatively comparable climates and heterogeneous vegetation structures that are representative of savannah wooded landscapes found across Southern Africa.
- Cattle and buffalo telemetry data have a temporal frequency of one hour and have been collected over different time periods for the three study sites. Concerning the buffalo telemetry data, several individuals were recorded at the same location at the same time, allowing to constitute groups of several individuals.
- Time series of Sentinel-2 satellite images for the year 2018 have been downloaded for all three study sites in order to characterize environmental variables at the landscape scale with a spatial resolution of 10 meters.
- Spatialized environmental data allowing the geographical location of natural and artificial water points exist for the three study sites. However, the Hwange/Dete study site has a more extensive database than the other two study sites considered.

Chapter 3

Literature review of the environmental drivers influencing the buffalo and cattle movements in space and time

Table of content

3.0 Preamble

3.1 The article

3.1.1 Introduction

3.1.2 Review article methodology

3.1.3 Environmental Drivers Influencing the Movements of Buffalo and Cattle and the Satellite Remote Sensing Tools to Characterize them

3.1.4 Discussion

3.1.5 Conclusion

3.2 Chapter summary

3.0 Preamble

Having learned about the existing dataset, the study sites and their hydrological, climatic, ecological and geographical characteristics, as well as the two focal animal species considered to focus the study on, this chapter focuses on discriminating the environmental variables that influence the buffalo and cattle movements in space and time, as well as the existing remote sensing methods to spatially and temporally characterize these environmental variables. To do so, a review article has been considered in order to present the results of this particular question in a comprehensive and potentially exploitable way by the whole scientific community specializing in animal movement ecology and wishing to become familiar with key concepts of remote sensing. The article was published in 2020 in the open-access and peer-reviewed journal “Remote Sensing” (<https://www.mdpi.com/journal/remotesensing>) that publishes regular research papers, reviews, technical notes and communications covering all aspects of remote sensing science, from sensor design, validation / calibration, to its application in geosciences, environmental sciences, ecology and civil engineering.

3.1 The article



remote sensing



Review

Remote Sensing of Environmental Drivers Influencing the Movement Ecology of Sympatric Wild and Domestic Ungulates in Semi-Arid Savannas, a Review

Florent Rumiano ^{1,2,*}, Elodie Wielgus ^{3,4,5,6,7}, Eve Miguel ^{8,9}, Simon Chamailé-Jammes ^{6,7,10}, Hugo Valls-Fox ^{6,7,11,12}, Daniel Cornélis ^{13,14}, Michel De Garine-Wichatitsky ^{4,5,15}, Hervé Fritz ^{7,16,17}, Alexandre Caron ^{4,5,18} and Annelise Tran ^{1,2,4,5}

¹ CIRAD, UMR TETIS, F-97490 Sainte-Clotilde, Réunion, France; annelise.tran@cirad.fr

² TETIS, Univ Montpellier, AgroParisTech, CIRAD, CNRS, INRAE, 34090 Montpellier, France

³ Division of Biology and Conservation Ecology, Manchester Metropolitan University, Manchester M1 5GD, UK; elodie.wielgus@stu.mmu.ac.uk

⁴ CIRAD, UMR ASTRE, F-34398 Montpellier, France; michel.de_garine-wichatitsky@cirad.fr (M.G.W.); alexandre.caron@cirad.fr (A.C.)

⁵ ASTRE, Univ Montpellier, CIRAD, INRAE, 34090 Montpellier, France

⁶ CEFÉ, Univ Montpellier, CNRS, EPHE, IRD, Univ. Paul Valéry Montpellier 3, 34090 Montpellier, France; simon.chamaille@cefe.cnrs.fr (S.C.); hugo.valls-fox@cirad.fr (H.V.)

⁷ LTSER France, Zone Atelier CNRS “Hwange”, Hwange National Park, Bag 62 Dete, Zimbabwe; herve.fritz@cnrs.fr

⁸ MIVEGEC, Univ. Montpellier, IRD, CNRS, 34090 Montpellier, France; eve.miguel@ird.fr

⁹ CREES Centre for Research on the Ecology and Evolution of Disease–Montpellier, 34090 Montpellier, France

¹⁰ Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, 0083 Pretoria, South Africa

¹¹ CIRAD, UMR SELMET, PPZS, 6189 Dakar, Senegal

¹² SELMET, Univ Montpellier, CIRAD, INRAE, Institut Agro, 34090 Montpellier, France

¹³ CIRAD, Forêts et Sociétés, F-34398 Montpellier, France; daniel.cornelis@cirad.fr

¹⁴ Forêts et Sociétés, Univ Montpellier, CIRAD, 34090 Montpellier, France

¹⁵ Faculty of Veterinary Medicine, Kasetsart University, 10900 Bangkok, Thailand

¹⁶ UCBL, UMR CNRS 5558, University of Lyon, 69007 Lyon, France

¹⁷ World Wildlife Fund, Washington, DC 20037-1193, USA

¹⁸ Faculdade de Veterinária, Universidade Eduardo Mondlane, 257 Maputo, Mozambique

* Correspondence: florent.rumiano@cirad.fr; Tel.: +33-638-2526-72

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Abstract: Interfaces between protected areas and their peripheries in southern Africa are subject to interactions between wildlife and livestock that vary in frequency and intensity. In these areas, the juxtaposition between production and conservation land uses in a context of increasing anthropisation can create issues associated with human-wildlife coexistence and raises concerns for biodiversity conservation, local development and livelihoods. This literature review aimed at addressing the need to consolidate and gather in one article current knowledge on potential uses of satellite remote sensing (SRS) products by movement ecologists to investigate the sympatry of wildlife/domestic ungulates in savanna interface environments. A keyword querying process of peer reviewed scientific paper, thesis and books has been implemented to identify references that (1) characterize the main environmental drivers impacting buffalo (*Syncerus caffer caffer*) and cattle (*Bos taurus* & *Bos indicus*) movements in southern Africa environments, (2) describe the SRS contribution to discriminate and characterize these

drivers. In total, 327 references have been selected and analyzed. Surface water, precipitation, landcover and fire emerged as key drivers impacting the buffalo and cattle movements. These environmental drivers can be efficiently characterized by SRS, mainly through open-access SRS products and standard image processing methods. Applying SRS to better understand buffalo and cattle movements in semi-arid environments provides an operational framework that could be replicated in other type of interface where different wild and domestic species interact. There is, however, a need for animal movement ecologists to reinforce their knowledge of remote sensing and/or to increase pluridisciplinary collaborations.

Keywords: African savanna; animal movements; earth observation imagery; remote sensing; sympatric wild and domestic ungulates; wildlife-livestock interface

1. Introduction

In Africa, human populations living at the edge of protected areas have significantly increased in recent years [1,2]. This burst in human population is a challenge for biodiversity conservation in protected areas (PA) and livestock production in adjacent communal lands (CL) where these land uses coexist [3]. At the PA-CL interfaces, interactions between wildlife, people and their livestock frequently occur [4,5] even when park or veterinary fences, largely detrimental to wildlife movements, exist [6–8]. This growing number of interactions potentially increases human/wildlife coexistence related issues [3] such as competition for resources inside/outside protected areas [9], predation of livestock by wild carnivores [10], crop destruction by wildlife [11], and risk of pathogen transmission between wild and domesticated species [12–14]. These complications associated with human/wildlife coexistence raise challenges for biodiversity conservation and local development. They impact local communities' livelihoods and well-being [15–18], and threaten the sustainable coexistence between stakeholders involved in the management of these land-uses. In this context, identifying and characterizing environmental drivers that condition animal movements in space and time is essential to assess the potential opportunities and threats associated with wild/domestic interactions in PA-CL interfaces.

The potential for SRS applications, regarding environment monitoring in general and animal conservation in particular, has been largely stressed [19,20]. Indeed, SRS techniques provide an increasing number of sensors [21–26] that may characterize the environmental drivers impacting animal movements at different space and time scales. Moreover, SRS offers continuous temporal follow-up data in areas where in-situ data are nonexistent and/or difficult to collect [27], as it is the case in the savanna landscapes in southern African PA-CL interfaces [28]. In these heterogeneous open environments with high variability in soil composition, topography, and subject to dynamic processes such as rainfall, fire, climate change, herbivory and human impacts [29–31], SRS could provide viable tools to predict biophysical measurements of cover, density, and biomass of savanna vegetation [32,33]. However SRS also faces difficulties in retrieving vegetation spectral response due to soil background, vegetation shadow, standing dead vegetation occurring in these arid and semi-arid areas [34,35]. Despite these limitations, combining SRS with recent advances in telemetry technology is key to assess wildlife/domestic animal interactions in savanna landscapes, especially at PA-CL interfaces [36–38].

The African buffalo (*Syncerus caffer caffer*) and cattle (*Bos taurus* & *Bos indicus*) are keystone species for conservation and production systems in southern African PA-CL interfaces. The understanding of their functional ecology constitutes an applied example on how SRS can be efficiently used to design a framework of animal movement analyses. The African buffalo is one of the “Big Five” [39] and contributes to consumptive and non-consumptive tourism [40,41], provides a source of proteins and income for local communities [42] and is an important member of the ungulate guild who shapes habitat heterogeneity in and outside protected areas where the human presence is low [43–46]. Cattle, in subsistence farming communities, provide draught power, source of protein, cash incomes, safety net and social status [47–49]. Buffalo and cattle are both grazer ungulates, close phylogenetically, sharing

common resources (i.e., forage and water) [50], and are thus likely to overlap in range and compete for resources, particularly in environments where resources are spatially segregated (e.g., savannas) [51,52]. Both species rely on their behavior and the management of the land use by humans to cope with constrained access to natural resources (e.g., access to artificial water, forage intake by the herder) [53,54]. Their shared use of space increases the likelihood of direct (i.e., the use of the same space at the same time) and indirect (i.e., the use of the same space at different times) contacts, which in turn promotes the risk of pathogen transmission [12,55–58], a threat to farmers and biodiversity conservation [4,13]. Given this complex ecological context, characterizing buffalo and cattle habitats to understand their movements in space and time in conjunction with currently available SRS applications and methodologies is necessary.

In this review article, we aim at (1) reviewing the main environmental drivers impacting buffalo and cattle movements in southern Africa interface environments, (2) describing the SRS contribution to discriminate and characterize these drivers in southern Africa interfaces. The underlying objective is to facilitate the uses of SRS by movement ecologists in order to improve wildlife/domestic animals management and conservation in different types of savanna interfaces across the globe. It is adding and completing previous works that focused on the link between SRS, environmental challenges and animal movement but in a wider ecological context [20,59].

2. Review Article Methodology

A literature review of peer-reviewed articles, thesis and books in English (such as defined in Grant and Booth (2009) [60]) has been conducted on the following topics: (i) behavioral and movement ecology of buffalo and cattle in southern Africa; (ii) existing remote sensing tools allowing the discrimination in time and space of determined environmental drivers. The Web of Science database was used to retrieve relevant references via a two steps keyword querying process without time constraint. At each step, a systematic screening based on the title and the abstract was first conducted to select the articles, books or thesis for full-text reading. Selected references bibliographies have also been read to extract additional relevant articles, book or thesis.

The first step was to discriminate the environmental drivers impacting buffalo and cattle movements in space and time. The different keywords combined in no particularly order in the first step were “buffalo”; “syncerus caffer”; “cattle”; “bos taurus”; “bos indicus”; “ungulates”; “southern africa”; “movement”. The search resulted in 787 references. After abstract screening and the removal of replicates, 87 peer-reviewed articles, thesis and books from 1975 to 2020 were included in the review ([Figure 3.1](#)). Among them, 29 (33.3%) articles concerned buffalo only, 15 (17.2%) cattle only, and 43 (49.5%) both species. Landcover & Vegetation, surface water, precipitation and savanna fire emerged as main environmental drivers impacting focal species (buffalo & cattle) ([Figure 3.1](#)).

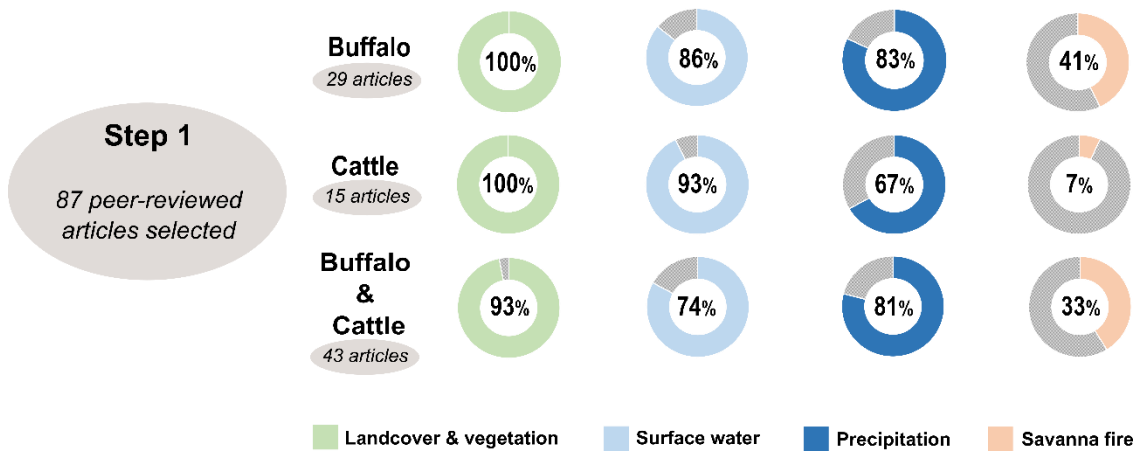


Figure 3.1. Environmental driver statistics of the step 1 bibliography. The percentage of articles identifying the environmental drivers of animal movements among all the peer-reviewed selected articles is presented according to the species considered (buffalo only, cattle only, buffalo & cattle).

The second step was to define the existing methodologies in remote sensing to characterize the different environmental drivers previously determined. The different keywords combined in no particular order in the second step were all the environmental drivers determined in the first step: “surface water”; “precipitation”; “rainfall”; “vegetation”; “fire” with the addition of the following keywords: “remote sensing”; “Earth observation imagery”; “landcover”; “land-use”; “spectral index”; “radar”; “optical”; “savanna”. The search resulted in 1140 references and, after abstract screening and the removal of duplicates, 240 articles from 1974 to 2020 were included in the review.

In total, 327 articles from 1974 to 2020, divided into 9 categories, have been selected and used as reference in this paper (Figure 3.2A). The “diverse” category includes the articles with general themes close to the study, but which cannot fit into the other specified categories. Two thirds of the selected peer-reviewed articles are about SRS, with a majority of them specifically focusing on Landcover & vegetation and surface water (Figure 3.2A). We observed an increase in publications related to SRS since the early 2000s and a steady frequency of peer-reviewed articles focusing on buffalo and cattle (Figure 3.2B).

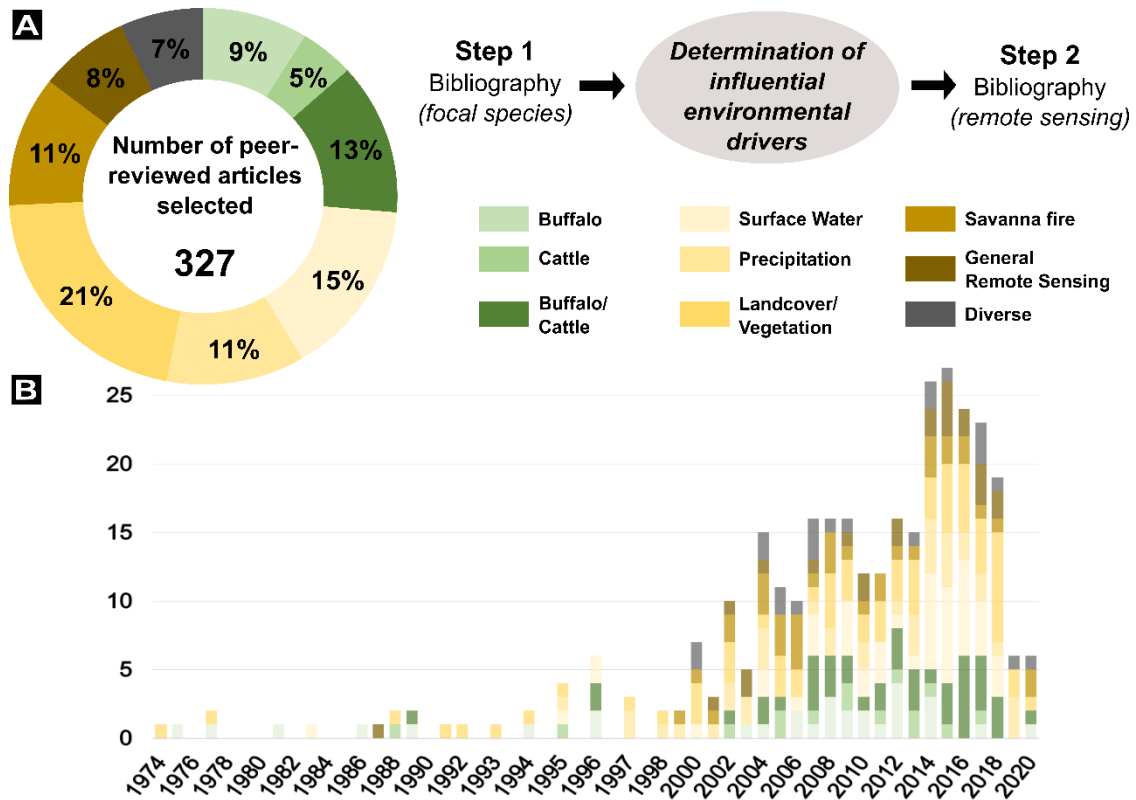


Figure 3.2. Statistics and chronology of the article bibliography by topic category. (A) The ring diagram represents the percentage of each category in relation to the total number of reviewed articles. (B) The horizontal axis of the histogram corresponds to the published year of the selected articles. The vertical axis corresponds to the number of published articles according to their respective categories.

3. Environmental Drivers Influencing the Movements of Buffalo and Cattle and the Satellite Remote Sensing Tools to Characterize them

The main environmental drivers (Landcover/vegetation, surface water, savanna fire and precipitation) identified through the reviewing process (Section 2) are illustrated through this section using the example of a buffalo/cattle interface localized in HNP, Zimbabwe ([Figure 3.3](#)). In this particular context, the two focal species interact at the interface between a national park and an adjacent CL ([Figure 3.3A](#)) where habitats cover a wide variety of environments and natural resources.

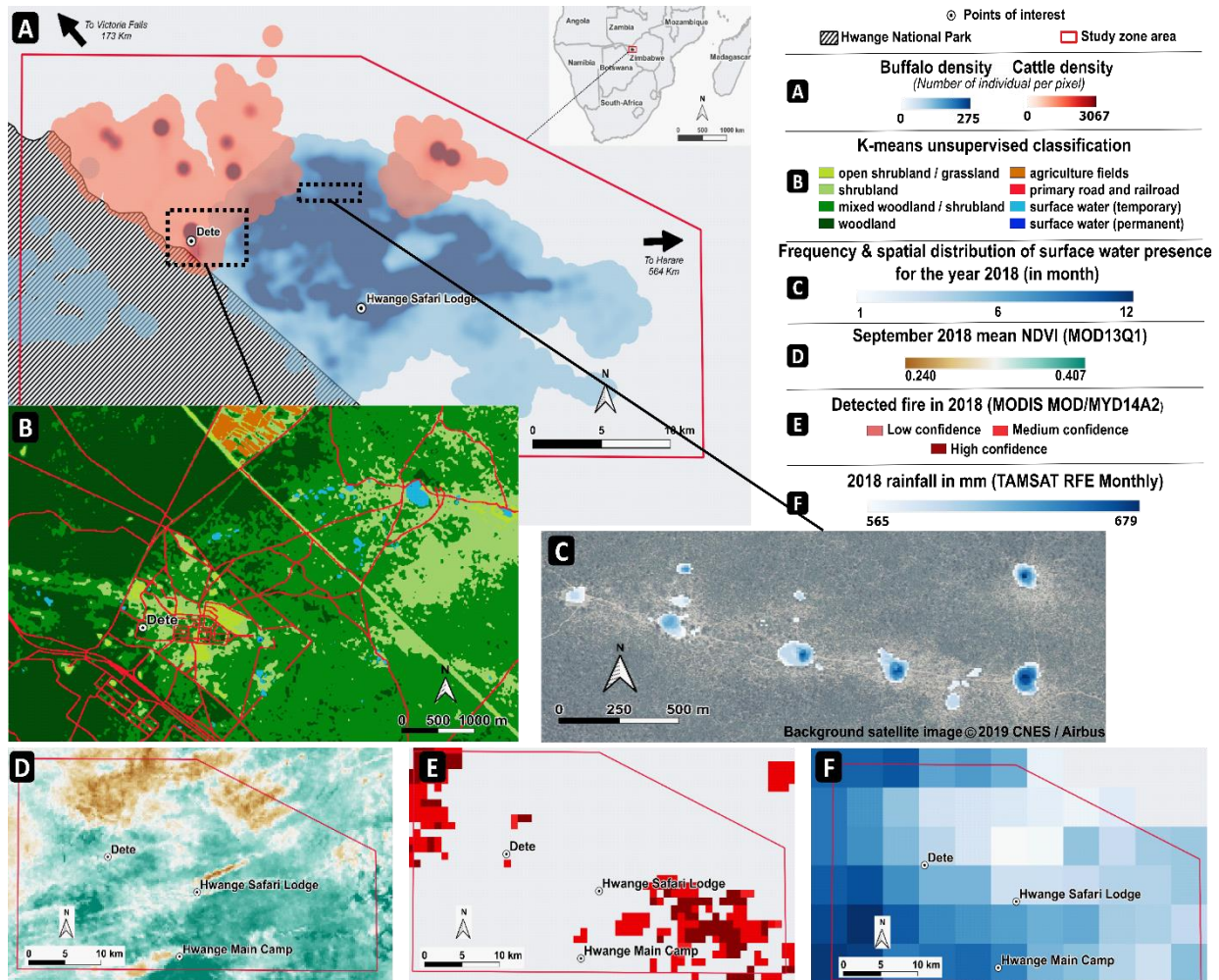


Figure 3.3. Illustrative examples of SRS-derived environmental drivers of buffalo and cattle movement in HNP, Zimbabwe (refer to supplementary materials for a complete description of the data used). (A) Map of the buffalo and cattle density based on GPS data set for both species (number of individual per pixel in the HNP interface ecosystem at 5m spatial resolution) [12]. (B) K-means unsupervised landcover classification map of Dete municipality next to HNP derived from Sentinel-2 imagery with a 10 m spatial resolution [61]. (C) Frequency and distribution of surface water presence at 10 m spatial resolution obtained via the Random Forest (RF) algorithm applied on a sentinel-2 image of March 2018 after the application of atmospheric corrections [61]. (D) Normalized Difference Vegetation Index (NDVI) map with a 250 m spatial resolution from the Moderate-Resolution Imaging Spectroradiometer (MODIS). (E) Map of fire detected in 2018 using the MOD14A2 Fire product with a 1 km spatial resolution. (F) Map of the yearly precipitation estimations by the Tropical Applications of Meteorology using SATellite data (TAMSAT V3.0) product with a 4 km spatial resolution [62,63].

3.1. Landcover

3.1.1. How Landcover and Vegetation Influences Cattle and Buffalo Movements

Landcover (cropland, forest, surface water, artificial cover, bare soil, human infrastructures,...) affects animal movements because it reflects differences in resource availability, habitat structure preferences and ease of travel [64–66]. Buffalo and cattle are ruminants and predominantly grazers [67–69]. They are associated with open environments, where grass species are more abundant [70], and the spatial and temporal variability of fodder resource drives the foraging responses of both species [71]. Seasonal shifts in the composition of their diet are common due to the availability of grass species [72,73]. During the dry season, i.e., when quantity and quality of food resources decrease, buffalo and

cattle adopt a selective and opportunistic switching between different types of habitat or concentrated feeding close to water sources [72,74]. Buffalo tend to avoid areas used by cattle due to strong dietary overlap [75,76], the presence of human activities, and can travel long distances to find suitable feeding resources during the dry season [71,77]. During the wet season, buffalo tend to select available feeding resources located close to watering points, limiting their daily travelled distances [70]. Cattle can range further away from their enclosures on their own, sometimes into protected areas in search of quality forage when the season is dry and when there is no fences surrounding the park [78]. In contrast, during the wet season, cattle focus on accessible and available shrub vegetation or low lying herbaceous vegetation at proximity of their respective enclosure and inside natural park in some instance [37]. Cattle are however prevented to enter agricultural fields during the growing season [79].

3.1.2. SRS Basics for Characterizing and Classifying Landcover

SRS is widely used to assess landcover [80–84]. Different types of satellite sensors ([Table 3.1](#)) record the electromagnetic radiations which characterize the landcover, may this be the radiation reflected (optical sensors), the radiation emitted (thermal infrared and passive microwave sensors) or the radiation scattered (active radar sensors) [85]. Their characteristics (spatial resolution, revisit time period, spatial coverage, data availability, spectral resolution—see [Table 3.1](#)) define their capacities to map different land cover types on a given study area.

Table 3.1. Small subset of Earth observation satellite systems allowing data acquisition that can potentially be used in the field of animal movement ecology.

Optical Remote Sensing Satellites							
Sensor Resolution	Satellite	Spatial Resolution	Revisit Time Period	Nb of Spectral Bands	Access	Data Availability	Used in Buffalo/Cattle Ecological Studies
Low Resolution	NOAA	1.1 Km	2 times a day	5	Open-source	1978-present	[86,87]
	MODIS	Bands 1-2 250 m / bands 3-7 500 m / bands 8-36 1 km	2 times a day	36	Open-source	1999-present	[29,54,67,79,87–89]
	Suomi NPP	Bands I1-5 375 m / bands M1-16 750 m	2 times a day	22	Open-source	2012-present	-
	Envisat MERIS	300 m	3 days	15	Open-source	2002-2012	-
	Sentinel-3	300 m	2 days	21	Open-source	2016-present	-
Medium Resolution	Landsat	Pan* 15 m / MS* 30 m / TIR* 60 to 100 m	16 days	4-11	Open-source	1972-present	[11,37,88,90]
	Sentinel-2	VNIR* 10 m / SWIR* 20 m / ACB* 60 m	5 days	13	Open-source	2015-present	[91]

	Aster	VNIR 15 m / SWIR 30 m / TIR 90 m	16 days	14	Open-source	1999-present	-
High Resolution	Spot	Pan 1.5 to 2.5 m / MS 6 to 10 m	26 days	4-5	Licensed	1986-present	[26]
	Ikonos	Pan 1 m / MS 4 m	1.5–3 days	5	Licensed	1995-2015	[54,92]
	Rapideye	MS 5 m	1–5.5 days	5	Licensed	2008-present	[26]
	ZY-3	Pan 2.1 m / MS 5.8 m	5 days	4	Licensed	2012-present	-
	GF-1 / GF-2	MS 5 m	4–5 days	5	Licensed	2013-present	-
	Planetscope - DOVEs	MS 3 m	Daily	4	Licensed	2017-present	-
Very-high Resolution	Quickbird	Pan 0.61 m / MS 2.24 m	2.7 days	5	Licensed	2001-2015	-
	WorldView	Pan 0.31 m / MS 1.24 m	1–4 days	4-17	Licensed	2007-present	[79]
	Geoeye	Pan 0.41 m / MS 1.64 m	3 days	5	Licensed	2008-present	-
	Pleiaides	Pan 0.7 m / MS 2.8 m	Sub-daily	5	Licensed	2011-present	-
	Skysat	Pan 0.9 m / MS 2 m	Sub-daily	5	Licensed	2013-present	-
Radar Remote Sensing Satellites							
Satellite	Frequency	Spatial Resolution	Revisit Time Period	Polarization	Access	Data Availability	Used in Buffalo/Cattle Ecological Studies
ERS-1/ERS-2	C-band (5.3 GHz)	30 m	35 days	VV	Open-source	1991–2001	-
Radarsat 1 Radarsat 2	C-band (5.3 GHz) C-band (5.405 GHz)	50 m 25m	24 days 24 days	HH VV-VH	Open-source Licensed	1995–present 2007–present	- -
Envisat ASAR	C-band (5.3 GHz)	12.5 m	35 days	VV	Open-source	2002–2012	-
TerraSAR-X / TanDEM-X	X-band (9.6 GHz)	5 m	11 days	HH-VV	Licensed	2007–present	-
Sentinel-1	C-band (5.405 GHz)	FR* 3.5 m / HR* 10 m and 25 m / MR* 25 m and 40 m	6 days	VV-VH	Open-source	2014–present	-
Alos PALSAR 1-2 Alos PALSAR 2	L-band (1.27 GHz)	SP* 9 × 10 m / DP* 19 × 10 m	46–14 days	VV VH HH HV	Licensed	2006–present	-

* Visible Near Infrared (VNIR) / Short-wave Infrared (SWIR) / Thermal Infrared (TIR) / Atmospheric Correction Bands (ACB) / Panchromatic (Pan) / Multi-spectral (MS) / Full Resolution (FR) / High Resolution (HR) / Medium Resolution (MR) / Single Polarization (SP) / Dual Polarization (DP)

Two main categories of classification methodologies are commonly used in SRS to produce landcover maps. Supervised classification methodologies use different machine learning algorithms (maximum likelihood, neural network ensembles, random forests (RF), ...) to discriminate user-determined landcover categories [93]. For example, the RF algorithm uses a set of decision trees [94] and is now widely used [95,96], with the advantages of reliable and rapid execution in processing time of large volume of variables and data [97,98]. Such approaches require the definition of a training dataset of the different classes to be distinguished before classification. On the other hand, unsupervised classifications methodologies are more automatic processes, relying on algorithms such as K-means or Agglomerative Hierarchical to discriminate landcover categories [99]. The two types of classification methods can be applied to classify either image pixels, based on their spectral or textural values, or objects, i.e., neighboring pixels with similar spectral values aggregated into "objects" prior to the classification process. In the latter case, additional object-specific features such as shapes, context features/neighborhood relation, scale-hierarchy relation can be used to characterize and classify the objects [100]. In all cases, ground-truthing data are required for accuracy assessment.

Optical satellite images such as MODIS and Landsat (Table 3.1) have been used extensively for land cover classification since the 1970s and have enabled the dissemination of freely available landcover map products (Table 3.2) that represent major landscape features on a global scale. These products provide an initial characterization of landscape features that can be useful considering landcover preliminary assessments in a particular study area and can be easily operated by users with little SRS knowledge. The recently launched ESA-S2-LC20 product (Table 3.2) is one good example and can fulfil such a task despite a moderate accuracy [101]. However, as their spatial resolution and typologies are possibly not adapted to the study of ungulates habitats, 'customized' landcover maps can be produced to better reflect the landscape complexity of a particular study area [102]. Implementing optical indexes of vegetation, soil (Table 3.3) and water (Table 3.4) can also potentially enhance landcover classification results [103,104].

Despite high capacities to produce landcover maps, optical satellite images are not without limitations (e.g., lack of cloud-free periods) [105] and synthetic aperture radar (SAR) images (Figure 3.4 and Table 3.1) can provide a reliable alternative to optical satellite images. SAR sensors produce their own source of illumination and therefore can operate in almost any weather condition, day or night, and penetrate different types of vegetation cover [106,107]. They have shown good results to classify landcover in general [108], forests [109] and biomass [110] in particular and are, as a result, increasingly used. Several studies have demonstrated the complementarity of SAR and optical data and concluded that using them together provides better results than using them separately [22,111,112], especially in tropical environments where the cloud coverage often hinders the use of optical satellite images [113].

Table 3.2. List of satellite remote sensing-based landcover products.

Product Name	Spatial Resolution	Data Availability	Sensor Used	Reference
Climate Change Initiative (CCI) LandCover V2	300 m	1992 to 2015– 2016–2017– 2018	MERIS Full and Reduced resolution / Spot VGT	[114]
MCD12Q1 0.5 km MODIS-based Global LandCover	500 m	2001–today	MODIS	[115]
Globeland30	30 m	2000 / 2010	Landsat TM, ETM7, HJ-1A/b	[116]
GLC 2000	1 km	2000	SPOT 4 VEGETATION	[117]
GlobCover 2005 V2.2 2009	300 m	2005 / 2009	MERIS FR	[118]
GLCNMO V.1-V.2-V3	1 km / 500 m	2003 / 2008 / 2013	MODIS	[119]
GLC Share	1 km	2014	MERIS-MODIS	[120]

GLC250 m CN (2001 / 2010)	250 m	2001 / 2010	MODIS	[121]
FROM-GLC (GLC, GLC-seg, GLC-agg, GC, GLC-hierarchy)	30 m	2010	Landsat TM, ETM+	[122]
Global 30m Landsat Tree Canopy (TCC) V.4	30 m	2000, 2005, 2010, and 2015	MODIS, Landsat TM, ETM+	[123]
Global Forest Change (GFC) - GLAD (Global Land Analysis & Discovery) lab at the University of Maryland (UMD)	30 m	2000 to 2019	Landsat TM, ETM+, OLI	[80]
Copernicus Global 100 m Landcover (CGLS-LC100)	100 m	2015	PROBA-V EO and GSD	[124]
ESA-S2-LC20, 20 m (over Africa)	20 m	2016	Sentinel-2A	[125]

3.1.3 SRS for Detecting Landcover and Vegetation Changes

Detection of landcover changes is a complicated and integrated process and there is no optimal and applicable approach to all cases [126]. Several studies have demonstrated the capacity of Landsat images, which offer the longest continuous record of medium-resolution satellite-based earth observation ([Figure 3.4](#)), to monitor long term environmental changes in savanna environments [127,128]. Optical remote sensing sensors allow to monitor the evolution of the vegetation through phenology based on the spectral signature of vegetation [129,130]. For example, the widely used normalized difference vegetation index (NDVI) ([Table 3.3](#)) [131] was demonstrated highly correlated with the vegetation photosynthetic activity [132–134], vegetation development and seasonal patterns, forage cumulative growth period quality and quantity assessments [135–137]. These properties allow monitoring and comparing vegetation phenology through space and time at different scales. The [Figure 3.3D](#), for example, represents one image (month of September 2018) of the MODIS MOD13Q1 NDVI time series, giving a spatial representation of the vegetation repartition across the HNP interface area.

NDVI was also found correlated with animal movements [138,139]. However, in savanna environments, the relevance of simple indexes such as the NDVI can be limited and must be used with caution. Using low spatial resolution satellite sensors (i.e., MODIS) or even medium resolution satellite sensors (i.e., Landsat or Sentinel-2), pixels are most of the time mixed pixels of varying proportion of trees, grasses and bare soil [140,141]. In that case, the use of soil-adjusted vegetation indexes ([Table 3.3](#)) may be used as complementary to enhance classification results and seasonal analyses of landcover evolution [142,143] when applied within the frame of animal movement studies.

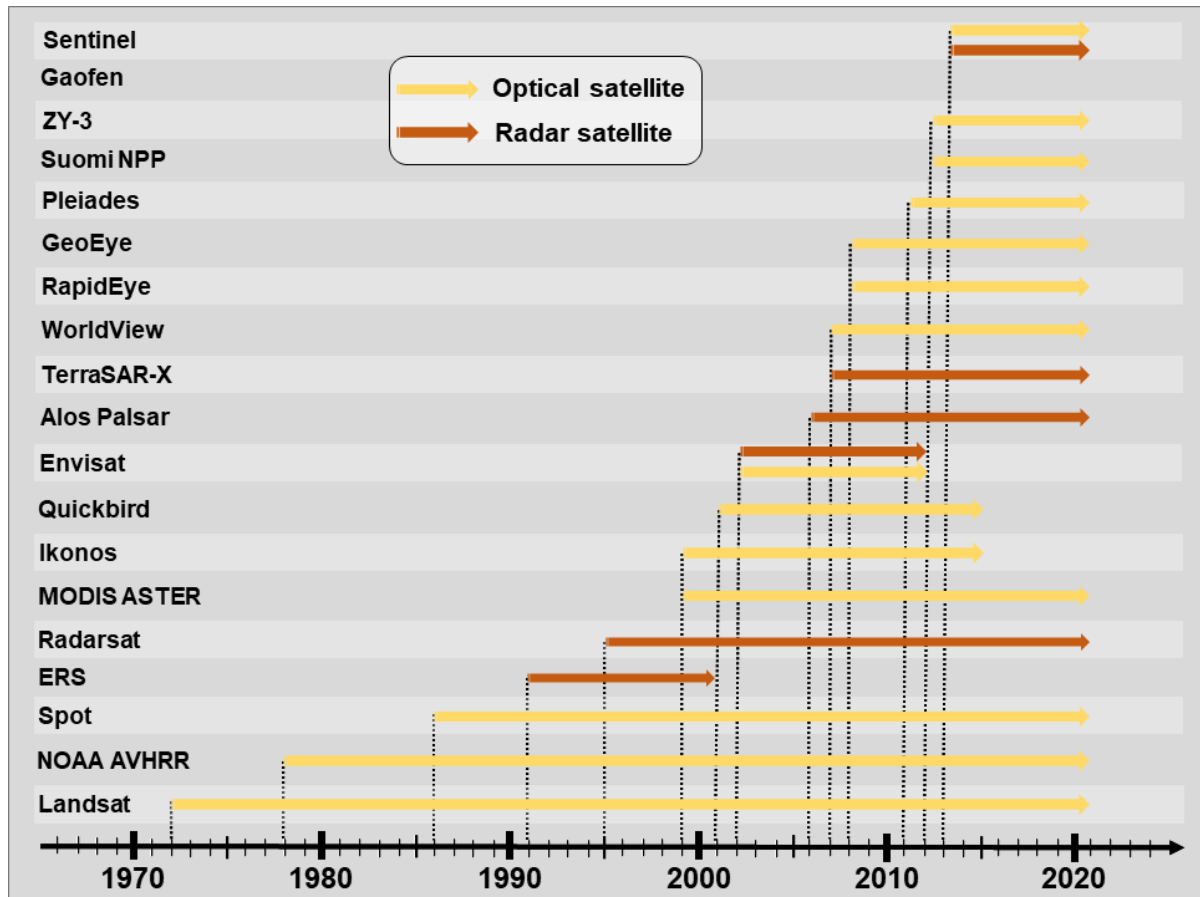


Figure 3.4. Earth observation optical and radar satellites commissioning and time of service chronology. The length of the arrow represents the continuity and the duration of the corresponding satellite program.

3.1.4. SRS to Characterize Landcover and Vegetation When Studying Animal Movements in Savanna Environments

Applying landcover classification to a savanna landscape can be challenging due to sparse cover, high background soil signal, and difficulty to differentiate between spectral signals of bare soil and dry vegetation [144]. Despite these limitations, Arraut et al (2018) produced a map of the vegetation structure of HNP in seven classes using 2013–2014 Landsat satellite images through a supervised classification process with an overall accuracy (OA) of 83.2% [102]. [Figure 3.3B](#) presents another example of a landcover map derived from an unsupervised classification (K-means algorithm) applied to a Sentinel-2 satellite image.

Such tailored SRS landcover maps have been used in different studies of buffalo and cattle ecology aiming at relating animal movements and landcover ([Table 3.1](#)). For example, Corn  lis et al. (2011) used a sylvo-pastoral vegetation map derived from 30 m resolution Landsat imagery to investigate the habitat preferences of buffaloes in W Regional Park (Burkina Faso, Benin, Niger) [88]. At local scale, very high spatial resolution sensors such as Worldview-2 and IKONOS were used ([Table 3.1](#)) to produce fine-scale landcover maps allowing the determination of resource use of cattle in communal lands in South Africa [79] and Zimbabwe [92].

Vegetation indexes ([Table 3.3](#)) provide a synthetic description of the vegetation spatio-temporal dynamics and several studies have related SRS derived vegetation indices such as the NDVI or the Enhanced Vegetation Index (EVI) ([Table 3.3](#)) to the spatio-temporal distribution and abundance of buffalo and other ungulates species at different scales [26,29,54,68,79,86,88,89,145–147]. For example, Naidoo et al. (2012a) used MODIS EVI time series to measure the greenness of the vegetation and

demonstrated the importance of this variable in explaining the variations in home range size of buffaloes in northeastern Namibia [29]. In two Australian savanna study sites, Handcock et al. (2009) showed that the tracks of cattle from GPS collars overlaid with a NDVI map derived from a 10 m resolution SPOT-5 image, highlighting a correlation between NDVI and cattle movements [26]. Using very high spatial resolution imagery, Zengeya et al. (2015) derived a fine scale EVI map from an IKONOS image to determine the proportion of cattle home range observed inside and outside a conservation area [54].

Table 3.3. Non-exhaustive list of spectral remote sensing indexes developed to discriminate vegetation and soil from optical satellite image analysis and that can be useful within the frame of animal movement studies in savanna environments.

Spectral Index	Calculation *	Reference	Used in Buffalo/Cattle Ecological Studies
Normalized Difference Vegetation Index (NDVI)	$(NIR - RED)/(NIR + RED)$	[148,149]	[26,68,79,86,88,145–147]
Enhanced Vegetation Index (EVI)	$2.5 \times [(NIR - RED)/((NIR + 6 \times RED - 7.5 \times BLUE) + 1)]$	[150]	[29,54,89,146]
Global Environmental Monitoring Index (GEMI)	$n = [n \times (1 - 0.25 \times n) - (RED - 0.125)]/1 - RED$ $n = [2 \times (NIR^2 - RED^2) + 1.5 \times NIR \times 0.5 \times RED]/NIR + RED + 0.5$	[142]	-
Soil Adjusted Vegetation Index (SAVI)	$[(1 + L) \times (NIR - RED)]/NIR + RED + L$ $L = 0.5$	[143]	-
Modified Soil Adjusted Vegetation Index (MSAVI)	$[2 \times NIR + 1 - \sqrt{(2 \times NIR + 1)^2 - 8 \times (NIR - RED)}]/2$	[151]	-
Modified Secondary Soil-Adjusted Vegetation Index (MSAVI2)	$0.5 \times [2 \times NIR + 1 - \sqrt{(2 \times NIR + 1)^2 - 8 \times (NIR - RED)}]$	[152]	-
Difference Vegetation Index (DVI)	$NIR - RED$	[153]	-
Optimized Soil-Adjusted Vegetation Index (OSAVI)	$(1 + Y \times [(NIR - RED)/(NIR + RED \times Y)])$ where $Y = 0.16$ (optimal value)	[154]	-
Soil Brightness Index (SBI)	$0.30372 \times BLUE + 0.27933 \times GREEN + 0.47434 \times RED + 0.55858 \times NIR + 0.508210 \times SWIR + 0.186312 \times MIR$	[155]	-
Two-band Enhanced Vegetation Index (EVI2)	$2.4 \times (NIR - RED)/(NIR + RED + 1)$	[156]	-
Modified Chlorophyll Absorption Ratio Index (MCARI)	$[(VNIR - RED) - 0.2 \times (VNIR - GREEN)] \times (VNIR/RED)$	[157]	-

* BLUE, GREEN, RED, NIR, MIR, SWIR: reflectance values in blue, green, red, near infrared, mid infrared and short-wave infrared, respectively. VNIR (visible and near infrared), SWIR1 and SWIR2: reflectance values from bands 5, 11 and 12 of Sentinel-2 respectively.

3.2. Surface Water

3.2.1. How Surface Water Distribution Influences Cattle and Buffalo Movements

The availability of surface water, artificial (e.g., solar-pumped, diesel generator) [158] or natural (e.g., dams, rivers) [159], is commonly cited to constrain movements and space-use of herbivores, including savanna buffalo [88,160–163] and cattle [164,165]. However, the influence of water sources in herbivore distributions is expected to change in response to variations in forage quality and quantity [166,167]. Buffalo are usually associated with areas close to water all-year-round and drink every day [90,168,169]. Similarly, cattle preferentially select areas close to water points, usually around their enclosures in order to optimize the ratio of energy expenditure to energy gain [79,170] and can also use boreholes which are never accessible to buffalo [90].

3.2.2. SRS Basics for Detecting Water and Water Dynamics

Optical SRS imagery can be efficient to discriminate water surface in different environments due to a wide range of sensors (Figure 3.4 & Table 3.1) with various spatial and temporal resolutions available [171–176]. Depending on surface water properties (i.e., size, river, pond, seasonal) to detect, different categories of sensors can be chosen [177]. However, their spatial resolution may affect their efficiency in accurately detecting surface water.

Many methodologies, from thresholding a single infrared band to the use of multi-spectral classification decision trees, have been developed to detect surface water via SRS [178–180]. They rely on the spectral signature of water, characterized by a quick reduction of reflectance from the blue to the near infrared wavelengths. Water indexes based on two or more spectral bands calculation (Table 3.4) and various spectral band combinations have been widely used to detect surface water [181,182] (see example in Figure 3.3C).

Other factors should also be considered as they potentially limit the satellite-based detection of surface water extent [183]: water depth, water turbidity variation, soil characteristics, vegetation cover, potential cloud cover and shadows. They all influence the water reflectance whatever the spatial resolution of the satellite images and influence thresholding values and the efficient use of water indexes. Despite these constraints, accurate methodologies can be developed to discriminate water by adding complementary spatial information to spectral indexes alone. Owen et al. (2015) for instance, have been able to accurately detect artificial waterholes across heterogeneous desert environments using Landsat 8 data combined with spectral indexes and texture analysis [184]

Table 3.4. Non-exhaustive list of spectral remote sensing indexes developed to discriminate water surfaces from optical satellite image analysis and that can be useful within the frame of animal movement studies in savanna environments.

Spectral Index		Calculation*	Reference
Normalized Difference Infrared Index	NDII	$(NIR - MIR)/(NIR + MIR)$	[185]
Normalized Difference Vegetation Index	NDVI	$(NIR - RED)/(NIR + RED)$	[148, 149]
Enhanced Vegetation Index	EVI	$2.5 \times [(NIR - RED)/(NIR + 6 \times RED - 7.5 \times BLUE + 1)]$	[150]
Normalized Difference Water Index	NDWI	$(GREEN - NIR)/(GREEN + NIR)$	[186]

Normalized Difference Water Index (Gao)	NDWI (Gao)	$(GREEN - SWIR)/(GREEN + SWIR)$	[187]
Modified Normalized Difference Water Index	MNDWI	$(GREEN - MIR)/(GREEN + MIR)$	[188, 189]
Normalized Difference Turbidity Index	NDTI	$(RED - GREEN)/(RED + GREEN)$	[188]
Normalized Difference Phytoplankton Index	NDPI	$(MIR - GREEN)/(MIR + GREEN)$	[188]
Automated Water Extraction Index	AWEInsh AWEIsh	$AWEInsh = 4 \times (GREEN - SWIR1) - (0.25 \times NIR + 2.75 \times SWIR2)$ $AWEIsh = BLUE + 2.5 \times GREEN - 1.5 \times (NIR + SWIR1) - 0.25 \times SWIR2$	[190]
Water Index	WI	$1.7204 + 171 \times GREEN + 3 \times RED - 70 \times NIR - 45 \times SWIR1 - 71 \times SWIR2$	[191]

* BLUE, GREEN, RED, NIR, MIR, SWIR: reflectance values in blue, green, red, near infrared, mid infrared and short-wave infrared, respectively. VNIR (visible and near infrared), SWIR1 and SWIR2: reflectance values from Bands 5, 11 and 12 of Sentinel-2, respectively.

Synthetic aperture radar (SAR) satellite images can be used independently or in combination with optical satellite images in order to detect surface water [192,193]. The recent increase in number of operational SAR sensors (Table 3.1 & Figure 3.4) has favored their use for surface water detection. Indeed, several SAR-based water detection methodologies have been developed such as the surface water detection through supervised and unsupervised classifications [194,195], thresholding [196,197], object-based image analyses [198,199] and hybrid approaches [200,201]. The application of these different methodologies led to the development of several surface water products (Table 3.5) [202–205].

The accuracy of the SAR-based surface water detection methodologies varies. Terrain shadowing due to the topography can result in a side-looking effect [197]. The importance of the vegetation layer can produce double-bounce scattering of the signal that increases the backscatter measured in the SAR image [206]. The strong wind that roughens the water surfaces can lead to misclassification errors and the threshold value to discriminate the surface water is dependent of the image quality acquisition and the type of landscape [193]. Nevertheless, surface water long-term monitoring has been successfully implemented in a savanna environment via a multi-SAR-system at high and very-high spatial resolution [207].

3.2.3. SRS to Detect Surface Water When Studying Animal Movements in Savanna Environments

SRS-based water products like the Global Surface Water (GSW) and the Global Water Body map (G3WBM / G1WBM) present the advantage to have a higher spatial resolution and temporal frequency compare to the other products listed in Table 3.5. These products are suitable to detect massive bodies of water at a continental scale and can be of interest for preliminary analyses, however they show strong limitations when trying to discriminate localized, small or seasonal surface water which are predominant in savanna environments [208]. Indeed, detecting surface water in savanna environments via remote sensing at a landscape scale remains challenging mostly because of surface water seasonality dynamics, landscape heterogeneity and variety in surface water area sizes and morphologies [208,209].

Increasing availability of free medium-resolution optical and radar satellite sensors such as Sentinel-1 and Sentinel-2 (Table 3.1) offers potentialities to accurately discriminate, via supervised

classification, surface water and surface water dynamics [210]. Among the different spectral remote sensing indexes developed to discriminate water surface from optical satellite images (Table 3.4), the MNDWI and NDWI are the most commonly used [211] and were identified as efficient discriminating indexes for the detection of surface water extent in savanna environments [177,212]. In the case of the HNP study area shown in Figure 3.3C, a time series of 12 Sentinel-2 images (one image per month for the year 2018) combined with the application of the RF algorithm on MNDWI and NDWI indexes (Table 3.4) was used to characterize the presence and seasonal dynamics of the surface water.

So far, water spectral indexes in combination with supervised classification have hardly been used in direct relation with buffalo and cattle movements, although their potential within this framework have already been stressed [212]. Recently, Naidoo et al. (2020) used the NDWI calculated from Sentinel-2 images to detect ephemeral water source in relation with buffalo and elephant movements in Namibia [91]. However, most of the reviewed studies integrating water into their analysis only used on-site observations of surface water [88,147,167] and natural or artificial waterholes [17,213–216].

Table 3.5. Non-exhaustive list of remote sensing-based water products.

Product Name	Developer	Spatial Resolution	Frequency	Data Availability	Reference
Global surface water (GSW)	EC JRC (European Commission Joint Research Center)/Google	30 m	Monthly Yearly	1984–2015 1984–2019	[217]
CCI global map of open water bodies (WBP V4.0)	ESA (European Space Agency) - climate change initiative(CCI)	300 m to 1 km	7 days–1 year	2000–2015	[218]
Global lakes and wetlands database (GLWD)	University of Kassel/ World Wildlife Fund (WWF)	1 km	1 year	2004	[219]
SRTM water body data product specific guidance (SWBD)	National Aeronautics and Space Administration (NASA)	90 m	1 year	2000	[220]
SAR-Based water body indicator (SAR-WBI)	ESA	150 m to 1 km	6 to 12 days	2005–2012	[221]
MOD44W	NASA	250 m	yearly	2000–2015	[222]
Copernicus WB	Copernicus program - ESA	300 m to 1 km	10 days	2014–present	[223]
Global 3-second/1-second water body map (G3WBM / G1WBM)	Department of Integrated Climate Change Projection Research, 4 Japan Agency for Marine-Earth Science and Technology	30 m to 90 m	1 year	2018	[224]

3.3 Fire Regimes

3.3.1 How Fire Influences Cattle and Buffalo Movements

Savanna is prone to fire due to the existence of a highly flammable continuous vegetation layer with ideal burning conditions during the dry season [225,226]. Savanna fires can thus affect herbivores movements, by impacting indirectly the quantity and quality of the grazing resources available [227] or by reducing cover to hide from predation [228]. Although most herbivores are attracted to the recently burned areas due to nutritious regrowth [229], buffalo habitat selection during the dry season appear to be strongly constrained by the occurrence of fire, probably due to a great reduction of the quantity of forage [75]. Fire can also affect the migration distance of buffalos during the wet season [146].

Movement patterns of cattle are also influenced by the occurrence of fire. In Kenyan savanna ecosystems, prescribed burning improved cattle forage intake but only in areas that cattle did not share with wildlife [230]. Savanna fires could, therefore, affect livestock-wildlife coexistence at the interfaces by altering the intensity and frequency of forage use [229].

3.3.2. SRS Basics for Detecting Fire and Fire Dynamics

Optical SRS can be used to spatially and temporally detect and characterize burnt area and burn severity [231–233] based on the detection of changes in the spectral signatures of vegetation [234] with a reflection reduction in the visible and near infra-red (NIR) spectral bands. Indeed, the charring and removal of vegetation are largely visible and detectable in the infrared [235].

Various SRS-based approaches have been developed to monitor fire [236,237], including aggregate active detection [238,239], multi-temporal composites analyses [240], the use of spectral indexes [241], including vegetation indexes such as NDVI or GEMI (Table 3.3), spectral mixture analysis [242], machine learning classification [243,244], time series change detection [245] and hybrid approaches mixing time series change detection with machine learning classification [246,247]. If these methods provide user friendly fire products (Table 3.6) and helpful fire spectral indexes (Table 3.7) by capturing most aspects of the spatial and temporal distribution of the fire effects, it can be difficult to relate them to actual burned area due to inadequate spatial and temporal resolutions, variability in cloud cover and differences in fire behavior [248]. Active fire detection algorithms may either : (i) underestimate the area burned in grassland and savanna ecosystems as the fire progresses rapidly across the landscape [249] and because small and low-intensity fires may not be detected [250]; (ii) overestimate the burned area for isolated fire points smaller than the pixel dimension [250]. In this instance, the MODIS fire products MOD14A2/MYD14A2 and MCD45A1 (Table 3.6) provide three categories of confidence (low, medium, high) of fire detection (Figure 3.3E), offering flexibility for a targeted use in accordance with the user's choice.

3.3.3. SRS to Characterize Fire when Studying Animal Movements in Savanna Environments

The Figure 3.3E shows an example of the MODIS fire product MOD14A2 (Table 3.6) at the HNP interface, illustrating the capacity of such product to depict with a 1km spatial resolution the active fire temporal and spatial dynamics and its potential for conducting seasonal- and inter-annual analyses. Despite the availability of numerous SRS-based fire products offering a wide range of applications (Table 3.6), according to our review only one of them has been used in relation with buffalo and cattle movement studies. Naidoo et al. (2012b) used the MODIS MOD14A2/MYD14A2 product to quantify the relative effect of dry season variables, including savanna fires, on subsequent wet season buffalo migration distance in a large study area running east-west between the northeast corner of Namibia, Angola and Botswana [146].

As shown by this example, and despite limitations, the data listed in Table 3.6 presents the advantage to describe fire phenomenon in relation with animal distribution and movement in regions with scarce fire information [251]. In well-documented areas, these data can potentially be used to complement existing fire databases. Combining better spatial resolution from new sensors such as Sentinel-3 (Table 3.1) and remote sensing-based fire products with designed spectral indexes to detect fire (Table 3.7) is promising. It could potentially reduce errors and uncertainties in satellite-derived fire dates and ignitions, and improve coverage of small fires. The recently launched FireCCI50 product (Table 3.6) offers an increased spatial resolution (250 meters) and a better burned area estimation compared to the MODIS fire products [249]. This spatial resolution could be useful when aiming to integrate fire assessment in animal movement study at the landscape scale in savanna environments.

Table 3.6. Non-exhaustive list of satellite remote sensing-based fire products.

Product Name	Spatial Resolution	Orbital Frequency	Data Availability	Reference	Use in Ungulates Ecological Studies
MOD14A2/MYD14A2	1 km	Every 8 days	2000–present	[252]	[29]
MCD45A1	500 m	Monthly	2000–present	[253]	-
MCD64A1	500 m	Monthly	2000–present	[248]	-
VIIRS 750 m active fire (VNP14)	750 m	twice/day (IR and day/night VIS/NIR channel) once/day (VIS)	2011–present	[254]	-
VIIRS 375 m Active Fire (VNP14IMG)	375 m	twice/day (IR and day/night VIS/NIR channel) once/day (VIS)	2016–present	[238]	-
Sentinel-3 SLSTR (level-2 FRP product)	1 km	Daily	2018–present	[255]	-
AVHRR Fire Detects from the Fire Identification, Mapping and Monitoring Algorithm (FIMMA)	1 km	Daily	1978–present	[256]	-
ESA FIRE_CCI	300 m	Monthly	2016–present	[257]	-
FireCCI51	250 m	Monthly	2001–2019	[258]	-

Table 3.7. Non-exhaustive list of spectral remote sensing indexes developed to discriminate fire from optical satellite image analysis and that can be useful within the frame of animal movement studies in savanna environments.

Spectral Index	Calculation *	Reference
Normalized Burned Ratio (NBR)	$(NIR - SWIR)/(NIR + SWIR)$	[258]
Burned Area Index (BAI)	$1/(NIR - 0.06)^2 + (RED - 0.1)^2$	[259]
Mid Infrared Burned Index (MIRBI)	$10 \times SWIR + 9.8 \times SWIR + 2$	[260]
Char Soil Index (CSI)	$NIR/SWIR$	[261]
Normalized Burn Ratio Thermal (NBRT)	$(NIR - SWIR \times TIR)/(NIR + SWIR \times TIR)$	[262]
Normalized difference Vegetation Index Thermal (NDVIT)	$(NIR - RED \times TIR)/(NIR + RED \times TIR)$	[262,263]

* RED, NIR, MIR, SWIR, TIR: reflectance values in red, Near Infrared, Mid Infrared, Short-wave Infrared and Thermal Infrared, respectively.

3.4. Precipitation

3.4.1. How Precipitation Influence Cattle and Buffalo Movements

In southern African savannas, the availability in time and space of natural resources (i.e., surface water and forage) is strongly dependent of the precipitation seasonal variations [88,264]. Most precipitation occurs during the wet season (November to April). However, the spatio-temporal distribution of precipitations in southern Africa is highly heterogeneous at medium-scale inducing specific movement patterns such as nomadism [265]. During the dry season (May to October), precipitation are lower or nonexistent, and the availability of natural resources decreases. This high heterogeneity in rainfalls dictates the behavior of wildlife [8].

Buffalos, like other ungulates of semi-arid savannas, are able to track precipitation events over large distances [88]. Buffalos living in wetter areas, such as in forested savanna habitats, tend to maintain smaller and constant home ranges than those in drier open savanna habitats [160,266]. In these more arid areas, natural resources are spatially unevenly distributed, forcing buffalos to travel longer distances in their search for forage and water [29,146,162]. In some areas however, smaller buffalo home ranges have been noticed during the dry season compared to the wet season [266–268].

Precipitation also affect cattle movement patterns through the combined influence on their grazing behaviors and the spatial grazing constraints imposed by livestock owners [269]. For example, cattle around Kruger National Park, South Africa, select forage with higher quantity and quality during the dry season but behave more like non-selective bulk grazers during the wet season, directly influencing their daily traveled distance [79].

3.4.2. SRS Basics for Measuring Precipitation

Satellite-based precipitation measurements with advanced infrared (IR), passive microwave (MW) and radar (SAR) sensors provide a complementary alternative to in-situ records [62,270] as they give a full spatial and temporal coverage with a good accuracy ([Table 3.8](#)) [271–278]. Yet, despite the growing collection of satellite-based rainfall measurement datasets providing near-real-time estimates [63], only a few high-resolution satellite-based products providing historical data at the daily time-step with real-time or near-real-time updates for the African continent are publicly available ([Table 3.8](#)). To improve the accuracy of rainfall estimations, the merging of satellite and gauge measurements have been designed, thus maximizing the benefits of each data type [279,280]. Noticeable differences can be found in the performance of the satellite precipitation estimates though [281]. Satellite-based precipitation products generally overestimate precipitation events under 200 mm/month and tend to underestimate daily time scale precipitation events compare to the decadal and monthly time scale precipitation events [272,282,283]. However, the main precipitation regimes and the spatial patterns of mean annual precipitation are well reproduced [281,284].

Satellite-based precipitation measurements have the advantage of providing full spatial coverage compared to the more accurate but spatially limited rain gauge data [285]. Furthermore, observational precipitation measurements over Africa include uncertainties that can bias analysis [286,287]. The TMPA 3B42 V7 (TRRM) offers the advantage of consistency at the daily time-scale [281]. It is a performing product for depicting inter-annual variations but offers a coarser spatial resolution ([Table 3.8](#)) which could be detrimental when studying animal movement at the landscape scale. Since 2019, the GPM IMERG v06 algorithm fuses the early precipitation estimates collected during the operation of the TRMM satellite (2000–2015) with more recent precipitation estimates collected during operation of the GPM satellite (2014–present). Therefore, the GPM IMERG v06 now offers 20 years of data coverage and can potentially be of interest regarding animal movement studies at the landscape scale regarding its spatial resolution of 0.1° and its broad coverage ([Table 3.8](#)).

The products that combine thermal infrared and passive microwave imagery such as RFE or CHIRPS ([Table 3.8](#)), perform comparatively well and outperform products which are only based on

thermal infrared imagery such as TARCAT (Table 3.8) [272]. They could be used in complement or independently with higher spatial resolution satellite-based precipitation products such as the GPM product (Table 3.8) to reliably assess precipitation at the landscape scale in seasonal-prone environments such as African savannas when lacking in-situ precipitation data.

Table 3.8. Non-exhaustive list of available satellite-based precipitation products.

Product Name	Temporal Resolution	Spatial Resolution	Data Availability	Coverage	In-Situ Calibration	Reference	Use in Ungulates Ecological Studies
TRMM (TMPA 3B42 V7)	3 hours	0.25°	1998–Mid 2019	50°S–50°N	yes	[288]	[29,146]
TRMM (TMPA 3B43 V7)	Monthly	0.25°	1998–Mid 2019	50°S–50°N	yes	[288]	[29,146]
PERSIANN-CDR	Hourly/Daily/ Monthly / yearly	0.25°	1983–present	60°S–60°N	no	[289]	-
GPCP (1dd)	Daily	1°	1996–present	90°S–90°N	no	[290]	-
GPCP V2.3	Monthly	2.5°	1979–present	90°S–90°N	no	[291]	-
CPC Global	Daily	0,5°	1979–present	90°S–90°N	yes	[292]	-
CMAP	Monthly	2,5°	1979–present	90°S–90°N	yes	[293]	-
Cmorph	30 min	0.25°	2002–2017	60°S–60°N	no	[294]	-
GPM (IMERG V06)	30 min / 3 hours / Daily	0.1°	2000–present	60°S–60°N	no	[295]	-
MSWEP V2	3 hours / Daily	0.1° / 0.5°	1979–2017	90°S–90°N	yes	[296]	-
SM2RAIN-ASCAT	Daily	0.5°	2007–2018	60°S–60°N	no	[297]	-
TAMSAT V3.1	Daily	0.0375°	1983–present	38°025N–35°9625S 19°0125W–51°975E	yes	[62,63]	-
CHIRPS v2p0	Daily	0.05°	1981–present	50°S–50°N	yes	[298]	-
ARC V.2	Daily	0.1°	1983–present	40°S–40°N	yes	[299]	-
RFE 2.0	Daily	0.1°	2001–present	40°S–40°N 20°W–55°E	yes	[300]	-
EPSAT-SG	15 min	0.0375°	2004–present	African continent	yes	[301]	-
MPE	15 min	0.0375°	2007–present	African & European continents	no	[302]	-

3.4.3 SRS to Measure Precipitation when Studying Animal Movements in Savanna Environments

Only the National Oceanic Atmospheric Administration (NOAA) African Rainfall Climatology (ARC V.2), the Climate Hazards Group InfraRed Precipitation with Station data version 2.0 (CHIRPS20) and the Tropical Applications of Meteorology using SATellite data and ground-based observations (TAMSAT V3.1) provide continually updated daily time-step data [63,303]. Therefore, due to their spatial and temporal resolutions ([Table 3.8](#)) they are potentially suitable for applications in animal movement studies in African savanna environments. [Figure 3.3F](#) shows a spatial representation of the TAMSAT V3.1 at the HNP interface while demonstrating the product capabilities to detect spatially contrasted precipitation within a relative extensive area (1192 km²). TAMSAT V3.1 ([Table 3.8](#)) is among the best product in terms of precipitation event detection at a spatial resolution of 0.0375° [304] but it may underestimate monthly rainfall measurements [284].

Despite the availability of these precipitation satellite-based products, the most commonly method to characterize precipitation in relation with animal movement and distribution remains the use of in-situ gauging stations data [170,305]. Only few studies have used satellite-derived precipitation data in relation with buffalo movements. Naidoo et al. (2012a, 2012b) used TRMM data ([Table 3.8](#)) to characterize which environmental factors, including precipitation, explain buffalo migration patterns [146], and variation in buffalo home range sizes in northeastern Namibia [29].

4. Discussion

The literature on the current knowledge on buffalo and cattle movements and their interactions was here linked to an inventory of available and relevant SRS tools to characterize the environmental drivers of these movements, found in savanna type landscape environment.

Landcover, surface water, savanna fire and precipitation emerged through this review as environmental drivers defining buffalo and cattle movements at the edge of protected areas in Africa and in southern Africa in particular. Optical and radar SRS are both currently operational to characterize these drivers and have already been used independently for several ecological applications, including animal movements [19,25,306] but have never been collectively linked in animal movement studies. The need of dynamic environmental products to analyze animal movement requires that the increasing number of SRS sensors, the multiple tools and the large quantity of data available become more accessible and easy to use to movement ecologists [307].

4.1. General Observations

Faced with an overabundance of available data, one should gain insight on data quality and the methods, algorithms and applications of using data in animal movement studies. SRS data must often be combined with in-situ measurements, which are sometimes not available, for validation purposes and accurately representation of environmental drivers. SRS has to be considered only as a partial view of the terrain and remain imperfect by definition [308]. Furthermore, the use of SRS products may be limited by the time-span of their availability, their spatial and temporal resolution and coverage, their spectral characteristics ([Table 3.1](#)). The revisit time period of a SRS product ([Table 3.1](#)) does not mean that it will be usable at the same frequency, as the quality of the image may not always be optimal at each acquisition (e.g., cloud cover, limited spatial extent that doesn't cover the desired area, ...).

These limitations often imply a trade-off between spatial and temporal resolutions [309] and/or between spatial resolution and spatial extent coverage [310]. For instance, high and very-high spatial resolution images are not necessarily appropriate for all research questions as they contain large amounts of data, heterogeneity of spectral values and diversity of objects in small spatial extents that can significantly complicate methodology applications [310]. Data pre-processing for a SRS derived application is not only costly in processing time and in expertise but also in financial resources. Naidoo

et al. (2012a) estimated that weekly acquisition of very high resolution Quickbird imagery ([Table 3.1](#)) to detect small ephemeral water sources within the frame of their study in relation with buffalo movements would have cost close to USD \$9 million [29]. One has to be aware of the computing capacities available, the allowed time and the appropriate algorithm for the completion of SRS analyses [34,311].

4.2. Landcover and Vegetation Characterization

Our review showed that the use of SRS to understand cattle or buffalo movement ecology mainly benefited from open-access products and standard image processing methods. EVI and NDVI are widely used vegetation indexes to characterize vegetation availability and evolution patterns in these studies [26,29,54,88,312]. However, other spectral indexes such as the Soil Adjusted Vegetation Index (SAVI) ([Table 3.3](#)) that eliminate soil-induced variations in vegetation indexes [143] have not been used at all in existing buffalo and cattle movement studies. The use of such spectral indexes could complement more classic vegetation indexes by overcoming certain associated limitations when characterizing savanna landscapes through SRS approaches (i.e., mixed pixels) [143,313,314].

Few studies listed in this review use high or very high-spatial resolution satellite images to characterize the landcover [54,79,89] comparatively to the studies that use medium or low-spatial resolution satellite images such as MODIS ([Table 3.1](#)) to derive spectral indexes [86,87,135] and Landsat or Spot ([Table 3.1](#)) to characterize landcover [11,70,88,90]. Indeed, high spatial resolution imagery is not necessarily appropriate for all research questions, especially because its limited spatial extent requires the acquisition of several images to cover large areas at a high financial cost [315]. High and very high spatial resolution images contain large amounts of data, heterogeneity of spectral values and diversity of objects that significantly complicate methodology applications such as landcover classification [310]. However, since 2015, open-source Sentinel-2 images ([Table 3.1](#)) bring a spatial resolution and a temporal continuity gain compared to other medium spatial resolution images that could potentially improve spectral indexes or landcover derivation over large areas while maintaining relevance in application for landscape scale analysis.

As the human and livestock populations grow in Africa [2,316], the pressure on protected areas' boundaries increases resulting in the transformation of natural landscapes and the creation of hard edges between protected areas and their surroundings by human infrastructures and activities (e.g., buildings, roads, cleaned land for cultivation, pasture, trees and grasses harvest) [68]. These two factors combined directly impact the movement of buffalo and cattle as they cross the natural park borders to find foraging or water resources. Human infrastructures including fences, human settlements and agricultural areas also represent potential barriers to animal movement. For example, movement rates of buffalos living near fences appear to be low [317] and large migratory movements are limited by fences [146] when they are not damaged by elephants [6]. SRS can play a fundamental role to characterize the human factors (infrastructures, activities) into the buffalo and cattle movement processes. For instance, crops can potentially provide an important resource for both buffalo and cattle during the wet season in southern African savanna even if both species are prevented to enter fields with growing crops (e.g., using different practices such as wildlife deterrent measures and livestock herding). Time series SRS derived vegetation indexes such as EVI or NDVI ([Table 3.3](#)) have been efficiently used as phenology indicators [318,319] combined with landcover classification [320], high-resolution optical and radar sensors [321] for crop and pasture monitoring and space delimitation. Concerning hardly distinguishable objects from space such as fences, human settlements and roads, the increasing availability of very high-resolution (Worldview-2, Pleiades, ...) satellite images ([Table 3.1](#)) offer a wide range of possibilities to characterize these landscape features via landcover object-based approach classification [23]. These methodologies could certainly be used independently or combined, bringing a wide range of indicators for animal movement and interactions analysis.

4.3. Surface Water Delineation

Several methods such as spectral indexes thresholding ([Table 3.4](#)), image classification, surface water spatial delineation through satellite image textures [184], have been efficiently used independently to map surface water bodies. However, the numerous remote sensing-based water products presented in [Table 3.5](#) have not been used in the different buffalo and cattle movement reviewed studies. Similarly, water spectral indexes listed in [Table 3.4](#) and SAR images ([Table 3.1](#)), with the exception of one study that used NDWI derived from Sentinel-2 images in relation with buffalo movements [91], have not been used despite their potential to improve classification algorithms and water detection in savanna environments [177,203,204,207,212]. This may partly result from a lack of knowledge about the existence and availability of SRS products in the movement ecology community, a major gap that this review aims to fill.

According to our review, the use of SRS offers a potential that remains to be explored regarding the detection of surface water at a landscape scale in savanna environments, as a driver of wild and domestic ungulates movements. Indeed, classification of surface water derived from optical and/or radar medium spatial resolution images ([Table 3.1](#)), could provide spatially delineated surface water areas and water resource seasonal variations at a landscape scale and on a monthly basis ([Figure 3.3B](#)), which constitutes a clear advantage in term of spatial representation over in-situ fixed referenced points.

4.4. Savanna Fire Characterization

SRS plays an important role in determining the spatial extent and timing of fires in savanna environments [244,322]. However,, few of the reviewed studies focusing on buffalo and cattle movements used satellite remote sensing-based fire products ([Table 3.6](#)) and none of them used designed optical images derived fire spectral indexes ([Table 3.7](#)) despite their proven efficiency [323]. Landsat and, increasingly, Sentinel-2 ([Table 3.1](#)) for example, are extensively used for medium spatial resolution fire scar mapping in savanna [250,324] and could provide potential improved results for studies that use lower spatial resolution images [146].

However, mapping fire severity is more challenging than just mapping the occurrence of fire. One major limitation of all optical SRS approaches is the presence of cloud cover that hinders the temporal continuity of the follow-up [325]. For animal movements studies, the severity of a given fire event is more relevant than its frequency and timing alone. To bypass such limitation, SAR images could be used. Philipp and Levick (2020), for example, demonstrated that C-band SAR data can contribute to effectively map fire severity in tropical savanna [325]. Characterizing savanna fire severity in addition of being able to locate fire events could also be useful for measuring more accurately the influence of human land use practices [326] and how it potentially affects animal movements.

4.5. SRS for Precipitation Characterization

According to our review, only the TRMM product ([Table 3.8](#)) have been used for buffalo and cattle movement studies [29,146]. This is probably because most of the satellite-based precipitation products are difficult to apprehend for non-specialists, thus compromising their potential use in animal movement studies. They usually present unconventional output file formats, non-standardised precipitation measurement units and uncommon map projection systems. Therefore, potential users need to access metadata that are most of the time difficult for non-SRS specialist to understand in order to assess satellite-based precipitation products usefulness. The mitigation of this constraint by simplifying the use of satellite-based precipitation products could be greatly beneficial for animal movement studies.

The use of satellite-based precipitation products combined with in-situ precipitation data when available remains paramount for more accurate estimations of precipitation trends at a local scale [272].

Additionally, algorithm performances of satellite-based precipitation products (Table 3.8) greatly vary depending on location, topography, local climate, and season [273,282,283]. This performance variability needs to be taken into account before choosing a satellite-based precipitation product for a specific application and in accordance with the study area geographical specifications.

4.6. Selection of Suitable SRS Products to Study Buffalo and Cattle Movements in Southern Africa

Choosing a set of SRS tools for the characterisation of environmental drivers influencing the buffalo and cattle movements is firstly driven by the question to be addressed (e.g., habitat selection, landscape scale movement patterns, long-distance migration, ...), which in turn defines the spatiotemporal scales to be considered [59]. Additional criteria such as the required SRS expertise, computing resources, and cost, may be taken into account too (see Section 4.1). Figure 3.5 provides an illustration of suitable SRS products for ecologists to characterize environmental drivers impacting animal movements in southern Africa according to their temporal and spatial resolution scales.

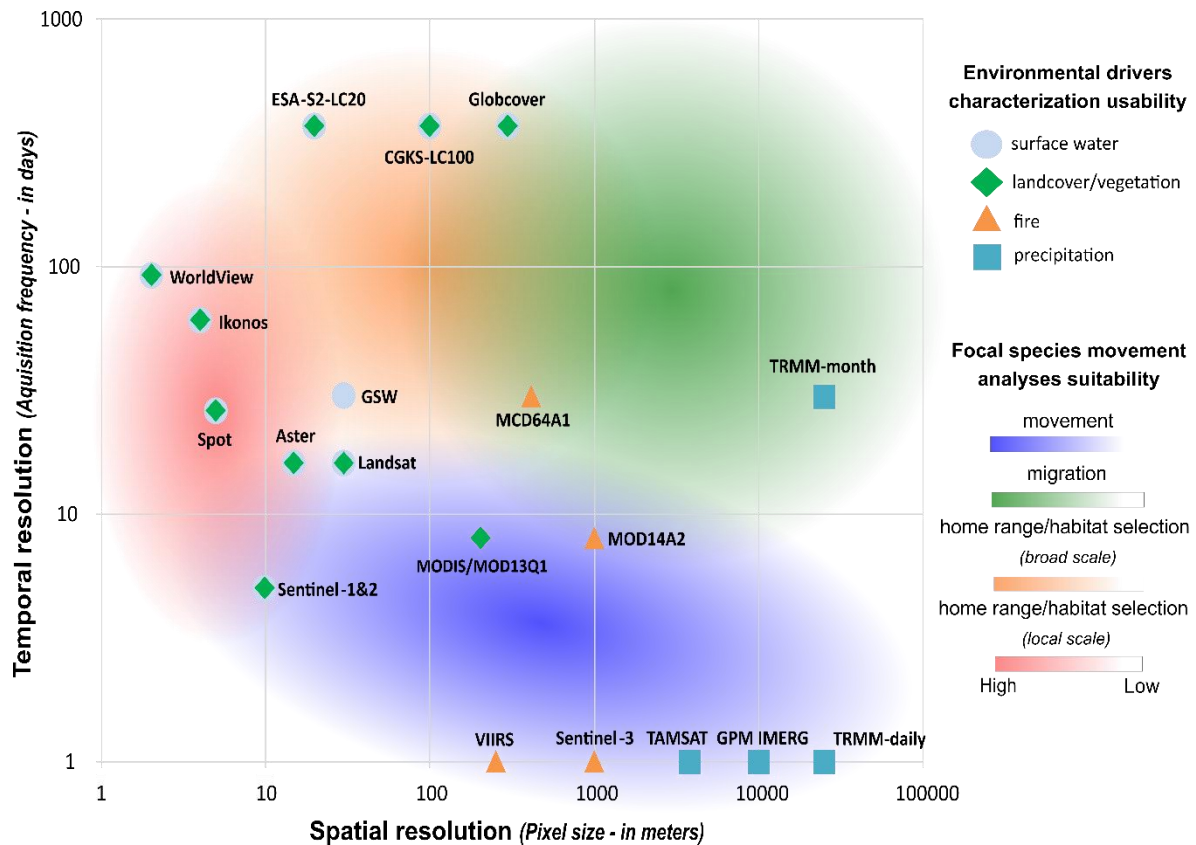


Figure 3.5. Suitable SRS products for ecologists to characterize environmental drivers impacting animal movements in semi-arid savannas landscapes. These SRS products are represented according to their temporal (ordinate axis) and spatial resolution scales (abscissa axis) and can be used for different type of analyses related to animal movements (movement patterns, home-range and habitat selection at broad and local scales, migration) [59]. We define the “movement” (represented in blue) as the motion initiated by a variety of methods that focal species use to move from one place to another. The “migration” (represented in green) is defined as long distance movements to a different environment involving periodical and cyclical dynamics in space and time. Home range and habitat selection (represented in orange at broad scale and in red at local scale) are considered as areas where focal species regularly move depending on natural resource selections and social interactions and behaviors. Note that the contours of the different analyses categories are blurred to emphasize the fact that there are no clearly established boundaries between these categories.

High and very high spatial resolution sensors can be used to provide fine-grain maps of landcover and water surface for habitat occupation and habitat selection studies at local scale. Very high spatial resolution images such as Worldview 2, Pleiades, or Ikonos images can be used to discriminate small objects within the landscape (i.e., fences, human settlements, road networks) and characterize landscape at fine scale (ideal for the study of small animal species with a small home range). However, they are costly and require remote sensing expertise and high computing power.

These fine-scale landcover maps can be combined with precipitation and savanna fires data at coarse spatial resolution but with a high temporal repetitivity for studies that focus on daily animal movements. For instance, precipitation TAMSAT 3.0 (Table 3.8) product is easily accessible and covers the entire African continent at 4.8 km of spatial resolution with daily, pentadal, decadal, monthly and seasonal temporal resolutions; recent VIIRS active fire images (Table 3.6) offer improved spatial and temporal resolutions compared to former fire products. These products are easy to use and do not require high computing power.

For studies focusing on animal movements at a coarser spatial and temporal scales, landcover and vegetation (Table 3.2), fire (Table 3.6) and water (Table 3.5) free products can be used for preliminary assessments in areas where in-situ data are difficult to collect or non-existent. These products are easily accessible online, easy to use for non-SRS specialists, well documented and require little computing power in order to cover large areas. In addition, they can be efficiently combined with higher spatial resolution and custom-made SRS products.

5. Conclusions

SRS extends the analytical capacity of ecologists in many fields including animal movement studies [20]. New SRS sensors are continuously launched thus expanding and increasing the potential applications of these tools (Figures 3.4 and 3.5). The Committee on Earth Observation Satellites (CEOS) reports that its member agencies are currently operating or planning more than 300 different satellite Earth observation missions by 2030, carrying over 900 different measurement instruments offering different spatial resolutions and spectral capabilities [327]. Medium-resolution Sentinel-1 and Sentinel-2 images (Table 3.1) are particularly promising in the field of animal movement as they provide continuous open-source data since 2014–2015 at a 10 meters spatial resolution with radar and optical sensors. However, given the SRS sensors and applications diversity, it is paramount to determine which SRS product is best suited for a given scale of analyses and how potential inherent limitations can affect the latter.

To facilitate the use of SRS products in ecological movement research studies, a better data accessibility such as the European Spatial Agency Sentinel program, which promotes open data, and training platforms to familiarize users with the utilization and the potentialities of SRS data, are needed. The collaboration of movement ecologists with remote sensing experts within a multi-disciplinary approach could also help to integrate more efficiently remote sensing products in ecological movement research.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1, The open-source data and developed products presented in Figure 3.3 are listed below: TAMSAT v3.0 data: the entire archive is available in direct download via batch process at <https://www.tamsat.org.uk/data/archive> with the script detailed at https://www.tamsat.org.uk/public_data/public_scripts/wget_TAMSATv3.0; The MOD/MYD14A2 (MODIS thermal anomaly product) data are available to download at <https://search.earthdata.nasa.gov/search> after login—Archived by National Aeronautics and Space Administration, U.S. Government, LP DAAC. <https://doi.org/10.5067/MODIS/MOD11A2.006>; The MOD/MYD13Q1 (MODIS vegetation product) data are available to download at <https://search.earthdata.nasa.gov/search> after login—Archived by National Aeronautics and Space Administration, U.S. Government, LP DAAC. <https://doi.org/10.5067/MODIS/MOD13Q1.006>; The Sentinel-2 images are freely available at <https://scihub.copernicus.eu/dhus/#/home> after login. The land cover map is available to download at CIRAD depository website: Rumiano, Florent; Miguel, Eve; Valls-Fox, Hugo; Chamailé-Jammes, Simon; Caron, Alexandre; Tran, Annelise, 2020, "Land cover map, Dete site, Hwangue National Park,

Zimbabwe", doi:10.18167/DVN1/BJJZJV, CIRAD Dataverse, V1; The surface water map is available to download at CIRAD depository website: Rumiano, Florent; Miguel, Eve; Valls-Fox, Hugo; Chamaillé-Jammes, Simon; Caron, Alexandre; Tran, Annelise, 2020, "Monthly surface water maps, Hwange National Park, Zimbabwe, 2018", doi:10.18167/DVN1/KPSYME, CIRAD Dataverse, V1, The buffalo and cattle GPS data access are subject to authors' authorization.

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3.2 Chapter summary

- 327 references (mainly peer-reviewed scientific articles) have been selected and analyzed.
- Surface water, precipitation, landcover and fire emerged as key drivers impacting the buffalo and cattle movements.
- These environmental drivers can be efficiently characterized by SRS, mainly through open-access SRS products and standard image processing methods.
- Applying SRS to better understand buffalo and cattle movements in semi-arid environments provides an operational framework that could be replicated in other type of interface where different wild and domestic species interact.
- Given the SRS sensors and applications diversity, it is paramount to determine which SRS product is best suited for a given scale of analyses and how potential inherent limitations can affect the latter.
- The collaboration of movement ecologists with remote sensing experts within a multi-disciplinary approach could help to integrate more efficiently remote sensing products in ecological movement research and solve the actual lack of knowledge that ecologists have with remote sensing applications and methods.

Chapter 4

Characterization of the study sites' environmental variables via satellite remote sensing

Table of content

- 4.0 Preamble**
 - 4.1 A three steps classification methodology**
 - 4.2 Characterizing the surface water**
 - 4.2.1 Methodological approach
 - 4.2.2 Results and descriptions
 - 4.3 Discriminating the agricultural areas**
 - 4.3.1 Methodological approach
 - 4.3.2 Results and descriptions
 - 4.4 Producing the final landcover maps**
 - 4.4.1 Methodological approach
 - 4.4.2 Results and descriptions
 - 4.5 Chapter summary**
-

4.0 Preamble

The purpose of this chapter is to describe in detail the satellite image classification methodologies used to characterize, at the landscape scale, the environmental variables influencing buffalo and cattle movements in space and time that were determined in the previous chapter. The results and analyses of the developed methodology are also detailed to provide a sense of accuracy of spatialized data that will be used as input in the mechanistic model later on in chapter 5, 6 and 7.

4.1 A three steps classification methodology

African savanna vegetation structure and pattern are heterogenous (Mishra and Crews 2014) and driven by rainfall, soils characteristics, geomorphology, herbivory, wildfire as well as anthropogenic activities (Coughenour and Ellis 1993). These biome's defining characteristics make landcover classification (abstract representation of the observed (bio)physical cover on the earth's surface using well-defined diagnostic criteria) of savanna environments particularly challenging as savanna vegetation types are often difficult to separate spectrally due to low inter-class separability and high intra-class variability (Sluiter & Pebesma, 2010) and because surface water is highly sensitive to changes in both climate conditions, and land-use/management practices (Andreu et al., 2019). However, the increasing number of SRS sensors allowing the use of time series datasets has drastically improved landcover classification potentiality and accuracy (Franklin et al., 2015). Indeed, intra-annual spectral variability of SRS images engendered by periodic vegetation life cycles and surface water seasonal variability can be measured and extrapolated (Liu et al., 2016). Several approaches to derive variables from time-series have been developed using a wide range of SRS sensors (Carrasco et al., 2019; Gómez et al., 2016; S. Xie et al., 2019). Regarding the spatial resolution of the SRS images used as classification reference input, low-resolution SRS images produce low accuracy with high uncertainty in savanna environments mainly due to small patches size of contiguous vegetation and heterogeneous classes with mixed vegetation (Mishra, Crews, and Okin 2014). Very high-spatial resolution SRS images (spatial resolution < 10 m) provide all the details required to

reproduce savanna vegetation complexity but are limited by small swath area, large data volume, low temporal frequency and high data cost (both financially and in computing capacity). Medium resolution SRS images (spatial resolution comprised between 10 and 30 m) such as Sentinel-2 or Landsat represent a good compromise in regard to landcover classification for landscape-level applications in savanna environments (Arraut, Loveridge, Valls, et al., 2018; Borges et al., 2020). However, in savanna environments, discriminating specific vegetation properties from medium-resolution imagery is methodologically challenging as soil background potentially affects the spectral contribution of vegetations (Huete, Jackson, and Post 1985).

To cope with challenges inherent to savanna environments pixel-based classification derived from medium-resolution SRS images, we've opted to divide our classification methodology into three separate and complementary steps ([Figure 4.1](#)), consisting in mapping the surface water as well as the agricultural areas separately from the other vegetation elements. With this approach, the pixels of Sentinel-2 images, constituting the input data used to train the classifier algorithm (in our case "Random Forest"), are more spectrally homogeneous. This homogeneity of the isolated spectral signal from a particular class of a landcover in contrast with all the other elements of the same landcover can significantly improve the classifier algorithm performance, thus limiting confusions in the output classifications (Andreu et al., 2019; Bellón, Bégué, Lo Seen, De Almeida, et al., 2017).

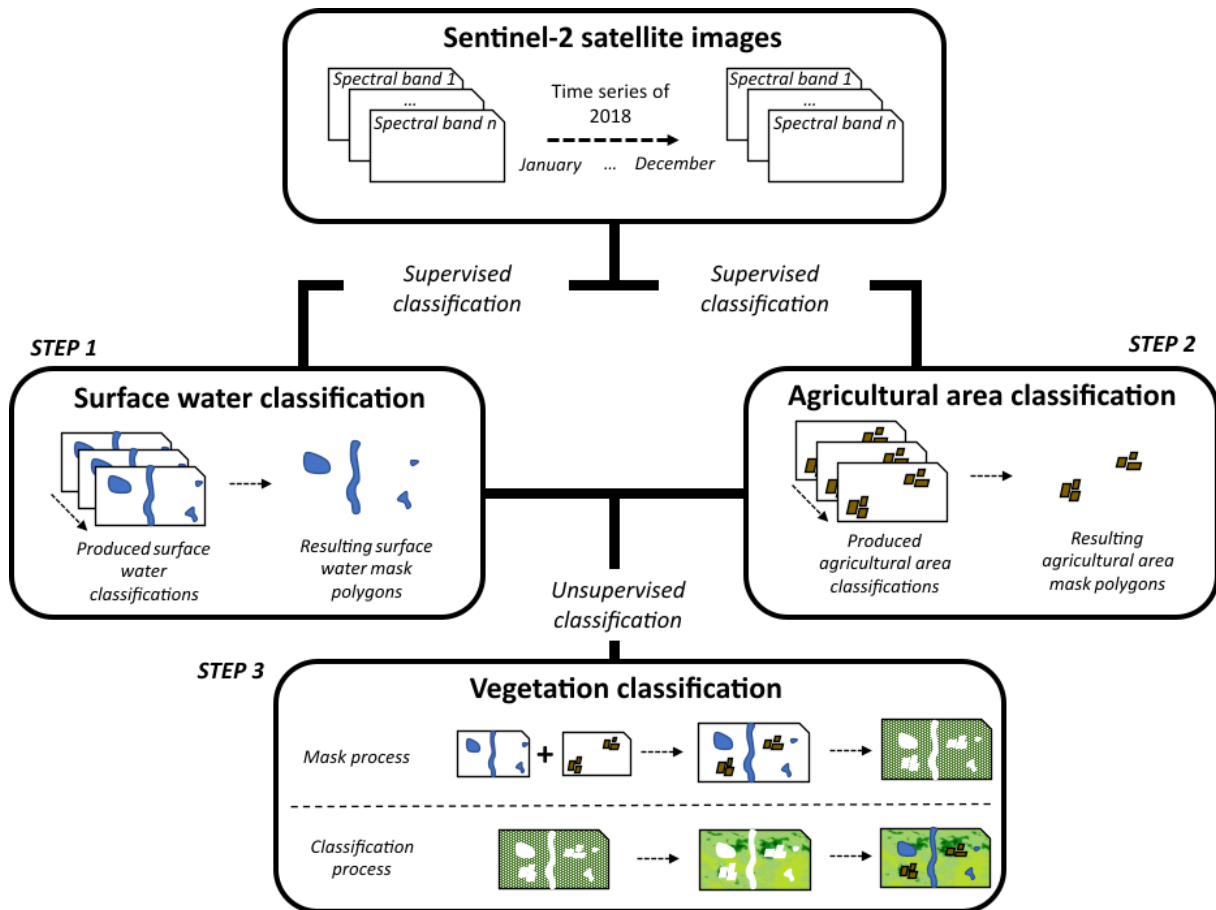


Figure 4.1: Landcover classification general methodology.

As described in Chapter 2, a time series of Sentinel-2 images has been considered for the classification process. A stack of the relevant Sentinel-2 bands or derived spectral indices has been selected and used as input for the considered classifier algorithm for each step (more details in [sections 4.2](#), [4.3](#) and [4.4](#)). A supervised classification of the surface water have been realized as a first step followed by a supervised classification of the agricultural area as a second step and an un-supervised classification of the vegetation as a third step. At the end of the two first steps, two derived polygons of the resulted classifications have been derived and merged to mask the input raster used in the un-supervised classification of the vegetation in step 3. The entire methodology process has been generically used for the three study sites.

4.2 Characterizing the surface water

4.2.1 Methodological approach

The modified normalized difference water index (MNDWI) (H. Xu, 2006) and the normalized difference water index (NDWI) (McFeeters, 1996) (see the Chapter 3 for the spectral indices calculation) have been derived from the sentinel-2 time series and used to classify the surface water. In addition to the two spectral indices, the Short Wave Infrared (SWIR) band has been used to complete the input SRS image dataset ([Figure 4.2](#)). A stack of the three selected bands have been realized for each month of the time series and used as input dataset for the classification process ([Figure 4.2](#)). Two classes (i.e., “surface water” and “other”) have been determined and 50 polygons for each of the two classes served as reference samples via image interpretation. Within the total amount of extracted pixel values, 300 pixel values have been randomly selected for each of the two classes in 50 iterations and have been redistributed following a 50/50 ratio to supply the training and the validating datasets respectively. The 50/50 ratio has been chosen as it allows a more reliable comparison between training and validation datasets than a ratio with a lower proportion of validation samples (Mercier et al., 2018). The training and validation datasets have then been integrated into a Random Forest (RF) classifier algorithm to monthly classify the entire SRS images dataset for each of the three study sites. RF has been chosen as it requires simple parametrization while being reliable and rapid in its execution as well as being able to efficiently process large volume of variables and data (Pelletier et al., 2016). The classification process has then been produced 50 times to consider the algorithm stochasticity and select the best classification iteration amongst the 50 iterations produced. At the end of the classification process ([Figure 4.2](#)), the resulted raster have been vectorized to allow the manual removing of the false positive pixels wrongly classified as “surface water”. The month of March has been chosen as the month of reference as it corresponds to the period of the year when the surface water reaches its maximum spatial extension. The obtained reference vector layer has then been used as a template to mask all of the false positive pixels present in the other months of the time series. The same process has been reproduced for each of the three study sites. At the end of the post-classification process ([Figure 4.2](#)), three time series of monthly classified surface water maps have been produced at the spatial scale of 10 meters ([Figure 4.3](#)).

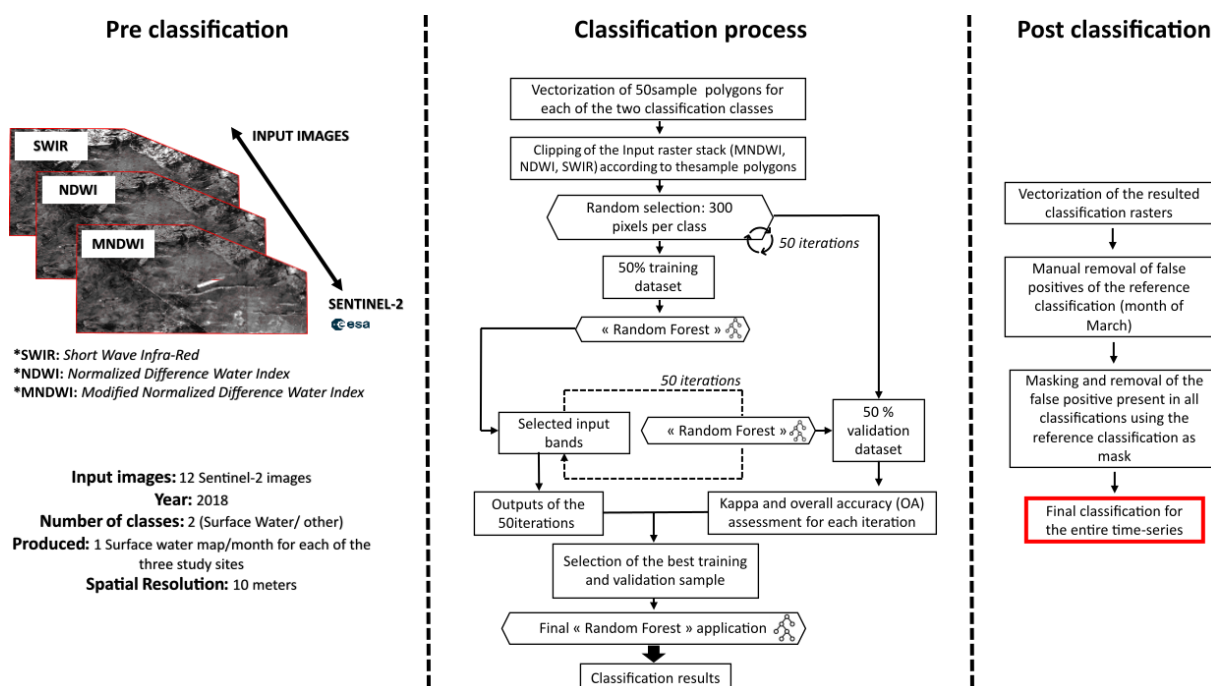


Figure 4.2: Diagram describing the pre-classification, the classification and the post classification stages of the surface water supervised classification methodology

To validate the resulting surface water classifications, the overall accuracy as well as the Kappa indicators have been derived for each of the 50 RF classification iterations (Figure 4.2). The kappa index measures the degree of agreement among independent observations of the same phenomenon (i.e., inter-rater reliability) as well as the consistency in ratings of the same observer across multiple instances of a given observation (i.e., intra-rater reliability) for categorical data (McHugh, 2012). The OA corresponds to the percentage of well classified pixels compared to the total number of pixels present within the classified image (Alberg et al., 2004). As all statistical index, the kappa and OA are not exempt of limitations and have to be used with caution (Pontius and Millones 2011). The average results of the 50 classification iterations regrouping the entire time series were compiled into a two dimensions confusion matrix (Stehman, 1997) for each of the three study sites where the OA and Kappa have been calculated. Each row of the confusion matrix represents the actual instances of a specific class while each column represents the predicted instances of a specific class. Specific to Hwange/Dete, another validation process took advantage of an existing in-situ reference dataset regrouping the localizations of surface water points (see Chapter 2 for more details on the in-situ surface water localization dataset and Chapter 6 for more details on the validation process using the in-situ surface water localization dataset).

4.2.2 Results and descriptions

The resulting classifications highlight the different hydrological morphologies of the three study sites ([Figure 4.3](#)). Indeed, Hwange/Dete is characterized by a succession of surface water ponds of varying size, unevenly distributed throughout the territory. These surface water ponds are impacted by seasonal variations with a maximum area reached in March and close to 6 km² for the year 2018 ([Figure 4.4](#)) compared to a total mapped surface area of 1191 km². The supervised classification of water surfaces via the use of Sentinel-2 medium resolution satellite images allowed the detection of surface water ponds with diameters well below 500 meters ([Figure 4.3](#)), thanks to a spatial resolution of 10 meters. The time series highlighted a significant seasonal fluctuation of surface water ponds detected each month of the year 2018. The areas of detected surface water ponds varied from 6.1 km² in March to 0.62 km² in December, a ratio of 1 to 10 ([Figure 4.4](#)). This variation in water area detected by the supervised classification of the time series corresponds to the seasonal variations in rainfall observed over the Hwange/Dete study site (see [section 2.1.1.1](#)).

In Gonarezhou/Malipati and Kruger/Pesvi, the hydrological morphology corresponds to a river system with some small surface water ponds unevenly distributed throughout the two study sites ([Figure 4.3](#)). In Gonarezhou/Malipati, the surface areas of the detected water bodies vary with the season ([Figure 4.4](#)). For the year 2018, it varied from 8 km² in March to 1.2 km² in January, a ratio of 1 to 6.7. The total surface area covered by the surface water remains relatively small in contrast with the total mapped surface area of the Gonarezhou/Malipati study site (i.e., 1696 km²). The intra-annual variation of the surface water area detected by the supervised classification through the entire time series follows the intra-annual seasonal rainfall pattern of the Gonarezhou/Malipati area (see [section 2.1.2.1](#)), which is similar to the one observed in Hwange/Dete despite different hydrological morphologies.

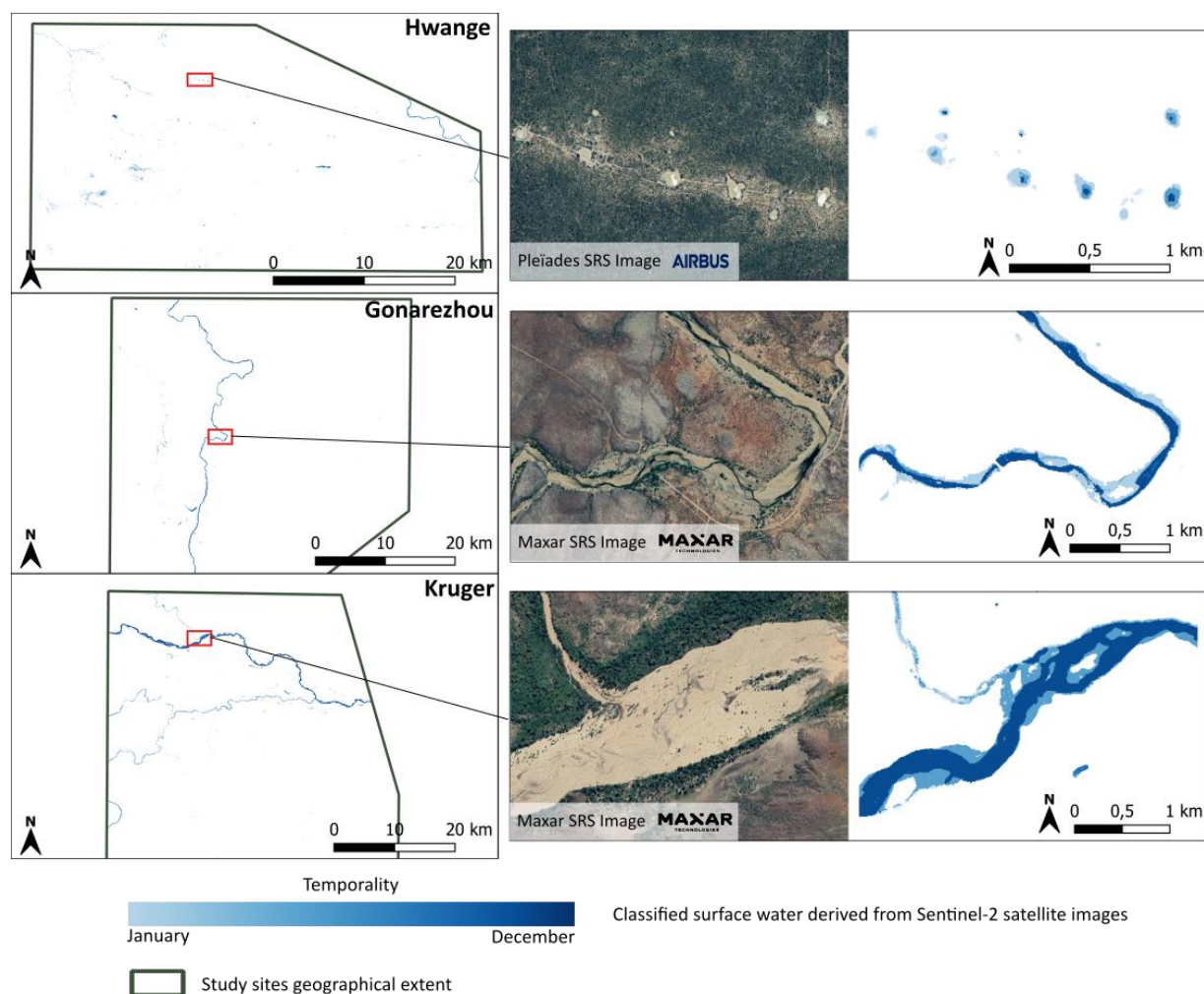


Figure 4.3: Surface water classification results for the three study sites

In Kruger/Pesvi, the surface areas covered by the detected surface water is more important compared to the two other study sites. The maximum surface area of the detected surface water reached 17.4 km^2 in February while the minimum surface area of the detected surface water reached 2.2 km^2 in November (Figure 4.4), a ratio of 1 to 7.9. It is important to note that, even if the surface area of the detected surface water fluctuates during the year, the seasonal pattern is not similar to the ones observed in the two other study sites with two noticeable peaks in detected surface water area in August and December (Figure 4.4). The Limpopo River, which flows through the Kruger/Pesvi study site is subject to hydrological flow variations due to anthropogenic activities and in particular to the water management in relation to hydroelectric dams installed on its course as well as the sustainability of irrigation developments (van der Zaag et al., 2010). The surface area covered by the detected surface water in regard to the total mapped surface area of the Kruger/Pesvi study site (i.e., 2037 km^2) remains small.

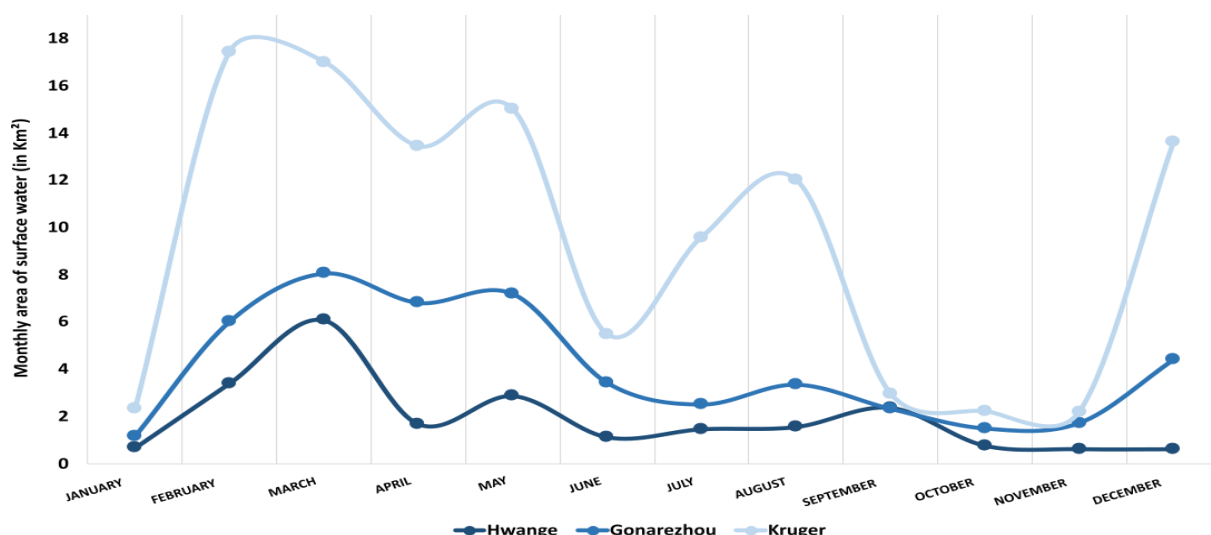


Figure 4.4: Temporal evolution of the monthly surface area of the surface water (in km²) detected by the supervised classification for the three study sites

If the surface water supervised classification time series managed to detect the study sites surface water areas at the landscape scale while translating ecological and climatic patterns observed in these areas, their accuracy performances are contrasted ([Figure 4.5](#)). Indeed, the supervised classification is less accurate in Hwange/Dete with a kappa index of 0.75 and an OA of 0.88 compared to the Gonarezhou/Malipati (kappa index of 0.97 and OA of 0.99) and the Kruger/Pesvi (kappa index of 0.93 and OA of 0.97) study sites. The amount of surface water classified as other types of landcover in Hwange/Dete is by far superior to the other study sites as the surface water areas are formed by small surface water ponds and are, as a result, more easily confused with other types of landcover with similar or closed spectral signal. Indeed, this is particularly true during the driest months (i.e., May, August, and September) ([Figure 4.5](#)) as the surface water become scarce and the surface water ponds reduce in size, making them less easily detectable and more easily confused with vegetation landcover categories where the proportion of bare soil in the spectral value of the pixel is important. In Gonarezhou/Malipati and Kruger/Pesvi, the river hydrological morphology configurations make the surface water more easily detectable through the use of a supervised classification performed from medium resolution satellite images such as Sentinel-2 images, since theoretically, the areas constituted by the water bodies are more extended in space, generating bigger objects with more homogeneous spectral signals. However, as in Hwange/Dete, contrasts exist in these two study sites when looking at the intra-annual surface water supervised classification accuracy ([Figure 4.5](#)). In Gonarezhou/Malipati, March and December are concerned with the lowest accuracies in contrast with the relative steady accuracies observed throughout the year while in Kruger/Pesvi, only the month of July shows a decrease in accuracy compared to the rest of the year. Due to the high overall accuracy values throughout the supervised classification of the time series both in Kruger/Pesvi and in Gonarezhou/Malipati, these punctual decreases of accuracy

values are more related to residual artifacts of the applied atmospheric corrections on the Sentinel-2 images (see [section 2.2.2](#)) than to seasonal changes in landscape structure or surface water abundance.

For the three study sites, the confusion is more pronounced for water pixels classified as other types of landcover than the other types of landcover pixels classified as surface water. This reflects a tendency of the RF algorithm to overestimate the presence of surface water within the landscape, even if this confusion must be put into perspective in view of the overall satisfactory performance of the three supervised classifications.

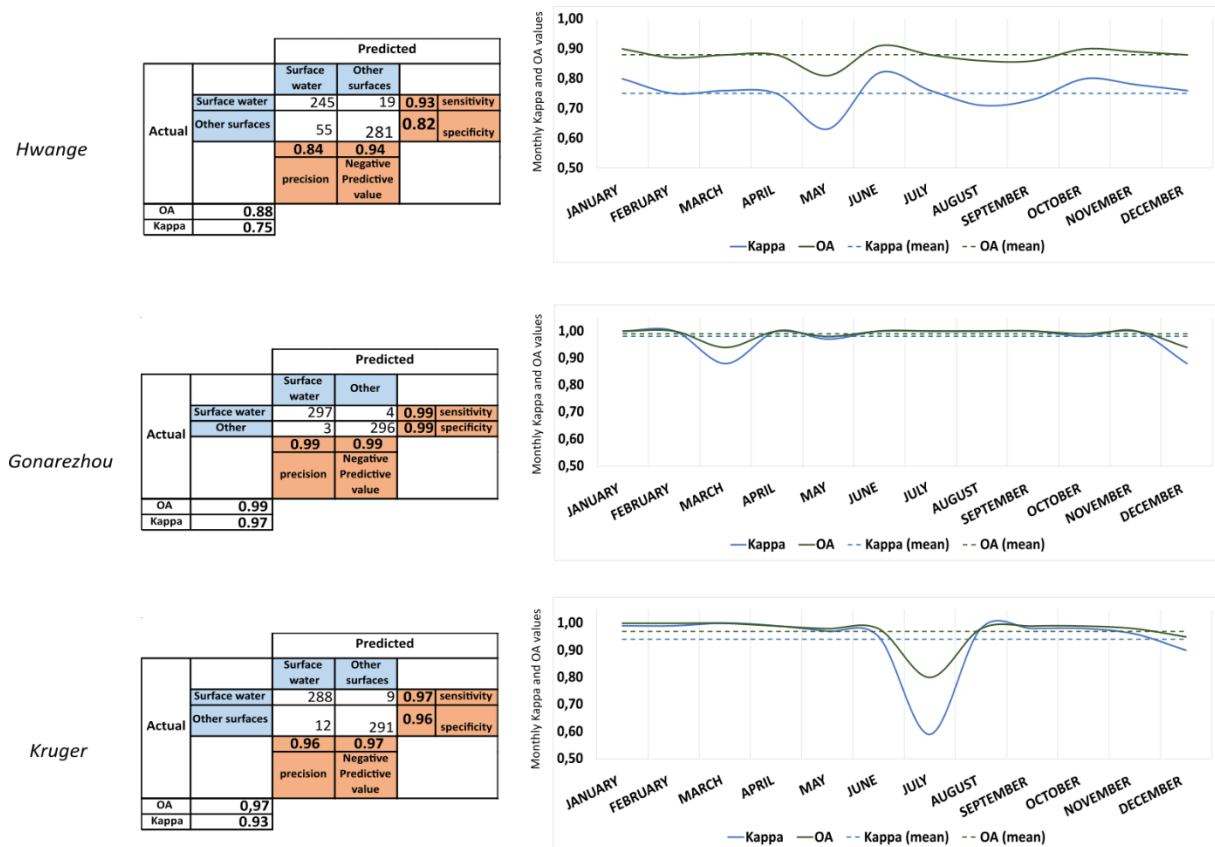


Figure 4.5: Confusion matrices of supervised surface water classifications for the three study sites

4.3 Discriminating the agricultural areas

4.3.1 Methodological approach

The methodological approach used for the supervised classification of the agricultural area is similar as the one described in [section 4.2.1](#) for water surfaces. However, two differences compared to the surface water classification methodology have to be noticed. The first difference is that only one month was used within the Sentinel-2 satellite image series ([Figure 4.6](#)). The month of March has been chosen as it corresponds to the period of the year when the peak of the wet season occurs ([Figure 4.4](#)) and where the contrast between the vegetation and the bare soil is the strongest. The second difference is the fact that other spectral indices have been used as SRS images dataset input for the pixel values extraction via reference polygons sampled. A combination of Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI) and Soil Adjusted Vegetation Index (OSAVI) (see Chapter 3 for the spectral indices calculation) have been considered to classify agricultural areas. These spectral indices have been used extensively and proved to be efficient in previous studies to characterize agricultural area using medium spatial resolution SRS images such as the one used in this supervised classification methodology (Bellón, Bégué, Lo Seen, De Almeida, et al., 2017; Y. Zhao et al., 2020). Two classification classes (i.e., “agricultural area” and “other”) have been determined to train and validate the RF classifier algorithm ([Figure 4.6](#)). At the end of the post-classification process, one map of the classified agricultural area at 10 meters of spatial resolution for each of the three study sites have been produced ([Figure 4.7](#)). To validate the accuracy of the agricultural area classifications, the same process as described in [section 4.2.1](#) has been reproduced, using confusion matrices ([Figure 4.8](#)).

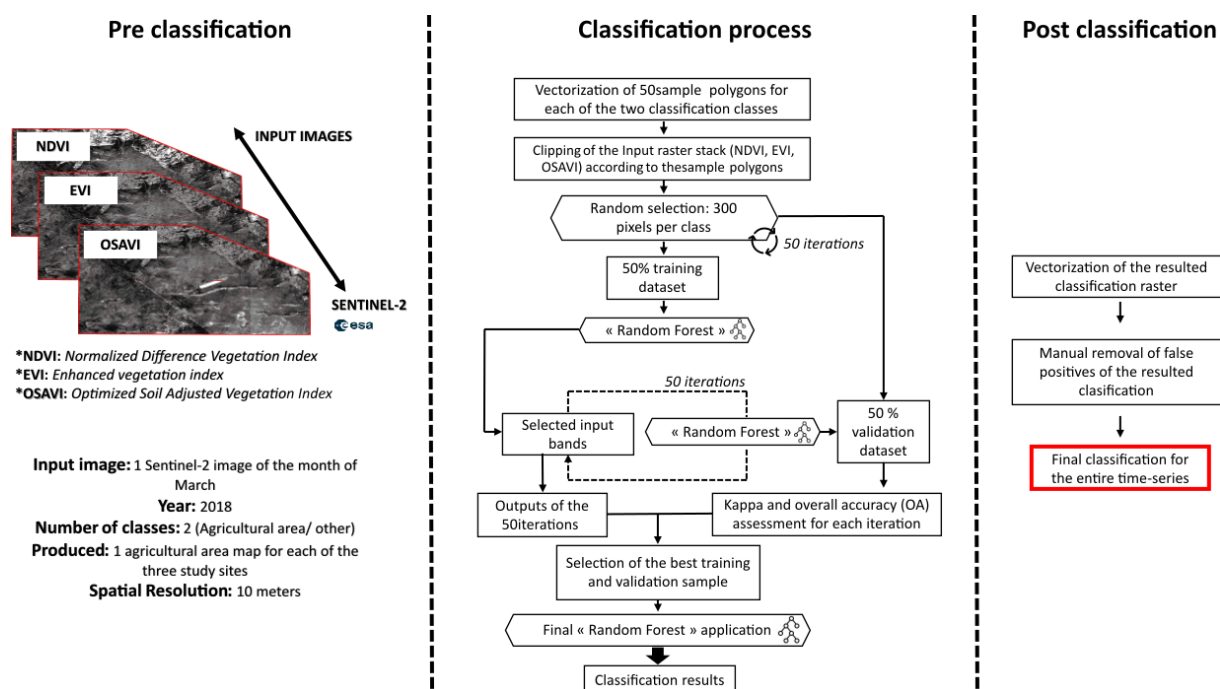


Figure 4.6: Diagram describing the pre-classification, the classification and the post classification stages of the agricultural area supervised classification methodology

4.3.2 Results and descriptions

The spatial distribution of agricultural areas detected by the supervised classification is very contrasted according to the study sites. In Hwange/Dete, the agricultural areas are grouped close to each other, forming a quasi-homogeneous space with marked contrasts to other landcover types (Figure 4.7). On the other hand, in Gonarezhou/Malipati and Kruger/Pesvi, the detected agricultural areas are more unevenly distributed throughout the mapped territories, forming patches with smaller surface areas, blending more into an heterogeneous landscape (Figure 4.7). In comparison with the other types of landcover, the percentage of the agricultural areas is more pronounced in Hwange/Dete with 5% of the total classified surface area (Figure 4.10B), covering an area of 59,5 km². In Gonarezhou/Malipati, the percentage represented by the agricultural areas is comparable with 4% of the total classified surface area covering an area of 68,3 km² while being far less inferior in Kruger/Pesvi with a percentage of only 0,8% (Figure 4.10B) and covering an area of 15,6 km².

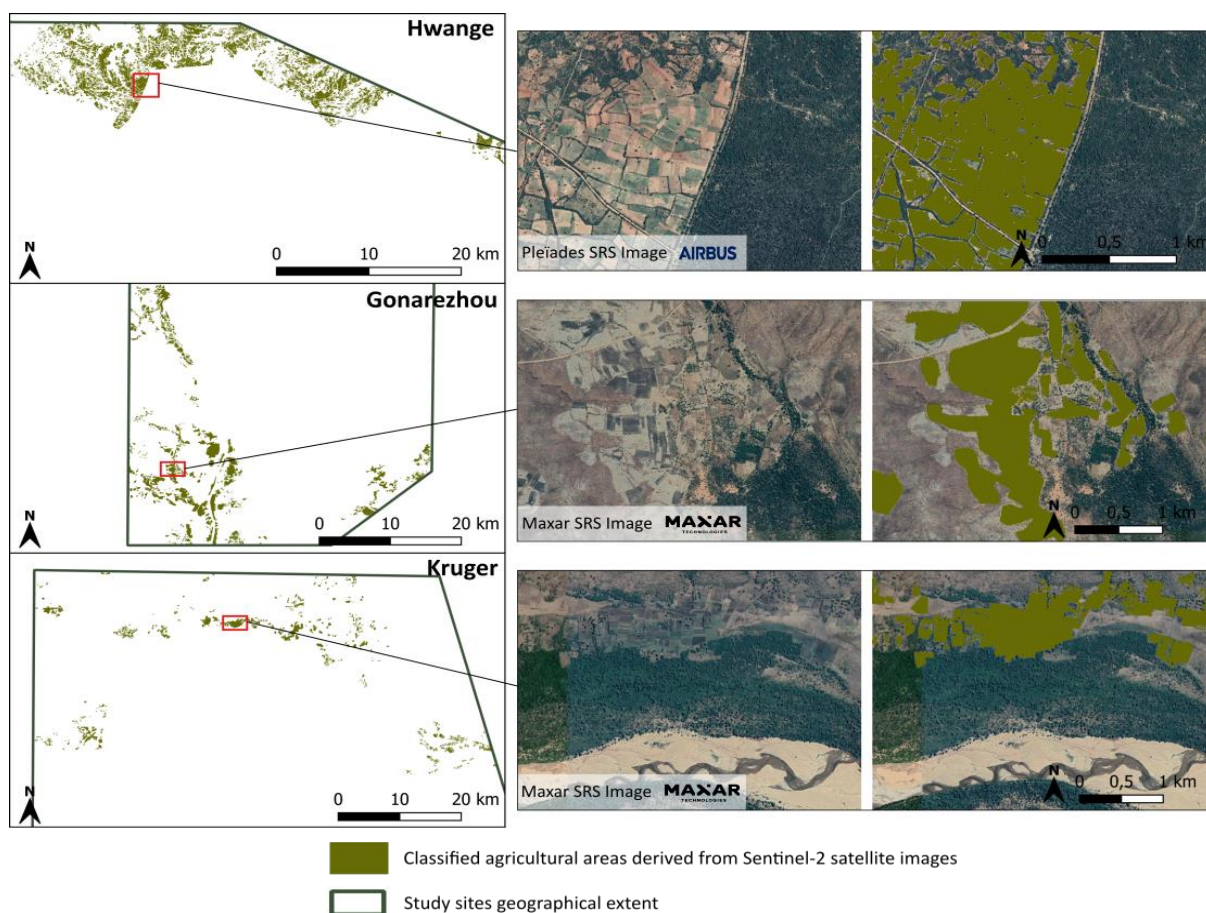


Figure 4.7: Maps of supervised water surface classification results for the three study sites

The accuracy of the agricultural areas supervised classifications is contrasted according to the study sites (Figure 4.8). In Hwange/Dete the supervised classification performed better with a kappa index of 0.83 and an OA of 0.91 compared to the Gonarezhou/Malipati (kappa index of 0.53 and OA of 0.77) and the Kruger/Pesvi (kappa index of 0.66 and OA of 0.83) study sites. These results confirmed the importance played by the landscape configuration and the existing degree of contrast between the different types of landcover. Unlike surface water, the spectral signal of agricultural surfaces is more difficult to isolate from the spectral signal of other types of vegetation cover. Hwange/Dete has better classification results because the agricultural areas are densely grouped in space, forming an homogeneous space that contrasts with other surrounding vegetation types. However, this existing contrast does not prevent the RF algorithm from overestimating the classification of agricultural areas into other types of vegetation cover while other types of vegetation cover are practically not classified as agricultural areas (Figure 4.8). The contrasting results observed in Kruger/Pesvi and Gonarezhou/Malipati can be explained by the tendency of the RF algorithm to confuse both agricultural areas with other types of vegetation cover and the other types of vegetation cover with agricultural areas in similar proportions (Figure 4.8).

The supervised classification of the agricultural areas at the landscape scale allows to visually assess the precise location as well as the main clusters of agricultural areas in the three study sites ([Figure 4.7](#)). The post-classification step consisting of the manual correction of the pixels wrongly classified as agricultural areas while being in fact other types of vegetation cover pixels ([Figure 4.6](#)) has therefore been facilitated as most of the false positive pixels were located in areas far from the detected agricultural area clusters.

Hwange

		Predicted			
Actual		Agricultural area	Other		
	Agricultural area	253	5	0.98	sensitivity
	Other	47	295	0.84	specificity
		0.86	0.98		
		precision	Negative Predictive value		
OA	0.91				
Kappa	0.83				

Gonarezhou

		Predicted			
Actual		Agricultural area	Other		
	Agricultural area	229	70	0.77	sensitivity
	Other	71	230	0.76	specificity
		0.76	0.77		
		precision	Negative Predictive value		
OA	0.77				
Kappa	0.53				

Kruger

		Predicted			
Actual		Agricultural area	Other		
	Agricultural area	253	55	0.82	sensitivity
	Other	47	245	0.84	specificity
		0.84	0.82		
		precision	Negative Predictive value		
OA	0.83				
Kappa	0.66				

Figure 4.8: Confusion matrices of supervised agricultural area classifications for the three study sites

4.4 Producing the final landcover maps

4.4.1 Methodological approach

Three Sentinel-2 red-edge bands (i.e., Sentinel-2 band 5, band 6 and band 7 that are located between the red and the Near Infrared of the electromagnetic spectrum) have been masked with manually digitalized polygons of road networks as well as with vectorized surface water and agricultural area polygons resulting from the two previous classifications ([Figure 4.1](#)). These three bands have been used as input SRS image dataset for the unsupervised classification as it has been established that the red-edge bands inclusion into classification scheme positively impacts the characterization of vegetation classes and improve overall classification accuracies (Schuster, Förster, and Kleinschmit 2012). The three produced masked raster have then been used to classify four classes of vegetation and landscape characteristics for Hwange/Dete (i.e., woodland, mixed-woodland-shrubland, shrubland, mixed shrubland-grassland) and five classes of vegetation and landscape characteristics for Gonarezhou/Malipati and Kruger/Pesvi (i.e., woodland, mixed-woodland-shrubland, shrubland, mixed shrubland-grassland, bare soil) ([Figure 4.9](#)) via a pixel-based non-supervised K-means clustering classification method (Burrough, van Gaans, and MacMillan 2000). The K-mean algorithm is a classical distance-based algorithm that evaluates similarity or dissimilarity of the pixel values by the distance to each cluster center for each of the pre-determined classes (Shan, 2018) and has been chosen as it proved its efficiency for SRS landcover classification (Chen and Peter Ho 2008). After the clustering of all pixels present in the input raster, the resulting classes were labelled in correspondence with the “a priori” class assessment previously realized via photo-interpretation of a very high satellite image (i.e., Pleiades). 40 reference polygons per class have been manually digitalized for each of the three study sites to compensate for the lack of an in-situ landscape description database and used as reference polygons for the validation of the unsupervised classification. These reference polygon datasets have then been used to derive the confusion matrices and calculate the OA and the Kappa index ([Figure 4.11](#)). A satisfaction threshold was established at an OA higher than 0.7 and a kappa index strictly superior to 0.6 to combine multiple accuracy quantifications, thus qualifying the relevance of the classification produced (Shao et al., 2019). In the case where the classification result is judged not usable (corresponding to the retroactive loop “NO” – [Figure 4.9](#)), the application of a k-means is repeated until a classification reach a satisfactory level of accuracy. At the end of the unsupervised classification process, the resulting vegetation classification raster have been merged with the previously

produced surface water, agricultural areas and road network polygons (Figure 4.1), thus assembling the final landcover maps for the three study sites (Figure 4.10A).

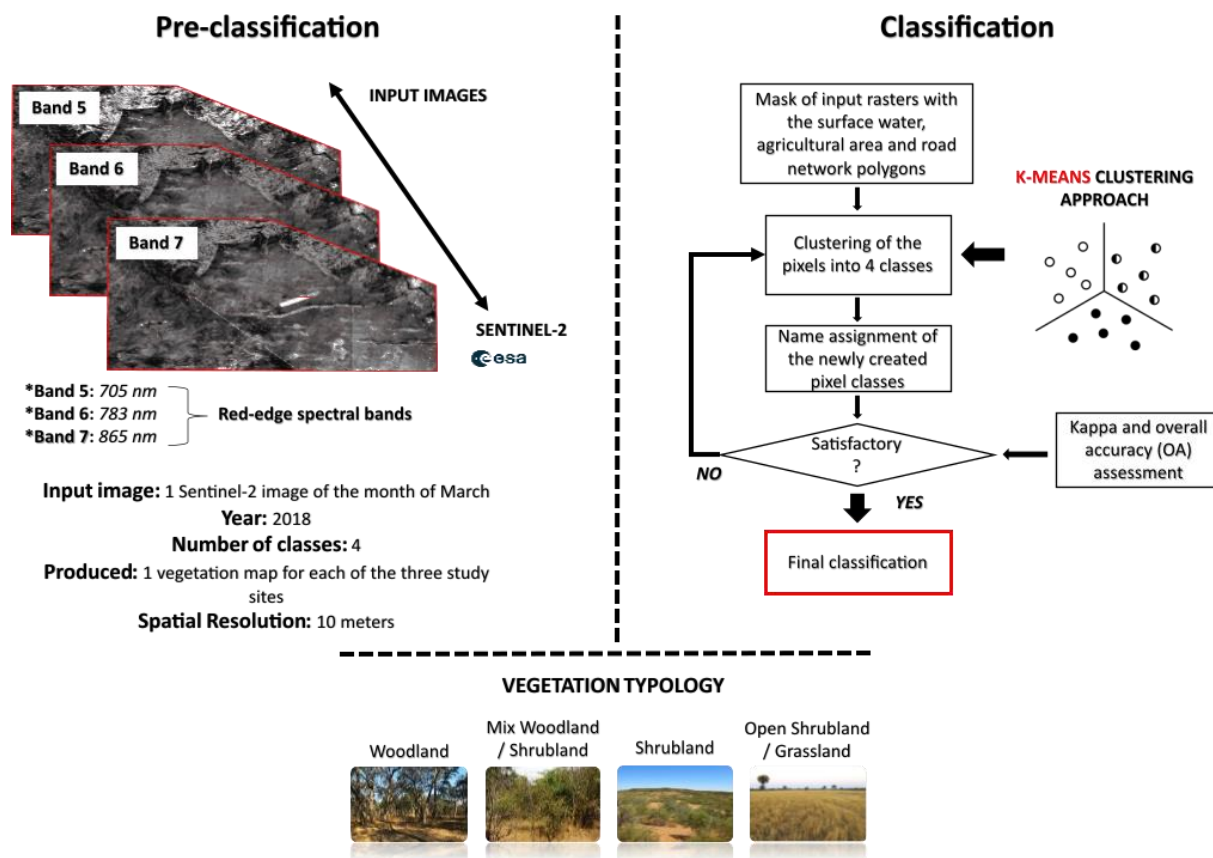


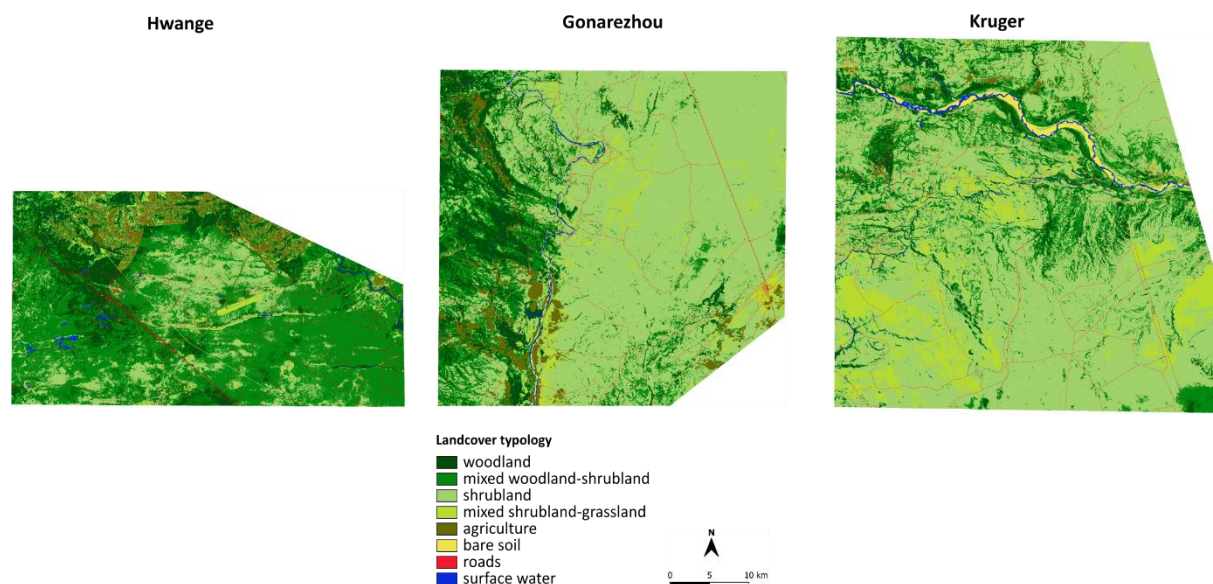
Figure 4.9: Diagram describing the pre-classification, the classification as well as the chosen vegetation typology of the vegetation unsupervised classification methodology.

4.4.2 Results and descriptions

The produced landcover maps for the three study sites highlight a contrast in the landscape spatial configuration and intrinsic composition between Hwange/Dete from one hand and Gonarezhou/Malipati and Kruger/Pesvi from the other end. In Hwange/Dete the landcover is more wooded across the mapped area and is composed of mostly closed landscapes, with the exception of areas in closed proximity with surface water where the vegetation opens up (Figure 4.10A). The woodland covers an area of 175,5 km² and the mixed-woodland shrubland covers an area of 660.4 km², representing 14.7% and 55.5 % of the total classified surface area respectively (Figure 4.10B). Interestingly, the most open areas where the landcover classes “shrubland” and

“mixed-shrubland-grassland” are found (these landcover categories represent 20.3% et 1.9% of the total classified surface area, covering areas of 242.1 km² and 22.8 km² respectively) correspond to the territory mainly frequented by GPS collared buffalo (see [Figure 2.5](#) in [section 2.2.1.2](#)).

A



B

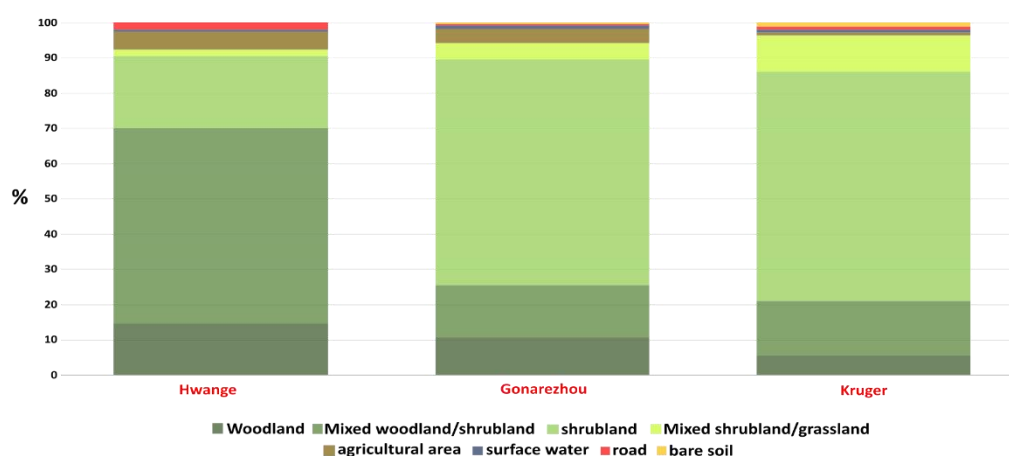


Figure 4.10: A) Maps of the three study sites landcover classifications. B) Percentage share of each landcover class relative to the total area of the landcover classification for each of the three study sites

In Gonarezhou/Malipati, the landcover changes drastically whether the observed landcover is located on the eastern or western side of the Mwenezi river that flows from north to south ([Figure 4.10A](#)). On the eastern side of the river, the landscape is more wooded as “woodland” and “mixed woodland shrubland” composed the majority of the landcover types present in this particular area (these landcover categories represent 10.7% et 14.7% of the total classified surface area, covering areas of 181.7 km² and 250 km² respectively). However, on the western side of the river, that corresponds to the Gonarezhou National Park (see [Figure 2.3](#) in the [section 2.1.2.1](#)),

the landscape is more open and composed primarily of “shrubland” and “mixed-shrubland-grassland” that cover a wider area and represent 88.7% et 76.8% of the total classified surface area, covering areas of 181.7 km² and 250 km² respectively ([Figure 4.10B](#)).

In Kruger/Pesvi, the wooded landcover is present in closed proximity of the Limpopo River that flows eastward and becomes rarer the further away from the river ([Figure 4.10A](#)). The “woodland” and “mixed woodland shrubland” landcover categories represent 5.5% et 15.7% of the total classified surface area, covering surface areas of 111.5 km² and 320.5 km² respectively ([Figure 4.10B](#)). The landscape is however more open in comparison with the other study sites as the “mixed-shrubland-grassland” landcover category is more present, covering an area of 208.6 km² that represent 10.2% of the total classified surface area ([Figure 4.10B](#)). Nevertheless, it is the “shrubland” landcover category that covers the most extensive area by far with a surface area of 1323.8 km², representing 65% of the total classified surface area ([Figure 4.10B](#)).

The accuracy of the unsupervised vegetation classification is rather consistent and steady for the three study sites ([Figure 4.11](#)). In Hwange/Dete, the kappa index is 0.67 and the OA is 0.75. In Gonarezhou/Malipati and Kruger/Pesvi, these accuracy indicators are slightly inferior with a kappa index of 0.64 and 0.66 and an OA of 0.71 and 0.73 respectively ([Figure 4.11](#)). It is slightly inferior to other realized supervised classifications of savanna environments (e.g., in Kenya Hunter *et al.*, 2020 obtained a classification with an OA of 0.82 while covering a smaller study area) but similar to other non-supervised classification using the K-means clustering approach (e.g., in Brazil Filippi *et al.*, 2009 obtained a classification with a maximum OA of 76.84). For the three study sites, the confusions concern the landcover categories that are closer in foliage and vegetation composition from one another. The “woodland” is often mistaken as the “mixed woodland shrubland” and the “mixed woodland shrubland” is often incorrectly classified as “shrubland”. Depending on the landcover categories, the precision of the k-mean algorithm varies greatly ([Figure 4.11](#)). Indeed, the landcover categories that contrast the most in term of spectral signal according to the degree of opening and closing of the foliage and vegetation composition, such as the “woodland” and “mixed-shrubland-grassland”, present the best accuracies (e.g., in Hwange/Dete, the “woodland” is classified with a precision of 0.91 and the “mixed-shrubland-grassland” with a precision of 0.85). On the contrary, the landcover categories that are heterogeneous in term of foliage and vegetation composition, hence having a contrasting spectral signal, such as the “shrubland” and the “mixed woodland shrubland”, are not as well classified as the other landcover categories (e.g., in Hwange/Dete the “shrubland” and the “mixed woodland shrubland” are both classified with a precision of 0.58).

Hwange

		PREDICTED						
		woodland	mixed woodland-shrubland	shrubland	mixed shrubland-grassland	sum	precision	
ACTUAL	woodland	32	8	0	0	40.00	0.80	
	mixed woodland-shrubland	3	29	8	0	40.00	0.73	
	shrubland	0	4	31	5	40.00	0.78	
	mixed shrubland-grassland	0	0	12	28	40.00	0.70	
	sum	35.00	41.00	51.00	33.00	120.00	160.00	
	precision	0.91	0.71	0.61	0.85	160.00		
	OA	0.75						
	Kappa	0.67						

Gonarezhou

		PREDICTED						
		woodland	mixed woodland-shrubland	shrubland	mixed shrubland-grassland	bare soil	sum	precision
ACTUAL	woodland	28	10	2	0	0	40.00	0.70
	mixed woodland-shrubland	11	19	10	0	0	40.00	0.48
	shrubland	0	4	29	7	0	40.00	0.73
	mixed shrubland-grassland	0	0	9	31	0	40.00	0.78
	bare soil	0	0	0	5	35	40.00	0.88
	sum	39.00	33.00	50.00	43.00	35.00	142.00	200.00
	precision	0.72	0.58	0.58	0.72	1.00	200.00	
	OA	0.71						
PC	0.64							

Kruger

		PREDICTED						
		woodland	mixed woodland-shrubland	shrubland	mixed shrubland-grassland	bare soil	sum	precision
ACTUAL	woodland	31	8	1	0	0	40.00	0.78
	mixed woodland-shrubland	11	24	5	0	0	40.00	0.60
	shrubland	0	8	28	4	0	40.00	0.70
	mixed shrubland-grassland	0	2	10	28	0	40.00	0.70
	bare soil	0	0	1	5	34	40.00	0.85
	sum	42.00	42.00	45.00	37.00	34.00	145.00	200.00
	precision	0.74	0.57	0.62	0.76	1.00	200.00	
	OA	0.73						
Kappa	0.66							

Figure 4.II: Confusion matrices of the unsupervised vegetation classifications for the three study sites

4.5 Chapter summary

- A three steps methodology have been chosen to characterize the surface water as well as the landcover at the landscape scale with a spatial resolution of 10 meters for the three study sites.
- To classify the surface water, a supervised classification method using a Random Forest algorithm have been designed and applied on Sentinel-2 satellite images time series. As a result, three time series of surfaces water (one for each of the study sites) have been produced, detailing the spatiotemporal availability of surface water at a landscape scale.
- The same methodological principles have been applied to classify the agricultural areas at the three study sites. This particular step have been conducted in order to discriminate agricultural areas from the rest of the vegetation structure thus improving the capacity to characterize vegetation landcover with limited confusions.
- An unsupervised classification using the K-mean clustering approach have been used to classify the vegetation structure of the three study sites. Four vegetation types have been discriminated: i) woodland, ii) mixed woodland-shrubland, iii) shrubland, and iv) mixed shrubland-grassland.
- Overall, the classification method based on a pixel-based approach is simple, reproducible, uses open-source data and software and provides accurate results for a wide range of ecological applications requiring landscape scale landcover data over an extensive surface area.

Chapter 5

A spatialized mechanistic animal movement model based on collective movements of self-propelled individuals

Table of content

5.0 Preamble

5.1 Overview of the animal movement ecology

5.2 Mathematical models follow two paradigms

5.2.1 Statistical models

5.2.2 Mechanistic models

5.3 The choice of a mechanistic model based on collective movements of self-propelled individuals

5.3.1 The individual versus the collective

5.3.2 The synthesis of the two, when individuals influence the collective

5.4 Spatializing the model and combining it with SRS data

5.4.1 The notion of space in animal movement modelling

5.4.2 The language “Ocelet”

5.5 Chapter summary

5.0 Preamble

This chapter marks a transition in that it addresses the issue of spatial modeling and follows on from Chapters 3 and 4 which were primarily focused on the remote sensing aspects of the thesis. The chapter below defines in detail the field of research of animal movement ecology, gives a state of the art of all spatial modeling methods used in this specific research field with their respective strengths and weaknesses, and describes the spatialization process of the animal movement model used in this thesis, and in particular through the description of the spatial modeling language Ocelet developed internally at CIRAD.

5.1 Overview of the animal movement ecology

Animal movement ecology has developed to a particular discipline within the broader research field of ecology and benefited strongly in recent years from telemetry data to explore the causes, mechanisms, and patterns of animal movement in space and time. This discipline primarily aims to understand consequences of animal movements on the ecology and evolution operating across heterogeneous/homogeneous landscapes at individual, population, and community scales (Cagnacci et al., 2010). Adding to these primary objectives, underlying objectives aim at addressing management and conservation questions, at determining the success or failure of management or conservation interventions, and at monitoring spatiotemporal environmental changes in relation with animal behaviors (Miller et al., 2019). Indeed, measuring the position in space and time of a free-living animal allows to relate the determined animal to its immediate environment, thus apprehending the fate of individuals (e.g., interrelations between individuals within the same animal species or with other animal species) as well as the structure and dynamics of populations and communities within changing ecosystems (Hanski & Hanski, 1999; Swingland et al., 1983; Turchin, 2015).

At first, animal movement ecology that started during the 1950s was primarily focused on improving management strategies by understanding where animals were moving and how they were using natural resources (Miller et al., 2019). The notion of animal's home range, originally

defined by Burt as “*an area traversed by the individual in its normal activities of food gathering, mating, and caring for young*” (Burt, 1943), was predominantly used to tackle this particular objective. Later, the concept of home range evolved through the development of statistical modeling of space use, and spatially explicit mechanistic models (Kie et al., 2010). However, until recently there was no general consensus on the framework to address animal movement mechanisms (Börger, Dalziel, and Fryxell 2008; Kie et al. 2010), as movement mechanisms are very diverse among animal life forms (Holyoak et al., 2008). In regard to these recurring confusions, today’s animal movement ecology quantifies movement patterns to make inferences about likely behaviors (Turchin, 2015). A general framework emerged ([Figure 5.1A](#)) as animal movement ecology considers animal movements as interactions between internal (e.g., intention, instinct, basic needs) and external factors (e.g., environment, other individuals of the same species or other animal species), movement and navigation capacities (e.g., speed, alignment, cohesion), producing observed qualitative and quantitative movement paths (Nathan et al., 2008). These interactions inserting themselves into four paradigms (i.e., biomechanical, random, cognitive and optimality) that represent different approaches to analyze, describe and quantify animal movement ([Figure 5.1B](#)). However, if the general framework developed by Nathan et al. 2008 allows to potentially link analyses of movement paths and studies of movement mechanisms, thereby better understanding the interactions between animal movement and ecological processes, a wide array of methodological approaches exist and are extensively used, leading to multiple interpretations and potential confusions. In animal movement ecology, synthesis as well as the generic aspect of the methods commonly used remains a challenge. In that regard, animal movement modelling methodologies must be chosen with care according to initial research hypotheses.

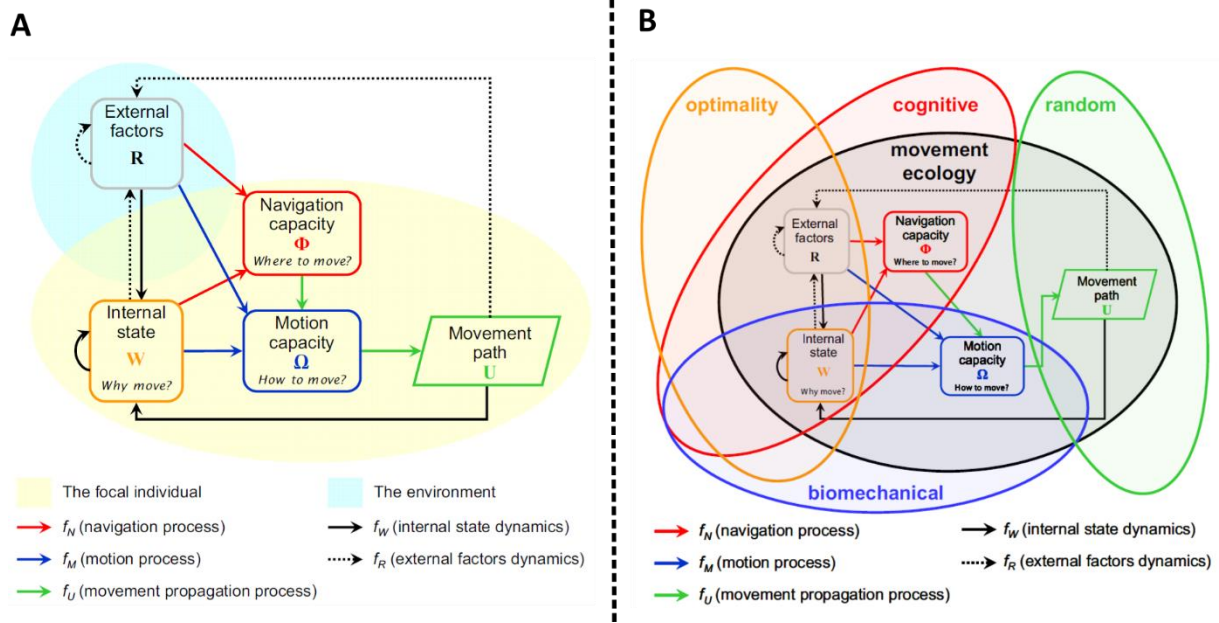


Figure 5.1: These two figures are extracted without modification from (Nathan et al., 2008). A) Diagram representing a general conceptual framework for movement ecology. B) Diagram representing the relationships (the three colored arrows) the different compartments of the general conceptual framework for movement ecology as well as different scientific disciplines (the four colored circles) in which the movement of organism is being studied while considering the organization of the general conceptual framework for movement ecology.

5.2 Mathematical models follow two paradigms

We consider the modelling process as a conceptual framework that aims to reproduce a real or proposed system by abstraction (Figure 5.2). By definition, a modelling process impacts all aspects of a given research as it is closely linked to the chosen discipline, theme and study locations, the initial research hypothesis, the quality and quantity of available data, the speed with which the model can be developed, the validity of the model, the speed of experimentation, as well as the confidence that is placed in the model results (S. Robinson, 2008). All simulation models are simplifications of a perceived reality and are subjective in essence (Zeigler, Muzy, and Kofman 2018). Mathematical modelling corresponds to the application of this conceptual framework (Figure 5.2) by the translation of a given system via mathematical reasoning following two methodological approaches that can be used independently or in combination : a statistical modelling approach and a mechanistic modelling approach.

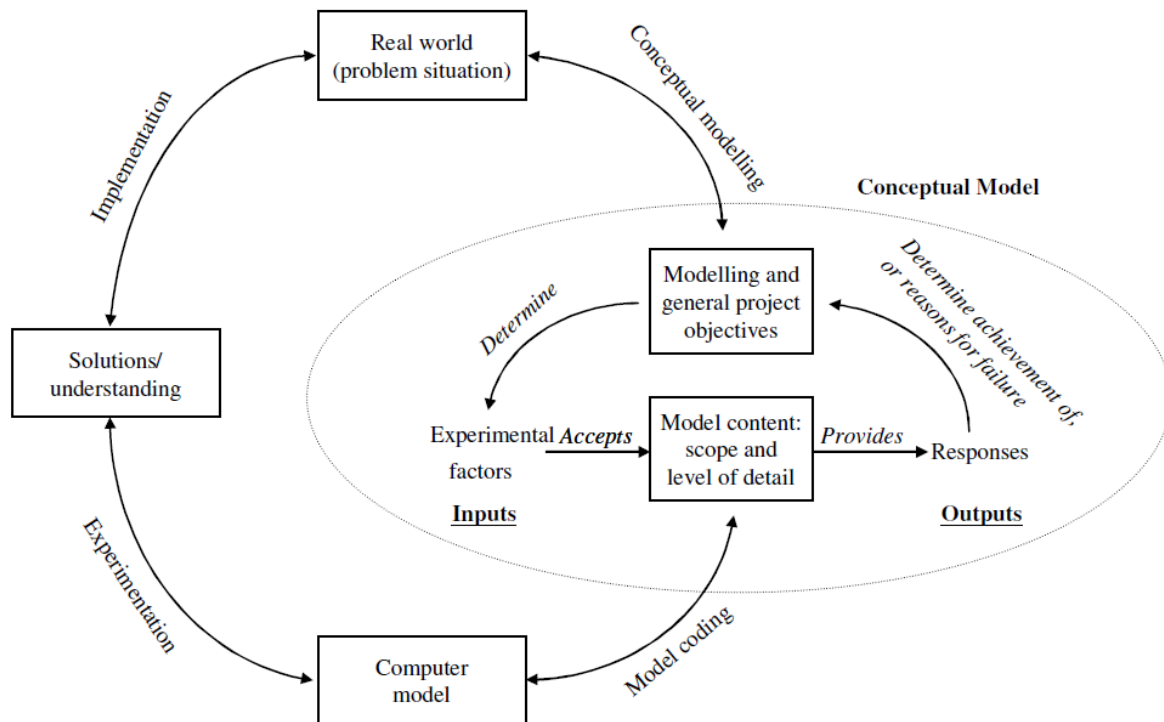


Figure 5.2: This figure is extracted without modification from (S. Robinson, 2008) and consists of a diagram representing the conceptual model in the simulation project life-cycle. This conceptual model can serve as a foundation to build any desired models that aim at reproducing complex ecological systems.

5.2.1 Statistical models

The mathematical formulation of a statistical model (also named empirical model) does not intent on describing realistic cause and effect between model parameters and a predicted response, or to reproduce/simulate phenomenon inherent to general ecological functions and mechanisms, but to efficiently condense empirical facts to provide an understanding of a specific research hypothesis based on correlative relations (Wissel, 1992). For example, it is possible to incorporate a specific animal trait information based on statistics into a given model for ordinal response in order to identify the main reasons why animal species differ in their environmental response (Warton et al., 2015). It can be considered that three major components compose a statistical modelling approach in ecology: i) an ecological component, ii) a data component, and iii) a statistical component (Austin, 2002). The ecological component consists of the ecological knowledge, theories, and assumptions to be used or tested in a given study. The data component is formed dependently of decisions made regarding the quality and quantity of the input data (i.e., telemetry data). How the data have been collected, measured, or estimated are key elements to be considered. The statistical component corresponds to the choice of one particular or several statistical methods, error functions and significance tests that linked the two other

components to determine the capacity of the designed statistical model to successfully answer the initial research hypothesis (Austin, 2002). Non exhaustive and commonly used statistical models to describe animal movement are step-space model (SSM) (Patterson et al., 2008), stochastic differential equations (SDEs) (Preisler et al., 2004) or hidden Markov model (HMMs) (Langrock et al., 2012). These models are usually calibrated and validated by statistical measurements of various level of complexity such as generalized linear model (GLM), generalized additive model (GAM), classification and regression tree (CART), artificial neural network (ANN), random forest (RF) or root mean square error (RMSE) (Dormann, 2020). Regarding animal movement ecology, statistical models are dynamic and assume a hierarchical structure between various different metrics such as velocity or displacement, distances between successively observed positions, headings (i.e., compass directions), changes of directions (i.e., turning angles), ... (Patterson et al., 2017). Three main categories encompass the variety of these dynamic statistical models (Hooten and Johnson 2017): i) point process models (Brost et al., 2015), ii) discrete-time dynamic models (McClintock et al., 2012) and iii) continuous-time dynamic models (D. S. Johnson et al., 2008).

Statistical modelling approaches for the analysis of individual or collective animal movements can be overly complex, both in their design and in terms of the computational power required to calibrate and validate them (Patterson et al., 2017). This can lead to a lot of effort in vain on trying to understand aspects of a possibly unrepresentative dataset. On the other end, some statistical animal movement models can also be too simplistic as they rely on one or few parameters to understand a vast array of complex behaviors (Patterson et al., 2017). It is important to keep in mind that statistical models are closely dependent of the quality and quantity of input telemetry data, and as such can be biased if the time frequency and regularity are inconsistent or if the continuity of data is compromised due to instrumental difficulties as well as environmental and animal behavioral influences (Hooten & Johnson, 2017). Statistical models have to be chosen carefully depending on the temporal and spatial scales of the given study, the number and type of the considered focal animal species as well as the scale on which the given study aims at understanding the animal movement patterns (i.e., individual, population or community). Statistical models have been extensively used to understand animal movements (Essington, 2021; King, 2014). For example, Hooten, Scharf and Morales, 2019 designed a statistical model in continuous-time to provide direct inference about gains and losses associated with physiological processes based on buffalo movements in heterogeneous environments.

5.2.2 Mechanistic models

Mechanistic models base predictions on our understanding of cause–effect relationships (Guisan and Zimmermann 2000) as they describe empirical knowledge by formalizing them into mathematical formulas or simulations. Mechanistic models are a formalization of knowledge on the functioning of a given system. This knowledge is often derived from observational data that are therefore essential to model specific processes. Indeed, mechanistic models do not focus primarily on predicted precisions, but rather on theoretical correctness of the predicted response (Pickett, Kolasa, and Jones 2010). The mechanistic model approach requires a conceptualization of a hypothesis centered on how a given system works and how considered variables are interconnected within this system (Ellis et al., 2020). It usually follow a five step process: i) problem identification, hypothesis generation and definition of the general framework of the study, ii) model conceptualization, iii) data collection that precisely describe mechanisms intended to be modeled, iv) model development based on the choice of mathematical equations to reproduce specific mechanisms or assumptions of particular mechanisms, and v) model evaluation through statistical, graphical, sensitivity, behavior, and scenario analyses. Mechanistic models can either have a system of equations simple enough to make an analytical calculation of the solutions or have too many retractions associated with a complex system making analytical solution applications impossible. In that case, simulations are processed step by step through the calculation of differential equations (Busenberg, 2012). Discriminating essential and nonessential components of a mechanistic model is crucial as it determines the assignment of the appropriate equation structure between components and indicates the required level of model complexity needed (Ellis et al., 2020). The model outputs will usually give valuable information on requirements to add more complexity and/or restructure the model, implying strong back-and-forth interventions between model developments and data-based experimental works, which are commonly used to parametrize the model in addition with empirical and bibliographical knowledge.

In regard to animal movement ecology, mechanistic movement models have seen recent methodological advances, where animal space-use as well as environmental conditions are now viewed as direct or indirect factors that mechanistically influence the movement of animal species individuals and/or collective (Morales & Ellner, 2002; Rumiano et al., 2020). Mechanistic approaches that consider such factors include ecological diffusion models (Hefley et al., 2017; P. J. Williams et al., 2017), resource selection function (RSF) (Manly et al., 2007), as well as the step selection function (SSF) (Thurfjell, Ciuti, and Boyce 2014) and its translation into a probability density function of space use through stochastic simulations (Signer, Fieberg,

and Avgar 2017) or a master equation (Potts et al., 2014). All these mechanistic model approaches identify the mechanisms driving animal movement, allowing a more explicit assessment of the ecological processes at play in comparison with statistical models (Potts and Lewis 2014).

If mechanistic models allow extrapolations as they can potentially produce predictions outside the range of used input data, they do have some limitations as well. The spatial and temporal scale on which a mechanistic model can efficiently operate is a central challenge in ecology in general (Levin, 1992). Applying such models is currently limited to relatively small systems (Cabral, Valente, and Hartig 2017). Mechanistic models face issues concerning calibration and data availability. Indeed, if mechanistic models are not constrained by data, increasing the model complexity may result in exponentially increasing uncertainties, rendering the model useless even if it is structurally correct. For example, the fitting procedure of an animal movement mechanistic model requires animal locations to be independent samples from the input dataset (Potts & Lewis, 2014). Yet, obtaining an independent set of location points usually requires using a small subsample of the input data, which can mean discarding a lot of information (Moorcroft and Barnett 2008).

Despite these challenges, one could argue that more mechanisms are needed to understand the complexity so common in nature (Evans et al., 2013). However, simple mechanistic models will remain useful to address specific questions and users have to carefully balance model complexity. In the end, one key advantage of mechanistic models is that they are flexible and modular, offering the possibility to experiment with the complexity trade-off and, as a result, assess model generality (Evans et al., 2013). Furthermore, mechanistic models can also be used effectively in combination with statistical models to enhance the capacity to describe, apprehend and simulate complex systems (Caradima et al., 2021).

5.3 The choice of a mechanistic model based on collective movements of self-propelled individuals

5.3.1 The individual versus the collective

Choosing a model to describe an ecological mechanism such as animal movement requires considering the scale at which the movement is applied. Do we favor to model a set of individual

movements or a collective movement of individuals to model the animal movements in space and time? Should interactions between individuals be considered as influential in regard to animal movements? Answering these questions while complementing initial research hypothesis conditions the choice of the modeling method to be used to simulate any given animal movement mechanisms a priori.

Individual based models (IBMs) constitute a more favored starting point for building animal movement models as this modelling approach explicitly recognizes the discreteness of the population and the stochastic nature of the movement dynamics (Black & McKane, 2012). Indeed, IBMs can potentially capture a large range of phenomena even if the results are frequently numerical in nature, making any theoretical understanding difficult (DeAngelis and Grimm 2014). IBMs are mechanistic model well suited to incorporate spatial landscapes in a realistic manner and to simulate complex behaviors in populations (DeAngelis, 2018) and have, for example, been used to spatially model ungulate grazers (Proaktor, Coulson, and Milner-Gulland 2007). However, a main limitation of this modelling approach is the lack of formal structure and methods of analysis compared to what mechanistic models with mathematical constraints (e.g., SSF) offer (Donald L. DeAngelis and Grimm 2014), despite standardization efforts such as the overview, design concepts, and details (ODD) protocol (Grimm et al., 2010).

Another individual scale approach, very close from the IBMs in terms of modeling principles, consists of Agent-based models (ABMs). These models have a finite number of individuals in the modeled system, each “agent” having an arbitrary given number of attributes or parametrized degrees of freedom (Grimm et al., 2005). They differ from IBMs as relationships between individuals are explicitly established. The IBMs, on the other hand, do not initiate relationships between the individuals of a given model, individuals being autonomous (DeAngelis & Grimm, 2014). For that reason, ABMs are able to capture the fine-scale effects of individual movements in driving dynamics within populations (Watkins et al., 2015) and consist of a bottom-up approach as each agent can learn and adapt their own behavior while responding to other agents and changes in the environment (McLane et al., 2011). This property as an advantage over top-down approaches (e.g., statistical models such as RSF) as it enables extensive exploration on the effects and implications of any type of changes that could potentially occur within the modeled system. In term of mitigating conservation management strategies, ABMs can play an important role indeed (Grimm et al., 2005). However, ABMs are complex in their design (i.e., more rules, quantitative parameter estimation, complex sensitivity analyses) and tuning them can be difficult as the more parameters there are, the more they influence each other (Schulze et al., 2017). Moreover, ABMs are much less tractable than a mechanistic model based on fewer mathematical equations and have a lower genericity potential.

Complementary to the individual scale modelling approaches, collective movement models are getting more and more recognition as recent technological advances dramatically improve the ability to collect data on the movements of animal groups (Hughey et al., 2018). Within the field of animal movement, the importance of social dynamics on both fine-scale (Russell et al., 2017) and broad-scale processes (Sigaud et al., 2017) is stressed, thus influencing the utilization of such model to reproduce animal movements. The possibility to couple extensive amounts of collected environmental data with the analytical capacities of mathematical movement models enable statistical inference of animal movement mechanisms and drivers (Hooten et al., 2017). If multi-agent ABMs have been used to simulate collections of interacting individuals (DeAngelis 2018; Couzin et al. 2002), several studies have introduced static quantitative observables into swarm models to effectively reproduce individual interactions within a collective (Eriksson et al., 2010). Such swarm model methodologies include the distribution of inter-individual distances, swarm density, polarity, sharply defined edges, and anisotropy (Viscido, Miller, and Wethey 2002; Ballerini et al. 2008; Cavagna et al. 2008). All these model methodologies can potentially be used to efficiently compare the output of a simulation model to in-situ observations of a given ecological/biological system depending on the abundance and quality of the in-situ data (e.g., telemetry data, empirical knowledge) used to calibrate the model. However, even if swarm models can provide valuable insights on the type of interactions occurring within an animal group/herd and more broadly on the groups general movement dynamics, the model's inferred interaction rules (e.g., repulsion, attraction, alignment,...) can potentially produce the same statistical observables even with different parameter values (Eriksson et al., 2010b). In turn, this can produce redundancy and an incapacity to reproduce specific behaviors.

As knowledge of animal movements accumulate, there has been an increasing appreciation that many movement processes must be considered using a wide array of modelling approaches. The preferred use of IBM and ABM is to study "emergent" properties at a given system scale from rules defined for individuals. The counterpart is that it is often very difficult to explain the exact causes of this emergence. IBMs, ABMs and collective movement models are all relevant but have to be chosen accordingly in regard to their intrinsic strengths and weaknesses.

5.3.2 The synthesis of the two, when individuals influence the collective

Many of animal movement modelling approaches usually neglect potential interactions between different animals as most of them assume that the movement of one individual within a group is representative of the group's overall movement (Morales et al., 2010). This assumption, mainly

correlated to the intention of advantaging model's simplification over its complication, can introduce an analysis bias, thus limiting the ability of a model to reproduce movement dynamics at different spatial and temporal scales. Indeed, animals often do not move independently of each other (Camazine et al., 2020). Therefore, understanding the distribution of individuals in space requires scaling-up from individual movement patterns to groups of individuals and, according to the scope and aim of the study, to populations of groups (Okubo et al., 2001). In this instance, the temporal scale becomes important as interactions between the group structure of a population and the movement of individuals can be relevant at longer time scales (Fryxell et al., 2007) as well as on relatively short temporal scales (Couzin et al., 2005; Eftimie et al., 2007). Moreover, movement responses of individuals to the changing spatial distributions of resources can not only influence their individual movement but also that of the entire group (Gaillard et al., 2010).

To model the movements of an entire group while considering the individual movements within the group, self-propelled particle (SPP) models are considered. These models capture physical properties (e.g. alignment, distance, cohesion) between neighboring individuals in self-organized swarms (Langrock et al., 2014). In SPP models, all individuals must adhere to basic mechanistic rules in which the forces of attraction (e.g., social interactions such as vigilance or interspecies relationship status) and repulsion (e.g., avoiding collisions with closed neighbors, safe space) are optimized within an interaction zone to maintain coordinated group movements (Mann, 2011; Strömbom, 2011). In SPP models, individuals consider their closed neighbors at discrete time intervals as well as being virtually considered similar to one another (Conradt et al., 2009). Collective motions can be envisioned without a leader (Grégoire & Chaté, 2004; Vicsek et al., 1995) but also with a leader (Ferdinandy et al., 2017), thus changing the configuration of individuals within the group and introducing a classification among them. SPP models have been developed extensively (Dowd & Joy, 2011; Polansky & Wittemyer, 2011; Yates et al., 2010) following the trend of technological advances in tracking individuals (Kays et al., 2015).

The main advantage of the SPP models is that they allow to translate detailed, intricate, and complex phenomenon such as individual interactions within animal groups in “minimal” rules composed of few parameters to catch crucial and universal properties that may be present in a wide variety of systems (Grégoire & Chaté, 2004). Empirical knowledge as well as observed data can fuel these models (Langrock et al., 2014), making them well-suited for a wide range of studies, especially when in-situ data are lacking or in insufficient number to validate a statistical model for instance. However, depending on the spatial and temporal scales of the study, limitations can occur as it can be difficult to model the level of detail entailed by animal

interactions at the landscape scale and with temporal frequency inferior to the hour. In this configuration, precise high resolution telemetry data as well as a large number of collared individuals are necessary to calculate the interactions metrics needed to calibrate the model parameters. Despite this constraint, SPP model can be a good alternative to avoid modelling design complexity inherent to ABMs or the important number of data required as input associated with statistical modelling approaches (Schliehe-Diecks et al., 2012) while reproducing animal movements at individual and group scales (see Chapter 6 for more detail).

5.4 Spatializing the model and combining it with SRS data

5.4.1 The notion of space in animal movement modelling

Spatial structure and organization of a given system is now usually acknowledged as an essential prerequisite to accurately model ecological processes (Dieckmann et al., 2000; Kareiva & Wennergren, 1995). It is now common knowledge that the degree of interrelation and influence between animal individual and the surrounding environment depends both simultaneously on animal movements and environmental change dynamics (Morales et al., 2010). While many studies of animal movements focus on apprehending the dynamics at the population and individual scales in space, the underlying connections between the intrinsic movement of an animal and its immediate environment is rarely addressed and described because a bidirectional spatial modelling of these connections are required at different spatial and temporal scales to be properly assessed (Fryxell et al., 2005; Revilla & Wiegand, 2008). Adding time as another dimension to space into a model requires the implementation of the model's inputs into a platform geared for manipulating spatialized data such as geographic information systems (GIS) to extrapolate and analyze the model outputs. This procedure may prove to be complicated and non-intuitive as GIS are still, to this day, suffering from an intrinsic limitation of not properly handling the time dimension (Comber & Wolter, 2019). Likewise, modeling approaches that consider time first face limitations in regard to spatial information as the latter cannot be dissociated with movement data and evolve independently (Peuquet, 2001). Merging movement data with a self-evolving geographical context implies to develop multi-dimensional (i.e., space and time) movement models to effectively measure the influence of a changing environment on the behavior of moving individuals or group of individuals (Onsrud & Kuhn, 2016). In regard to this particular challenge, an intuitive environment platform able to link all the dimensions of a

movement model in an intuitive and scalable way could prove to be a valuable tool to facilitate the development of such approach.

5.4.2 The language “Ocelet”

Several domain specific languages (DSL) that allow the simulation of heterogeneous entities in spatialized and temporalized complex systems through their interactions exist today. Amongst them, the most noticeable are CORMAS (Bousquet et al., 1998), NetLogo (Levy et Wilensky, 1999), GAMA (Taillandier et al., 2012) and Ocelet (Degenne et al., 2009). The Ocelet DSL allows the synthesis of top-down (e.g., systems dynamics) and bottom-up (e.g., ABMs) modeling approaches by focusing on their “common denominator” which are embodied by the interactions (Degenne & Lo Seen, 2016).

The Ocelet DSL is designed around five main concepts that are: entity, service, relation, scenario and datafacer (Degenne et al., 2009) ([Figure 5.3](#)). It is based on the concept of interaction graph (Harary, 1969), where each element of the system (entity) is represented by one specific vertex of the graph, and where the graph’s edges between the vertices carry the functions describing the relations between the entities (interaction functions). Each entity has different characteristics, called properties, which can be assigned to other entities if required and allow to establish potential relations in between them. A service (e.g., update of the trajectory, or the individual movement – [Figure 5.3](#)) can complement the entity in addition to the properties by assigning functions that characterize given abilities inherent to a given entity. The datafacer is a generic way to bind entities and datasets, independently of their spatial form: vectors (i.e., point, line, and polygon geometries) and raster (i.e., matrix of pixels) (Castets, 2015). Three levels of model specification are denoted by (Degenne, 2012): i) “The level of individuals”, where the types of entities in the model are described, their properties defining their state, and the rules (service) defining their behavior, ii) “The level of interactions”, where the exchanges between the entities are governed and defined via the concept of interaction graphs, iii) “The level of the system and its dynamics”, which allows the organization of a scenario modeling the spatiotemporal dynamics of a defined system. Indeed, the initial state of the model and the simulation steps are set within the scenario that contains an ordered sequence of operations that are executed during a simulation run to represent the changes occurring in a geographical area over a period of time (Degenne et al., 2009).

The ability of the Ocelet DSL to incorporate heterogeneous spatialized data by attributing them the status of entity or assigning them as one or several entity's properties, offers the capacity to the user to establish relations between complementary spatialized and temporal information inherent to a complex system. For example, it is possible to implement an entity of an animal species telemetry data as spatialized vector points with a temporal property and put them in relation with another entity of remote sensed surface water represented as a spatialized raster with the same temporal property. By establishing an interaction graph between these two implemented entities, it is therefore possible to assign a wide range of functions to translate the design of the desired model with a set of rules detailed within a scenario. Such rules could be “a restriction applied to the animal species to get closer to the surface water during the dry season”. This example shows how numerous the possibilities are and how easily they can be used to implement different types of models (e.g., ABMs, SPP) to translate animal movements at different spatial and temporal scales while using heterogeneous data.

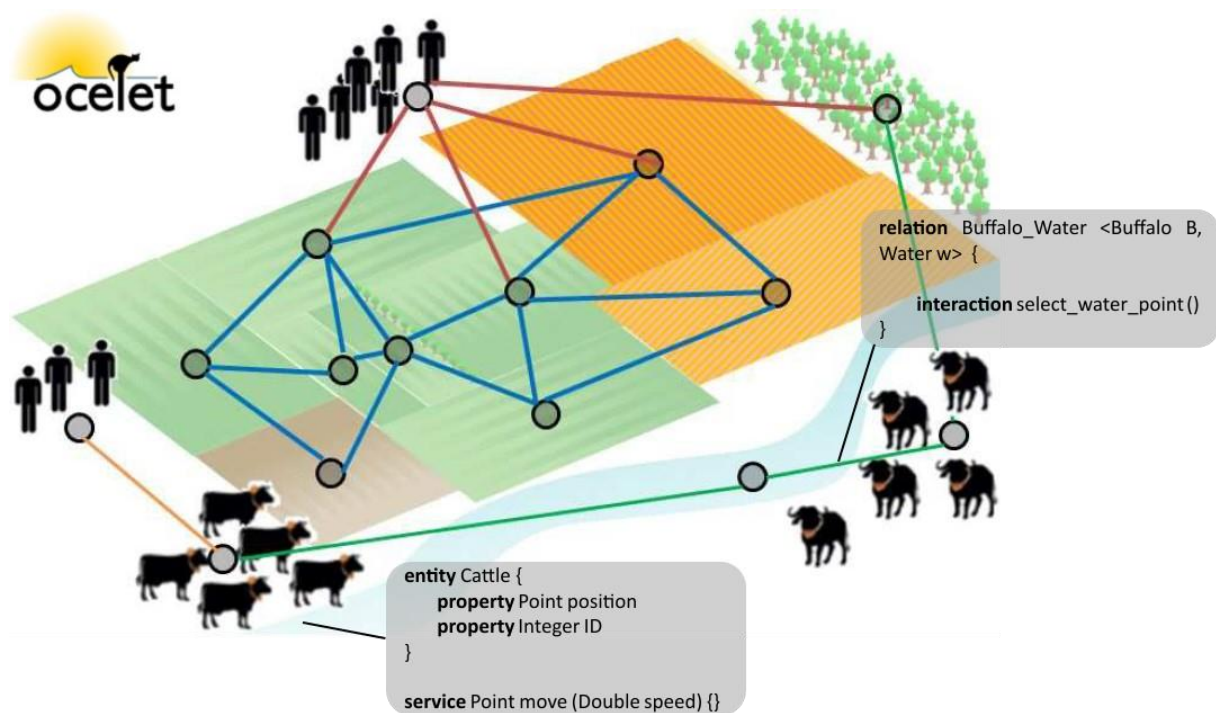


Figure 5.3: This figure have been adapted from (Degenne & Lo Seen, 2016) and represent a schematic diagram showing an practical example of different entities in interaction. Circles are the vertices, and colored lines, the edges, of a graph. Lines represent spatial (blue), functional (orange), hierarchical (red) and social (green) relationships between the entities (Buffalo, cattle, water, landcover and herders), on which interaction functions can be applied. The gray boxes are examples of Ocelet language syntax to develop an entity and a relation.

5.5 Chapter summary

- Animal movement ecology primarily aims to understand consequences of animal movements on the ecology and evolution operating across heterogeneous/homogeneous landscapes at individual, population, and community scales
- Mathematical models mainly follow two paradigms dictated by the statistical approach and the mechanistic approach. Statistical models efficiently condense empirical facts to provide an understanding of a specific research hypothesis based on correlative relations. Mechanistic models base predictions on the understanding of cause–effect relationships as they formalize them into mathematical formulas or simulations.
- The advantages and disadvantages of individual and collective movement models have been assessed. Self-propelled particle models provide an adequate solution as they avoid modelling design complexity inherent to ABMs or the important number of data required as input associated with statistical modelling approaches while reproducing animal movements at individual and group scales.
- The domain specific language “Ocelet” can incorporate heterogeneous spatialized data by linking them within an interaction graph in the form of entities on which are assigned a set of particular properties. This language offers the capacity to the user to establish relations between complementary spatialized and temporal information inherent to a complex system.

Chapter 6

Combined use of remote sensing and spatial modelling: When surface water impacts buffalo (*Syncerus caffer caffer*) in savanna environments

Table of content

6.0 Preamble

6.1 The article

6.1.1 Introduction

6.1.2 Material & Method

6.1.3 Results

6.1.4 Discussion

6.1.5 Conclusion

6.2 Application of the buffalo movement model in two other W/L interfaces

6.2.1 A movement model that also considers the landcover

6.2.2 Application in Gonarezhou/Malipati and Kruger/Pesvi

6.3 Chapter summary

6.0 Preamble

This chapter first presents, in the form of an article published in the scientific journal "The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences" that was also subject of an oral presentation in the framework of the International Society for Photogrammetry and Remote Sensing (ISPRS) Congress 2021 in front of peers and colleagues, the mechanistic movement model developed to simulate the movements of buffalo at the collective and individual scale in regard to the surface water availability in space and time at the specific study site of Hwange/Dete. In a second step, this chapter details the application of this same model on the other two study sites (i.e., Gonarezhou/Malipati and Kruger/Pesvi) and its modification with the implementation of the ability to consider landcover in addition to surface water to determine buffalo movements in space and time. This work, which was the subject of a Master 2 internship, has the particularity of testing the generality of the mechanistic movement model by applying and validating it in different W/L interface configurations.

6.1 The Article

The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences, Volume XLIII-B3-2021 XXIV ISPRS Congress (2021 edition)

COMBINED USE OF REMOTE SENSING AND SPATIAL MODELLING: WHEN SURFACE WATER IMPACTS BUFFALO (*SYNCERUS CAFFER CAFFER*) MOVEMENTS IN SAVANNA ENVIRONMENTS

F. Rumiano ^{1,2 *}, C. Gaucherel ³, P. Degenne ^{1,2}, E. Miguel ^{4,5}, S. Chamaillé-Jammes ^{6,7,8}, H. Valls-Fox ^{6,7,9,10}, D. Cornélis ^{11,12}, M. de Garine-Wichatitsky ^{13,14,15}, H. Fritz ^{7,16,17}, A. Caron ^{5,13,14,18}, A. Tran ^{1,2,5,13,14}

¹ CIRAD, UMR TETIS, F-97490 Sainte-Clotilde, Réunion, France

² TETIS, Univ Montpellier, AgroParisTech, CIRAD, CNRS, INRAE, 34090 Montpellier, France

³ AMAP, IRD, CIRAD, CNRS, INRAE, Univ Montpellier, 34398 Montpellier, France

⁴ MIVEGEC, Univ. Montpellier, IRD, CNRS, 34090 Montpellier, France

⁵ CREES Centre for Research on the Ecology and Evolution of Disease–Montpellier, 34090 Montpellier, France

⁶ CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ. Paul Valéry Montpellier 3, 34090 Montpellier, France

⁷ LTSE France, Zone Atelier CNRS “Hwange”, Hwange National Park, Bag 62 Dete, Zimbabwe

⁸ Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, 0083 Pretoria, South Africa

⁹ CIRAD, UMR SELMET, PPZS, 6189 Dakar, Senegal

¹⁰ SELMET, Univ Montpellier, CIRAD, INRAE, Institut Agro, 34090 Montpellier, France

¹¹ CIRAD, Forêts et Sociétés, F-34398 Montpellier, France

¹² Forêts et Sociétés, Univ Montpellier, CIRAD, 34090 Montpellier, France

¹³ CIRAD, UMR ASTRE, F-34398 Montpellier, France

¹⁴ ASTRE, Univ Montpellier, CIRAD, INRAE, 34090 Montpellier, France

¹⁵ Faculty of Veterinary Medicine, Kasetsart University, 10900 Bangkok, Thailand

¹⁶ UCBL, UMR CNRS 5558, University of Lyon, 69007 Lyon, France

¹⁷ World Wildlife Fund, Washington, DC 20037-1193, USA

¹⁸ Faculdade de Veterinaria, Universidade Eduardo Mondlane, 257 Maputo, Mozambique

Commission VI, WG VI/4

KEY WORDS: remote sensing, spatial modelling, mechanistic model, animal movement, surface water, African buffalo, ungulates, savanna

ABSTRACT:

In semi-arid savannas, the availability of surface water constrains movements and space-use of wild animals. To accurately model their movements in relation to water selection at a landscape scale, innovative methods have to be developed to i) better discriminate water bodies in space while characterizing their seasonal occurrences and ii) integrate this information in a spatially-explicit model to simulate animal movements according to surface water availability. In this study, we propose to combine satellite remote sensing (SRS) and spatial modelling in the case of the African buffalo (*Syncerus caffer caffer*) movements at the periphery of Hwange National Park (Zimbabwe).

An existing classification method of satellite Sentinel-2 time-series images has been adapted to produce monthly surface water maps at 10 meters spatial resolution. The resulting water maps have then been integrated into a spatialized mechanistic movement model based on a collective motion of self-propelled individuals to simulate buffalo movements in response to surface water.

The use of spectral indices derived from Sentinel-2 in combination with the short-wave infrared (SWIR) band in a Random Forest (RF) classifier provided robust results with a mean Kappa index, over the time series, of 0.87 (max = 0.98, min = 0.65). The results highlighted strong space and time variabilities of water availability in the study area. The mechanistic movement model showed a positive and significant correlation between observations/simulations movements and space-use of buffalo's herds (Spearman $r = 0.69$, $p\text{-value} < 10^{-114}$) despite overestimating the presence of buffalo individuals at proximity of the surface water.

* Corresponding author

1. INTRODUCTION

In semi-arid environments such as southern African savannas, the availability of surface water constrains movements, distributions and space-use of wild animals (Chamaillé-Jammes et al., 2016). Having the capacities to monitor, through space and time, surface water availability at a landscape scale can potentially enable the characterization of wild animal movements in relation to this natural resource. The simulated distribution of wildlife in space and time resulting from the modelling of the relationship between an animal species and its water requirements could then be used to address human/wildlife coexistence related issues such as competition for resources inside/outside protected areas (Young et al., 2005), crop or livestock destruction by wildlife (Valls-Fox, 2015), and risk of pathogen transmission between wild and domesticated species (Caron, Miguel, Gomo, Makaya, Pfukenyi, Foggin, Hove, & de Garine-Wichatitsky, 2013; Miguel, Grosbois, Caron, Boulonier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & de Garine-Wichatitsky, 2013).

The advent of satellite telemetry using global positioning system (GPS) allows to determine temporal and spatial position of animals in a given area with high precision, temporal accuracy and position updates available in rapid frequency 24 hours a day (Cagnacci et al., 2010). This breakthrough in technology enabled to better apprehend how and why animals move (Kays et al., 2015). Combining this technology with satellite remote sensing (SRS) generates opportunities for studies such as natural resource suitability mapping (Remelgado et al., 2018) or species–environment interactions mapping (Sheeren et al., 2014). Indeed, SRS provides an array of tools and methodologies to discriminate environmental variables (e.g., surface water) at different spatial and time scales in areas with partial or no in-situ data coverage (Alsdorf et al., 2007). This is particularly true in the current context of increasing number and variety of SRS sensors (Paganini et al., 2018). For example, several studies have been combining GPS telemetry data with SRS in savanna environments to investigate the relationship between resource gradients and overlap between wild and domestic herbivores (F. M. Zengeya et al., 2015) or to assess the impact of small-scale ephemeral water sources on wildlife (Naidoo et al., 2020), greatly expanding our understanding of ecological functioning in relation to animal movement as a result. Since 2015, Sentinel-2 satellites provide 10m spatial resolution SRS images with a revisit frequency of 5 days that can potentially be combined with GPS telemetry data to conduct landscape scale ecological analysis. Applications and studies in the field of ecology using this technology need to be further developed in conjunction with spatial modelling.

Spatial models of animal movement taking into account biotic and abiotic drivers as well as behavioral mechanisms have been developed in recent years (Moorcroft, 2012; Westley et al., 2018). Mechanistic modelling approaches can take into account fine-scale ecological processes (e.g., environmental changes and animal responses) that underlie ecosystem functions (i.e., watering behavior of a focal species) and incorporates changes in ecosystem properties (e.g., inter-species competition for water resources) in response to changes in the environment (e.g., climate and water resource changes) (Rastetter et al., 2003). Models that describe the collective motion of groups of self-propelled agents (Gregoire et al., 2003; Huepe & Aldana, 2008) can simulate herd dynamics easier than hard-to-calibrate

individual-based models. Such ‘swarm’ models are parsimonious as they use few parameters (i.e., speed, alignment, cohesion) to mimic a group of individuals (Eriksson et al., 2010; Gregoire et al., 2003; Vicsek et al., 1995b) and are a way to control the amount of self-organization within a herd of a specific species (i.e., the degree of alignment and cohesion of the individuals’ headings). However, dynamic animal movement models that combine SRS with GPS telemetry in order to specifically characterize species–environment interactions in space and time at a landscape scale are lacking. Indeed, SRS derived environmental data are rarely used in combination with spatial modelling although the understanding of animal movement and their associated ecological mechanisms could benefit from such approaches (Neumann et al., 2015; Rumiano et al., 2020).

Thus, the objectives of this study are two-fold: i) developing a method to map surface water at a landscape scale accounting for seasonal variations in a savanna type area near the Hwange National Park (Zimbabwe) using Sentinel-2 satellite images, and ii) integrating the resulting surface water maps in a spatialized mechanistic animal movement model, with the example of the African buffalo (*Syncerus caffer caffer*), a keystone species for conservation and production systems in southern African interfaces (Cornélis et al., 2014).

2. MATERIAL & METHOD

2.1 Study area

Our study area is located North West of Zimbabwe in the Matabeleland North Province (18°37' S, 26°52' E) ([Figure 6.1](#)). More specifically, it lies at the northern periphery of Hwange National Park (HNP), within the Sikumi Forest Area (SFA) that is under the management of the Forestry Commission of Zimbabwe since 1968 and covers an area of approximately 200 km² sharing an open boundary with HNP (14650 km²). In this ecosystem, wildlife coexists with human activities such as cattle herding, firewood and thatching grass harvesting and tourism (Valls-Fox et al., 2018). Human settlements and agricultural fields are located only a few hundred meters away from the unfenced SFA boundaries (Guerbois et al., 2013). The vegetation of the area can be characterized as semi-arid wooded savannas with patches of grassland. Surface water is naturally provided by pans and springs, most of which dry-up during the dry season (May to September). Solar powered pumping stations are also present in the area and ensure year-round water availability. Annual rainfall approximates 600 mm per year in average with an inter-annual variability coefficient of 25 % between 1928-2005 (Chamaillé-Jammes et al., 2006). However, drought severity and inconsistency of rainfall increased in the area during the twentieth century (Chamaillé-Jammes, Fritz, et al., 2007).

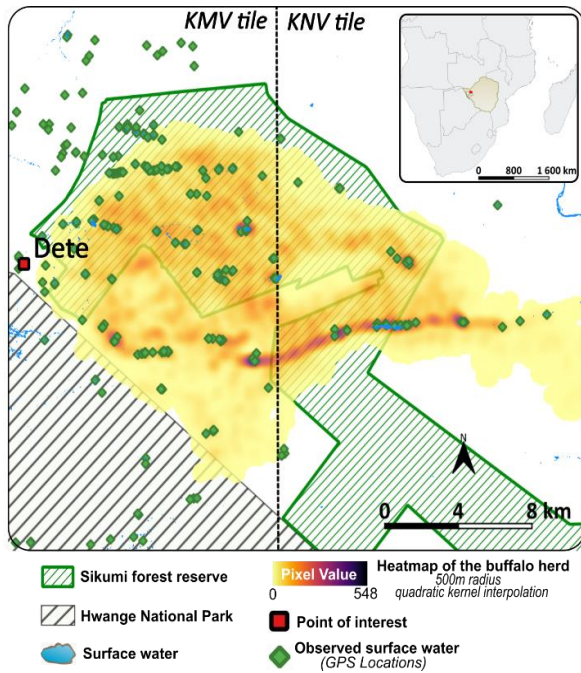


Figure 6.1. Map of the study area and display of the data used in the study

2.2 Data

Telemetry data: 8 buffalo individuals have been monitored in the area from April 2010 to April 2014 by ultra-high frequency (UHF) collars (manufactured by African wildlife Tracking) set with a 1 hour frequency signal (Miguel, 2012; Valls Fox, 2015). Three groups of respectively three individuals (from April 20th 2010 to August 18th 2011), four individuals (from November 14th 2011 to September 9th 2013) and four individuals (from March 12th 2013 to April 15th 201) have been constituted. Each group represents buffaloes that are present at the same time in the same area (Figure 6.1).

Remote sensing data: 24 Sentinel-2 satellite images of a complete year, corresponding to one image per month for the two tiles (T35KNV & T35KMV), necessary to spatially cover the entire area, have been downloaded in level 1C (Top Of Atmosphere reflectance and orthorectified images) via the Copernicus Open Access Hub. As no Sentinel-2 images were produced at the time of the telemetry data acquisition, we have chosen images from the year 2018 which is representative of the annual rainfall precipitation measured via Tropical Applications of Meteorology using SATellite data and ground-based observations (TAMSAT) compared to the years where the telemetry data have been collected. Only the images with less than 10% of cloud cover have been considered. As no images were cloud free for the month of February 2018, the series was completed by two images from February 2019, one per tile.

Reference polygons derived from image interpretation: For each Sentinel-2 image and each land-use types to be classified (“surface water” and “other”), a set of 100 reference polygons have been evenly vectorised over the study area.

Surface water ground truth data: These data consist in GPS coordinates locating surface water collected on the field

during previous studies conducted in the area (Guerbois, 2012; Miguel, 2012; Valls Fox, 2015) (Figure 6.1).

2.3 Methodology

The methodology is structured in separate phases (Figure 6.2).

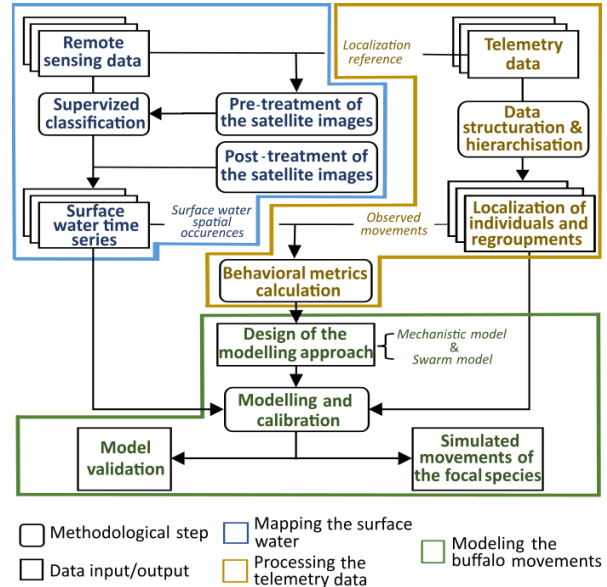


Figure 6.2. Flowchart combining remote sensing data with telemetry data to model the focal species movements

2.3.1 Mapping the surface water

Pre-treatment: The Sen2Cor v2.8 application (Sen2Cor, European Space Agency) has been used to apply atmospheric corrections, thus transforming LIC images to level L2A (Top Of Canopy) images. The 20 meters spatial resolution spectral bands have been resampled by bilinear interpolation to 10 meters spatial resolution before being projected to the WGS84/UTM35S projection system and clipped to the study zone spatial extent. Following (Y. Du et al., 2016), the modified normal difference water index (MNDWI) and the normalized difference water index (NDWI) have been calculated and stacked with Sentinel-2 short-wave infrared (SWIR) band. At the end of the pre-treatment, 24 three-layer rasters (NDVI, MNDWI, SWIR), 12 (one per month) for each of the two tiles covering the study area, composed the image corpus used in the supervised classification process.

Classification: The reference polygons (c.f. 2.2) have been used to clip the 24 pre-treated multi-layer raster stacks to create training and validation raster samples. These raster samples were then randomly selected with a 50/50 ratio towards training and validation and used in the random forest (RF) classifier (Breiman, 2001). The 50/50 ratio has been chosen as it allows a more reliable comparison between training and validation samples than a ratio with a lower proportion of validation samples (Mercier et al., 2018). RF algorithm was chosen because of its advantages of simple parametrization, reliable and rapid execution in processing time of large volume of variables and data and its proven efficiency in satellite image landcover classification (Pelletier et al., 2016). The RF algorithm has then been applied on all the 24 pre-processed multi-layer rasters to obtain a classification at 10 meters of spatial resolution.

Post-classification: For each classified raster image, the pixels classified as ‘water’ have been vectorised to allow the manually removal of the noise pixels (false positives). As the water surfaces reach their maximum spatial extents in March, when the peak precipitation occurs, the two derived classification images of the month of March (one per tile) have been selected to map the maximum water extent in the area. The resulted vector layers of the month of March have then been used as a template to mask all of the noise pixels present in the 11 other months of the year vector layers.

Surface water classification validation: The surface water ground truth data (c.f. 2.2) were used to validate the classification when being located directly on a surface water polygon or within a 100m buffer area around the surface water polygon. Reference polygons derived from image interpretation (c.f. 2.2) have been used as training and validation references to apply a cross-validation on two classification accuracy indicators (i.e. overall accuracy (OA) and Kappa index) and test the robustness and stability of the classification method. 50 iterations of classification using randomly selected reference polygons were performed to run the cross-validation.

2.3.2 Processing telemetry data

Behavioural metrics calculation: In-situ telemetry data (c.f. 2.2) have been used to calculate the movement’s speed of buffaloes. The speed value gathering 75% of the values of the speed distribution observed within the three buffalo groups ($v_1, v_2, v_3 = 0.48, 0.45, 0.46$ km/h resp.) determines the distance v_0 that buffaloes are able to cover in one model time step (10 minutes) in the following modelling section. In addition, the median distance between individuals of a same group has been calculated and mean/median daily distances covered between water points by buffalo have been calculated for validation.

Identification of behavioural phases. African buffalo drink water daily (Cornélis et al., 2014). The telemetry in-situ data have been used in accordance to correlate the speed and the probability for individuals to be near the surface water every hour over a period of 24 hours for the entire duration of the telemetry data measurement (Figure 6.3). As a result, two distinct phases were identified: a watering phase (from 9am to 7pm) and a free wandering phase (from 7pm to 9am).

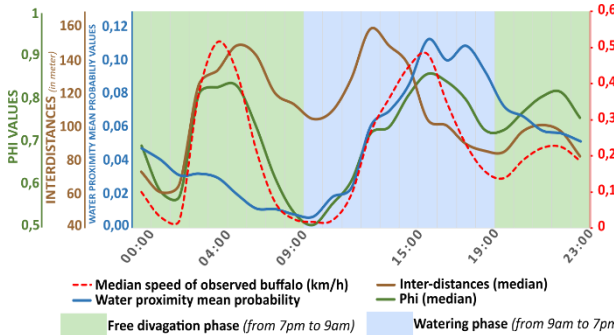


Figure 6.3. Mean probabilities of the observed buffalo to be nearby (< 100m, shaded zone) surface water as a function of the time of the day (blue line), superimposed to the median speed of the observed buffalo (red dashed line), the median interdistance (brown line) and the phi values (green line)

2.3.3 Modelling the buffalo movements in space and time

Choice of the modelling language: The domain specific language Ocelet has been used to build the animal movement model (Degenne & Lo Seen, 2016). This language has the capacity to integrate spatial entities in vector and raster format and create relations between them to simulate spatio-temporal dynamics. The developed spatial model is composed of three main interacting spatial entities: (i) the buffalo individuals, (ii) the herd, (iii) the surface water.

Animal modelling approach: To model buffalo movements in space and time, a model of collective motion of self-propelled individuals (Gregoire et al., 2003) has been chosen, as it is parsimonious and mimics a wide range of movements. Derived from the Vicsek model (Vicsek et al., 1995) in which individuals interact at short distances, the model induces an overall cohesion of a population of individuals through space and time (Gregoire et al., 2003). Hence, the model highlights specific properties: no leader in the herd, noisy environment and/or communications, local interactions. In the model, buffalo move at discrete time steps by a fixed distance v_0 , their direction defined for each time step t as an angle θ_t^t :

$$\theta_t^{t+1} = \arg \left[\alpha \sum_{j \neq i} \vec{v}_j^t + \beta \sum_{j \neq i} \vec{f}_{ij}^t \right] + \eta \xi_t^t \quad (1)$$

where α controls the herd alignment that corresponds to the sum of individual’s speed vectors \vec{v}_j ($j \neq i$), while β controls the herd cohesion expressed as the sum of the vectors \vec{f}_{ij} that link two individuals i and j , and η the noise that represents the uncertainty with which the direction of each individual is influenced by neighbouring individuals (ξ being a random angle, comprised between $-\pi$ and π). The cohesion force \vec{f}_{ij} (Gregoire et al., 2003) between each pair of individuals i and j is expressed as follows:

$$\vec{f}_{ij} = \vec{e}_{ij} \begin{cases} -\infty & \text{if } r_{ij} < r_c, \\ \frac{1}{4} \frac{r_{ij} - r_e}{r_a - r_e} & \text{if } r_c < r_{ij} < r_a, \\ 1 & \text{if } r_{ij} > r_a \end{cases} \quad (2)$$

where \vec{e}_{ij} represents the unit vector along the segment going from individual i to individual j within a defined distance of interaction r_0 and r_{ij} between individuals i and j . \vec{f}_{ij} is defined by several parameters (Table 6.1) that are representative of buffalo’s herd behaviour. These values are based on empirical knowledge and in-situ observations.

Parameter	Definition	Value
v_0	Buffalo speed	0.46 km/h*
r_0	limit of interaction distance	500m**
r_c	distance of repulsion	5m**
r_e	equilibrium distance	10m**
r_a	minimal distance	150m**
α – free divagation	60	***
α – watering phase	90	***
β	40	***
η	0.2	***

Table 6.1. Model parameters estimated from telemetry data (*), expert knowledge (**), or calibration (***)

Calibration: To control the animal movement modeled we used two integrated indices calculated at each timestep t (Figure 6.3). The first one is the Phi order parameter (φ) that summarizes the averaged alignment of the herd:

$$\varphi^t \equiv \frac{1}{N} \left| \sum_{j=1}^N e^{i\theta_j^t} \right| \quad (3)$$

where N is the total number of individuals. The second indicator is the median interdistance that reflects the averaged cohesion of the herd. For the simulated data, φ and interdistance values have been calculated from four randomly selected individuals within the modeled herd of 200 individuals to level with the observed data where four individuals make up the herd at most (cf. 2.2). The absolute differences between the observed and simulated values of φ and interdistance have been calculated. We have then chosen the parameters tryptic (α , β and η) minimizing the difference between observations and simulations for both behavioral phases. The interdistance distributions being non-normal, the Kullback–Leibler (KL) divergence (Kullback & Leibler, 1951) has been chosen for the distribution comparison purposes. The parameters β and η have been calibrated in comparison with the free wandering phase interdistance distribution of the observed data. Once calibrated, β and η remained constant during the watering phase as the cohesion between individuals and the noise to be added to the equation have been considered identical for the two phases. The α parameter has been calibrated for each phase by minimizing the differences between observed and simulated φ distributions. For testing every combination of the parameters tryptic (α and $\beta \in [1:100]$, $\eta \in [0.2:0.6]$) 33 iterations of simulation for each of the three observed herds (cf. 2.2) have been conducted.

Model behavior: Buffalo move randomly in every direction during the free wandering phase (c.f. 2.3.2) following the set α , β and η values determined by the calibration. During the watering phase (c.f. 2.3.2), buffalo take the direction of the closest surface water only changing the α value. The α value is then set to 0 when the herd reaches the proximity of the surface water. α remains unchanged until the beginning of the free wandering phase when the cycle repeats itself.

Validation: The centroids calculated from four randomly selected individuals within the simulated herd have been compared with the centroid derived from observed individuals. Spatial density rasters of the centroids have been computed using a quadratic kernel shape from planar distances with a search radius of 500m at a 10m spatial resolution. The model being stochastic, 50 iterations for each of the three herd groups, considering the entirety of their respective time periods (c.f. 2.2), have been conducted for the simulation and used to derive a final simulated median raster. Concerning the observed data, the same method of density calculation have been used for each of the three groups, also considering the entirety of their respective time periods, before deriving the final observed median raster. In the end, the simulated median raster has been subtracted to the observed median raster to measure quantitatively and spatially their differences. Spearman correlation coefficients have also been calculated from 1000 iterations of 1000 randomly selected sample pixels on the observed and simulated median rasters.

3. RESULTS

3.1 Monthly surface water maps

In total, 290 ponds have been identified through the classification of Sentinel-2 images time series, highlighting strong seasonal patterns of water spatial distribution and availability, with only 24 ponds detected in August, the driest month of the season, and 17 water ponds that have been detected every month of the time series, indicating that 94% of the surface water depend on the season.

The mean OA value of the time series, both tiles combined, is 0.93 (min 0.82 – max 0.99) and the mean kappa index value is 0.87 (min 0.65 – max 0.98), with temporal and spatial fluctuations (Figure 6.4). Kappa index and OA values are higher for the KMV tile than for the KNV tile (Figure 6.1) during the dry season (May to September) but lower during the wet season (November to April) (Figure 6.4).

For the validation of the water classification with the use of the observed data, 85% of the GPS points referencing the presence of surface water (c.f. 2.2) have been detected when applying a buffer of 100m around the polygon classified as surface water and 60% have been detected without applying a buffer.

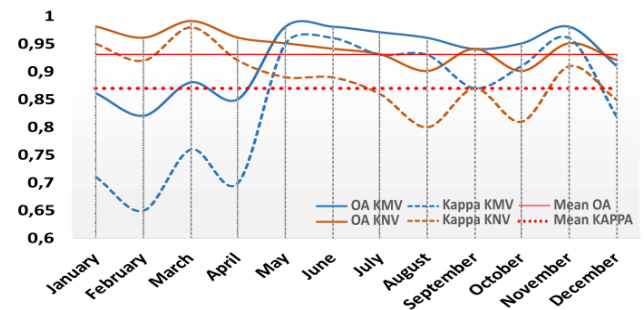


Figure 6.4. Kappa index and overall accuracy (OA) of water classification along to the year for the two Sentinel-2 tiles (KMV and KNV)

3.2 Calibration results

For the free wandering phase (c.f. 2.3.2), α has been set to 60, β at 40 and η at 0.2 (Table 6.1). For the watering phase (c.f. 2.3.2), the value of α has been set to 90, confirming the initial assumption that the weight of the alignment would be more pronounced during the watering phase when all the individuals take the direction of the closest surface water.

3.3 Results of modelling buffalo movements in relation with surface water

The model is stochastic as each buffalo individuals can choose a random direction following an angle from 0° to 360° at the beginning of every free wandering phases (c.f. 2.3.2). As a result, each simulation produced a specific centroid trajectory of 200 buffalo individuals that can then be compared to the observed centroid trajectory of 4 individuals for the entire observed time period or over a different time period (Figure 6.5). We observe that the area covered by simulated centroid trajectories is comparable in size to the area covered by the observed centroid trajectory although simulated centroid trajectories tend to extend further. The shape of simulated centroid and observed centroid trajectories follow the same general pattern. We note different round trips made within the area covered by the different centroid trajectories as well as recurrent use of specific surface water locations.

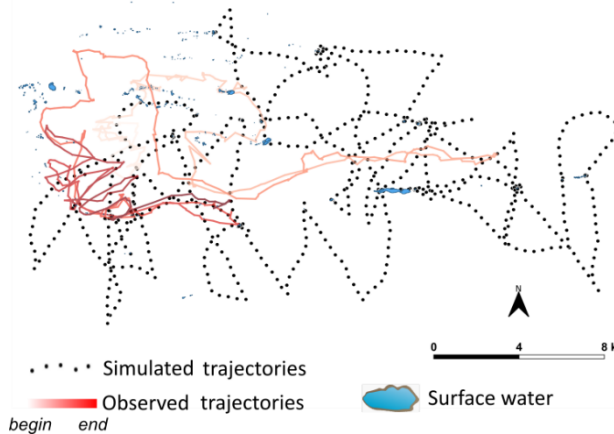


Figure 6.5. Observed and simulated herd' centroids trajectories comparison for a period of one month. The observed trajectory is symbolized by the graduated red line (from light red that symbolizes the beginning of the period to dark red that symbolizes the ending of the period). The black dot points represents the simulated herd' centroids trajectory.

Overall, the model tends to overestimate the presence of buffalo near water ponds and underestimate their presence in peripheral areas (Figure 6.6A). Even if overestimated, validation results demonstrate the model capacity to simulate the movement of buffaloes towards the surface water. Indeed, simulated and observed median density rasters were significantly correlated (Spearman $r = 0.69$, $p\text{-value} < 10^{-114}$). Most of the differences between the densities are small (Figure 6.6B). The model, however, fails in reproducing the densities observed outside the proximity of surface water ponds (Figure 6.6A), explaining the differences between the observed and simulated densities for the pixel's density values superior to 0.25 (Figure 6.6B). During the free-divagation phase, buffalo may take random paths away from their territory before turning around and heading back to the

nearby surface water. This feature of the model explains why the territory covered by buffalo in the simulations is larger than that observed (Figure 6.6A).

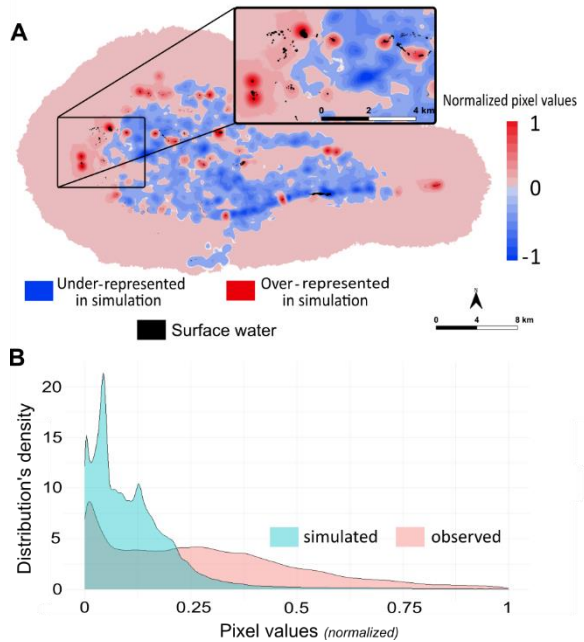


Figure 6.6. A) Difference of density map between observed and simulated herd's centroids trajectories. B) Graph representing the distributions of pixel values in the simulated and observed median density rasters (c.f. 2.3.3)

4. DISCUSSION

4.1 Mapping the surface water via SRS in savanna

Detecting surface water in semi-arid savanna using SRS at a landscape scale remains challenging due to surface water seasonality dynamics, landscape heterogeneity, presence of shades, and variety in surface water area sizes and morphologies (Moser et al., 2014). However, increase availability of free medium-resolution satellite sensors such as Sentinel-2 provides potentialities to characterize, via supervised classification of combined MNDWI and NDWI indices, surface water presence and dynamics at landscape scale (Y. Du et al., 2016). Even if most studies focusing on buffalo movements only use in-situ observations of surface water (Zvidzai et al., 2013), SRS is increasingly used (Naidoo et al., 2020) and can be a valuable asset in areas that are difficult to access and where it is almost impossible to collect in-situ data. The surface water classification methodology developed in this study is efficient (c.f. 3.1) but may be limited by the spatial resolution of the SRS images used for input. Indeed, the use of satellite optical sensors such as Sentinel-2 images can show its limit when trying to detect the small ponds (surface $< 1,000 \text{ m}^2$) or the surface water that may be hidden by the vegetation. The use of very-high SRS images in combination with hydrologic modelling (Soti et al., 2010) or time series of medium spatial resolution could be an improvement.

4.2 The mechanistic animal movement model

The mechanistic movement model, even if it requires significant development and implementation costs, is less dependent of a correlation between ecological processes and environment properties than an empirical model (Gaucherel, 2018). By mathematically simulating interactions and mutual constraints among ecological processes, mechanistic models improve the ecological realism and extrapolation to different environments of a given model (Kearney & Porter, 2009). By using a swarm model to mechanistically model buffalo herd movements, the knowledge of individual behaviours is reduced but the potential to develop animal movement models in area where in-situ data are lacking or expensive to collect is increased. It is important to keep in mind that the model developed in this study somehow neglects individual characteristics as only their interactions with neighbours are considered. As a result, interaction rules between individuals, mostly quantitative, can generate the same statistical variables leading to redundancy and model similarity (Eriksson et al., 2010). In this particular instance, agent-based modelling can provide alternative approaches but usually implies greater complexity in design (i.e., more rules, quantitative parameter estimation, complex sensitivity analyses) for tuning the model (Schulze et al., 2017), is much less tractable than mechanistic equation-based models and has a lower reproducibility potential.

4.3 Limits of the designed model

Only eight buffalo individuals have been monitored by telemetry and, at best, only four individuals were simultaneously recorded within the same area at the same time, thus partially reproducing the dynamics of a herd. Indeed, a buffalo herd is composed of at least 200 individuals in our study area (Miguel, Grosbois, Fritz, Caron, de Garine-Wichatitsky, et al., 2017). Given the few individuals used to calibrate buffalo herd behaviour, proven dynamics such as fission-fusion within buffalo herds (Wielgus et al., 2020) are not reproduced by the model. Despite this limitation, the model has been able to coherently simulate the movement of 200 buffalo individuals influencing each other's direction in relation with surface water availability (c.f. 3.3). Monitoring more individuals and integrating this data in the calibration process should potentially strengthen the model's capacity to reproduce buffalo herd dynamics. Moreover, if surface water directly impacts buffalo movements in space and time (Chamaillé-Jammes et al., 2016), other environmental variables may be taken into account to accurately simulate buffalo movements at the landscape scale (Rumiano et al., 2020). Indeed, the temporal structuration of the model in two behavioural phases (cf. 2.3.2) translates an oversimplification of buffalo ecological functioning. For example, times when buffalo are feeding in between the two behavioural phases have not been taken into account, leading to an underestimation of the presence of buffalo in areas located at the periphery of surface water. On the other hand, the trends of the model to overestimate the presence of buffalo at proximity of detected surface water may be due to the quality of SRS-derived surface water maps. Indeed, all the surface water have not been detected due to their small size, vegetation covering and potential draining at the time of satellite image acquisition, de facto reducing the choice of surface water locations that buffalo can reach in simulations compared to what happens in reality.

4.4 Perspectives

Perspectives of this first modelling study of buffalo movements in semi-arid savanna using SRS include the integration of other environmental variables (e.g., browsing areas, vegetation structure, ...) and human infrastructures (e.g., agricultural fields, roads, ...) to simulate more realistic buffalo movements. By adding more key factors influencing the buffalo's movements to the model, the latter could potentially be adapted to the study of contacts between wildlife and domesticated species at the interface between communal and protected areas. The present study provides an original modelling framework allowing the integration of SRS-derived environmental variables to address complex questions on disease propagation, ecological interactions between species or animal management.

5. CONCLUSION

The ecological and animal movement model developed in this study demonstrated how a mechanistic model can be spatialized and combined with remote sensing data to simulate buffaloes' movements in relation with surface water availability at a landscape scale. For the first time to our knowledge, we proposed to model buffalo at the individual and collective scales in heterogeneous environments by the use of a parsimonious swarm model. This simple and replicable framework can be considered as an alternative to the existing modelling tools in the understanding of animal movement in regard to water selection in several ecological contexts and environments.

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6.2 Application of the buffalo movement model in two other W/L interfaces

The reflections and results presented in this section are the result of a Master 2 internship carried out during 5 months between February and June 2021 by Victor Dufleit (Dufleit, 2021), then a student in the Master “Biodiversité, écologie et évolution” (BEE) specialization “Écologie Évolutive et Fonctionnelle” (EEF) at the University of Paris I Panthéon-Sorbonne.

6.2.1 A movement model that also consider the landcover

As detailed in [Chapter 2](#), the Gonarezhou/Malipati and the Kruger/Pesvi study sites are ecologically, geographically and hydrologically contrasted with the Hwange/Dete study site. To adapt the model, initially developed to the Hwange/Dete study site configuration, to the Gonarezhou/Malipati and the Kruger/Pesvi study sites, changes regarding the model's capacity to apprehend the hydrological spatial configuration had to be processed. The water points in the Hwange/Dete study site are mainly small water ponds ([Figure 4.3](#)), and the movement of simulated buffalo towards a selected water point by taking the centroid of the corresponding water polygon as the "target" works accordingly as the centroid of the polygon corresponds to the location of a specific water point. This is not the case for the Kruger/Pesvi and Gonarezhou/Malipati study sites which are crossed by rivers ([Figure 2.3](#) and [Figure 2.4](#)). Initially, these rivers were represented in the original environmental data by a single polygon, whose centroid did not necessarily correspond to a particular water area. In addition, observation of GPS collar data showed that buffalo drink at different locations in the rivers. It was therefore chosen to divide the polygons characterizing these rivers into multiple smaller polygons, each with its own identifier. Watering areas in these rivers were identified from GPS records near the rivers, and the median size of these areas has been calculated for both study sites and used to divide the river polygons (Gonarezhou/Malipati, Mwenezi River: 1300m; Kruger/Pesvi, Limpopo River: 750m).

The movement model detailed in the [section 6.1.2](#) was considering the surface water as the only environmental driver influencing the buffalo movements in time and space. Therefore, in order to measure the impact of landcover on buffalo movements over time and space and improve the model's reproduction of buffalo's herd trajectories, the movement model has been modified to consider, in addition to the surface water, the landcover. Indeed, certain landcover classes (e.g.,

mixed shrubland/grassland) can represent feeding areas for a herd, particularly grassy areas, as buffalo are browsers (Cornélis et al., 2014). It has also been shown that buffalo can feed on the leaves and fruits of certain trees (Cornélis et al., 2014), so shrub and forest areas were also considered attractive to buffalo during their feeding periods. Therefore, based on probability metrics extrapolated from the buffalo telemetry (Figure 6.7), the model behavioral and temporal structures have been modified accordingly (Figure 6.8). The buffalo day was thus redivided into five different phases to account for two new phases, active movement in search of a grazing area and resting/rumination, corresponding to the observed velocity measurements (Figure 6.7A). The watering phase was kept as it was, the free divagation phase was shortened to stop before the increase in speed observed around 3 am (Figure 6.7A). The watering phase was kept as it was, the free divagation phase was shortened to stop before the increase in speed observed at around 3 a.m (Figure 6.8). A new phase began, which was termed active movement, where the buffalo moved in relation to the nearby landcover (Figure 6.8).

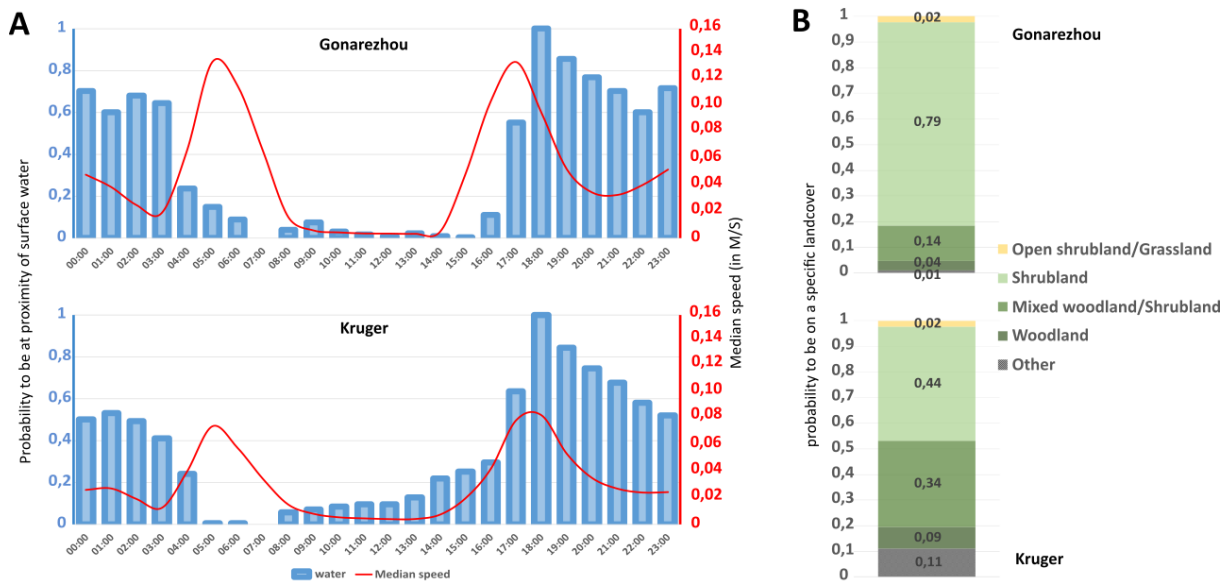


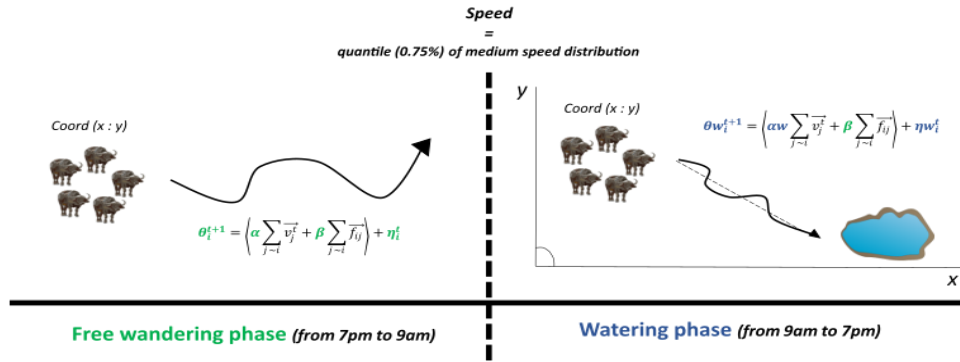
Figure 6.7: A) Medium speed of buffalo in relation to the probability to be at proximity of the surface water depending on the hour of the day. B) Probability for buffalo to be on a specific landcover in regard to the entire duration of the telemetry data recording period for each of the study sites.

A preferential targeting system has been created (Figure 6.8) based on the methodology used in Step Selection Function (SSF) studies (Thurfjell et al., 2014). At each hour, a new "target" is determined. A buffer zone, which radius corresponds to the maximum distance d covered by the buffalo in one hour, is created around the position of the herd ($d = 750\text{m}$ at Kruger/Pesvi and 1035m at Gonarezhou/Malipati), values determined after removing outliers, (value greater than $1.5 \times \text{quartile } 0.75$). All pixels of the landcover raster within this buffer then become potential targets. Each pixel is assigned a probability p according to the equation (1)

$$p = P_i * n_i \quad (1)$$

where P_i is the preference associated with landcover i (Figure 6.7A) and n_i is the proportion of pixels of land cover i present in the buffer. A target is then selected considering the probability associated with each pixel (Figure 6.7A). The buffalo then move towards this target. A new target is determined every hour, an interval over which observed buffalo behavior in relation to landcover has been extrapolated (extrapolation corresponding to the frequency of recording the location of the buffalo equipped with GPS collars).

Movement model in relation to water availability



Movement model in relation to water availability and landcover selection

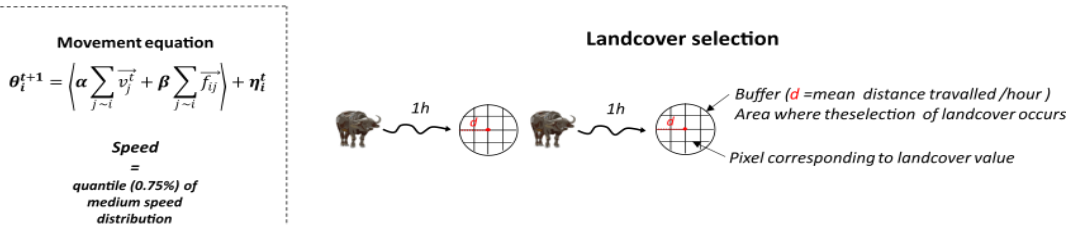
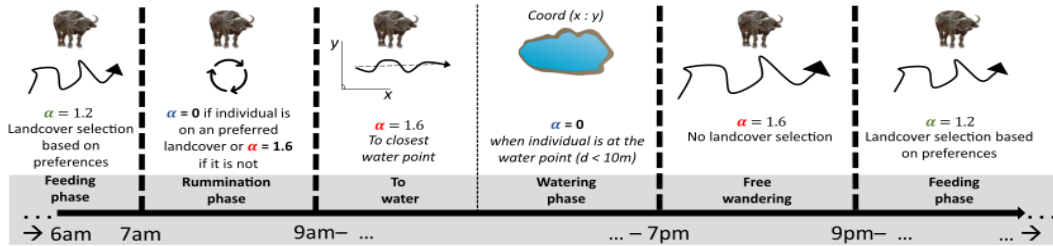


Figure 6.8: Evolution of the buffalo movement model. The later transitioned from a movement model considering surface water only with two behavioral phases to a movement model considering surface water as well as landcover with five behavioral phases.

The selection process occurs during the “feeding phase where buffalo keep moving while taking the direction of the most suitable landcover corresponding to the pre-determined preference probabilities ([Figure 6.7B](#)). The last phase, in which the observed speeds decrease ([Figure 6.8](#)), was named “rumination phase” and can be considered as a phase in which the buffalo stop to rest and ruminate. In this phase, the landcover on which the herd is standing is checked every hour. If the herd is on a landcover considered favorable (Mixed shrubland/grassland, Shrubland, Mixed shrubland/woodland), the α of the model that regulate the alignment of the individuals within the collective is set to 0, forcing the buffalo movements to be governed only by the noise η and the cohesion β . As the result, the herd's movements are restricted to a relatively small area and is almost static in space. If, at the time of the landcover check, the herd is on unfavorable ground cover (e.g., Woodland, Other) the buffalo behave similarly to the free divagation phase. They continue their random movements in their directions until they reach a favorable landcover.

With these modifications, the movement model is able to consider both the availability of the water resource and its spatial distribution, as well as the different types of landcover corresponding to the buffalo's preferences in offering potential food sources and suitable areas for resting and rumination.

6.2.2 Application in Gonarezhou/Malipati and Kruger/Pesvi

Looking at one trajectory output simulated in the Kruger/Pesvi Study site as an illustration example, the movement model that only considers surface water ([Figure 6.9A](#) - map located in the middle) follows the model's behavioral phases implemented ([Figure 6.8](#)). The trajectory starts in a random direction and then move in the direction of the surface water at the beginning of the watering phase. Once the surface water reached, the buffalo slow down and stop until the next free roaming phase begins. At this point, a new random direction is given to the buffalo's individuals until the next watering phase begins. The simulated trajectory is very straight for this model, giving a strong impression of going back and forth ([Figure 6.9A](#) – map located in the middle). Concerning the trajectory output simulated by the movement model considering the surface water as well as the landcover ([Figure 6.9A](#) – map located in the right), i) the free divagation and watering phases trace rectilinear trajectories comparable to the model considering only the surface water, ii) the active movement phase with landcover preference presents relatively scattered clusters of points with some backtracking depending on the

landcover preferences and the stochastic buffalo's locations, and iii) the rumination phase is characterized by a cluster of points in a restricted area when the buffalo are on a landcover that is favorable to them. In this specific simulation ([Figure 6.9A](#) – map located in the right), the buffalo are attached to a much smaller geographic area than with the movement model considering only the surface water and the trajectory produced by the model considering surface water and landcover is more consistent with the observed trajectory ([Figure 6.9A](#) – map located in the left).

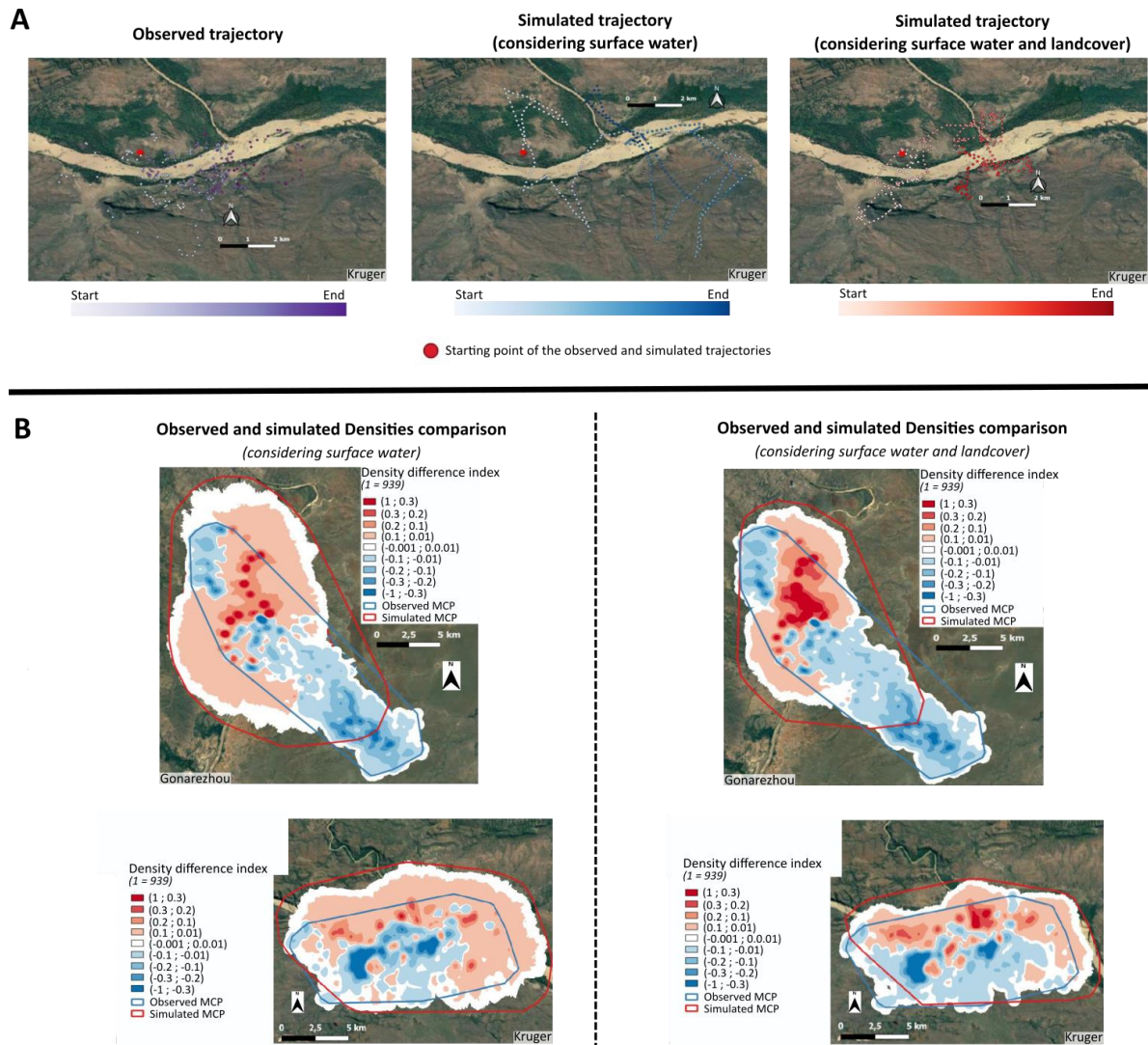


Figure 6.9: A) Maps of the buffalo herd centroids observed and simulated trajectories at the Kruger/Pesvi study site, for one iteration (concerning the simulations) over a period of 15 days. B) Heat maps of density differences (simulated-observed) for Gonarezhou/Malipati (above) and Kruger/Pesvi (below) and the observed and simulated MCP obtained with the two different buffalo movement models. The model considering surface water only (on the left) and the model considering surface water as well as landcover (on the right).

The MCPs simulated by the movement model considering only the surface water ([Figure 6.9B](#) – maps located in the left) and the movement model considering the surface water as well as the

landcover (Figure 6.9B – maps located in the left) are close to those observed (Figure 6.9B), although in Gonarezhou/Malipati, an area unexplored by the simulated buffalo in the south-east can be seen (Figure 6.9B – maps located in the top). We also observe that the high values of over-estimations are not very widespread in space for all the simulations. All the movement models overestimate the density of buffalo herds at the centroids of the water polygons used, this is particularly true at Gonarezhou (Figure 6.9B – maps located in the top). Herd density is underestimated in some Mixed shrubland/grassland and woodland areas south of the river in Kruger/Pesvi (Figure 6.9B – maps located in the bottom). This underestimation persists with the movement model considering the surface water as well as the landcover. The simulated MCP have an area closer to the observed one for the model considering the surface water and the landcover. This observation is related to the trajectories simulated by this model (Figure 6.9A – map located in the right), resulting in an increase of the overall values of simulated densities and strong densities over-estimations more extensively spread in space for the two study sites (Figure 6.9B – maps located in the right).

The average ρ ranges varies from 0.80 to -0.05 for the "water" model with the maximum for Kruger/Pesvi group 1 and the minimum for Gonarezhou/Malipati groups 1 and 3 (Table 6.2). For the "water/landcover" model, mean ρ values range from 0.72 to -0.26 (Table 6.2) maintaining the same hierarchy in values as for the "water" model. It should be noted that at the Kruger/Pesvi study site, the higher the simulation time the higher the average ρ (Table 6.2).

	Simulation time	"water" model		"water/landcover" model	
		$\bar{\rho}$	$\overline{p\ value}$	$\bar{\rho}$	$\overline{p\ value}$
K1	455 days	0,66	<0,05	0,53	<0,05
K2	52 days	0,15	<0,05	-0,14	<0,05
K3	54 days	0,38	<0,05	-0,03	0,06
K4	462 days	0,66	<0,05	0,53	<0,05
K5	568 days	0,78	<0,05	0,62	<0,05
K6	264 days	0,80	<0,05	0,72	<0,05
G1	871 days	-0,05	<0,05	-0,26	<0,05
G3	401 days	0,02	0,11	-0,19	<0,05

Table 6.2: Table that present the results of the Spearman correlation tests for the "water" and "water/landcover" models. These tests were performed with the observed and simulated median density raster obtained considering the entirety of the simulation duration for each buffalo groups (K corresponding to the Kruger/Pesvi buffalo groups and G corresponding to the Gonarezhou/Malipati buffalo groups).

Despite the more realistic simulated trajectories produced by the landcover model in terms of morphology (because they are more random and less rectilinear) and in terms of spatial

representation (because the produced MCP are less extensive), the densities produced are less faithful to observed densities ([Figure 6.9B](#)). However, these results are strongly linked to the spatial distribution of natural resources (e.g., water surface and landcover) and to the geographical location of the starting point of the simulated trajectories. It is also important to note that the model is stochastic and that the correlations between observed and simulated densities vary strongly from one iteration to the next.

6.3 Chapter summary

- An existing classification method of satellite Sentinel-2 time-series images has been adapted to produce monthly surface water maps at 10 meters spatial resolution.
- The use of spectral indices derived from Sentinel-2 in combination with the short-wave infrared (SWIR) band in a Random Forest (RF) classifier provided robust results with a mean Kappa index, over the time series, of 0.87 (max = 0.98, min = 0.65). The results highlighted strong space and time variabilities of water availability in the study area
- The resulting water maps have been integrated into a spatialized mechanistic movement model based on a collective motion of self-propelled individuals to simulate buffalo movements in response to surface water at the Hwange/Dete study site.
- The mechanistic movement model showed a positive and significant correlation between observations/simulations movements and space-use of buffalo's herds (Spearman $r = 0.69$, $p\text{-value} < 0.05$) despite overestimating the presence of buffalo individuals at proximity of the surface water.
- The mechanistic movement model only considering the surface water have been replicated and tested in the two other study sites.

- The mechanistic movement model has been modified with the implementation of the ability to consider landcover in addition to surface water to determine buffalo movements in space and time.
- The genericity of the modified mechanistic movement model has been tested by applying and validating it in different W/L interface configurations (i.e., Gonarezhou/Malipati and Kruger/Pesvi).
- More realistic simulated trajectories have been produced by the mechanistic movement model considering the surface water and the landcover in terms of morphology (because they are more random and less rectilinear) and in terms of spatial representation (because the produced MCP are less extensive).
- The ρ values range from 0.72 to -0.26, maintaining the same hierarchy in values as for the previous mechanistic movement model.

Chapter 7

Spatial modelling of contacts between wildlife and livestock in Southern Africa

Table of content

7.0	Preamble
7.1	The article
7.1.1	Introduction
7.1.2	Method
7.1.3	Results
7.1.4	Discussion
7.2	Chapter summary

7.0 Preamble

This chapter details, in the form of a scientific paper, not yet submitted, the mechanistic model for simulating buffalo-cattle contacts at the three study sites considered in this thesis. The objective is to better understand potential contacts between domestic and wildlife at three different wildlife/livestock interfaces by combining remote sensing and spatial modeling to simulate the movements of African buffalo (*Syncerus caffer caffer*) and domestic cattle (*Bos taurus*, *Bos indicus*) at the landscape scale. The movement and contact model presented in this chapter synthesizes all the methodological and thematic steps presented in the previous chapters of this manuscript.

The submission of the article is planned by the end of 2021 knowing that the article has only been reviewed by the thesis supervisors and not by all the associated co-authors. For now, The open-access Ecography journal (<https://onlinelibrary.wiley.com/journal/16000587?tabActivePane=undefined>) is targeted for publication. Ecography is owned by the Nordic Society Oikos (NSO), and publishes papers focused on broad spatial and temporal patterns, particularly studies of population and community ecology, macroecology, biogeography, and ecological conservation. It is particularly suited to communicate the developed model to the ecologist scientific community.

7.1 The article

Research

Spatial modelling of contacts between wildlife and livestock in Southern Africa

Florent Rumiano, Pascal Degenne, Alexandre Caron, Cédric Gaucherel, Eve Miguel, Michel de Garine-Wichatitsky, Simon Chamaillé-Jammes, Hugo Valls-Fox, Hervé Fritz, Annelise Tran

F. Rumiano (<https://orcid.org/0000-0001-8615-7161>) ✉ (florent.rumiano@cirad.fr), P. Degenne (<https://orcid.org/0000-0003-0062-8511>), A. Caron (<https://orcid.org/0000-0002-5213-3273>), C. Gaucherel (<https://orcid.org/0000-0002-4521-8914>), M. deGariné Wichatitsky (<https://orcid.org/0000-0002-5438-1473>), S. Chamaillé-Jammes (<https://orcid.org/0000-0003-0505-6620>), H. Valls-Fox (<https://orcid.org/0000-0001-7482-1205>), H. Fritz (<https://orcid.org/0000-0002-7106-3661>), A. Tran (<https://orcid.org/0000-0001-5463-332X>)

The open interfaces between protected areas and rural communal lands in southern Africa are characterized by semi-arid savannas where wildlife-livestock interactions vary in frequency and intensity. In a context of increasing anthropization, the multiplication of these interactions may facilitate human-wildlife conflicts such as competition for natural resources, livestock predation, crop destruction by wildlife, and/or the risk of pathogen transmission between wild and domestic species. To better understand potential contacts between domestic and wildlife at these wildlife/livestock interfaces, we combine remote sensing and spatial modeling to simulate the movements of African buffalo (*Syncerus caffer caffer*) and domestic cattle (*Bos taurus*, *Bos indicus*) at the periphery of three national parks in Zimbabwe and South Africa. Surface water and vegetation, the primary determinants of movement for these ungulate species, have been classified and mapped from a time series of medium resolution Sentinel-2 satellite images. The resulting classification maps were then integrated into a mechanistic mathematical model of collective movement of individuals interacting in relation to one another according to group cohesion and alignment. This stochastic model allowed the simulation of herd movements and the location of contact areas and their seasonal dynamics in space and time. The model outputs were compared to GPS collar location data of 34 individuals (16 buffalo and 18 cattle). The results show a high spatial and seasonal variability of contacts between buffalo and cattle in the three study areas, and a landscape scale correspondence between the modeled and observed contact area spatial extensions (distance between centroids of the observed and simulated contact areas are strictly inferior to 3.1 km). These initial results illustrate the potential of spatial modeling combined with remote sensing to generically simulate animal movements at the landscape scale while offering opportunities to manage these interfaces through, for example, a coupling with epidemiological modelling.

Keywords: remote sensing, spatial modelling, mechanistic model, animal movement, surface water, landcover, African buffalo, cattle, savanna, wildlife-livestock interface

Introduction

The current footprint of human societies and their extractive activities increase the need for natural resources while producing the fragmentation of

natural areas (A. Hansen & Defries, 2007). This phenomenon particularly pregnant in developing countries de facto conditions humans and their domestic animals to live more and more in proximity to natural areas and wildlife (Wittemyer et al., 2008), thus multiplying the number of

wildlife-livestock interfaces (WLI). WLI are defined as the physical space in which wild and domestic species, as well as humans, overlap in range and potentially interact (Caron et al., 2021). These interactions occur between natural ecosystems as defined by Ostrom (2009). Within WLI, wild and domestic animal movements between land uses (e.g., communal land and protected areas) determine the spatial overlap and the potential direct and indirect contacts between species (Ferguson & Hanks, 2012). From an anthropocentric perspective, the so-called “human-wildlife conflicts” (HWC) that potentially constitute threats to human agricultural activities as a whole and human life in particular (Madden 2004) are characterized by events such as livestock depredation by carnivores (Eklund et al., 2017), crop destruction by wildlife (Gross et al., 2018), increased competition for shared natural resources (Treves et al., 2006), hunting or illegal poaching (Warchol et al., 2003), and disease transmission (Decker et al., 2010). Given the complexity of HWC locally, WLI are in the epicenter of economic, social, health and conservation issues (Frank, Glikman, and Marchini 2019), conducting stakeholders, including scientists to design policy-relevant pathways toward human-wildlife coexistence (König et al., 2020) and coadaptation (Carter, Baeza, and Magliocca 2020). Indeed, livestock husbandry and subsistence agro-pastoralism prevail in Southern African WLI, (Caron, Miguel, Gomo, Makaya, Pfukenyi, Foggin, Hove, & Garine-Wichatitsky, 2013), impacting conservation within these multiple use areas (Fynn et al., 2016). In Southern Africa, WLI are mainly located in semi-arid savannas in which the spatial distribution and availability of natural resources (e.g., forage and surface water, ...) are conditioned by seasonal variations and the footprint of human activities as well as agricultural expansion (Chagumaira et al., 2016). This spatial distribution of natural resources influences, in turn, how animal use a landscape and the abundance of animal species (G. Wang et al., 2006). In Southern African savannas, forage and surface water become resources that cannot be substituted during the dry season (Valls-Fox, De Garine-Wichatitsky, et al., 2018) and, as a result, their respective availability becomes a key determinant of animal distribution at the landscape scale (Ogutu, Reid, et al., 2014). In Southern African WLI, competition for natural resources occurs in areas suitable for the development and occurrence of these resources (Chamaillé-Jammes, Valeix, and Fritz 2007) and can potentially lead to depletion effects as they are often regrouped in delimited areas for a limited timeframe (Shrader et al., 2008).

African buffalo (*Syncerus caffer caffer*) and domestic cattle (*Bos taurus*, *Bos indicus*), keystone animal species for conservation and production systems in Southern Africa, are large bovid species, principally grazers with similar body size, that rely on and compete for the same natural resources when sympatric (Fynn et al., 2016; Odadi et al., 2011). Given the particular context occurring in southern African WLI, it is crucial to understand the drivers of resource selections by wild and domesticated animal species to mitigate HWC, including the risk of pathogen transmission (Miguel, Grosbois, Caron, Boulinier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & Garine-Wichatitsky, 2013) by characterizing the spatiotemporal distribution of natural resources (Wiens, 1989), animal movements patterns (Benhamou, 2014) as well as their respective foraging and watering decisions (Owen-Smith, Fryxell, et Merrill 2010; Valls-Fox et al. 2018).

Spatial models that simulate animal movements at a landscape relative to biotic and abiotic drivers and including behavioral mechanisms have recently been the subject of several studies (Westley et al., 2018). In conjunction with the development of spatialized animal movement models, the democratization of the combined use of telemetry using global positioning system (GPS) (Kays et al., 2015) and satellite remote sensing (SRS) (Remelgado et al., 2018) in animal movement ecology further strengthens the potential to develop mechanistic model approaches that reproduce fine-scale ecological processes (e.g., landscape scale animal movements and inter-individual contacts) and underlie ecosystem functions (e.g., watering and foraging behavior of a focal species) in response to changes in the environment (e.g., seasonal variabilities of natural resources). In that regard, a spatialized mechanistic mathematical model simulating buffalo movements in relation to surface water seasonal availability characterized by SRS at the landscape scale (spatial resolution of 10 meters) have been recently developed in a WLI in Zimbabwe (Rumiano et al., 2021).

Considering the overgrowing risk of disease transmission between wildlife and livestock (and potentially humans) (Miguel, Grosbois, Caron, Boulinier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & Garine-Wichatitsky, 2013) induced by their direct or indirect contacts in space and time, this study proposes 1) to build on the buffalo movement model developed by Rumiano et al. 2021, to include cattle movements according to the collective motion of groups of self-propelled individuals (Gregoire, Chate, and Tu 2003) as well as to consider landcover in addition to the surface

water as environmental drivers of animal movements, 2) to use this spatialized mechanistic mathematical model to apprehend and discuss the role played by the environmental variables that potentially condition the frequency and intensity of the two focal animal species contacts in three different WLI located at the periphery of protected areas in Zimbabwe and South Africa.

Method

Study area

The three study sites ([Figure 7.1](#)) are located on the periphery of protected areas in Zimbabwe (i.e., Hwange National Park (HNP) referred in the article as “Hwange/Dete”, Gonarezhou National Park (GNP) referred in the article as “Gonarezhou/Malipati” and in South Africa (i.e., Kruger National Park (KNP) referred in the article as “Kruger/Pesvi”) where conflicts between human

areas outside national parks essentially consist of subsistence farming with small-scale livestock production and rainfed agriculture (from November to March). Small herds are bred extensively with on average 12 heads of cattle and small ruminants (goats and a few sheep) per herder (Miguel, Grosbois, Caron, Boulinier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & Garine-Wichatitsky, 2013). In these areas, domestic and wild animal movements between natural and anthropogenic compartments are frequently observed in both directions (Chigwenhese et al., 2016; Dube et al., 2010) and contacts between Africa buffalo and domesticated cattle have been observed (Miguel, Grosbois, Caron, Boulinier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & Garine-Wichatitsky, 2013) despite the fact that incursions of livestock into protected areas are strictly forbidden in Zimbabwe and in South Africa (Chigonda, 2018). The intensity and frequency of contacts varied among the study sites (represented by the width of the arrows in [Figure 7.1](#)), emphasizing different buffalo

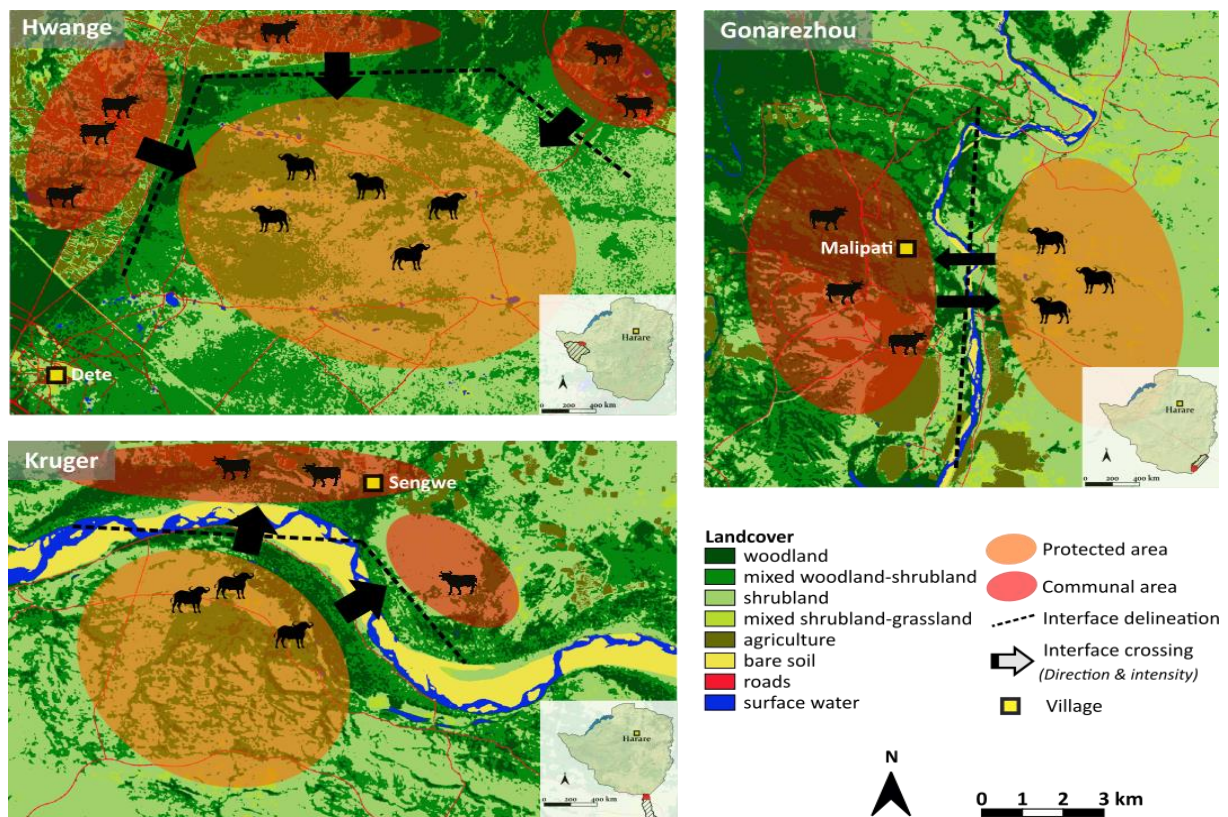


Figure 7.1: Location maps of the three study areas. Only the contact areas between buffalo and cattle are represented.

communities and wildlife are increasing (Mutanga et al., 2017; Guerbois, Chapanda, and Fritz 2012) and where boundaries between protected areas and communal areas are often permeable (i.e., river, railroad, or road) and without barriers. For the three study sites, human activities in communal

and cattle contact configurations. Based on the statistical analyses developed in a previous study (Miguel, 2012), the rate of cattle incursion inside protected areas (expressed as a percentage of the overall time recorded by the GPS collars placed on targeted cattle) was 6.9% in Hwange/Dete, 3% in

Gonarezhou/Malipati and 0.2% in Kruger/Pesvi. Concerning the rates of buffalo incursion into communal areas, it was of 0.05% in Hwange/Dete, 7.46% in Gonarezhou/Malipati and 58% in Kruger/Pesvi.

The three study sites are located in semi-arid climate with annual mean temperatures of 22°C and mean annual precipitation ranging from 450 to 650 mm for Hwange/Dete (Chamaillé-Jammes, Valeix, and Fritz 2007) and mean annual temperatures ranging from 25°C to 27°C and mean annual precipitation ranging from 300 to 600 mm in both Gonarezhou/Malipati and Kruger/Pesvi. On average and excluding climatic anomaly (e.g., drought), the dry season occurs from April-May to October-November and the wet season from November to March for the three study sites. The vegetation found in these areas is typical of a highly heterogeneous dystrophic wooded savanna (Arraut, Loveridge, Valls, et al., 2018). The woody cover increases with distance from water pans (Chamaillé-Jammes et al., 2009) and the open grassland is located along drainage lines. In Hwange/Dete, the surface water is mainly composed of seasonal natural pans of different sizes widely distributed across the area complemented with artificial pans fed by underground water pumping stations during the drier months. In Gonarezhou/Malipati and Kruger/Pesvi, the surface water is composed of river systems having water along their entire courses during the wet season. During the dry season, intermittent river branch inside the riverbed as well as ephemeral rain fed natural pans located on sandstones are present and constitute a primary water resource for wild and domestic animal species alike.

Telemetry data

Ultra-high frequency Global Positioning System (GPS) collars manufactured by African Wildlife Tracking have been used in previous studies (Miguel, 2012; Valls Fox, 2015) to monitor the movements and contacts between selected cattle and buffalo herds simultaneously in the three sites with a one hour frequency. In total, 10 cattle and 4 buffalo individuals were monitored in Hwange/Dete, while 4 cattle and 8 buffalo individuals as well as 4 cattle and 4 buffalo individuals were monitored at Kruger/Pesvi and Gonarezhou/Malipati respectively (Appendix 1). The data (Appendix 1) have been pre-processed in order to derive metrics allowing the design and validation of the movement model used in this

study. Pre-processing processes included 1) the re-projection of the entire telemetry dataset, the correction of outlier data and the harmonization of time-delays, all following the methodology developed by (Wielgus, 2020), 2) the grouping of buffalo and cattle telemetry data by locations and time of recording for each of the three study sites to derive herd entities sharing the same location at the same time (Appendix 1).

Remote sensing data

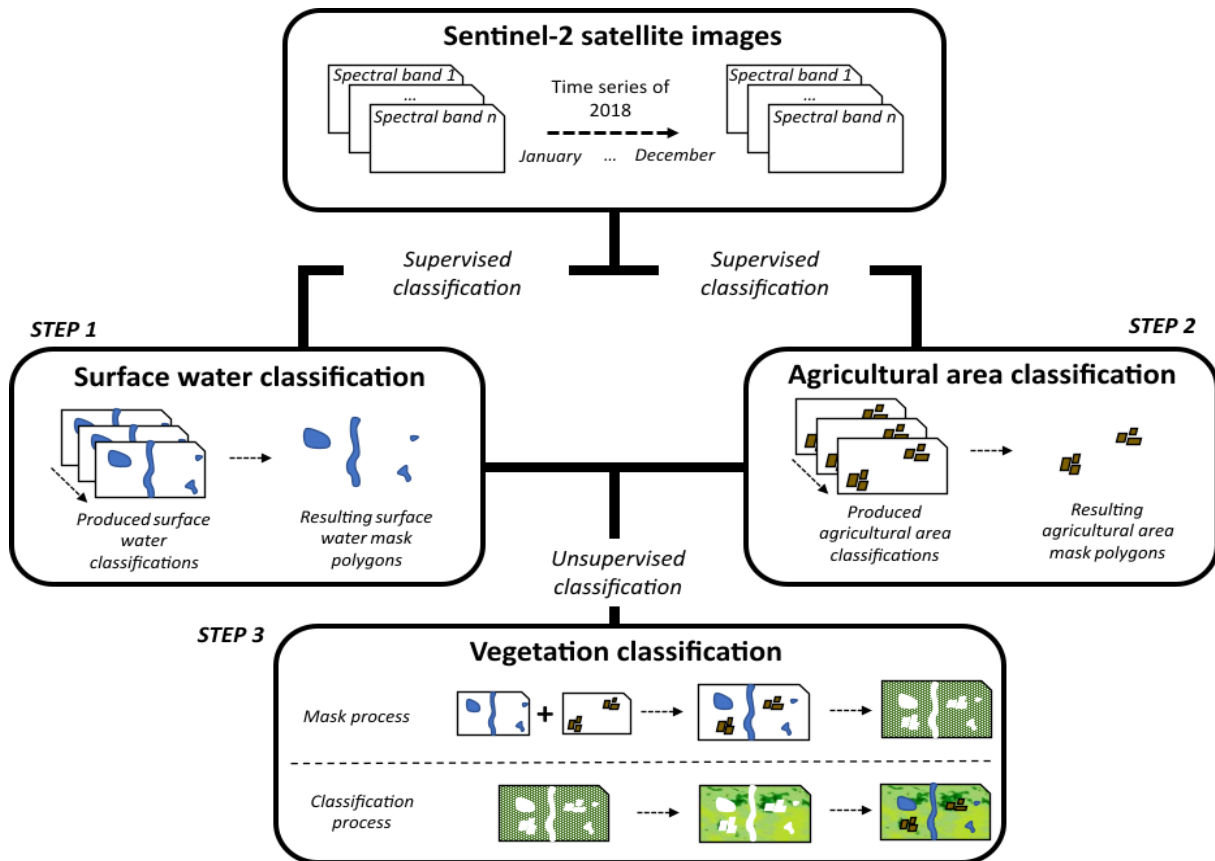
72 Sentinel-2 satellite images (Drusch et al., 2012) acquired in 2018 and covering the three study sites have been downloaded in level 1C which provides Top of Atmosphere reflectance and orthorectified images (Appendix 2). The Sen2Cor v2.8 application (Sen2Cor, ESA, <http://step.esa.int/main/third-party-plugins-2/sen2cor/>) has been used to apply the atmospheric corrections, thus transforming L1C images to level L2A (Top of Canopy) images. 6 tiles were necessary to cover the entire study zone spatial extent (Appendix 2). The dates of the image selected represent days with less than 10% of cloud cover for the entire year 2018 with one image per month for each tile. For the month of February however, no images were cloud free in 2018. As a result, Sentinel-2 satellite images from February 2019 have been selected instead (Appendix 2). The 20 meters spatial resolution spectral bands of the L2A Sentinel-2 images have been resampled by bilinear interpolation to 10 meters spatial resolution before being projected to the WGS84/UTM35S and WGS84/UTM36S projection systems and clipped to correspond to the respective spatial extent of the three study sites.

Discrimination of surface water

The discrimination of the surface water corresponds to the first step of a three steps classification process (Figure 7.2)

Classification: The calculation of the modified normalized difference water index (MNDWI) and the normalized difference water index (NDWI) derived from sentinel-2 have been used to classify the surface water, following Du et al. 2016. The supervised classification using the Random Forest (RF) algorithm have then been applied using the methodology developed in Rumiano et al. 2021. After the application of the RF algorithm, three time series (one for each of the study site) of classified surface water at 10 meters of spatial resolution have been obtained.

Figure 7.2: Classification general process



Post-classification: For each classified raster image, the pixels classified as “surface water” have been vectorized to allow the removal manually of the noise pixels (false positives). As the water surfaces reach their maximum spatial extents in March, when the peak precipitation occurs, the classification images of the month of March (one per tile) have been selected to map the maximum water extent for each of the three study sites. The resulted vector layers of the month of March have then been used as a template to mask all of the noise pixels present in the 11 other months of the year vector layers.

Classification validation: The three sets of reference polygons have been used as training and validation references to apply a cross-validation on two classification accuracy indicators (i.e., overall accuracy (OA) and Kappa index) and test the robustness and stability of the classification method. 50 iterations of classification using randomly selected reference polygons were performed to run the cross-validation for each of the three study sites.

Classification of the landcover

The classification of the landcover is divided into two steps that correspond respectively to the

agricultural area classification (step 2) and the landcover classification per se (Step 3) that take part of the three step general classification process ([Figure 7.2](#))

Classification of agricultural areas: A combination of Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI) and Soil Adjusted Vegetation Index (OSAVI) (Fern et al., 2018) for the month of March (month of the year corresponding to the peak of the wet season and where the contrast between the vegetation and the bare soil is the strongest) and derived from Sentinel-2 images have been realized. These spectral indexes have been considered for the agricultural areas supervised classification as they have been used extensively and proved to be efficient in previous studies to characterize agricultural areas using medium spatial resolution SRS images (Bellón, Bégué, Lo Seen, De Almeida, et al., 2017; Y. Zhao et al., 2020). A supervised classification using a set of 50 reference polygons for the two classification classes (i.e., “agriculture areas” and “other”) to derive data from the combination of the three produced spectral indexes images for each of the three study sites has been integrated into a RF algorithm. The reference polygons have been extrapolated from photo-interpretation of a very-high SRS image (i.e., Pleiades) and have been split into a 50/50 ratio to

constitute a reliable comparison between training and validation samples (Mercier et al., 2019). The resulting classification raster have then been vectorized to manually detect and remove false positives.

Classification of other vegetation areas: Afterwards, three Sentinel-2 red-edge bands (i.e., band 5, band 6 and band 7 that are located between the red and the Near Infrared of the electromagnetic spectrum) have been masked with manually digitalized polygons of road networks as well as with vectorized surface water and agricultural area polygons resulting from the two previous classifications. It has been established that the red-edge bands inclusion into classification scheme positively impacts the characterization of vegetation classes and improve overall classification accuracies (Schuster, Förster, and Kleinschmit 2012). The three produced masked raster have then been used to classify five classes of vegetation and landscape characteristic (i.e., woodland, mixed-woodland-shrubland, shrubland, mixed shrubland-grassland, bare soil) for each of the three study sites via a pixel-based non-supervised K-means clustering classification method (Burrough, van Gaans, and MacMillan 2000).

Post-classification: For each of the study sites, the produced raster from the non-supervised classification have been combined with their respective surface water, agricultural area, and road network raster to form a final landcover classification raster of an eight elements typology (Figure 7.1) at 10 meters of spatial resolution.

Classification validation: To validate the accuracy of the agricultural area classifications, the same method as the surface water have been used (as described in the previous section). Concerning the validation of the non-supervised classification of the vegetation and landscape characteristic, three sets of reference polygons (one for each study site) comprising of 50 reference polygons per class have been manually digitalized. The digitalization has been done “a priori” before the classification by photo-interpretation of a very high satellite image (i.e., Pleiades) for the three study sites to

compensate for the lack of an in-situ landscape description database. The reference polygon datasets have then been used to calculate the OA and the Kappa index of the realized vegetation classifications.

A spatialized movement model

Choice of the modelling language: The developed spatial model is composed of six main interacting spatial entities: (i) the buffalo individuals, (ii) the buffalo herd, (iii) the cattle individuals, (iv) the cattle herd, (v) the surface water, (vi) the landcover. The domain specific language Ocelet (Degenne & Lo Seen, 2016) has been used to specialized the model and create the relations between the different spatial entities of the model.

Animal modelling approach: A model of collective motion of self-propelled individuals (Gregoire et al., 2003) has been chosen to model the two focal species movements at the individual and herd scales as developed in Rumiano et al. 2021. In this particular model, all individuals move from their starting location to the next at discrete time steps by a fixed distance v_0 , their direction defined for each time step t as an angle θ_i^t :

$$\theta_i^{t+1} = \arg \left[\alpha \sum_{j \neq i} \vec{v}_j^t + \beta \sum_{j \neq i} \vec{f}_{ij} \right] + \eta \xi_i^t \quad (1)$$

See Rumiano et al. 2021 for more details concerning the equation (1). The herd's cohesion force \vec{f}_{ij} that link two individuals i and j and that is regulated by β is expressed as follows:

$$\vec{f}_{ij} = \vec{e}_{ij} \begin{cases} -\infty & \text{if } r_{ij} < r_c, \\ \frac{1}{4} \frac{r_{ij} - r_e}{r_a - r_e} & \text{if } r_c < r_{ij} < r_a, \\ 1 & \text{if } r_{ij} > r_a \end{cases} \quad (2)$$

Refer to Rumiano et al. 2021 for more details. \vec{f}_{ij} (2) is defined by several parameters (Table 7.1) that are representative of buffalo and cattle's herd behavior . These values are based on empirical knowledge and in-situ observations.

Parameters	Definition	Values	Values
		Buffalo	Cattle
v_0	Buffalo speed	0.46 km/h*	0.46 km/h*
r_0	limit of interaction distance	500m**	300m**

r_c	repulsion distance	5m**	0.5m**
r_e	equilibrium distance	10m**	5m**
r_a	minimal distance	150m**	150m**
α – free divagation	alignment regulation	1.2***	1.2***
α – toward water and kraal phases	alignment regulation	1.6***	1.6***
β	cohesion regulation	1***	1***
η	noise regulation	0.4***	0.4***

Table 7.1: Model parameters estimated from telemetry data (*), expert knowledge (**), or calibration (***)

Buffalo and cattle contact model configuration and behavior

The developed buffalo and cattle contact model is constituted of two main blocs, the buffalo movement model, and the cattle movement model (Figure 7.3), that interact with one another and determine the geographical location, frequency and temporality of the buffalo and cattle contacts at the three studied WLI interfaces.

The buffalo movement model is divided into five phases per 24-hour period (Figure 7.3) that are based on buffalo behavior (i.e., median speed per hour) derived from telemetry data (Rumiano et al., 2021) (Appendix 3). The first phase corresponds to the “rumination phase” where $\alpha = 0$ (buffalo movements are only influenced by the cohesion of individuals, which is equivalent to standing still) when each individual is located over a suitable landcover determined by their preferences (Appendix 4) or keep moving ($\alpha = 1.6$) until they reach a suitable landcover. The second phase is the “to water” phase where buffalo move towards the closest surface water from the buffalo’s herd centroid position at the beginning of the phase. Once buffalo individuals are within 10 meters of the targeted surface water point, the “watering phase” starts and α take the zero value. At the end of the “watering phase”, the “free wandering” phase where buffalo individuals randomly move across space occurs to signify their departure from the surface water point towards their feeding areas. The “feeding phase” starts with a selection of suitable landcover determined in the same fashion as the “rumination phase” to signify areas suitable for feeding. After the “feeding phase”, the buffalo starts their “rumination phase” once again, thus marking the end of a daily cycle that repeats itself for the duration of the simulation.

The cattle movement model is constituted of five phases per 24-hour period (Figure 7.3) that are based on cattle behavior (i.e., median speed per

hour) derived from telemetry data (Appendix 3). The first phase corresponds to the free wandering phase where cattle roam randomly across the space and outside the kraal (local name for an enclosure where herders keep their cattle during the night close to their homestead, to prevent predation and theft) from 6am to 8am. During the first phase, outside the cropping seasons (from May to November in Hwange/Dete, from May to October in Kruger/Pesvi and from July to December in Gonarezhou/Malipati) (Miguel, 2012; Perrotton et al., 2017), cattle are allowed to move in agricultural areas to feed on secondary agricultural products. On the other end, during the cropping season (from December to April in Hwange/Dete, from November to April in Kruger/Pesvi and from January to June in Gonarezhou/Malipati), cattle are herded away from growing fields. To cope with this herder’s decision, the selection of landcover pixels occurs within a polygon. This polygon represents the extent of a buffer corresponding to the average maximum daily travelled distance from kraal by cattle cropped by a determined angle interval polygon (i.e., -60° to $+60^\circ$) that follows the direction of \vec{v} (speed vector of the cattle’s herd) (Figure 7.3). The second phase starts at 8am, when cattle move towards the selected surface water point. The selection process is influenced by the cropping season as the landcover composition present within an empirically determined buffer (50 meters) around the surface water point is considered. For example, during the cropping

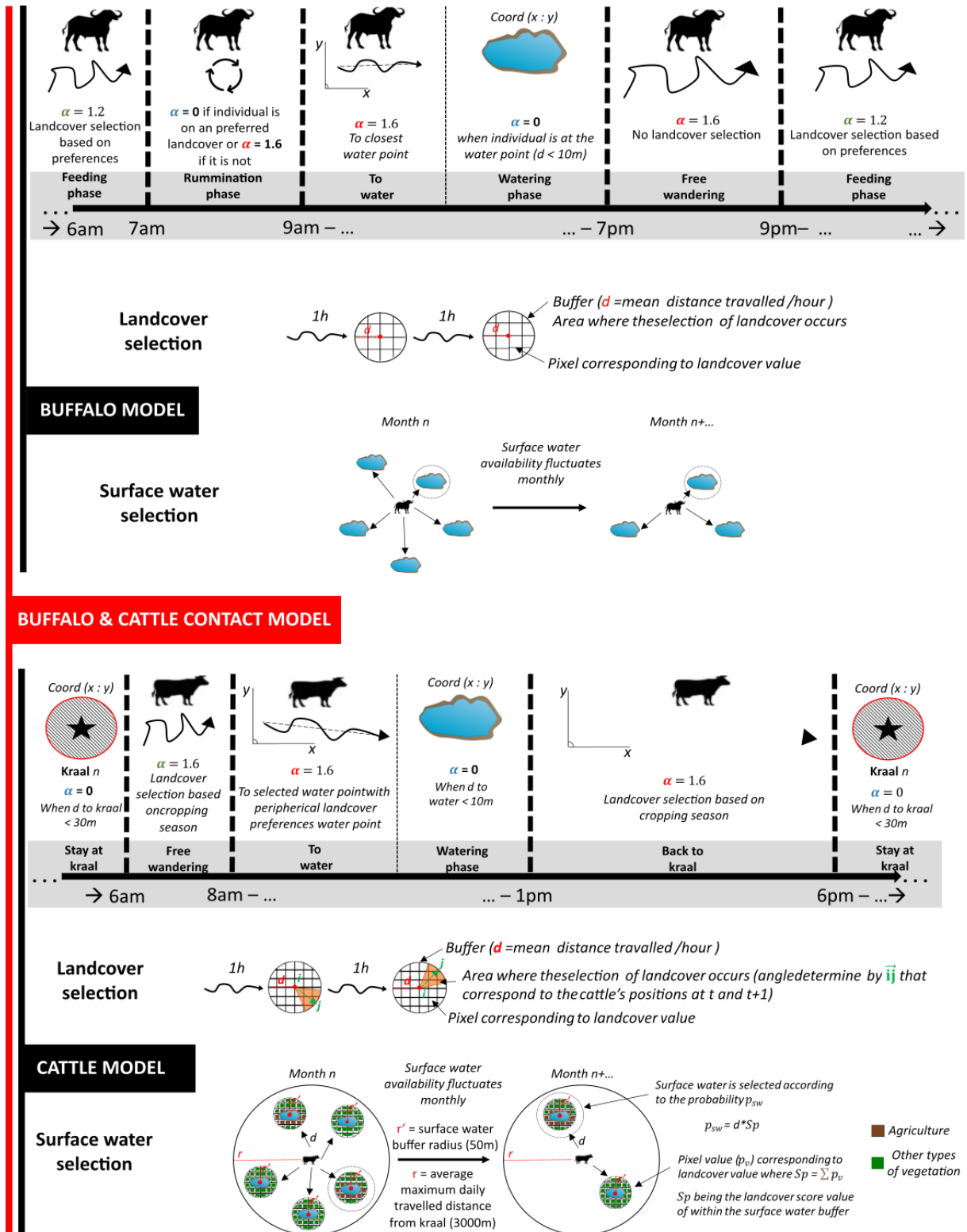


Figure 7.3: Diagram representing the designed behavioral chronologies of the two focal species movement models as well as their respective landcover and surface water selection processes

season, crop pixels present within the buffer are given a zero value, making them non attractive by cattle. This, in turn, is going to affect the total buffer landcover score value indexed to the corresponding surface water point. The more agricultural area there is in the buffer, the smaller

the indexed surface water point score will be, reducing the chances of the latter to be selected. The distance separating the cattle's herd centroid from the surface water point centroid is also affecting the probability of the surface water selection as it is a multiplier of the total buffer

landcover score value. The [Figure 7.3](#) presents the example of the non-cropping season water selection case where surface water with agricultural landcover present within the buffer have a higher probability to be selected ([Figure 7.3](#)). Once within a distance of 10 meters of the selected surface water point, α take the zero value until the end of the “watering phase” (phase three) and the beginning of the “go back to kraal” phase (phase four). In the fourth phase, cattle starts moving towards their respective kraal at 1pm while selecting the landcover over which they can freely move according to the cropping season, repeating the same section process as describe in phase one. Once cattle’s herd centroid is located within 30 meters of their respective kraal, α take the zero value until 6am to signify the herd’s resting period at the same geographical location (fifth phase). This fifth phase marks the end of a daily cycle that repeats itself for the duration of the entire simulation.

Validating the spatial movement model

One herd of 200 buffalo individuals for each of the buffalo groups derived from the in-situ telemetry datasets (Appendix 1) have been simulated based on buffalo herd size observations in the three study sites (Miguel, Grosbois, Fritz, Caron, de Garine-Wichatitsky, et al., 2017). Three simulated periods have been synchronized with the respective recording periods of each of the three constituted buffalo groups derived from the observed telemetry data (Appendix 1). As observed groups never exceeded 7 individuals recorded at the time in the same location (Appendix 1), it has been decided to base the analyses on datasets that are composed of centroids calculated from four randomly selected buffalo individuals within the simulated herds and the centroids derived from the constituted groups of in-situ buffalo individuals (Appendix 1). Concerning the simulated datasets, only one centroid per hour (out of the centroid calculated every 10 minutes) have been extracted to fit with the in-situ centroid datasets that have been recorded with a one hour frequency (see section “two focal species”). The same approach has been applied to the cattle simulated and in-situ datasets with the notable difference that simulated cattle herds were constituted of randomly numbered of individuals within an interval of 5 to 15 individuals in accordance with the field observations (Miguel, 2012). Considering the stochasticity of the model, 10 iterations have been made for every buffalo and cattle movements simulations.

For every simulated and in-situ centroid dataset, maximum convex polygons (MCP) have been computed each month and for the entire period ([Figure 7.4](#)). The maximum MCP (MCP-max) corresponds to the maximum spatial extent of one of the 10 iteration by superposition of all of them whereas the minimum MCP (MCP-min) corresponds to the intersection area of the 10 iterations MCPs. Derived buffalo and cattle MCPs of the same study site have then been intersected to extract the zone of contact between the two species in the shape of a polygon (the MCP-max contact area being represented by the yellow line and the MCP-min contact area by the dashed black line in [Figure 7.4](#)). In addition to these zone of contact polygons, spatial density raster of the simulated and in-situ centroid datasets for the entire period and for every month have been computed using a quadratic kernel shape from planar distances with a search radius of 100m at 100m spatial resolution. For the simulated centroid datasets, mean and sum density raster have been derived from the 10 iterations density raster corresponding to the same group and the same simulated period (i.e., monthly and the entire period). For the in-situ centroid datasets, buffalo and cattle groups of the same study site have been combined before deriving monthly density raster and entire period density raster using the same methodology. All the density raster values have been normalized within a range of 0 to 1 in order to harmonize the density raster dataset and facilitate the analyses. These rasters have then been clipped to the corresponding zone of contact polygon extents allowing the calculation of mean, sum and median density of buffalo and cattle contact within these zones of contact for every month and for the entire duration of the simulations ([Figure 7.4](#)).

Results

Environmental variables characterized at a landscape scale

Surface water: The mean overall accuracy (OA) of the time series surface water supervised classification for Hwange/Dete is 0.88 while the kappa index is 0.75, the OA is 0.99 while the kappa is 0.97 for Gonarezhou/Malipati and the OA is 0.97 while the kappa is 0.93 for Kruger/Pesvi (Appendix 5). The supervised surface water classification accuracy is very high for the three study sites despite some disparities. Indeed, the supervised classification was not as efficient in Hwange/Dete in comparison to the two other sites. Accuracy

variations within the Hwange/Dete time series surface water supervised classification are also noticeable with an OA ranging from 0.81 to 0.91 and a kappa ranging from 0.63 to 0.82. For the two other study sites, the classification accuracy remains stable for the entire time series.

Landcover: The mean overall accuracy (OA) of the time series agricultural area supervised classification for Hwange/Dete is 0.91 while the kappa index is 0.83, the OA is 0.77 while the kappa is 0.53 for Gonarezhou/Malipati and the OA is 0.83 while the kappa is 0.66 for Kruger/Pesvi (Appendix 5). Overall, the supervised classification accuracy was optimal concerning Hwange/Dete but more nuanced concerning Gonarezhou/Malipati and Kruger/Pesvi with an equivalent number of confusions between the two classification classes (i.e., “agricultural areas” and “other”) (Appendix 5). The agricultural area classifications of Gonarezhou/Malipati and Kruger/Pesvi remain usable as most of the extensive agricultural areas have been correctly detected after qualitative analyses (i.e., accuracy assessment via the superposition of a very-high SRS image and the produced classification).

Concerning the non-supervised classifications of the three study sites vegetation according to the chosen typology (Figure 7.1), the OA and kappa are

0.75 and 0.67 for Hwange/Dete, 0.71 and 0.64 for Gonarezhou/Malipati, and 0.73 and 0.66 for Kruger/Pesvi (Appendix 5). The classification accuracy is comparable for the three study sites with an overprediction of the shrubland class that is confused equally with the mixed-woodland-shrubland class and the mixed-shrubland-grassland class. The mixed-woodland-shrubland class is also confused with the woodland class although the confusion is less pronounced in Hwange/Dete. Overall, the woodland, the mixed-shrubland-grassland and the bare soil classes are well classified (Appendix 5).

Modelling the buffalo and cattle contacts

In Hwange/Dete, the observed contact area has an area of 38.4 km² while the simulated contact area defined by the MCP-max has an area of 56.2 km² and the contact area defined MCP-min an area of 27.2 km². Although similar in their morphology, the observed contact area and the simulated contact area are not overlapping, the simulated contact area being closer to the communal area (Figure 7.4). The distance separating the centroids of the observed area and the different simulated contact areas are in the range of 2.2 to 3.1 km (Figure 7.4). In Gonarezhou/Malipati, the observed contact area has an area of 15.7 km² while the

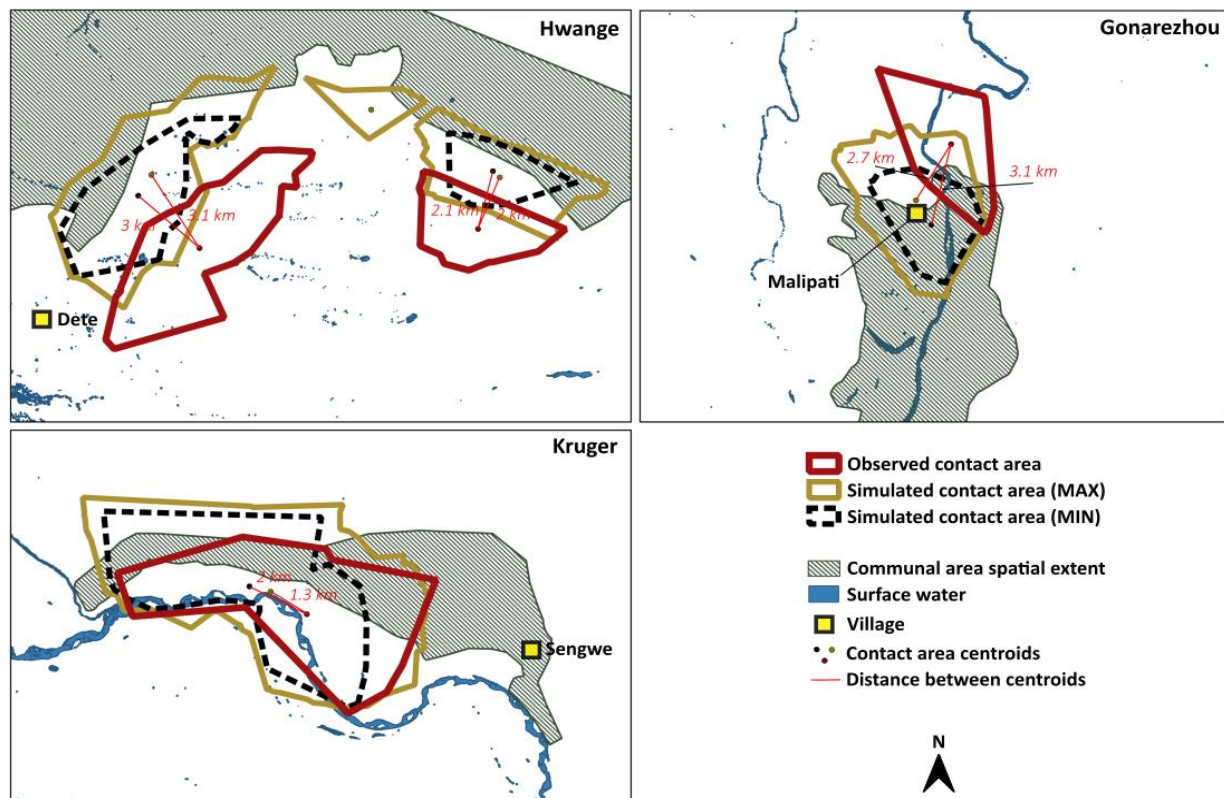


Figure 7.4: Maps representing the observed and simulated contact area spatial extensions in regard to the proximity of the communal area for the three study sites

simulated contact area defined by the MCP-max has an area of 24.7 km² and the contact area defined MCP-min an area of 11.7 km². Within comparable surface area range, observed and simulated contact area are not perfectly superposed as their respective centroids have distances that range from 2.7 to 3.1 km. The simulated contact areas are located, as in Hwange/Dete, more deeply into the communal area (Figure 7.4). In Kruger/Pesvi, the observed contact area has an area of 40.7 km² while the simulated contact area defined by the MCP-max has an area of 68.9 km² and the contact area defined MCP-min an area of 43.1 km². While the simulated contact area defined by the MCP-max over-estimates the area of contact, the simulated contact area defined by the MCP-min is quite comparable to the observed contact area. All the contact areas are located within the same area as they superposition and respective morphology are similar. The distances from the contact areas respective centroids range from 1.3 km to 2 km (Figure 7.4).

In Hwange/Dete, the monthly variations of the observed mean density are well reproduced when considering the mean density of the contact area

(Figure 7.5). When comparing the monthly variations of the observed sum density, the annual trend is well reproduced when considering the sum density of the contact area defined by the MCP-max, especially during the maximum sum density peak in March and the second sum density peak in November (Figure 7.5). In Gonarezhou/Malipati, the monthly variations of the observed mean density is once again more comparable when focusing on the mean density of the contact area defined by the MCP-min, although the seasonal pattern is not well reproduced (Figure 7.5). Indeed, the mean density peak in March is not reproduced by the model simulations and the mean density peak of September is simulated with a one month delay. When comparing the monthly variations of the observed sum density, the model simulations tend to over-estimate the density all year round when taking into account the sum density of the contact area defined by the MCP-max despite the fact that the period with the lowest density values from September to January is well reproduced when considering the contact area defined by the MCP-min (Figure 7.5). In Kruger/Pesvi, the overall behavior of the monthly variations of the observed mean density is well reproduced, although both mean density of the

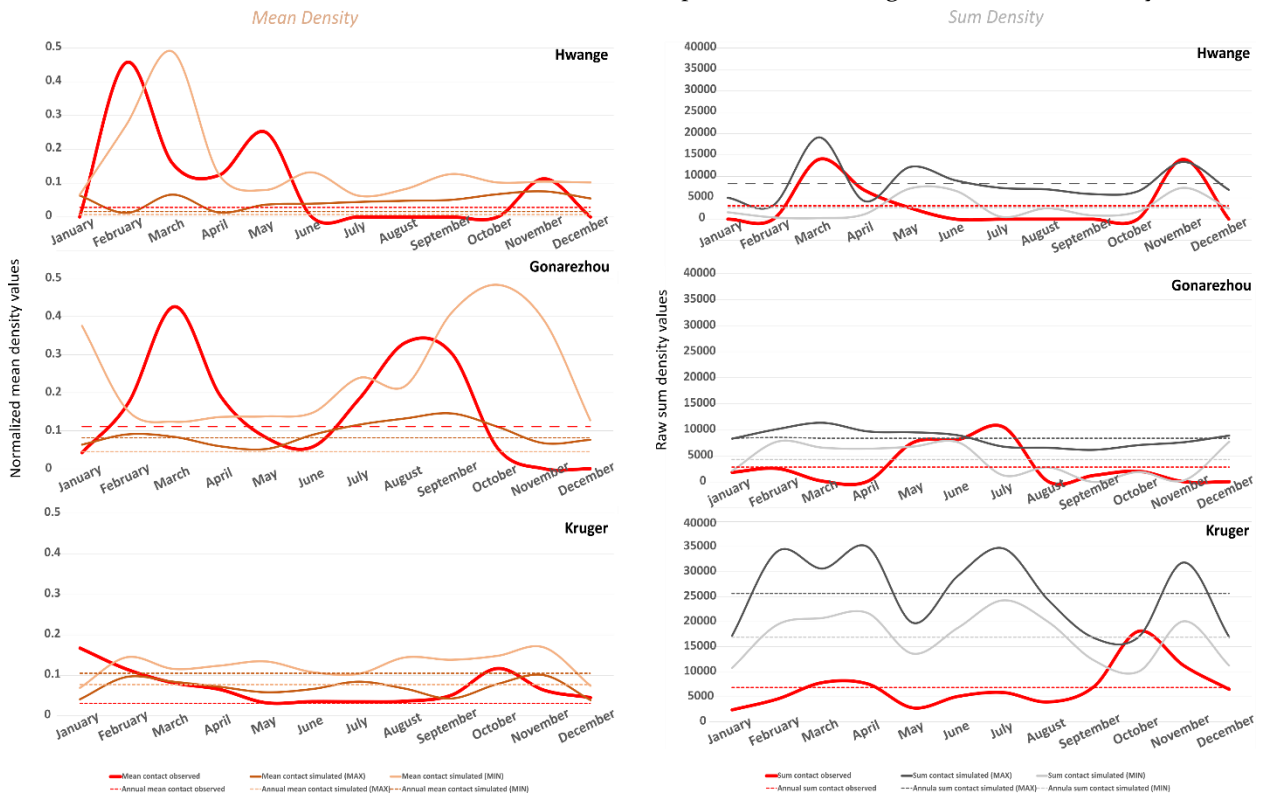


Figure 7.5: On the left, line chart representing the monthly variations of the mean density for the observed contact area and the simulated contact areas. On the right, line chart representing the monthly variations of the sum density for the observed contact area and the simulated contact areas

defined by the MCP-min, especially the peak of mean density observed from January to June

contact area defined by the MCP-min and the MCP-max are slightly over-estimated (Figure 7.5).

The same observation can be made when considering the monthly variations of the sum density ([Figure 7.5](#)).

Discussion

Ecological implications

The model demonstrated the capacity to reproduce seasonal patterns of contact between buffalo and cattle in three different WLI by considering only two environmental variables (i.e., surface water and the landcover) and livestock practices. With a set of simple rules combining basic daily resources requirement (i.e., water and grazing) and herding practices (i.e., avoidance of growing crop fields), the model simulated the movement of buffalo and cattle and their areas and intensity of contacts in three different interface areas in southern Africa. The observation of modelled vs. observed areas of inter-species overlap and contact in space and time ([Figure 7.4](#)) as well as the monthly variations of the mean density for the observed contact area and the simulated contact areas ([Figure 7.5](#)) provide a sense of overall replicability of ecological patterns by the model. For example, in the different landscape, it the distribution of available surface water that concentrates spatially animal movements around surface water and create interfaces. The necessity of both buffalo and cattle to look daily for a surface water in the vicinity of where they are at any time prevent them of “escaping” from the interface area and the model replicates just that. In addition, the model’s ability to consider grazing behaviors improve on the capacity to reproduce buffalo and cattle movements as we know that grazing behaviors strongly influence the two focal species respective movements in space and time (Rumiano et al., 2021).

However, despite coherent model’s outputs, there are significant differences in predictions between the model outputs and the behavior of the observed data. Factors related to the method and to variables (environmental, ecological, data related) can explain these differences in predictions. The fact that cattle are sent farther than the search for the nearest available water source could potentially suggest political claims to the forestry zone by the herders and/or ancestral practices as well as other “beliefs” linked to specific surface water points. The grazing practices could explain the drift of the contact zone towards the interior of the park, especially in the Hwang/Dete study site. Concerning buffalo, they seem to move less towards the communal land boundary than the

model predicts, which means that there are behavioral factors that could explain this particular trend such as the already documented avoidance of cattle by buffalo (Valls et al., 2018). In addition, the time lags exist between the date chosen to characterize the environmental variables by remote sensing (i.e., 2018) and the recording years of the in-situ buffalo (Appendix 1) and cattle (Appendix 2) telemetry data. The surface water characterized during the year of the SRS satellite images does not correspond exactly in its spatial and temporal repartition with the one that occurred during the year when the telemetry data have been collected, thus introducing bias between the observed and predicted focal species movements and contacts at the landscape scale. Another factor concerns the ability to detect, at the landscape scale, all the environmental variables even if the classification results seem optimal (see the section Results). Any classification is inherently imperfect because it is subjective and based on validation tools that can be subject to caution (Pontius and Millones, 2011). Given the landscape heterogeneity of our three study sites and the strong presence of trees, it is possible that some watering ponds under tree canopy have not been correctly detected as they could have been located. In addition, some watering ponds are ephemeral and only related to rainfall occurrences as well as soil properties in semi-arid savanna environments (Soti et al., 2010). They could have been missed given the temporal frequency of the SRS time series used by the developed surface water classification methodology (one satellite image per month was used to classify water surfaces). Also, it is important to note that the model is based on the analysis of the collective behavior of the targeted species in their respective environments (Appendix 4). However, regarding cattle, only one individual per herd was used as reference. For buffalo, at best 7 individuals constituted the reference of a herd, whereas the herds observed on site are close to 200 individuals (Miguel, 2012). Thus, model parameters such as speed of movement, preference for a particular type of vegetation, distance from the kraal, time of day, and frequency of use of watering holes provide only a partial and incomplete view of the ecological behavior of these animal species in their respective environments. Nevertheless, the model, in its current configuration, allows us to make some observations that reflect the different influences of surface water availability and landcover on the frequency and intensity of contact between buffalo and cattle at the three study sites. In Hwange/Dete, the intensity of contact is the greatest during the cropping season and during the wet season, when

the water resource is abundant (Figure 7.5). It is between December and May that herders drive their cattle herds into protected areas to avoid cultivated fields damages (Amon et al., 2013), thus corroborating the observed trends of the model output simulations in this particular study site. In Gonarezhou/Malipati, two peaks of contacts between buffalo and cattle were observed (Figure 7.5). The first peak during the cropping season in March represent the attraction of buffalo for forage in agricultural areas. The model was unable to reproduce this trend as the agricultural areas were not considered to be a buffalo landcover preference based on observations extrapolated from the three study sites for genericity purposes (Appendix 3). The second peak of activity, occurring from August to November, corresponds to the dry season. As surface water availability is reduced to a handful of pools in the Mwenezi riverbed during the dry season and the river being closed to communal areas, contacts between buffalo and cattle become more frequent. Surface water seasonal variability as well as potential forage resource provided by agricultural areas are the two factors driving contact between buffalo and cattle in Gonarezhou/Malipati. In Kruger/Pesvi, the model outputs follow similar patterns with the highest peaks of contacts occurring during the cropping season in January and at the end of the dry season in October.

Epidemiological implications

Having the capacity to apprehend the ecological and human induced processes that drive the frequency, intensity, and localization of inter-species contacts at the WLI scale through mechanistic mathematical models can potentially improve the capacity to quantify and characterize HWC including pathogen circulation between wild and domestic animal species within specific multi-host systems (Caron et al., 2015; Roche et al., 2012). One of the advantages of mechanistic mathematical model is that they require few empirical data to reproduce complex ecological processes such as movements, watering and foraging amongst others (Rastetter et al., 2003). In that regard, such models are promising as they may help guide future data collection or elucidate certain traits (e.g., targeted species habitat preferences, herding decisions) of potential host animal species in areas where in-situ data is lacking or residual (Doherty & Driscoll, 2018). While some models have explored the sensitivity of pathogen dynamics to dispersal and migration rates (L. A. White et al., 2018), few studies compared animal movements and contacts in relation to spatially

explicit landscape on pathogen transmission (Lane-deGraaf et al., 2013; Tracey et al., 2014). Pathogen transmission models with mechanistic representations of animal movements in space and time remain scarce (Fofana and Hurford 2017) and there is a need to fill this gap (L. A. White et al., 2018).

Our results indicate that interspecific contacts, possibly leading to disease transmission, are clustered and driven by the seasonality of natural resources (Guerrini et al., 2019) and herding practices at the three studied WLI. We argue that this information provides opportunities to improve pathogen management, by controlling access to key natural resources (i.e., forage and surface water) or adapting livestock and/or wildlife management practices in order to reduce the frequency of buffalo-cattle contacts. However, pathogen circulations amongst hosts vary along a gradient from direct to indirect transmission (Altizer, Harvell, and Friedle 2003). Therefore, the definition of what is a relevant contact in regard to pathogen transmission varies according to the pathogen of interest and the considered space-time windows (Wielgus et al., 2021) that define potential infectious contacts between focal animal species. The temporal and spatial scales from which contacts are characterized will determine the potentiality of a spatialized movement and contact model, such as the one developed in this study, to be of used to pathogen transmission assessments. Indeed, pathogen dynamics are different depending on whether we consider a direct transmission pathogen such as foot and mouth disease (FMD) or a vector-borne pathogen such as Rift Valley Fever (RVF) for example. Indeed, there is no guarantee that the transmission process, data collection (i.e., SRS data and telemetry data) are necessarily taking place at the same spatial and temporal scale (Riley et al., 2015). Forecasts of pathogen transmission based on potential host movement alone can be questioned when pathogen-environment interactions (e.g., pathogen movement, rates of growth or decay, or the length of vector life history stages) occur at time scales comparable with the host-pathogen interactions themselves (e.g., lengths of latent and infectious periods) (Dougherty, Seidel, Carlson, Spiegel, et al., 2018).

Mechanistic mathematical movement and contact models could be combined or potentially replace ecological niche modelling as proxy for pathogen circulation as the latter often considers host-pathogen systems as only one coupled phenomenon (Kearney & Porter, 2009). It could drastically improve the characterization of average and/or seasonal host movement patterns,

especially in the case of free-ranging or semi-free ranging hosts such as buffalo and cattle and be part of an integrative solution to develop real-time early warning system for pathogen transmission risk assessment.

Room for improvements

Mechanistic mathematical models require significant development and implementation costs but is less dependent of a correlation between ecological processes (e.g., movements, contacts, watering,...) and environment properties (e.g., surface water, forage, ...) compared to empirical models (Gaucherel, 2018). The capacity of such mechanistic model to develop interactions between animal behavior and related environment variables improve the capacity to describe holistic ecological functioning (Kearney & Porter, 2009) in areas where in-situ data are lacking or expensive to collect as well as when knowledge on focal animal behavior is limited. Despite genericity potential as shown by the results of this study, mechanistic mathematical models are mostly based on quantitative assessments in their design which can lead to output redundancy and similarity (Eriksson et al., 2010). Intra-herd dynamics are reduced to parameters defining the herd's cohesion (see "A spatialized movement model" section) when in reality more complex dynamics are occurring, such as the fusion-fission dynamics of buffalo herds (Wielgus et al., 2020) or cattle herding decisions influenced by collective social determinants (Valls-Fox, Chamailé-Jammes, et al., 2018). Agent-based modelling could provide alternative approaches to simulate movement and contact of focal animal species. However, these types of models usually imply greater complexity in design (i.e., more rules, quantitative parameter estimation, complex sensitivity analyses), are much less tractable than mechanistic mathematical models, have a lower reproducibility potential and require more empirical knowledge on specific focal species ecological behaviors and relation to environmental variables (Schulze et al., 2017). Model sensitivity analyses (Frey and Patil 2002) could help to find the right balance between the different parameters of the model (see "A spatialized movement model" as well as [Figure 7.3](#)) and improve the oversimplification of the two animal species ecological functioning. Indeed, even if the temporal structuration of the model in several behavioral phases ([Figure 7.3](#)) is based on empirical knowledge, bibliographical analyses and data extrapolation, it remains subjective and does not prevent, for example, an underestimation of the presence of buffalo in areas located at the

periphery of surface water (Rumiano et al., 2021) or the systematic return of the cattle to the kraal at the same time of the day ([Figure 7.3](#)). Currently, the model does not allow to extrapolate qualitative analyses such as the propensity of buffalo to avoid contact with livestock (Miguel, Grosbois, Caron, Boulonier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & Garine-Wichatitsky, 2013). The model output is constrained by the temporal scale of the in-situ telemetry data. By improving on the temporal resolution of field telemetry data, model outputs could be much more suited for qualitative analyses in regard to buffalo and cattle movements and contacts. Furthermore, several variables such as anthropogenic and climate changes as well as host heterogeneity could be considered and implemented into the current model as they play a crucial role in influencing the buffalo and cattle movements in space and time (Naidoo, Preez, et al., 2012).

The model developed in this study has the advantage of being easily scalable in addition to requiring little input data to produce consistent and usable results. The democratization of SRS technologies utilization by ecologists (Remelgado et al., 2018) coupled with the advances in technologies that remotely monitor animal's physiology and movements (Kays et al., 2015a) constitute opportunities to further enhance mechanistic mathematical models such as the one developed in this study. Implementing animal movements and contacts at the landscape scale into spatialized epidemiological models could prove to be solution amongst many to tackle the increasing risk of pathogen transmission at the WLI interface.

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Author contributions

Florent Rumiano: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Methodology (equal); Writing-original draft (lead); Writing-review & editing (lead). Pascal Degenne: Methodology (equal); Writing-review & editing (equal). Alexandre Caron: Conceptualization (equal); Data curation (equal); Methodology (supporting); Resources (equal); Writing-review & editing (lead). Cédric Gaucherel: Conceptualization (supporting); Methodology (equal); Writing-review & editing (equal). Eve Miguel: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Methodology (supporting); Writing-original draft (equal); Resources (lead). Michel de Garine-Wichatitsky: Writing-review & editing (supporting); Methodology (supporting); data curating (supporting). Simon Chamaille-Jammes: Data curation (supporting); Writing review & editing (supporting). Hugo Valls-Fox: Data curation (supporting); Writing review & editing (supporting). Hervé Fritz: data curating (equal); Writing-review & editing (supporting). Annelise Tran: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Resources (equal); Writing-original draft (lead); Writing-review & editing (lead).

Data availability statement

The Sentinel-2 images are freely available at <https://scihub.copernicus.eu/dhus/#/home> after login.

The land cover map are available to download at CIRAD depository website: Rumiano, Florent; Miguel, Eve; Valls-Fox, Hugo; Chamaille-Jammes, Simon; Caron, Alexandre; Tran, Annelise, 2020, "Land cover map, Dete site, Hwange National Park, Zimbabwe", doi:10.18167/DVN1/BJJZJV, CIRAD Dataverse, V1; Rumiano, Florent ; Miguel, Eve ; Caron, Alexandre ; Dupuy, Stéphane, Tran, Annelise, 2021, "Land cover map, Malipati site, Gonarezhou National Park, Zimbabwe", <https://doi.org/10.18167/DVN1/2SFOA5>, CIRAD Dataverse. Rumiano, Florent ; Miguel, Eve ; Caron, Alexandre ; Dupuy, Stéphane ; Tran, Annelise, 2021, "Land cover map, Sengwe site, Kruger National Park, Zimbabwe", CIRAD Dataverse.

The surface water map is available to download at CIRAD depository website: Rumiano, Florent; Miguel, Eve; Valls-Fox, Hugo; Chamaille-Jammes,

Simon; Caron, Alexandre; Tran, Annelise, 2020, "Monthly surface water maps, Hwange National Park, Zimbabwe, 2018", doi:10.18167/DVN1/KPSYME, CIRAD Dataverse, V1,

The buffalo and cattle GPS data access are subject to authors' authorization.

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Appendix I:

Buffalo and cattle telemetry data characteristics and specifications

BUFFALO

Study areas	Groups	Number of individuals	Individual id	Period of recording	Utilizations
Hwange/Dete	Gp 1	3	AU287/AU291 /AU297	20/04/2010 to 18/08/2011	Calibration/ validation
	Gp 2	4	SAT524/SAT526 /11456/11472	14/11/2012 to 28/09/2013	Calibration/ validation
	Gp 3	4	SAT526/11456 /11472/11473	03/12/2013 to 15/04/2014	Calibration/ validation
Gonarezhou/Malipati	Gp 1	3	B80/B83/B85	13/10/2008 to 03/03/2011	validation
	Gp 2	4	B80/B83/B84/B85	14/10/2008 to 19/11/2019	validation
Kruger/Pesvi	Gp 1	7	B31810/B34559/ B34564/B34567/ B34571/B34572 /B34575	31/10/2013 to 25/01/2015	validation
	Gp 2	7	B31805/B31810/ B31811/B31813/ B31817/ B31818/ B31820	25/07/2011 to 15/09/2011	validation
	Gp 3	5	B34562/B34563/ B34566/B34574/ B34576	20/12/2013 to 12/02/2014	validation
	Gp 4	4	B34562/B34566/ B34574/B34576	31/10/2013 to 06/02/2015	validation
	Gp 5	2	B1130/B8526	04/06/2010 to 24/12/2011	validation
	Gp 6	3	B1130/B8526/ B31808	25/07/2011 to 14/04/2012	validation

CATTLE

Study areas	Number of individuals	Individual id	Period of recording	Utilizations
Hwange/Dete	10	AU387	15/12/2010 to 15/08/2011	calibration/ validation
		AU388/AU389 AU390/AU392	20/04/2010 to 15/08/2011	
		U4	28/11/2012 to 22/11/2014	
		U6	30/11/2012 to 27/06/2014	
		U7	29/11/2012 to 23/01/2014	
		U8	29/11/2012 to 04/12/2014	
		U9	29/11/2012 to 21/11/2014	
Gonarezhou/Malipati	4	382/384/386	26/11/2009 to 16/05/2011	validation
		383	26/11/2009 to 21/10/2010	
Kruger/Pesvi	4	681/682 684/685	16/06/2010 to 25/07/2011	validation

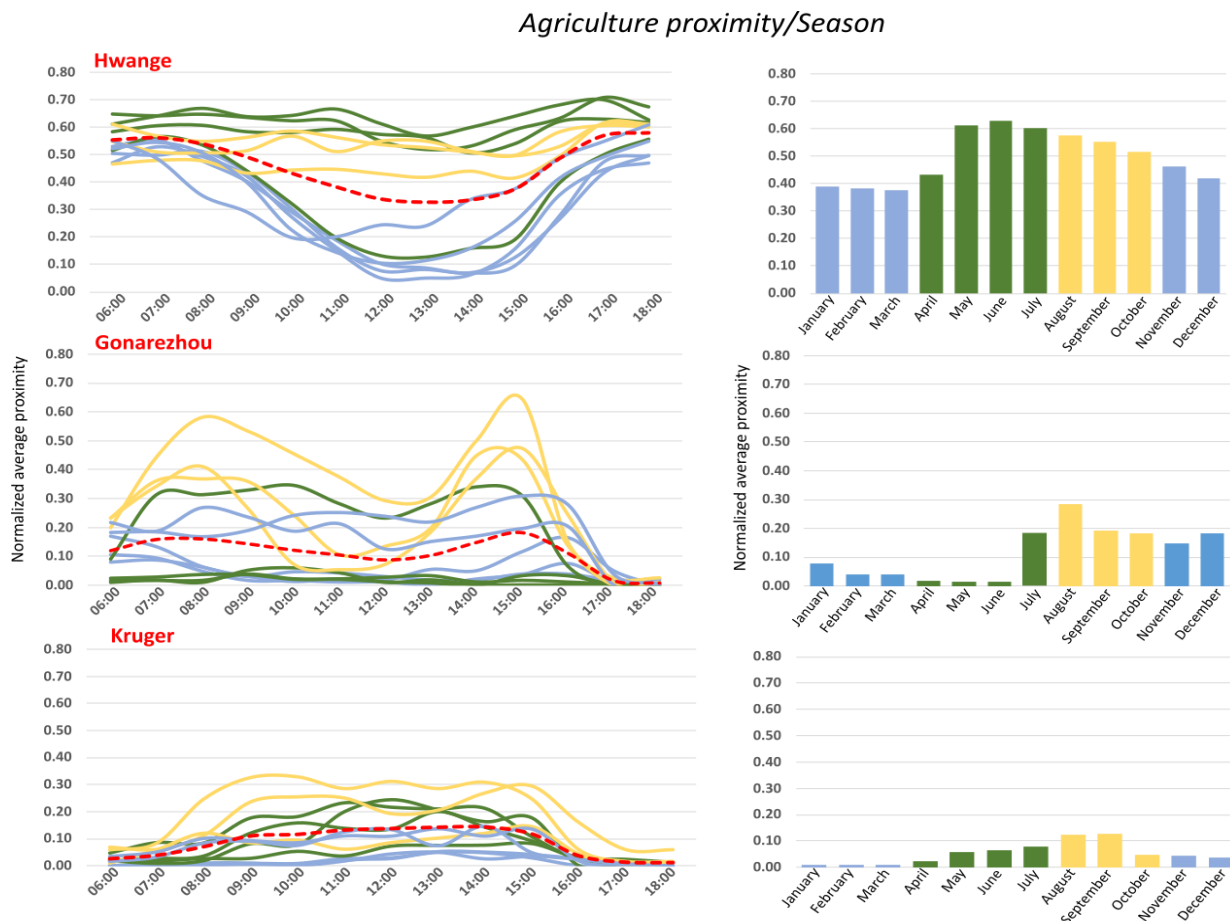
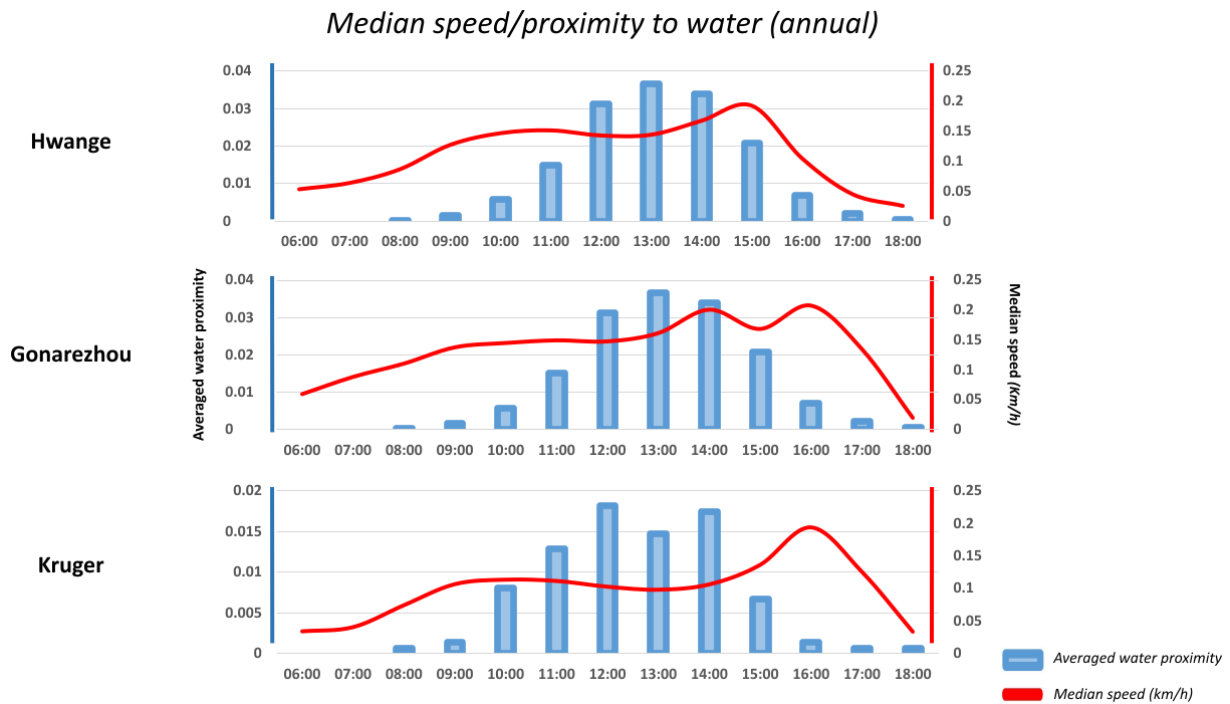
Appendix 2:

SRS Images specifications and characteristics

Name of the characteristics	Satellite image characteristics
Spatial and spectral resolutions	10 x 10 m B2 (490 nm), B3 (560 nm), B4 (665 nm), B8 (842 nm) 20 x 20 m B5 (705 nm), B6 (740 nm), B7 (783 nm), B8a (865 nm), B11 (1610nm), B12 (2190 nm)
Temporal resolution	5 days
Swath width	290 km
Tile size	100 x 100 km
References of selected tiles	T35KNV – T35KNU – T35KMOV – T35KMU – T35KLV – T35KLU
Dates of the downloaded tiles	T35KNV (2018-01-05 / 2019-02-24 / 2018-03-16 / 2018-04-20 / 2018-05-05 / 2018-06-04 / 2018-07-04 / 2018-08-18 / 2018-09-12 / 2018-10-12 / 2018-11-16 / 2018-12-21) T35KNU (2018-01-05 / 2019-02-24 / 2018-03-16 / 2018-04-25 / 2018-05-10 / 2018-06-14 / 2018-07-04 / 2018-08-18 / 2018-09-12 / 2018-10-12 / 2018-11-11 / 2018-12-11) T35KMOV (2018-01-08 / 2019-02-22 / 2018-03-14 / 2018-04-23 / 2018-05-03 / 2018-06-12 / 2018-07-02 / 2018-08-16 / 2018-09-15 / 2018-10-10 / 2018-11-19 / 2018-12-14) T35KMU (2018-01-13 / 2019-02-22 / 2018-03-14 / 2018-04-23 / 2018-05-03 / 2018-06-12 / 2018-07-02 / 2018-08-16 / 2018-09-15 / 2018-10-10 / 2018-11-14 / 2018-12-14) T35KLV (2018-01-08 / 2019-02-22 / 2018-03-14 / 2018-04-23 / 2018-05-03 / 2018-06-12 / 2018-07-02 / 2018-08-16 / 2018-09-15 / 2018-10-10 / 2018-11-14 / 2018-12-14) T35KLU (2018-01-08 / 2019-02-22 / 2018-03-14 / 2018-04-23 / 2018-05-03 / 2018-06-12 / 2018-07-02 / 2018-08-16 / 2018-09-15 / 2018-10-10 / 2018-11-14 / 2018-12-14)

Appendix 3:

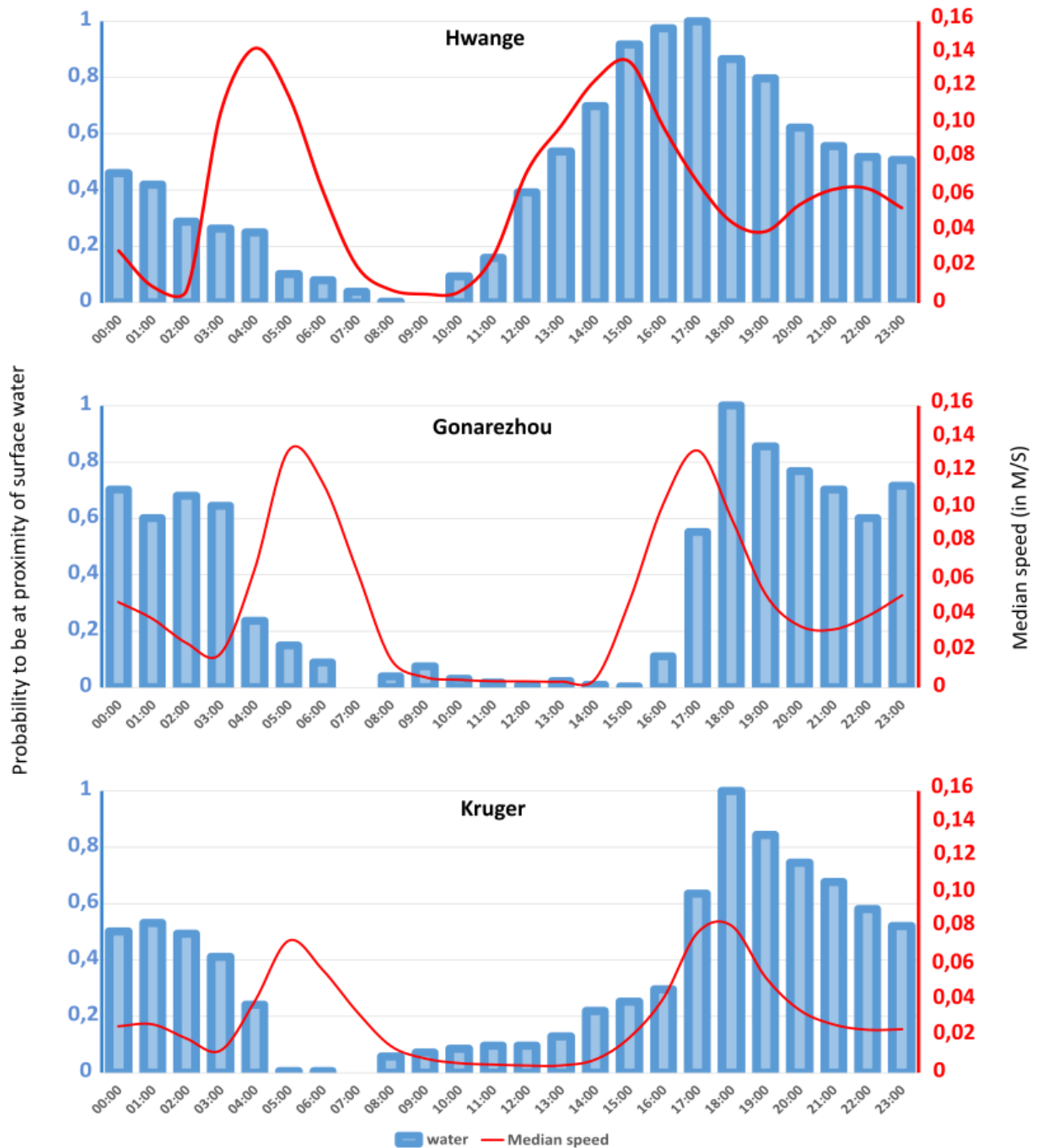
Graphs that describe cattle behaviors in relation with environmental variables (surface water and agricultural areas)



Appendix 4 :

Graphs that describe buffalo relation with surface water and landcover preferences

Median speed in relation to the probability to be at proximity to the surface water depending on the hour of the day



Probability for buffalo to be on a specific landcover in regard to the entire duration of the telemetry data recording period for each of the study sites

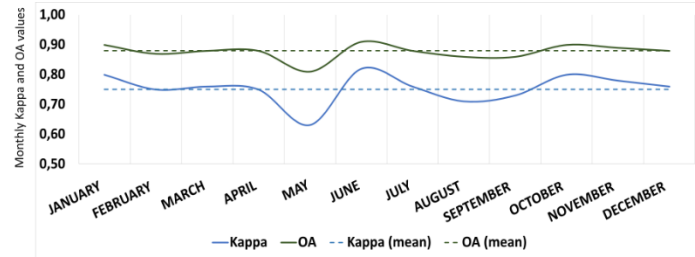


Appendix 5:

Confusion matrices of the **supervised surface water classifications**. These matrices represent the mean of the time series predicted and actual pixel counts for each of the three study sites.

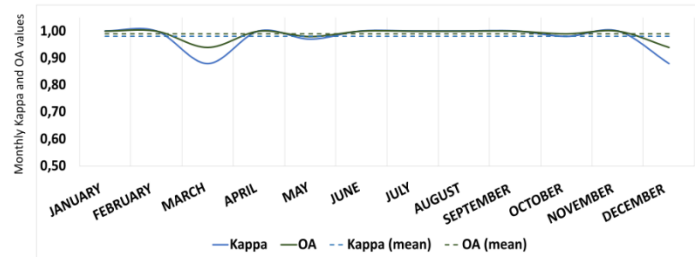
Hwange

		Predicted		
		Surface water	Other surfaces	
		Surface water	Other surfaces	
Actual	Surface water	245	19	0.93 sensitivity
	Other surfaces	55	281	0.82 specificity
		0.84 precision	0.94 Negative Predictive value	
OA		0.88		
Kappa		0.75		



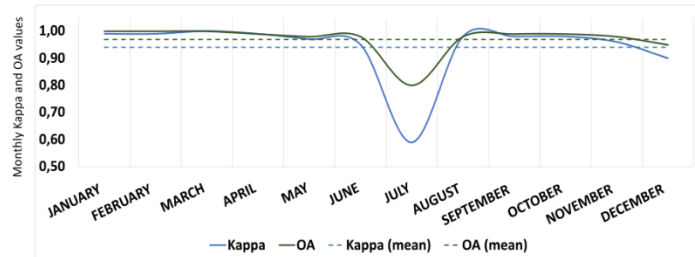
Gonarezhou

		Predicted		
		Surface water	Other	
		Surface water	Other	
Actual	Surface water	297	4	0.99 sensitivity
	Other	3	296	0.99 specificity
		0.99 precision	0.99 Negative Predictive value	
OA		0.99		
Kappa		0.97		



Kruger

		Predicted		
		Surface water	Other surfaces	
		Surface water	Other surfaces	
Actual	Surface water	288	9	0.97 sensitivity
	Other surfaces	12	291	0.96 specificity
		0.96 precision	0.97 Negative Predictive value	
OA		0.97		
Kappa		0.93		



Confusion matrices of the supervised agricultural area classifications. These matrices represent the mean of the time series predicted and actual pixel counts for each of the three study sites.

Hwange

		Predicted			
Actual		Agricultural area	Other		
	Agricultural area	253	5	0.98	sensitivity
	Other	47	295	0.84	specificity
		0.86	0.98		
		precision	Negative Predictive value		
OA	0.91				
Kappa	0.83				

Gonarezhou

		Predicted			
Actual		Agricultural area	Other		
	Agricultural area	229	70	0.77	sensitivity
	Other	71	230	0.76	specificity
		0.76	0.77		
		precision	Negative Predictive value		
OA	0.77				
Kappa	0.53				

Kruger

		Predicted			
Actual		Agricultural area	Other		
	Agricultural area	253	55	0.82	sensitivity
	Other	47	245	0.84	specificity
		0.84	0.82		
		precision	Negative Predictive value		
OA	0.83				
Kappa	0.66				

Confusion matrices of the non-supervised landcover classifications. These matrices represent the mean of the time series predicted and actual pixel counts for each of the three study sites.

		PREDICTED					precision	
		woodland	mixed woodland-shrubland	shrubland	mixed shrubland-grassland	sum		
Hwange	ACTUAL	woodland	32	8	0	0	40.00	0.80
		mixed woodland-shrubland	3	29	8	0	40.00	0.73
		shrubland	0	4	31	5	40.00	0.78
		mixed shrubland-grassland	0	0	12	28	40.00	0.70
		sum	35.00	41.00	51.00	33.00	120.00	160.00
		precision	0.91	0.71	0.61	0.85	160.00	
		OA	0.75					
		Kappa	0.67					

		PREDICTED					sum	precision
		woodland	mixed woodland-shrubland	shrubland	mixed shrubland-grassland	bare soil		
Gonarezhou	ACTUAL	woodland	28	10	2	0	40.00	0.70
		mixed woodland-shrubland	11	19	10	0	40.00	0.48
		shrubland	0	4	29	7	40.00	0.73
		mixed shrubland-grassland	0	0	9	31	40.00	0.78
		bare soil	0	0	0	5	35	40.00
	sum	39.00	33.00	50.00	43.00	35.00	142.00	200.00
	precision	0.72	0.58	0.58	0.72	1.00	200.00	
		OA	0.71					
	PC	0.64						

		PREDICTED					sum	precision
		woodland	mixed woodland-shrubland	shrubland	mixed shrubland-grassland	bare soil		
Kruger	ACTUAL	woodland	31	8	1	0	40.00	0.78
		mixed woodland-shrubland	11	24	5	0	40.00	0.60
		shrubland	0	8	28	4	40.00	0.70
		mixed shrubland-grassland	0	2	10	28	40.00	0.70
		bare soil	0	0	1	5	34	40.00
	sum	42.00	42.00	45.00	37.00	34.00	145.00	200.00
	precision	0.74	0.57	0.62	0.76	1.00	200.00	
	OA	0.73						
	Kappa	0.66						

7.2 Chapter summary

- Surface water and vegetation, the primary determinants of movement for these ungulate species, have been classified and mapped from a time series of medium resolution Sentinel-2 satellite images.
- The resulting classification maps have been integrated into a mechanistic mathematical model of collective movement of individuals interacting in relation to one another according to group cohesion and alignment. This stochastic model allowed the simulation of buffalo and cattle's herd movements and the location of contact areas and their seasonal dynamics in space and time. The movement and contact mechanistic model has been applied to the three study sites in order to assess its genericity.
- The model outputs have been compared to GPS collar location data of 34 individuals (16 buffalo and 18 cattle). The results showed a high spatial and seasonal variability of contacts between buffalo and cattle in the three study sites, and a landscape scale correspondence between the modeled and observed contact area spatial extensions (distance between centroids of the observed and simulated contact areas are strictly inferior to 3.1 km).
- These initial results illustrated the potential of spatial modeling combined with remote sensing to generically simulate animal movements at the landscape scale while offering opportunities to manage these interfaces through, for example, a coupling with epidemiological modelling

Chapter 8

General Discussions & perspectives

Table of content

8.1 Summary of the objectives and findings

8.1.1 The global approach

8.1.2 From a thematical standpoint

8.1.3 From a methodological standpoint

8.2 Limits and recommendations

8.2.1 On the telemetry data used

8.2.2 On the remote sensing methodology to characterize the environmental data

8.2.3 On the mechanistic movement and contact model

8.2.4 On the movement and contact model ecological simulations

8.3 Future directions and perspectives

8.3.1 Combing methodologies and approaches to detect and characterize a wide array of environmental variables at multi-temporal and spatial scales

8.3.2 Improving the intrinsic robustness of the mechanistic movement and contact model

8.3.3 Enhancing the model's capacities to reproduce ecological processes

8.3.4 Adding an epidemiological compartment to the movement and contact model

8.3.5 Towards an "Eco Health" approach

8.4 A last word

8.1 Summary of the objectives and findings

8.1.1 The global approach

This thesis had three main objectives. The first one was to develop a classification methodology allowing to characterize environmental factors, such as surface water and landcover, at the landscape scale (i.e., 10 meters of spatial resolution) and with pertinent temporal resolutions (i.e., intra-annual and inter-annual) in three different study sites. The second objective focused on developing a mechanistic model that enable the simulation of buffalo and cattle movements in space and time while considering the individual and collective dynamics of the focal species. And the third objective was to assess the nature, frequency, locations of buffalo and cattle contacts and interactions by combining the two spatialized models previously developed, as well as to test the generic aspect of the model by simulating buffalo and cattle movements and contacts in three different W/L interfaces with different ecological and geographical configurations.

This thesis is a continuation of scientific works conducted over the years on these geographical areas and made possible thanks to the collect and analysis of observational data (e.g., telemetry data) (Miguel, 2012; Valls Fox, 2015). The modelling approach developed during this work has always been considered as exploratory in the sense that it is a process-based method no longer based exclusively on data, but also considering spatial ecological processes.

The chosen general methodology approach is based on four main steps ([Figure 8.1](#)) detailed respectively in chapters 3, 4, 6 and 7 of this thesis manuscript. Chapter 3 synthesized the scientific literature to identify the environmental variables influencing the movements of the two target animal species over time and space. Chapter 4 detailed the methodology developed to characterize, via the classification of SRS images, the environmental variables considered (i.e., water surface and landcover) that influence the movements of the two focal animal species in space and time. Chapter 6 described in detail the principles of the spatialized mechanistic model to simulate buffalo movements in relation to seasonal variability of water surfaces in space and time. Chapter 7 explained the principles of the buffalo-cattle contact model as a function of water availability and the spatial structure of land use at the landscape scale in three different W/L interfaces. The other chapters allow us to contextualize and describe the ecological issues (Chapter 1 and Chapter 2), methodological issues (Chapter 5) and to discuss these

methodological choices and the results produced while considering the perspectives of this thesis work (Chapter 8).

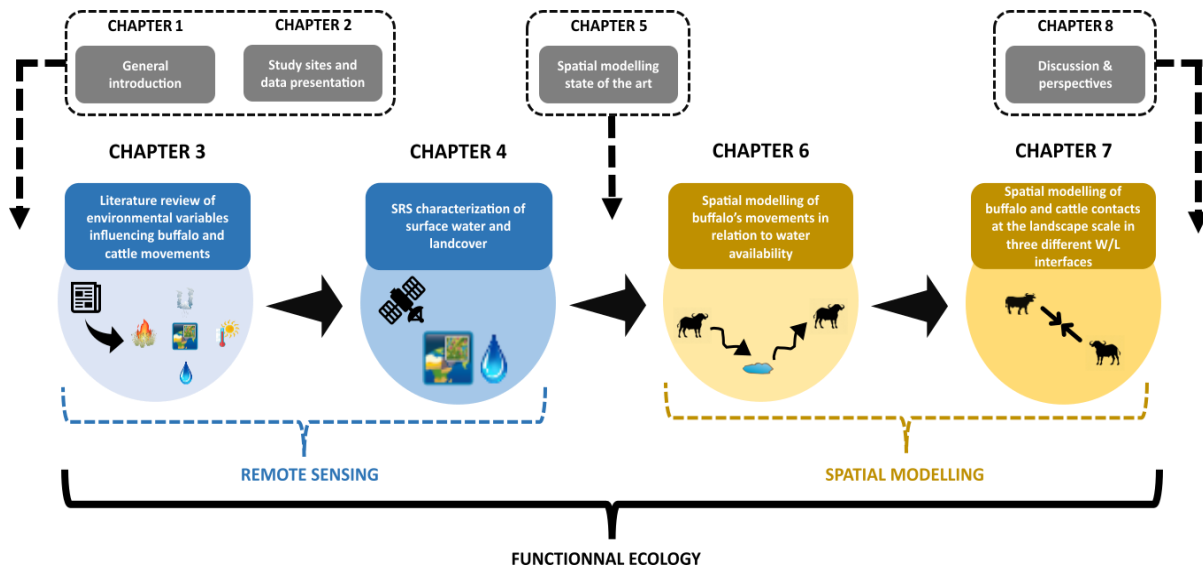


Figure 8.1: Figure synthesizing the thesis's general approach, the corresponding chapters in which the specific methodologies are detailed as well as the field of research associated with each of the chapter.

8.1.2 From a thematical standpoint

An extensive literature review (Rumiano et al., 2020) has been conducted to consolidate and gather current knowledge on potential uses of SRS to investigate the sympatry of wildlife/domestic ungulates in African savanna interface environments as well as identifying which environmental drivers influence the buffalo and cattle movements at the landscape scale (see chapter 3). In total, 327 references (e.g., scientific papers, thesis) have been selected and analyzed. Surface water, precipitation, landcover and fire emerged as key drivers impacting the buffalo and cattle movements. The results of this literature review emphasize need for animal movement ecologists to reinforce their knowledge of remote sensing and/or to increase pluridisciplinary collaborations (Chapter 3).

The three interfaces considered in this study have different geographical and ecological characteristics but all are concerned by a pronounced temporal and spatial variability of surface water as well as by highly heterogeneous landscapes in semi-arid climate (see chapter 2). These two common environmental characteristics de facto influence the availability of water and forage resources, conditioning and constraining the movements of buffalo and cattle in space and time (see chapter 6 and chapter 7). Wildfires are by essence very heterogeneous in their

amplitude and frequency in space and time. Their occurrence can impact the movements of buffalo and cattle but in a punctual and non-regular manner. Precipitations are also very localized and strictly condition the availability of water and fodder resources in Southern Africa. Therefore, surface water and landcover are the two environmental indicators that were chosen to spatially model buffalo and cattle movements (see Chapter 7). These two environmental variables can be efficiently characterized and discriminated in space and time at the landscape scale via the use of SRS (Rumiano et al., 2020).

Miguel, 2012 observations of cattle incursion into protected areas at Hwange/Dete, buffalo crossing communal boundaries at Gonarezhou/Malipati and Kruger/Pesvi have been reproduced with varying degrees of accuracy across study sites based on analysis of observed telemetry data (chapter 7). These results demonstrate that the implementation of two environmental factors (i.e., water surface and landcover) and one particular livestock practice (i.e., avoidance of growing crop fields) is sufficient to reproduce the spatiotemporal contact and movement patterns of buffalo and cattle at the landscape scale in three ecologically and geographically contrasted W/L interfaces.

The frequency and location of contacts between these two animal species is therefore to be put, first and foremost and before all other natural resources and ecological factors, in direct relation to the spatial distribution and temporal availability of the water resource. However, the impact of the distribution of the fodder resource as well as the behavior of the herders on the movements of these two animal species should not be neglected as they directly influence their potential contacts.

8.1.3 From a methodological standpoint

A simple three steps methodology, yet robust and reproducible, have been developed to characterize the surface water spatial availability within a time series and the landcover at a spatial resolution of 10 meters (Chapter 4). Using pixel-based supervised and unsupervised classifications methods on open-source SRS images (i.e., Sentinel-2), this methodology can easily be apprehended even by non SRS specialists. It allows to characterize complex and heterogeneous environments on wide areas at a landscape scale where in-situ data (e.g., GPS localized landscape samples, empirical knowledge on landscape structures) are lacking or non-existent. The entirety of the classification procedures have been developed using open-source

software (i.e., QGIS) and programming environments (i.e., R), making it accessible and reproducible even if computing and financial resources are limited.

A spatialized mechanistic approach integrating a self-propelled particle (SPP) model to simulate individual and collective movements in relation with the spatial and temporal variations of the surface water availability have been developed using the buffalo telemetry data of the three study sites as reference data for the model calibration and validation processes (see chapter 6). This modelling approach demonstrated how a mechanistic model can be spatialized and combined with SRS data to simulate animal movements in relation with a given environmental variable at a landscape scale. The development of this model tested and confirmed the capacity of a domain specific language such as Ocelet (see [section 5.4.2](#)) to efficiently model heterogeneous entities (i.e., buffalo individuals, buffalo's herd, surface water) in spatialized and temporalized complex systems through their interactions (chapter 6). For the first time to our knowledge, buffalo's movements at the individual and collective scales have been simulated in heterogeneous environments and at three different W/L interfaces by the use of a self-propelled particle model (also called parsimonious swarm model). This simple and replicable modelling framework can be considered as an alternative to the existing modelling tools in the understanding of animal movements in regard to water selection in several ecological contexts and environments.

The mechanistic model reproducing the buffalo movements in space and time at the landscape scale has then been completed by other entities such as cattle and the landcover to model the contacts between a wild and a domesticated animal species at the three considered W/L interfaces (Chapter 7). This model demonstrated that with a set of simple rules combining basic daily resources requirement (i.e., water and grazing) and herding practices (i.e., avoidance of growing crop fields), the buffalo and cattle movements as well as their respective areas and intensity of contacts in three different interface areas in southern Africa are simulated and reproduced. The observation of modelled vs. observed areas of inter-species overlap and contact in space and time (chapter 7) provides a sense of overall replicability of ecological patterns by the model. For example, in three different study sites with contrasting geographical and ecological configurations (see chapter 2), the movement and contact model confirmed that the distribution of available surface water spatially concentrates buffalo and cattle movements around surface water, thus generating potential localized interfaces. The necessity of both buffalo and cattle to look daily for a waterhole in the vicinity of where they are at any time prevent them of “escaping” from the interface area. This ecological pattern has been observed and is well known in the literature (Miguel, 2012; Valls-Fox, Chamaillé-Jammes, et al., 2018). However, for the first time to our knowledge, a spatialized mechanistic model manages to realistically replicate and predict this ecological dynamic at the landscape scale (Chapter 7).

Overall, this thesis reveals that applying SRS to better understand buffalo and cattle movements and contacts in semi-arid environments provides an operational framework that could potentially be replicated in other types of W/L interface where different wild and domestic species interact. Moreover, the implementation of a spatialized epidemiological compartment into the already developed mechanistic movement and contact model could potentially improve the general understanding and apprehension of the pathogen transmission and circulation between wild and domesticated species at the W/L interface.

8.2 Limits and recommendations

8.2.1 On the telemetry data used

The GPS collars used in this study allow continuous data collection and provide input data to examine the buffalo and cattle behaviors spatially and temporally with a frequency of one hour over varying periods of time in extensive areas (see [section 2.2.1](#)). However, the constraints (e.g., costs, difficulty of deployment) associated with the telemetry technology used in this study have limited the number of individuals to be monitored simultaneously within the same group (see [section 2.2.1](#)). Given our aim to translate individual but also collective movements of the buffalo and cattle, the composition of the telemetry data used did not give us enough information (i.e., time frequency and limited sample within targeted animal species populations) to refine the collective movements reproduced by the model. If the buffalo and cattle movement model is able to simulate individual movements influencing collective movement dynamics, the alignment and cohesion parameters regulating group dynamics were calibrated on Hwange with a maximum of four individual buffalo representing the collective (see Chapter 6). As a buffalo herd is composed between 50 and 600 individuals in the three study sites (Miguel, Grosbois, Fritz, Caron, Garine-Wichatitsky, et al., 2017) an average of 200 individuals have been considered. This constraint related to the composition of the data (i.e., gap concerning the number of observed individuals and measured individuals) introduces a bias that potentially impacts the metrics used by the movement model to accurately reproduce collective dynamics at the landscape scale and over a time frequency of one hour. Also, the one-hour frequency of the telemetry data did not allow to accurately measure the periods of rumination and rest that occur with finer temporal resolution (Cornélis et al., 2011; Kingdon, 2015). As a result, the design

of different behavioral phases inherent to the buffalo and cattle movement models have been simplified. This gap between the frequency of the focal animal species recorded positions and their known ecological behaviors has been compensated by extrapolating their localizations with the remotely sensed surface water and landcover at the same time frequency than the telemetry data (i.e., 1h). Finally, the social interactions between individuals have not been considered given the impossibility to derive such information from the telemetry dataset. This conscious oversight could introduce a bias into our developed movement models as social behaviors is considered as an important factor to understand the mechanisms for intra-group behaviors and inter-group encounters, especially for the buffalo in the case of fission/fusion events for instance (Wielgus, 2020).

Reducing the frequency of GPS location acquisition is often considered even if it means trading off the temporal resolution to maximize transmitter battery life and onboard memory storage (Hebblewhite & Haydon, 2010). Yet, long term and short term intrinsic animal behaviors create several levels of decisions that operate simultaneously to dictate animal movements (Benhamou, 2014). In that regard, assessing animal movements or behaviors only by considering GPS-locations can potentially lead to incomplete interpretations, therefore inaccurate movement models (Bastille-Rousseau et al., 2018). In this study, we have already integrated telemetry data with medium spatial resolution SRS imagery. However, the capacity to describe individual and collective movements as well as intra-group dynamics in space and time could be further improved by combining GPS collars with cost-efficient proximity loggers that could directly record synchronous contacts between a larger number of individuals (Robert et al., 2012), animal-borne video and environmental data collection systems (AVEDs) which record what the animal sees in the field (Moll et al., 2007), or Unmanned Aircraft System (UAS) that give high resolution images to study animal herd spatial composition and structure as well as intra-group interactions (Inoue et al., 2019; Vermeulen et al., 2013). Despite a variety of existing tracking device and their rapid development in the field of ecology (Kays et al., 2015), it is important to keep in mind that a given study can only answer a limited set of questions. Therefore, the choice and combination of tracking devices is fundamentally linked to the research questions asked, as are the costs and constraints involved in installing and monitoring such devices in the field.

8.2.2 On the remote sensing methodology to characterize the environmental data

Pixel-based classification approaches use the pixel as the basic analysis unit and have been proven to be efficient in extracting landcover information from SRS images (Mather & Tso, 2016) and have been the main used technique for classifying low/medium spatial resolution SRS images (Duro et al., 2012). In this study, pixel-based classification methods have been used to derive environmental variables (i.e., landcover and surface water) from medium SRS images (i.e., Sentinel-2) at the landscape scale (see chapter 4). These methods have been considered as pixel-based classification does not change the spectral properties of the pixels and have a higher chance of preserving landcover details in comparison to other classification methods such as object-based classification (Y. Chen et al., 2018). However, it is difficult to use complementary properties (e.g., topography) which may lead to the salt and pepper effect (i.e., noise pixels covering the majority of a given classified image) in classified maps (Y. Chen et al., 2017), especially in areas where the landcover is heterogeneous.

The choice of a classifier algorithm has also its importance as it determines the quality of the resulting classification based on training and validating data samples that represent the desired typology. In this study, the choice of the RF algorithm (Breiman, 2001) has been made for the supervised classifications of the surface water and agricultural areas as it requires simple parametrization while being reliable and rapid in its execution as well as being able to efficiently process large volume of variables and data in accordance with the spatial extent of the three study areas (Inglada et al., 2015) (see chapter 4). In addition, robust classification methods such as RF have shown that their performances are likely to remain unchanged even by adding insignificant features (i.e., landcover training and validation samples that are inadequately referenced) (Pelletier et al., 2016). For the non-supervised classification of the landcover, the K-means clustering approach (Burrough, van Gaans, and MacMillan 2000) has been used for its proven ability to efficiently classify SRS images with a low cost computing time (Chen and Peter Ho 2008). However, RF and k-mean algorithms are data dependent as they efficiently rely on the quality of the data given in input, especially for the RF algorithm (Pelletier et al., 2016). In both cases, it is crucial to spend a fair amount of time verifying the input training and validating samples as well as the input SRS images composition used by the classifier algorithms before computation in order to avoid classification bias and errors as much as possible. In this study, the training and validation samples have been assessed by photo-interpretation of a very-high satellite imagery to compensate the lack of in-situ collected data (see [section 4.2.1](#)). This approach is time and cost effective but can introduce bias that can be discussed and relativized

according to the desired use of the produced classifications, even after rigorous visual assessment based on empirical knowledge and result sharing amongst peers. Concerning the non-supervised classification, Sentinel-2 bands used as input SRS images for the k-means algorithm have been visually compared with the produced landcover maps to assess dissimilarities (see [section 4.4.1](#)). Despite these verifications relative to the user's interventions, the native characteristics of the SRS images used to produce the classifications influence their quality. Sentinel-2 SRS images used to produce and assess the classifications have several advantages (see [section 2.2.2](#)) but also face several limitations that can potentially affect the classification results (Transon et al., 2018). Indeed, the medium spatial resolution of the Sentinel-2 sensors (i.e., 10-20m) produces SRS images with mixed-pixels, which highly affects classification and detection performances (Y. Zhao et al., 2014). Sentinel-2 being equipped with optical sensors, they are not exempted of cloud covering and atmospheric perturbations than can potentially alter the spectral signal of each and every pixel present in the SRS image despite the application of cloud removal procedures (Ebel et al., 2021) or atmospheric correction (Main-Knorn et al., 2017). In that regard, accuracy assessment of classification derived from SRS images is paramount. To further validate the classification methodology developed in this study, accuracy assessments using the Kappa index (McHugh, 2012) and the OA index (Alberg et al., 2004) have been conducted of every produced classification (see [sections 4.2](#), [4.3](#) and [4.4](#)). Even if these indices are widely used in SRS classification accuracy assessment (Foody, 2002), they have limitations as it is argued for instance that the Kappa index *“attempts to compare accuracy to a baseline of randomness although randomness is not a reasonable alternative for map construction”* (Pontius & Millones, 2011). Classification maps and all the environmental variables (e.g., surface water, agricultural areas) derived from SRS images are subjective and must be considered as such and not as a ground truth. They do not dispense of in-situ assessments and have to be used with caution in accordance with a specific research problematic. For instance, the buffalo movement model developed in this thesis only takes into account detected water points to simulate buffalo movements in time and space (see [section 6.1.4](#)). Therefore, undetected surface water via SRS classification or surface water absent during the period of GPS measurements in the field, can strongly reduce the model's capacity to reproduce the observed buffalo movements. Thus, the performance of any given spatialized model is closely linked to the quality of the environmental data (e.g., SRS detected surface water, collected buffalo telemetry data) used as input.

8.2.3 On the mechanistic movement and contact model

To our knowledge, this study is the first to mechanistically model buffalo and cattle individual and collective movements as well as inter-species contacts at three different W/L interfaces. However, the observed population samples (i.e., observed telemetry data) represent a small proportion of the historic and current geographical range of the two studied species in their respective environments. In that regard, the developed movement and contact model can be considered as an exploratory model that need to be optimized, refined, and improved upon in order to respond in a more in-depth manner to particular sets of research questions related to the ecology of buffalo and cattle as well as the risk of pathogen transmission induced by the spatial and temporal contacts (direct and indirect) between these two species.

The mechanistic movement and contact model developed in this study is based on behavioral metrics that were extrapolated from the analyses done on the observed telemetry data (see chapters 6 & 7). These metrics then contributed to define a representative daily behavior based on a temporal frequency of one hour, thus composing a cycle of actions of 24 hours repeating over the entire duration of the simulation. Therefore, the designed behavioral mechanisms are closely linked to the observation of the data potentially introducing bias in the model outputs. Indeed, even if the mechanistic movement model induces stochasticity within the simulated spatial and temporal movements of the two focal species (see chapter 6 & 7), it does not completely free itself from the data and as a result, does not adopt a mechanistic approach purely based on empirical knowledge and bibliographical analyses. However, in order to limit bias and to test the generality of the model on three W/L interfaces with different ecological and geographical configurations, the calibration allowing to fix the alignment and cohesion of individuals influencing the collective movement was carried out only on the buffalo herds recorded at the Hwange study site (see chapter 6). These parameters remained unchanged for the buffalo and cattle movement simulations at the three study sites. However, it is important to note that a time lag between the temporal frequency of the simulation (set at 10 minutes) and the temporal frequency of the telemetry data (set at one hour) is occurring within the model.

Therefore, for the validation process, only the hourly model outputs from the simulations were extracted, thus losing details in the temporal simulation of the focal species movements. In addition, only the herd's centroids have been used to derive metrics (e.g., point density, maximum convex polygons) to efficiently compare the model outputs with the telemetry data and avoid dissimilarities in term of herd's composition. The contacts extracted from the

telemetry database were not in sufficient quantity at the three study sites to be significant enough in comparison to the produced simulated data, thus preventing the use of quantitative statistical tests. Therefore, the derivation of spatial qualitative metrics (e.g., MCP and point density maps) have been used to spatially compare the observed with the simulated movements and contacts data (Chapter 6 and 7).

8.2.4 On the movement and contact model ecological simulations

The movement and contact model produced coherent results in regard to what have been extrapolated from the observed telemetry data (Chapter 7). Differences in predictions between the model outputs and the behavior of the observed data are noted as the observed and simulated contact areas differ in their localization as well as in the total amount of their respective surface area. For the three study sites, the simulated and observed contact geographical overlays are not totally accurate (especially in Hwange/Dete) and their surfaces, even if they are in the same order of magnitude, are not quite similar (Chapter 7). Factors related to the method and to variables (environmental, ecological, data related) can explain these differences in predictions. The fact that cattle are sent farther than the search for the nearest available water source could potentially suggest political claims to the forestry zone by the herders and/or ancestral practices as well as other "beliefs" linked to specific surface water points. The grazing practices could explain the drift of the contact zone towards the interior of the park, especially in the Hwang/Dete study site. Concerning buffalo, they seem to move less towards the communal land boundary than the model predicts, which means that there are behavioral factors that could explain this particular trend such as the already documented avoidance of cattle by buffalo (Valls et al., 2018). Therefore, In-depth field studies in the form of semi-structured interviews (Harrell & Bradley, 2009) or multiple-choice questionnaires (Mathesius & Krell, 2019), supplemented by detailed information gathering and annotations using interactive and/or mental maps (Pánek, 2016) from different stakeholders (e.g., nature park agents, herders, local elected officials, village leaders) would significantly help to enrich empirical knowledge on buffalo and cattle ecological behaviors (e.g., watering, grazing) over time and space, as well as to give a detailed cartographic representation of the specific places of watering and grazing privileged according to the seasons and the herder's decisions. All of these data would be processed and analyzed in order to be integrated into the model in the form of calibration of already implemented ecological parameters (e.g., alignment, cohesion, frequency of water point use, seasonality of grazing areas), thus reinforcing the capacity of the model to translate a certain ecological reality as well as more detailed herder's decision impacting

domesticated species movements without harming the potential genericity of the model insofar as this questionnaire and mind map protocol can be reproduced on all types of study sites, and no additional parameters need to be added to the model in order to simulate movements and contacts.

8.3 Future directions and perspectives

8.3.1 Combining methodologies and approaches to detect and characterize a wide array of environmental variables at multi-temporal and spatial scales

The supervised and non-supervised pixel-based classification of spatial medium resolution SRS imagery developed in this study managed to accurately characterize the desired environmental variables (e.g., surface water and landcover) at the landscape scale while being open-access, semi-automated as well as reproducible. Remote sensing is a burgeoning field of research and is increasingly used in ecology where many methodologies are emerging, being tried, tested, and discussed (Pettorelli, Laurance, et al., 2014). This development of new methodologies in conjunction with an increasing number of SRS sensors (He et al., 2015) could potentially, by the combination and thoughtful use of the latter, improve the classification results obtained in this study.

To improve on the methodology developed to characterize surface water, the use of satellite aperture radar (SAR) images such as European Space Agency's Sentinel-1 could be decisive and potentially allow the detection of open surface water but also vegetated water bodies often found in savanna environments (Sankaran & Ratnam, 2013). A number of approaches automatically detect open water based on multi-temporal SAR imagery (Bioresita et al., 2018; Westerhoff et al., 2013). These methods could be used as starting point to design an integrative approach ready to be applied in the three study sites by combining optical and SAR SRS images with the use of a supervised classifier algorithm such as RF. Indeed, surface water has a low backscatter response due to its smooth texture in comparison with other types of landcover (Schlafler et al., 2016). As such, surface water can be efficiently identified and discriminated by SAR images, thus providing additional information to the classifier algorithm and potentially enhancing its global performance in detecting surface water. Moreover, (Hardy et al., 2019) developed an automatic

open and vegetated water bodies detection approach using Sentinel-1 SRS images segmentation and machine learning (extra trees classifier) that applied to training data automatically derived using ancillary data (e.g., digital elevation model, global water occurrence layer (Pekel et al., 2016)). The capacity to detect vegetated water bodies in addition to open surface water could allow the current surface water classification methodology (see [section 4.2.1](#)) to be not only more efficient in its overall detection performance but also in its accuracy and wider range of surface water spatial assessment.

Concerning the landcover detection, especially the vegetation cover, combining pixel-based and object-based classifications could constitute the way forward as both pixel-based and object-based classifications have been proven efficient in extracting landcover information from different remote sensing images (Blaschke et al., 2014; Lu & Weng, 2007). If these two approaches have their respective strengths and weaknesses, by combining the two, the overall robustness of the current landcover classification method (see [section 4.4.1](#)) can potentially be significantly improved. (Chen et al., 2018) developed a classification method through integration of pixel-based and object-based classifications for reducing the uncertainties in mixed objects and pixels present in medium spatial resolution SRS images, especially in area with heterogeneous landscape such as savanna environments (Huete et al., 1985). In this methodology, a pixel-based classification produces class proportions of pixels used to characterize the landcover details pixel by pixel. At the same time, the spatial relationships from object-based classification results and the spatial relationships between objects are employed to characterize the class spatial dependence of each pixel. In the end, the class proportions of pixels and the spatial dependence of pixels previously determined are combined to produce a classification by a linear optimization model in units of object (Y. Chen et al., 2018). The application of such methodology within the framework of this study could potentially reduce the current three steps classification methodology (see chapter 4) into a one-step methodology while increasing the overall accuracy of the obtained landcover classification.

Another methodological avenue that could be explored with the ambition to potentially improve the current methodology developed in this study (see Chapter 4) is the use of deep learning algorithms. Deep learning, artificial intelligence derived from machine learning where the developed algorithm is able to learn by itself, has become a growing trend in big data analysis recently and has been widely and successfully applied in SRS image classification via the use of deep convolutional neural network (Minetto et al., 2019). However, the deep convolutional neural network methods generally require a large amount of training data as well as a high computing power, both considered as limiting factors in the general application of these methods in SRS image classification. Nevertheless, more recently, an innovative method

emerged using generative adversarial networks based on unsupervised learning process (Duan et al., 2018). This approach combines generative and discriminative models as well as the incorporation of a non-local layer to the designed deep neural network in order to capture the non-local spatial relationships and improve the network performance. With such methods, the automated classified of high and very-high spatial resolution SRS images can be considered while providing very accurate results (Cheng et al., 2020; Y. Li et al., 2018). The use of deep learning algorithms could prove to be a very good opportunity in characterizing environmental variables such as landcover or human infrastructures with very fine details (from 30 centimeters of spatial resolution), provided enough computing power as well as sufficient monetary investment capacities.

In addition to SRS, unmanned aircraft system (UAS) technology (e.g., drone) is increasingly used in ecology (Anderson & Gaston, 2013; Baxter & Hamilton, 2018) as it has several advantages: i) user controlled survey and revisit time period allowing potential high temporal resolution, ii) balanced spatial resolution enabled by the ability to fly at low altitude and regulate it accordingly (Linchant et al., 2015), iii) low operating costs compared to manned airborne and satellite observation (Jurdak et al., 2015), iv) can embark various sensors and measuring devices (e.g., hyperspectral and multispectral sensors, Lidar, thermal sensors) based on the desired application (Anderson & Gaston, 2013), v) reduce interference and disturbance compared to direct surveys done by humans (Iv et al., 2006). However UAS monitoring for ecological studies involves important decisions such as planning flight paths and heights, considering regulations in effect in some areas (e.g., the use of drones to fly over national parks is strongly regulated today), as well as image acquisition and analysis that can all contribute to potential radiometric (e.g., contrasts in the acquisition image) and geometric (e.g., spatial) errors (J. L. Morgan et al., 2010). Consequently, trade-offs and decisions have to be made throughout the implementation of UAV surveys, from camera positioning or aircraft speed, to the choice of image-processing algorithm and embarked sensors (Baxter & Hamilton, 2018). Despite these constraints, the versatility and flexibility offered by the use of UAS widen the range of possibilities in addition to the already numerous applications offered by remote sensing. Large scale democratization of wildlife aerial surveys informing on herd composition, morphology, spatial and temporal location is now within grasp (Linchant et al., 2015). Moreover, used in conjunction with SRS applications UAS could reinforce the capacity to monitor additional environmental variables efficiently and at different spatial and temporal scales (e.g., topographic measurements at very high spatial resolution, measurements of soil and vegetation thermal heat). This could potentially improve our understanding of how environmental dynamics shape the ecology and conservation of large herbivores drastically by providing accurate and very high resolution image time series from which environmental variables can be derived.

8.3.2 Improving the intrinsic robustness of the mechanistic movement and contact model

Although the genericity of the mechanistic model of movements and contacts has been tested in this study (Chapter 7), the results produced by the model and their inherent uncertainties have not been established and objectively assessed. Indeed, the input to a model is subject to potential errors of measurement, absence of information, sampling design, out-of-date information, scaling errors, and misreading or poor conceptualization of the driving forces and mechanisms of a given system (Burrough et al., 2015). Therefore, by conducting uncertainty and sensitivity analyses on the model, it is possible to provide an understanding on how the model's parameters respond to changes in the inputs. Sensitivity analysis (Figure 8.2) study how the uncertainty in the output of the model can be apportioned to different sources of uncertainty in the model inputs (Saltelli et al., 2006). This analytic procedure could then drastically improve the capacity to determine the developed mechanistic model genericity potential. It could also allow to efficiently tune the model's parameters, determine minimum data standards, and establish priorities for updating the model.

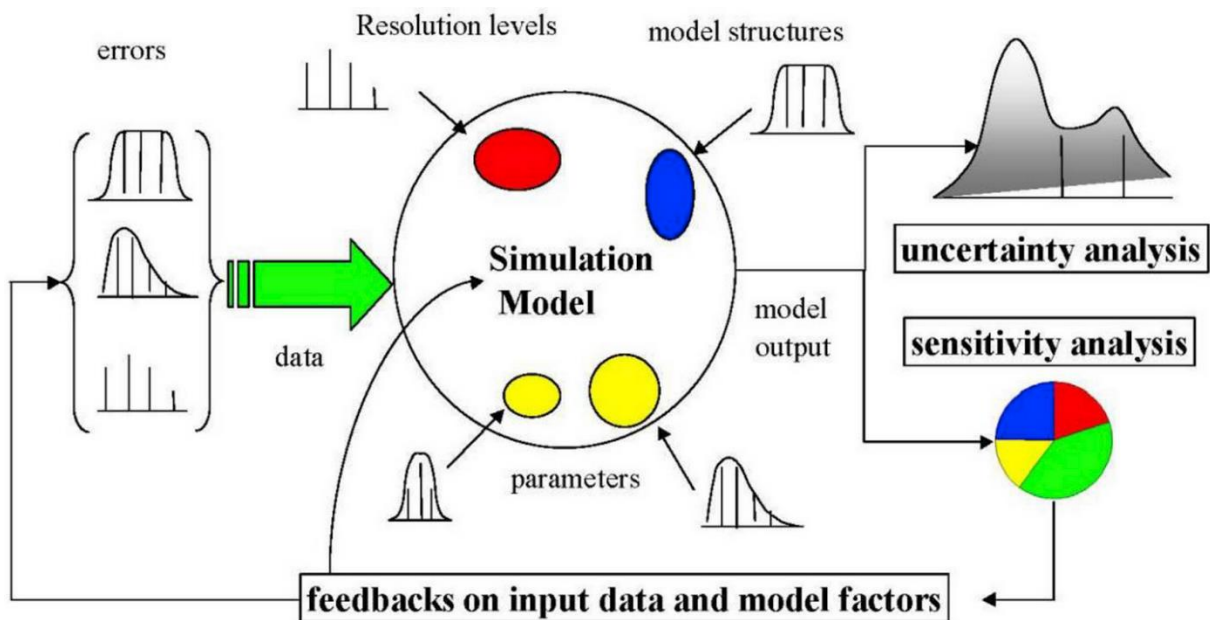


Figure 8.2: Figure extracted without modification from (Saltelli et al., 2019). This figure represents a schematic of an idealized uncertainty and sensitivity analysis. Uncertainty coming from heterogeneous sources is propagated through the model to generate an empirical distribution of the output of interest (grey curve). The uncertainty in the model output, captured for example by its variance, is then decomposed according to source, thus producing a sensitivity analysis.

Amongst the many sensitivity analyses developed for a wide range of models (Iooss & Lemaître, 2015; Saltelli et al., 2019), most of the existing sensitivity analyses present some conceptual issues when applied to spatial models (Lilburne & Tarantola, 2009). Some of the conceptual issues concern the need to represent a spatial input with a scalar value, and the desirability of being able to simulate auto-correlated inputs and analyze the effect of spatial structure (Lilburne & Tarantola, 2009). However, Variance-based sensitivity analyses such as the Sobol method (based on the decomposition of the variance) adapted by (Saltelli, 2002) and improved by (Tarantola et al., 2006) present several advantages when applied to a spatial model: i) the entire model input space is explored; ii) it is a model-free sensitivity measure that is independent of the model structure associated assumptions; iii) it is able to distinguish between first-order effects (i.e., the impact is comparable to the change) and higher-order effects (i.e., interaction modifications or change per capita effect) that account for interactions. This can prove to be useful in term of model improvement, parameter estimation, or model simplification; iv) it yields more robust sensitivity rankings than other measures such as analysis of variance or regional sensitivity analysis (Tang et al., 2007); v) spatial variable inputs are not required to be represented in a single scalar value; vi) it can equally be used to assess the sensitivity of time-dependent input or/and spatial-temporal input (Lilburne & Tarantola, 2009). The application of sensitivity analyses to the model developed in this study with the use of the Sobol method seems to be the natural and necessary next step.

If the movement and contact mechanistic model developed within the framework of this study is intended to be relatively simple with a deliberately limited number of adopted behavioral phases and parameters regulating the movements in time and space (chapter 6 and chapter 7), more complex mechanisms such as fusion/fission dynamics (Wielgus et al., 2020), influences of human infrastructures (Beyer et al., 2016) or inter-species interactions (Schoon et al., 2014) could be simulated by judiciously implementing additional spatialized data as model's input. Such data could be the human infrastructures (e.g., fences, settlements) derived from very-high spatial resolution SRS images (e.g., Pleiades Neo SRS images from Airbus with a 30 cm spatial resolution), high resolution telemetry data (with a frequency of 1 minute) of more individuals within the same herd as well as other animal species (e.g., predators, bridge host animal species) that drive the food competition/avoidance/pathogen transmission dynamics. These input data could reinforce the development of test scenarios to validate or invalidate assumptions based on field observations and bibliographical research regarding the influence of the environmental variables on the buffalo and cattle movements and contacts at the W/L interface. Moreover, by adding these additional data, one could verify their relative importance in regard to model accuracy performances, providing a general validation framework confident analyses,

extrapolations, and confirmations. The optimal model input determined, the intrinsic parameters regulating the movements of the modeled species could then be efficiently optimized or modified. The implementation of other self-propelled particle (SPP) models such as the Cucker-Smale model (Cucker & Smale, 2007) or models with multiple interaction radii (Couzin et al., 2002) (see Yates et al. 2010 for an extensive review of SPP models) in addition to the (Grégoire & Chaté, 2004) model already developed within the movement and contact model could allow to test, compare and choose the most adequate in reproducing the individual and collective movements and contacts, thus reinforcing the model adaptability and genericity.

Important modifications could be applied to reinforce the general robustness and genericity capacities of the already developed movement and contact model. By definition, a model is never static and in constant evolution. Having this constant in mind, the model have been developed as modular and flexible in order to optimize its use and application in a wide array of ecological problematics occurring in various ecosystems and environments.

8.3.3 Enhancing the model's capacities to reproduce ecological processes

Ecological processes are particularly difficult to model as they are numerous and difficult to separate from each other in terms of their explanatory importance (Joergensen & Fath, 2011). The aim is not to model as many ecological processes as possible, but to determine those that will have an essential impact on a particular behavior of a target animal species. Through the development of a model, it is a question of identifying trends and confirming or refuting hypotheses in a simple, generic, and reproducible way to promote its apprehension and therefore its utilization by multiple stakeholders in a variety of ecological configurations and contexts (May, 2019).

In the case of the movement and contact model developed in this thesis, several avenues of reflection exist to improve its ability to understand and apprehend the ecological processes of buffalo and cattle at the W/L interface scale. One of the first avenue would be to test different environmental scenarios and then analyze the impact of these scenarios on the movements and contacts of buffalo and cattle at the landscape scale. Based on the principle that the movements of the two focal species are a function of the spatial and temporal availability of water and forage resources, simulating a drought by modifying the spatial distribution and availability of environmental resources in the model input for example, would result in movement and contact patterns that could be compared to similar ecological patterns under normal conditions. This

would potentially provide indications on the degree of explanatory influence of the environmental indicators determined on the movements and contacts of buffalo and cattle within their respective environments. In addition, applying these scenarios to the three study sites would give us an indication of the developed model's generality in the sense that the different model's outputs produced would constitute potential comparative indicators of the relative weight played by the environmental variables in determining buffalo and cattle contact areas. These indicators would then be analyzed in contrast with the landscape configuration of the three study sites to ascertain which one mostly influences the buffalo and cattle movements and contacts. These drought scenarios could be configured via the different climate models already existing (Eyring et al., 2016) and applicable at the landscape scale, as Southern Africa is particularly affected by the consequences of climate change (e.g., increase in average temperatures, alteration of rainfall frequency and intensity) (Davis & Vincent, 2017).

The second avenue would be to consider and integrate into the model other animal species (e.g., carnivores, similar trophic animal species within herbivores) in addition to the two target species already considered. Africa is home to more ungulates than any other continent, with the greatest species richness (30 species) found in the grass-dominated savannahs (Shorrocks & Bates, 2015). In savanna environments, many herbivore species, including ungulates, are known to be bottom-up regulated (especially the larger herbivore species) (Codron et al., 2007), which can potentially result in competition and increase interaction for browse and grass between herbivores especially when food availability is limited (Hopcraft et al., 2010). This competition for resources is likely to influence animal movement in regard to specific species interactions. In addition, predation can play a crucial role in conditioning the movements patterns and interactions of not only wild herbivores but also domesticated species. For example, herbivores may reduce the risk of predation proactively, by occupying more secure habitats, by being vigilant and by restricting their movements at times when carnivores are most active (Owen-Smith, 2019). Taking these behaviors into account by the model could only strengthen its ability to predict the landscape-scale movements of buffalo and cattle and therefore their potential contacts within W/L interfaces where they permanently cohabit with other animal species. Even if it means adding complexity into the model it could, in turn, simulate more accurate ecological processes (i.e., wild and domestic animal species movements and contacts). This could prove to be decisive as Southern African W/L interfaces face an increasing infectious diseases' threats in multi-hosts transmission contexts aggravated by climate change and biodiversity erosion (Johnson et al., 2020). Indeed, it is urgent to understand how pathogens are maintained in the environment, which implies characterizing the spatio-temporal dynamics of wild animal host communities and their role in the chain of diseases transmission (i.e., reservoir, cul de sac, bridge species) more accurately (Gortazar et al., 2015).

8.3.4 Adding an epidemiological compartment to the movement and contact model

Having the capacity to model the movement and contacts spatially and temporally between wildlife and livestock at the landscape scale offers a wide range of opportunities to expand the model's functionalities. Amongst those functionalities could be the implementation of an epidemiological compartment where the movements and contacts of the two focal species in relation with their direct environment (e.g., surface water and landcover) would be the starting point of pathogen transmission modelling. Pathogen transmission at the W/L interface are driven by animal behavior, social structure, and spatial overlap but also by the pathogen characteristics (e.g., survival, transmission pathways) as well as environmental and climatic factors (e.g., landscape composition and structure, amount of precipitation) (Plowright et al., 2017). These mono-specific pathogen transmission factors potentially affect, in turn, the inter-species pathogen transmission dynamics. Facing this multifactorial system, the selection and design of an epidemiological modeling compartment into an already developed mechanistic model will need to be adapted on the characteristics of a specific pathogen as well as the data available to calibrate and assess such approach (Martínez-López et al., 2021). Several modelling approaches could be envisioned to understand and apprehend mechanisms involved in pathogen transmission dynamics, to quantify transmission rates, to assess how the animal population movements and contacts in relation with environmental variables influence pathogen transmission. Such models potentially providing means to identify optimal control strategies are (Miller et al., 2019): compartment based models (e.g., Multi host Susceptible, Infectious, or Recovered (SIR) model) and agent-based models (e.g., network-based models, coupled map lattice).

Multi-host SIR models simulate pathogen dynamics in multiple host species explicitly, separating these dynamics in different species while considering similar or different transmission mechanisms in each species and integrating spatial and environmental modulators of disease transmission (Huyvaert et al., 2018). For each host or vector animal species considered, independent processes determining transitions among compartments (e.g., disease transmission, demographic dynamics, movements, and contacts, ...) are designed. These compartments are then linked through the specific transmission process (depending on the considered pathogen) of infectious individuals to susceptible individuals (Manlove et al., 2019). This modelling approach could bring the capacity to infer differences in transmission rates (therefore transmission heterogeneity) within and between potential susceptible and host animal species at the population scale. Their relative movements and contacts in space and time

thanks to the contacts rates and locations provided by the already developed movement model would also be considered.

To simulate pathogen transmission and circulation processes at both individual and collective scales, where control strategies need to be fine-tuned to a complex system, a spatially explicit agent-based models (ABMs) could be considered (see chapter 5). Characteristics of a selected pathogen (e.g., infection rates, ability to survive in the environment), agents (considered focal animal species attributes and behaviors), as well as interactions between agents and interactions between agents and environmental variables would constitute all the elements of the desired epidemiological model, following the procedures already developed in research studies (e.g., (Martínez-López et al., 2011; Ward et al., 2015). However, such modeling approach should be carefully designed as ABMs usually require a lot of computing power, are more difficult to replicate, and are subject to caution when fitting the data for validation purposes (Martínez-López et al., 2021). Moreover, they are still a number of challenges to solve regarding wildlife epidemiological modelling as most of the commonly used epidemiological parameters (e.g., incubation period, susceptibility, infectiveness, clinical signs, role of environmental factors) are difficult to estimate, and isolated, spatialized filed epidemiological data are hard to collect.

Epidemiological models that explicitly include contact networks and spatial structure have become increasingly used (Huyvaert et al. 2018). However, it is important to note that estimating contacts remains challenging and usually only possible at small scales (see chapter 7) while factors influencing interactions, and as a result pathogen transmission, may vary from one area to another (Miguel, Grosbois, Caron, Boulinier, Fritz, Cornélis, Foggin, Makaya, Tshabalala, & Garine-Wichatitsky, 2013). The spatial and temporal scales have to be carefully determined as models integrating the ability to simulate complex phenomenon at different spatial scales within a same temporal time frame can be complex. Indeed, W/L interfaces are dynamic environments evolving as the environment changes in space and time (Vercauteren et al., 2021). ABMs may capture all this complexity and describe ecological/epidemiological processes as they actually occur but a complex model does not necessarily ensure more credible results (Martínez-López et al., 2021). A model should not be more complex than necessary to fulfill its goals but, at the same time, transdisciplinary approaches are increasingly considered as necessary to efficiently apprehend wildlife livestock pathogen transmission (De Garine-Wichatitsky et al., 2021).

8.3.5 Towards an “Eco Health” approach

Pathogen transmissions from wildlife to livestock increases mortality and reduce livestock productivity, thus causing economic damages to the agricultural sector through indirect losses associated with cost of control, loss of trade, decreased market values and food insecurity (Dehove et al., 2012). In addition, pathogen transmission from livestock to wildlife poses potential threats to entire ecosystems, affecting biodiversity as well as modifying animal's behavior and composition of animal populations (Daszak et al., 2000). The economic, social, health and ecological consequences associated with the inter-species transmission of pathogens within animal communities are maintained and amplified by anthropic actions. The conversion of natural habitats into production landscapes, the intensification of international travel and wildlife trade are all facilitating exposure to novel pathogen communities (Patz et al., 2008). The decreasing wildlife diversity and the isolation of ecological communities through habitat fragmentation reinforce the circulation of pathogens and their transmission (Keesing et al., 2010). Facing these global issues, standard public health approaches that are based on the one host/one pathogen relationships are out of date, all the more so as some consequences associated with the current pathogen transmission trend have yet to be realized.

Until recently, spill-over/spill-back or reservoir hosts frequencies were analyzed within localized animal populations living in W/L interfaces and considered as static epidemiological and ecological functions (Siembieda et al., 2011). Now, pathogen transmission is considered as dynamic, diverse, and bidirectional with transmission phenomenon occurring freely within and between wildlife and livestock species at the W/L interface scale (Wells et al., 2018). This change of paradigm is explained by the emergence of integrated approaches to health such as One Health, EcoHealth and Planetary Health (Buse et al., 2018; Lerner & Berg, 2017). The EcoHealth approach (Box 1) is difficult to conduct as it relies on both empirical and flexible, context-specific methodologies (Charron, 2012). However, six principles have been designed to facilitate the integration and implementation of such approach in a variety of case study: i) system thinking that can connect the different components of W/L interfaces (e.g., the ecology, socio-cultural context, the governance and the economy) at different temporal and spatial scales to apprehend the ecology of a particular pathogen, ii) transdisciplinary research that implies the collaboration of a multitude field of research as well as the gathering of academic and non-academic actors to tackle health issues at the W/L interface, iii) participation to include local stakeholders and populations such as farmers and community members, thus diversifying the shared knowledge and creating potential viable alternatives, iv) sustainability as all the tools and methodologies developed within the frame of an EcoHealth approach have to protect ecosystems and improve

degraded environments, v) gender and social equity as the EcoHealth approach promotes the suppression of unequal and unfair sanitary situations that impact the health and well-being of already vulnerable populations, vi) knowledge to action as a process involving a wide variety of stakeholders, where research, tools and methodologies produce knowledge that are, after collegial consultation, integrated into co-designed management options.

BOX 8.1

The definition of the EcoHealth approach by Dominique F. Charron

“ Ecosystem approaches to health (or EcoHealth research) formally connect ideas of environmental and social determinants of health with those of ecology and systems thinking in an action-research framework applied mostly within a context of social and economic development. Ecosystem approaches to health focus on the interactions between the ecological and socio-economic dimensions of a given situation, and their influence on human health, as well as how people use or impact ecosystems, the implications for the quality of ecosystems, the provision of ecosystem services, and sustainability ” (Charron, 2012)

So far, examples integrating these various principles are few (Charron, 2012) but research projects adopting part or the entirety of EcoHealth principles start to emerge. The Hum-Ani project supported by the BNP Paribas Foundation through its “Climate & Biodiversity Initiative” and led by Eve Miguel, researcher in Ecology and Epidemiology at the French National Research Institute for Sustainable Development (IRD) is one example amongst many (see <https://en.ird.fr/project-hum-ani-contacts-among-animals-and-humans-and-infectious-risk>).

This project aims to understand how loss of biodiversity and climate change influence the contacts between wildlife and domesticated animals, thus increasing the risk of pathogen circulation and transmission amongst and in between them. This transdisciplinary project is based on the combination of three main research pillars that are the ecology, the epidemiology, and the social sciences. The conceptualization of the research questions, the team composition and the partnership have all been thought of as part of an integrative approach.

The movement and contact model developed in this thesis followed a pluri-disciplinary approach as it combines several fields of research such as remote sensing, spatial modelling, and ecology. The model’s capacities to integrate heterogenous spatialized data, to simulate at

different temporal and spatial scales, to consider multiple animal species at individual and collective scales as well as to be implemented with additional complementary features make this mechanistic model the perfect tool to address animal population health issues at the interface scale while considering using it to promote an EcoHealth approach. This thesis lays the conceptual foundations of what could be the first step in the construction of a generic model allowing to combine complementary disciplines while remaining within the methodological framework imposed by the principles of the EcoHealth approach. The developed model can already demonstrate the influence of environmental variables on the contacts and movements of a wild and a domesticated animal species at the landscape scale in its current state (see chapter 6 and chapter 7). After optimization and improvement, this mechanistic model could be a formidable tool to apprehend, explain and prevent the risk of pathogen transmission between wildlife and livestock at the W/L interface scale while being used as a catalyst for exchange, discussion, and education within the scientific community but also among local populations and stakeholders. Such methodological tool could be beneficial as it could potentially convince, by incarnating a concrete application of an EcoHealth approach, of the need to radically shifting attitudes toward wildlife (De Garine-Wichatitsky et al., 2021). While the challenges concerning the health and well-being of human and animal populations are ever increasing due to climate change and anthropic pressure, it is urgent to consider wildlife more as an asset than a problem to be controlled (du Toit et al., 2017) as well as to properly establish collective and aligned strategic use of ecological complementarities between livestock and wildlife in order to promote coexistence (Fynn et al., 2016). We humbly hope that this thesis will encourage multi-disciplinary approaches in order to collectively solve major ecological issues that face W/L interface in Southern Africa but also in other parts of the world.

8.4 A last word

Currently, discussions regarding human–nature interactions, which will surely affect W/L interfaces, are numerous. Questions are being raised about land sparing (for biodiversity protection) versus land sharing (Fischer et al., 2014), about the role of protected areas and how multi-use landscapes must be managed (Sayer, 2009), and about sustainable use versus protectionist ideologies (Cretois et al., 2019). The science of coexistence that is being opposed to the science of spared landscapes (i.e., protected areas) promotes the presence of wildlife in multi-use landscapes. However, the strategic utility and practicality of such science are contested (Linnell et al., 2020).

Pastoralism as well as human societies in general need to reinvent themselves to determine their respective contributions to future food and nutrition security systems worldwide, while reducing their impact on the climate, the environment and wildlife. Globally, pastoralism constitutes on average 37% of the agricultural gross domestic product (Alexandratos & Bruinsma, 2012) and is one of the most important and rapidly expanding commercial agricultural sectors worldwide (Thornton, 2010). Considering this trend, spatialized mechanistic model inserted into an “Eco Health” approach considering livestock, wildlife, humans, and environment in constant interactions could contribute to achieve a fair balance and mutual benefits across sectors (Kleczkowski et al., 2019) and mitigate the increasing risk of pathogen transmission between wild and domestic animal species at the W/L interface. We believe that such approach needs to be further developed and encouraged by the scientific community and designed as a diagnostic tool to support decision-making in a constantly changing world. This thesis humbly promotes the resilience of ecosystems within virtuous and encompassing dynamics for both animal welfare and the welfare of human societies.

Synthèse Générale de la thèse

L'utilisation combinée de la télédétection et de la modélisation spatiale pour la mobilité animale - Application à l'étude des contacts entre espèces animales sauvages et domestiquées afin d'appréhender le risque de transmission d'agents pathogènes en Afrique australe

Table des matières

- 9.1** Contexte général
 - 9.2** Une thèse structurée en trois temps
 - 9.3** Approches méthodologique
 - 9.4** Principaux résultats
 - 9.5** Eléments de discussion et perspectives
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9.1 Contexte général

En Afrique australe, les populations humaines vivant sur des terres communales situées en bordure d'aires protégées ont considérablement augmenté ces dernières années (Cleland & Machiyama, 2017; Wittemyer et al., 2008). Cette explosion de la population humaine favorise les contacts entre la faune sauvage, les hommes et leur bétail dans les zones où ils coexistent (Bengis, Kock, & Fischer, 2002; de Garine-Wichatitsky et al., 2013). Par conséquent, les zones d'interface sont confrontées à plusieurs problèmes liés à la coexistence entre l'homme et la faune sauvage (Andersson et al., 2017) et parmi eux, le risque de transmission d'agents pathogènes entre les espèces sauvages et domestiques (Caron et al., 2013; Miguel et al., 2013). Depuis plusieurs décennies (e.g., l'épidémie du SIDA ayant officiellement commencée en 1981), le nombre de maladies humaines émergentes ou ré-émergentes a considérablement augmenté, et parmi celles-ci, 75% ont une origine zoonotique. Les ongulés sont partie intégrante des sociétés humaines de par les activités d'élevage et sont considérés comme l'un des principaux groupes d'espèces responsables des zoonoses (Woolhouse et al., 2012). La proximité spatiale entre les populations a été clairement identifiée comme l'un des facteurs de risque cruciaux dans la transmission d'agents pathogènes entre espèces (Roche et al., 2012). Cependant, la nature, la fréquence et la localisation de ces contacts entre ongulés sauvages et domestiques restent largement inconnues. Bien que l'utilisation d'outils telles que la télémétrie ou encore la télédétection permettent le suivi dans le temps et dans l'espace d'espèces animales, il existe encore de nombreux verrous techniques et scientifiques afin de mesurer, analyser le mouvement animal en relation avec l'environnement. Par exemple, les mouvements des espèces animales sauvages sont-ils comparables aux mouvements des espèces animales domestiquées ? Est-ce que le rapport à l'environnement de chaque espèce animale conditionne leurs mouvements respectifs ? Comment simuler, dans le temps et l'espace les mouvements d'espèces animales avec des données hétérogènes ?

Dans ce contexte, la présente thèse, qui s'inscrit dans le cadre du projet TEMPO (TElédétection et Modélisation sPatiale pour la mObilité animale), vise à 1) Caractériser les variables environnementales, à l'échelle du paysage, qui influencent potentiellement les mouvements d'une espèce d'ongulés sauvages (le buffle - *Syncerus caffer caffer*) et d'une espèce d'ongulés domestiques (les vaches - *Bos taurus* & *Bos indicus*) à trois interfaces différentes situées en Afrique australe, et plus particulièrement au Zimbabwe (Hwange/Dete, Gonarezhou/Malipati and Kruger/Pesvi), 2) Développer un modèle mécaniste pour simuler les mouvements des deux espèces animales cibles, à l'échelle de l'individu et du troupeau, en relation avec la saisonnalité des eaux de surface et le type d'occupation du sol représentatif de leurs environnements

respectifs, 3) Déterminer la nature, la fréquence et la localisation des contacts entre les deux espèces animales cibles, le rôle joué par les variables environnementales (i.e., les eaux de surface et l'occupation du sol) et les comportements des éleveurs, en l'occurrence, en combinant les modèles mécanistes de mouvements développés.

9.2 Une thèse structurée en quatre temps

Bien que cette étude s'inscrive dans la continuité des travaux scientifiques menés depuis des années sur ces zones géographiques et est rendue possible grâce à la collecte et l'analyse de données d'observation (e.g., données de télémétrie) (Miguel, 2012; Valls Fox, 2015), l'approche de modélisation développée au cours de ce travail est exploratoire dans le sens où il s'agit d'une méthode basée principalement sur des connaissances issues de la littérature scientifique, de l'expérience scientifique ainsi que de l'expérience de terrain de l'ensemble des contributeurs.

Cette thèse repose sur une approche pluridisciplinaire en combinant plusieurs disciplines complémentaires et est structurée suivant quatre étapes méthodologiques principales ([Figure 9.1](#)) détaillées respectivement dans les [chapitres 3, 4, 6 et 7](#) de ce manuscrit de thèse. Le [chapitre 3](#) a synthétisé la littérature scientifique afin d'identifier concrètement les variables environnementales influençant les déplacements des deux espèces animales cibles dans le temps et l'espace (ce chapitre est représenté sous la forme d'un article scientifique déjà publié). Le [chapitre 4](#) a détaillé la méthodologie développée pour caractériser, via l'utilisation de méthodes de classification dérivées des images SRS, les variables environnementales considérées (i.e., les surfaces en eau et l'occupation du sol) qui influencent les mouvements des deux espèces animales cibles dans l'espace et le temps. Le [chapitre 6](#) a décrit en détail les principes du modèle mécaniste spatialisé permettant de simuler les mouvements des buffles en fonction de la variabilité saisonnière des surfaces en eau dans l'espace et le temps. Le [chapitre 7](#) a expliqué les principes du modèle de contact buffles-vaches en fonction de la disponibilité en eau et de la structure spatiale de l'occupation du sol à l'échelle du paysage dans trois interfaces W/L différentes. Les autres chapitres permettent de contextualiser et de décrire les enjeux écologiques et thématiques ([chapitre 1](#) et [chapitre 2](#)), les enjeux méthodologiques ([chapitre 5](#)) et de discuter ces choix ainsi que les résultats produits en considérant les perspectives de ce travail de thèse ([chapitre 8](#)).

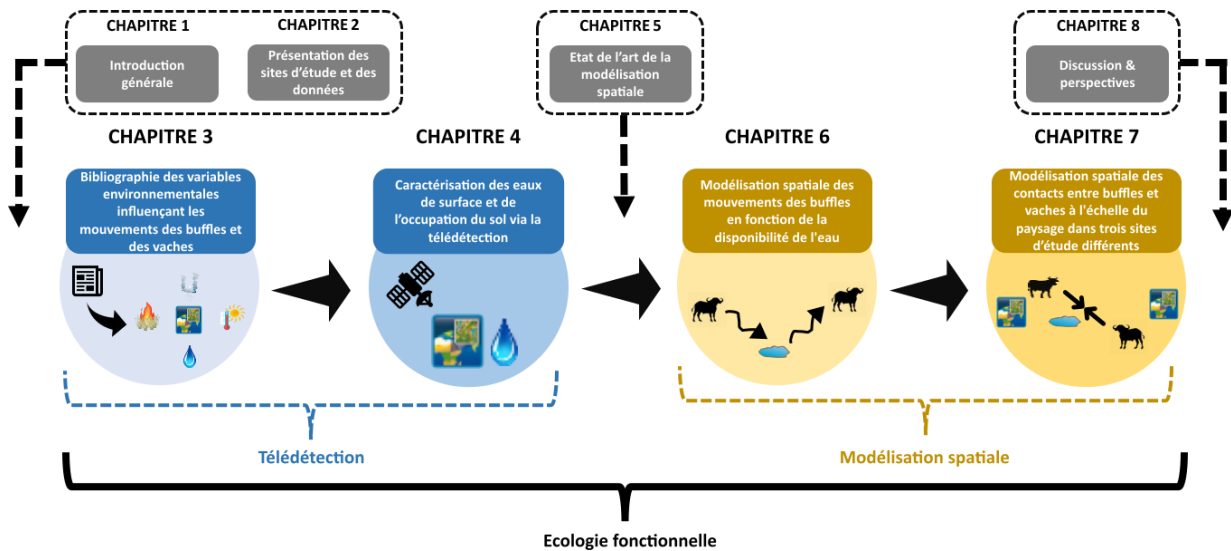


Figure 9.1: Figure synthétisant l'approche générale de la thèse, les chapitres correspondants dans lesquels les méthodologies spécifiques sont détaillées ainsi que le domaine de recherche associé à chacun des chapitres. Les chapitres figurant en gris sont des chapitres de contextualisation du travail de thèse réalisé.

9.3 Approches méthodologiques

Les trois interfaces considérées dans cette étude présentent des caractéristiques géographiques et écologiques différentes mais sont toutes concernées par une variabilité temporelle et spatiale prononcée des eaux de surface ainsi que par des paysages très hétérogènes, typiques des savanes arborées s'épanouissant en climat semi-aride (voir [chapitre 2](#)). Ces deux caractéristiques environnementales communes influencent de facto la disponibilité des ressources en eau et en fourrage, conditionnant et contraignant les mouvements des buffles et des vaches dans l'espace et le temps (voir [chapitre 6](#) et [chapitre 7](#)). Après analyse de la littérature scientifique, les eaux de surface, les précipitations, l'occupation du sol et les feux de savane sont apparus comme des facteurs clés ayant un impact sur les mouvements des buffles et du bétail. Les feux de savane sont par essence très hétérogènes dans leur amplitude et leur fréquence dans l'espace et le temps. Leur occurrence peut impacter les déplacements des buffles et des vaches mais de manière ponctuelle et non régulière. Les précipitations sont également très localisées et conditionnent la disponibilité des ressources en eau et en fourrage en Afrique australe. Pour ces raisons, les eaux de surface et l'occupation du sol sont les deux indicateurs environnementaux qui ont été choisis pour modéliser spatialement les mouvements des buffles et des vaches car ils peuvent être efficacement caractérisés et discriminés dans l'espace et le temps à l'échelle du paysage via l'utilisation de la télédétection (Rumiano et al., 2020).

Une méthodologie simple en trois étapes, reproductible, a été développée pour caractériser la disponibilité spatiale et saisonnière des eaux de surface, pour discriminer les surfaces agricoles et pour déterminer l'occupation du sol à l'échelle paysagère, soit à une résolution spatiale de 10 mètres ([chapitre 4](#)). Des méthodes de classifications supervisées (pour la classification des eaux de surface et des surfaces agricoles) et non supervisées (pour les classifications de l'occupation du sol) basées sur l'approche pixels des images satellitaires open-source (i.e., Sentinel-2) ont été développées. Cette méthodologie permet de caractériser des environnements complexes et hétérogènes sur de larges zones à l'échelle du paysage où les données in-situ (par exemple des échantillons de paysage localisés par GPS, des connaissances empiriques sur les structures du paysage) sont manquantes ou inexistantes. L'ensemble des procédures de classification a été développé à l'aide de logiciels (i.e., QGIS) et d'environnements de programmation (i.e., R) libres, ce qui le rend accessible et reproductible même si les ressources informatiques et financières sont limitées. De plus, cette méthodologie peut être facilement appréhendée même par des non spécialistes en télédétection, ce qui accroît potentiellement son usage dans le champ disciplinaire de l'écologie.

Une approche de modélisation mécaniste spatialisée intégrant un modèle de particules autopropulsées (SPP) pour simuler les mouvements individuels et collectifs en relation avec les variations spatiales et temporelles de la disponibilité en eau de surface a été développée (voir [chapitre 6](#)). Les données de télémétrie des buffles des trois sites d'étude ont été utilisées comme données de référence pour les processus de calibration et de validation du modèle (voir [chapitre 6](#)). Le modèle mécaniste a été spatialisé en utilisant le langage métier Ocelet, spécialisé dans la modélisation de dynamiques spatiales (Degenne, 2012). Ce langage repose sur le concept de graphe d'interactions (Harary, 1969) afin de manipuler l'information géographique au sein d'un environnement de développement (voir [Chapitre 5](#)).

Le modèle mécaniste reproduisant les mouvements du buffle dans l'espace et le temps à l'échelle du paysage a ensuite été complété par d'autres entités telles que les vaches et l'occupation du sol pour modéliser les contacts entre une espèce animale sauvage et une espèce animale domestiquée sur les trois sites d'étude considérés (voir [chapitre 7](#)).

9.4 Principaux résultats

Revue littéraire :

Une analyse bibliographique approfondie (Rumiano et al., 2020) a été réalisée afin de consolider et de rassembler les connaissances actuelles sur les utilisations potentielles de la télédétection

pour étudier la sympatrie des ongulés sauvages/domestiques dans les environnements d'interface de savane d'Afrique australe et pour identifier les facteurs environnementaux qui influencent les mouvements des buffles et des vaches à l'échelle du paysage (voir [chapitre 3](#)). Au total, 327 références bibliographiques (e.g., articles scientifiques, thèses) ont été sélectionnées et analysées après référencement et utilisation de mots clé (i.e., "eau de surface" ; "précipitations" ; "pluie" ; "végétation" ; "feu" avec l'ajout des mots-clés suivants : "télédétection" ; "imagerie d'observation de la Terre" ; "couverture du sol" ; "utilisation du sol" ; "indice spectral" ; "radar" ; "optique" ; "savane"). Les eaux de surface, les précipitations, l'occupation du sol et les feux de savane sont apparus comme des facteurs environnementaux clés ayant un impact sur les mouvements des buffles et des vaches au sein des environnements de savane arborée d'Afrique australe. Les résultats de cette revue de la littérature scientifique soulignent la nécessité pour les écologistes du mouvement animal de renforcer leurs connaissances en matière de télédétection et/ou d'accroître les collaborations entre différentes disciplines scientifiques comme l'écologie fonctionnelle et la géomatique par exemple (voir [chapitre 3](#)) afin de caractériser plus efficacement les variables environnementales à différentes échelles spatiales et temporelles sur des zones d'étude où les données observées peuvent manquer ou trop coûteuses et difficiles à collecter.

Classification :

La précision de la classification supervisée des eaux de surface est très élevée pour les trois sites d'étude malgré quelques disparités (voir [chapitre 4](#)). En effet, la classification supervisée n'a pas été aussi efficace à Hwange/Dete par rapport aux deux autres sites d'étude. Les variations de précision dans la classification supervisée des eaux de surface de la série temporelle de Hwange/Dete sont également notables. Pour les deux autres sites d'étude, la précision de la classification reste stable pour l'ensemble de la série temporelle.

Concernant classification des surfaces agricoles, la précision de la classification supervisée des surfaces agricoles est optimale pour Hwange/Dete mais plus nuancée pour Gonarezhou/Malipati et Kruger/Pesvi avec un nombre équivalent de confusions entre les deux classes de classification (i.e. "zones agricoles" et "autres"). Cependant, la discrimination des surfaces agricoles pour Gonarezhou/Malipati et Kruger/Pesvi restent exploitables et sont avant tout concernées par des pixels faux positifs (voir [chapitre 4](#)).

Les classifications non supervisées de l'occupation du sol des trois sites d'étude selon la typologie choisie (voir [chapitre 4](#)) ont des résultats comparables. Pour les trois sites d'étude la classe des zones arbustives est principalement confondue avec la classe des forêts mixtes. La classe des forêts mixtes et des arbustes est également confondue avec la classe des forêts, bien que la confusion soit moins prononcée à Hwange/Dete. Dans l'ensemble, les classes de forêt, d'arbustes mixtes et de prairies et de sols nus sont bien classées (voir [chapitre 4](#)).

Modélisation :

L'approche de modélisation choisie a démontré comment un modèle mécaniste peut être spatialisé et combiné avec des données de télémétrie et de télédétection pour simuler les mouvements des animaux en relation avec une ou des variables environnementales caractérisées à l'échelle du paysage. Le développement de ce modèle a testé et confirmé la capacité d'un langage spécifique au domaine tel que Ocelet (voir [section 5.4.2](#)) à modéliser efficacement des entités hétérogènes (i.e. individus de buffles, troupeau de buffles, eau de surface) dans des systèmes complexes spatialisés et temporisés à travers leurs interactions ([chapitre 6](#)). Pour la première fois à notre connaissance, les mouvements des buffles à l'échelle individuelle et collective ont été simulés dans des environnements hétérogènes et sur trois sites d'étude différents par l'utilisation d'un modèle « Self-propelled particle » (SPP). Ce cadre de modélisation nécessitant peu de paramètres et reproductible peut être considéré comme une alternative aux outils de modélisation existants dans la compréhension des mouvements des animaux par rapport à la sélection de l'eau dans plusieurs contextes et environnements écologiques.

Le modèle de mouvements et de contacts entre les buffles et les vaches a démontré qu'avec un ensemble de règles simples combinant les besoins quotidiens en ressources de base (c'est-à-dire l'eau et les ressources fourragères) et les pratiques d'élevage (c'est-à-dire éviter les champs de cultures en croissance), les mouvements des buffles et des vaches, ainsi que leurs zones respectives et l'intensité des contacts dans trois zones d'interface différentes en Afrique australe, sont simulés et reproduits. L'observation des zones de chevauchement et de contact inter-espèces modélisées et observées dans l'espace et le temps (voir [chapitre 7](#)) donne une idée de la reproductibilité globale par le modèle des systèmes écologiques étudiés. Par exemple, au sein de paysages hétérogènes, c'est la distribution de l'eau de surface disponible qui concentre spatialement les mouvements des animaux autour des points d'eau et crée des interfaces potentielles entre espèces animales sauvages et domestiques. La nécessité pour les buffles et les vaches de chercher quotidiennement un point d'eau les contraint au sein d'une zone d'interface délimitée par la répartition spatiale de la ressource en eau et l'évolution de sa disponibilité. Le modèle parvient à reproduire cette dynamique spatio-temporelle (voir [chapitre 7](#)).

Cette étude révèle que la combinaison de la télédétection et de la modélisation spatiale pour mieux comprendre les mouvements et les contacts des buffles et des vaches dans les environnements de savane arborée semi-arides fournit un cadre opérationnel qui pourrait potentiellement être répliqué dans d'autres types d'interfaces où différentes espèces sauvages et domestiques interagissent. La capacité de produire des cartes de contacts potentiels peut, à terme, permettre d'estimer le risque, sa localisation et prioriser ainsi la surveillance. De plus,

l'implémentation d'un compartiment épidémiologique spatialisé dans le modèle mécaniste de mouvement et de contact déjà développé pourrait potentiellement améliorer la compréhension générale et l'appréhension de la transmission et de la circulation des pathogènes entre les espèces sauvages et domestiques à l'échelle spatiale des interfaces entre espaces communaux et aires naturels protégées.

9.5 Éléments de discussion et perspectives

La classification supervisée et non supervisée basée sur les pixels de l'imagerie satellitaire à moyenne résolution spatiale développée dans cette étude a réussi à caractériser avec précision les variables environnementales souhaitées (par exemple, l'eau de surface et la couverture végétale) à l'échelle du paysage tout en étant en accès libre, semi-automatique ainsi que reproductible. La télédétection est un domaine de recherche de plus en plus utilisée en écologie où de nombreuses méthodologies émergent, sont essayées, testées et discutées (Pettorelli, Laurance, et al., 2014). Ce développement de nouvelles méthodologies en conjonction avec un nombre croissant de capteurs satellite (He et al., 2015) pourrait potentiellement, par la combinaison et l'utilisation réfléchie de ces derniers, améliorer les résultats de classification obtenus dans cette étude. Plusieurs méthodes peuvent ainsi potentiellement être envisagées afin d'améliorer la méthode de classification développée dans le cadre de cette thèse : i) l'utilisation de l'imagerie satellitaire radar (SAR) pour détecter les surfaces en eau (Sankaran & Ratnam, 2013), ii) la combinaison des classifications orientées pixel et orientées objet (Blaschke et al., 2014; Lu & Weng, 2007), iii) l'utilisation d'algorithmes d'apprentissage profond comme la classification d'images satellitaires via l'utilisation d'un réseau de neurones convolutifs profonds (Minetto et al., 2019), iv) la technologie des systèmes d'aéronefs sans pilote (UAS) (par exemple, les drones) qui est de plus en plus utilisée en écologie (Anderson & Gaston, 2013; Baxter & Hamilton, 2018).

Bien que la généricité du modèle mécaniste des mouvements et des contacts ait été testée dans cette étude (voir [chapitre 7](#)), les résultats produits par le modèle et leurs incertitudes inhérentes n'ont pas été établis et évalués objectivement. En effet, les données d'entrée d'un modèle sont sujettes à des erreurs potentielles de mesure, d'absence d'informations, de plan d'échantillonnage, d'informations obsolètes, d'erreurs d'échelle et de lecture erronée ou de mauvaise conceptualisation des forces motrices et des mécanismes d'un système donné (Burrough et al., 2015). Par conséquent, en effectuant des analyses d'incertitude et de sensibilité sur le modèle, il serait potentiellement possible de fournir une compréhension sur la façon dont

les paramètres du modèle répondent aux changements opérés sur les données utilisées en entrée du modèle. L'analyse de sensibilité étudie comment l'incertitude dans la sortie du modèle peut être attribuée à différentes sources d'incertitude dans les entrées du modèle (Saltelli et al., 2006). Cette procédure analytique pourrait améliorer considérablement la capacité à déterminer le potentiel de généralité du modèle mécaniste développé tout en ajustant efficacement les paramètres du modèle pour corroborer la structure de ce dernier. Cela permettrait également d'identifier les régions critiques dans l'espace en fonction des données d'entrée, de déterminer les normes minimales de données d'entrées et d'établir les priorités pour la mise à jour du modèle.

La capacité de modéliser spatialement et temporellement les mouvements et les contacts entre la faune sauvage et le bétail à l'échelle du paysage offre un large éventail de possibilités pour étendre les fonctionnalités du modèle. Parmi ces fonctionnalités, on pourrait mettre en œuvre un compartiment épidémiologique où les mouvements et les contacts des deux espèces animales cibles en relation avec leur environnement direct (e.g., les eaux de surface et l'occupation du sol) seraient le point de départ de la modélisation des transmissions et des circulations d'agents pathogènes. Les transmissions et les circulations de pathogènes aux interfaces entre faune sauvage et bétail sont déterminées par le comportement des animaux, la structure sociale et le chevauchement spatial, mais aussi par les caractéristiques des pathogènes (e.g., les voies de transmission) ainsi que par des facteurs environnementaux et climatiques (e.g., la composition et la structure du paysage, la quantité de précipitations) (Plowright et al., 2017). Face à ce système multifactoriel, la sélection et la conception d'un compartiment de modélisation épidémiologique dans un modèle mécaniste déjà développé devront être adaptées en fonction des caractéristiques d'un pathogène spécifique ainsi que des données disponibles pour calibrer et évaluer une telle approche (Martínez-López et al., 2021). Plusieurs approches de modélisation peuvent être envisagées pour comprendre et appréhender les mécanismes impliqués dans la dynamique de la transmission des agents pathogènes, pour quantifier les taux de transmission, pour évaluer comment les mouvements et les contacts des populations animales en relation avec les variables environnementales influencent la transmission des agents pathogènes et, à terme, pour identifier les stratégies de contrôle optimales (Miller et al., 2019) : modèles basés sur les compartiments (par exemple, le modèle SIR (Susceptible, Infectious, or Recovered) multi-hôte) et modèles basés agents (e.g., modèles basés sur les réseaux).

Le modèle de mouvement et de contact développé dans cette thèse a suivi une approche pluridisciplinaire car il combine plusieurs domaines de recherche tels que la télédétection, la modélisation spatiale et l'écologie. Les capacités du modèle à intégrer des données spatialisées hétérogènes, à simuler à différentes échelles temporelles et spatiales, à considérer de multiples

espèces animales à l'échelle individuelle et collective, ainsi que sa modularité font de ce modèle mécaniste un outil utile pour aborder les questions de santé des populations animales à l'échelle des interfaces bétail/faune sauvage tout en envisageant de l'utiliser pour promouvoir l'approche « EcoHealth » (Charron, 2012). En effet, cette thèse pose les bases conceptuelles de la construction d'un modèle générique permettant de combiner des disciplines complémentaires. Le modèle développé peut déjà démontrer l'influence des variables environnementales sur les contacts et les déplacements d'une espèce animale sauvage et d'une espèce animale domestique à l'échelle du paysage dans son état actuel (voir [chapitre 6](#) et [chapitre 7](#)). A terme, après optimisation et amélioration, ce modèle mécaniste pourrait être un formidable outil pour appréhender, expliquer et prévenir le risque de transmission de pathogènes à l'interface bétail/faune sauvage tout en servant de catalyseur d'échange, de discussion et de transfert de compétences au sein de la communauté scientifique mais aussi auprès des populations locales et des divers acteurs concernés (e.g., institution publiques). Un tel outil méthodologique pourrait être bénéfique car il pourrait potentiellement convaincre, par la capacité de poser un diagnostic concret des contacts entre faune sauvage et domestiquée à l'échelle des interfaces, de la nécessité de changer radicalement les attitudes envers la faune sauvage (De Garine-Wichatitsky et al., 2021). Alors que les défis concernant la santé et le bien-être des populations humaines et animales ne cessent d'augmenter en raison du changement climatique et de la pression anthropique, il est urgent de considérer la faune sauvage davantage comme un atout que comme un problème à contrôler (du Toit et al., 2017) ainsi que de bien établir une utilisation stratégique collective et alignée des complémentarités écologiques entre le bétail et la faune sauvage afin de promouvoir une coexistence vertueuse (Fynn et al., 2016). Nous espérons humblement que cette thèse encouragera les approches pluridisciplinaires afin de résoudre collectivement les problèmes écologiques majeurs auxquels les interfaces bétail/faune sauvage sont confrontées en Afrique australe mais aussi dans d'autres parties du monde.

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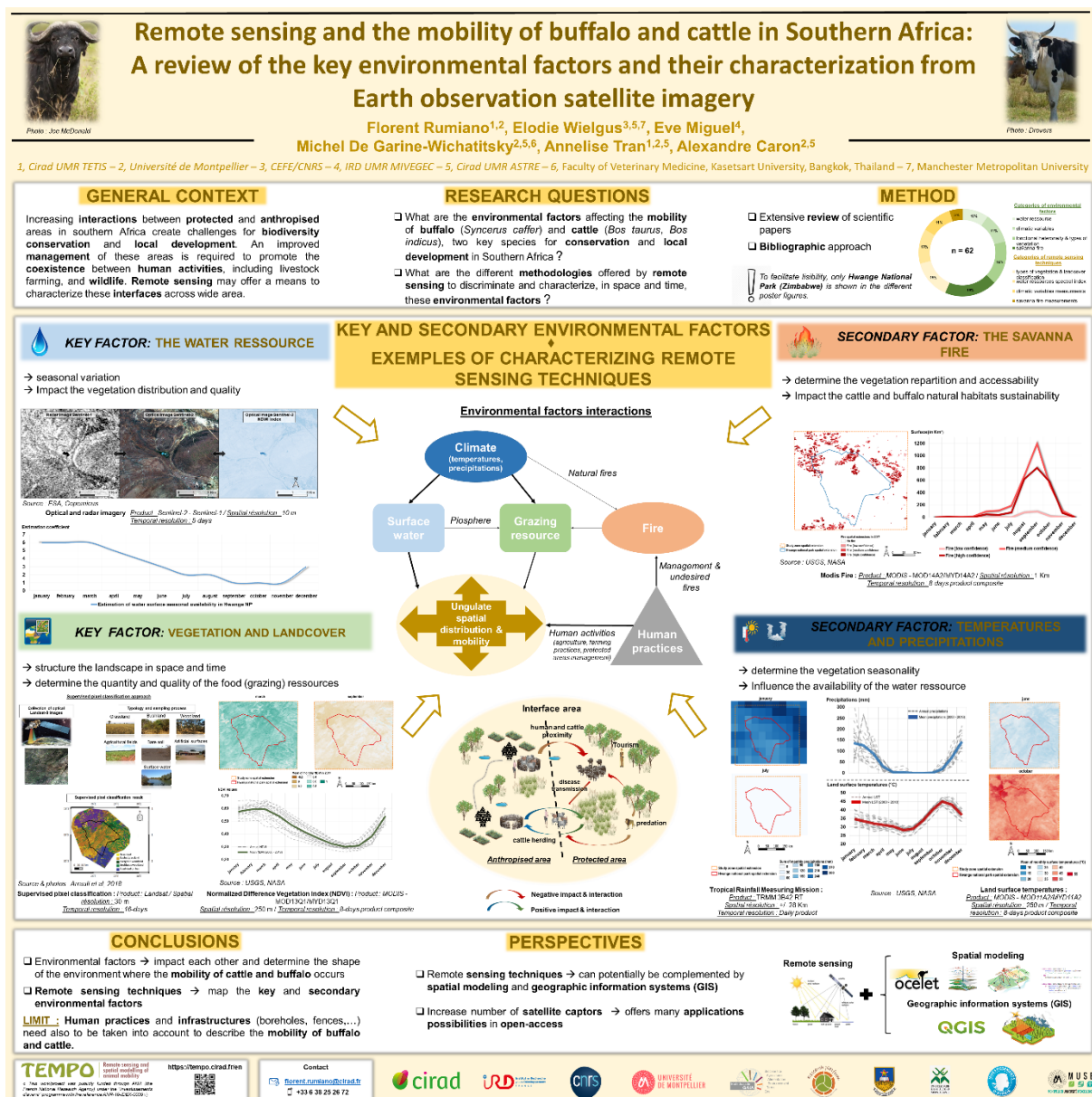
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List of poster, oral communications, publications, and award

1) Poster

- **Rumiano Florent, Wielgus Elodie, Miguel Eve, De Garine-Wichatitsky Michel, Tran Annelise, Caron Alexandre.** Remote sensing and the mobility of buffalo and cattle in Southern Africa: a review of the key environmental factors and their characterization from Earth Observation satellite imagery. Gordon Research Conference, Animal Movement as a Link Between Ecology, Evolution and Behavior, Barga, Italie, March 3rd 2019/ March 8th 2019. 2019. <https://www.grc.org/movement-ecology-of-animals-conference/2019/>



2) Oral communications

- **Gordon Research Conference**, Animal Movement as a Link Between Ecology, Evolution and Behavior, Barga, Italie, March 3rd 2019/ March 8th 2019. 2019
<https://www.grc.org/movement-ecology-of-animals-conference/2019/>
- **2019 and 2021 Ecole internationale de recherche d'Agreenium (EIR-A) seminars**, Dijon, France, April 1-5, 2019 and April 19-22, 2021
<https://www.agreenium.fr/taxonomy/term/118/all/feed/feed>
- **XXIVth The International Society for Photogrammetry and Remote Sensing (ISPRS) Congress**, Nice, France, July 5-9, 2021
<https://www.isprs2022-nice.com/>
- **REP21**, Les « Rencontres d'Ecologie des Paysages » (REP), Rennes, France, October 11-14, 2021
<https://rep21.sciencesconf.org/>

3) Publications

- **Rumiano F., Gaucherel C., Degenne P., Miguel E., Chamaillé-Jammes S., Valls-Fox H., Cornélis D., de Garine-Wichatitsky M., Fritz H., Caron A., and Tran A.** Combined use of remote sensing and spatial modelling: When surface water impacts buffalo (*Syncerus caffer caffer*) movements in savanna environments. *Int. Arch. Photogramm. Remote Sens. Spatial Inf. Sci.*, XLIII-B3-2021, 2021, 631–638.
<https://doi.org/10.5194/isprs-archives-XLIII-B3-2021-631-2021>
- **Rumiano F., Wielgus E., Miguel E., Chamaillé-Jammes S., Valls-Fox H., Cornélis D., Garine-Wichatitsky M.D., Fritz H., Caron A., Tran A.** Remote Sensing of Environmental Drivers Influencing the Movement Ecology of Sympatric Wild and Domestic Ungulates in Semi-Arid Savannas, a Review. *Remote Sensing*, 2020, 12, 3218.
<https://doi.org/10.3390/rs12193218>

4) Produced data

Landcover data:

- **Hwange study site:** Rumiano, Florent; Miguel, Eve; Valls-Fox, Hugo; Chamaillé-Jammes, Simon; Caron, Alexandre; Tran, Annelise, 2020, "Land cover map, Dete site, Hwange National Park, Zimbabwe", <https://doi.org/10.18167/DVN1/BJJZJV>, CIRAD Dataverse, V1
- **Gonarezhou study site:** Rumiano, Florent; Miguel, Eve; Caron, Alexandre; Dupuy, Stephane; Tran, Annelise, 2022, "Land cover map, Malipati site, Gonarezhou National Park, Zimbabwe", <https://doi.org/10.18167/DVN1/2SFOA5>, CIRAD Dataverse, V1

- *Kruger study site*: Rumiano, Florent; Miguel, Eve; Caron, Alexandre; Dupuy, Stéphane; Tran, Annelise, 2022, "Land cover map, Pesvi site, Kruger National Park, Zimbabwe", <https://doi.org/10.18167/DVN1/ZLIQIL>, CIRAD Dataverse, V1

Surface water:

- *Hwange study site*: Rumiano, Florent; Miguel, Eve; Valls-Fox, Hugo; Chamaillé-Jammes, Simon; Caron, Alexandre; Tran, Annelise, 2020, "Monthly surface water maps, Hwange National Park, Zimbabwe, 2018", <https://doi.org/10.18167/DVN1/KPSYME>, CIRAD Dataverse, V1
- *Gonarezhou study site*: Rumiano, Florent; Miguel, Eve; Caron, Alexandre; Dupuy, Stéphane; Tran, Annelise, 2022, "Monthly surface water maps, Gonarezhou National Park, Zimbabwe, 2018", <https://doi.org/10.18167/DVN1/O9COVW>, CIRAD Dataverse, V1
- *Kruger study site*: Rumiano, Florent; Miguel, Eve; Caron, Alexandre; Dupuy, Stéphane; Tran, Annelise, 2022, "Monthly surface water maps, North Kruger National Park, 2018", <https://doi.org/10.18167/DVN1/DAVZUY>, CIRAD Dataverse, V1

5) Award

- **Laureate of the Fulbright France** – French / American Commission, 2020 P.h.D. Fulbright National program, https://fulbright-france.org/laureats_list