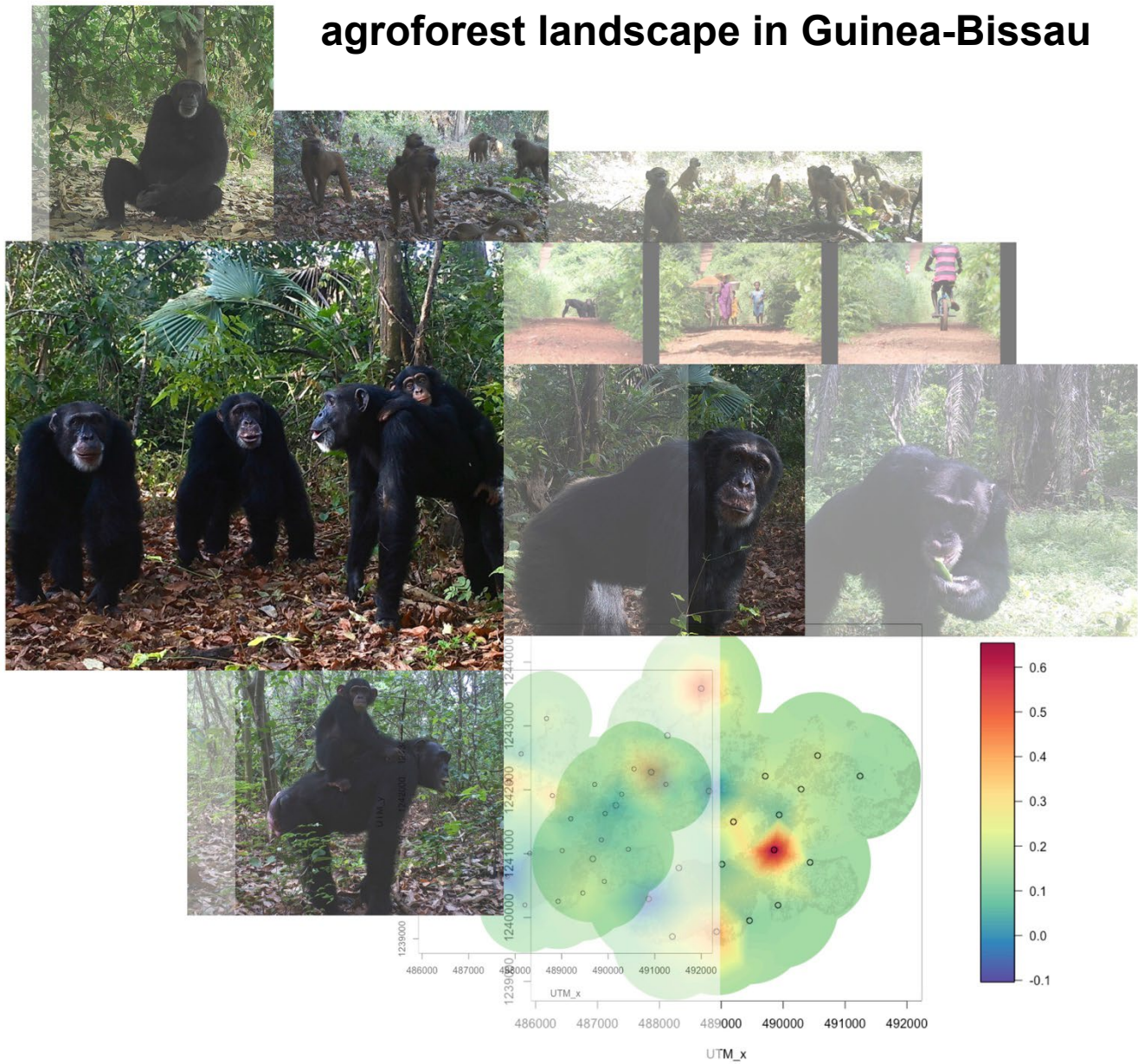


# Zooming in on human-wildlife coexistence: primate community responses in a shared agroforest landscape in Guinea-Bissau



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Thesis submitted in partial fulfilment of the requirements of  
the award of Doctor of Philosophy

September 2019



## Abstract

In this thesis I explore how humans and nonhuman primates, including chimpanzees, share the space in a coastal forest-agriculture-village landscape mosaic at Cantanhez National Park (NP), southern Guinea-Bissau (West Africa). I integrate data from arboreal and terrestrial camera traps with habitat surveys, remote sensing and interviews with local people. For the first part of this thesis I use arboreal and terrestrial camera trap occupancy modelling across the landscape to investigate patterns of occurrence of seven primate species. Based on the *landscape of fear* concept, in Part 2 I combine camera trap based-Bayesian spatiotemporal models with interview data to investigate chimpanzee-human interactions at one focal site within the park (Caiquene–Cadique). Some primates showed high sensitivity to anthropogenic influences particularly king colobus (*Colobus polykomos*) and Guinea baboon (*Papio papio*). King colobus was the rarest primate and showed a strong avoidance of villages. Baboons largely relied on forest, and in the rainy season their distribution was severely constrained to areas away from human land uses. The highly restricted spatial occurrence of king colobus and baboons is likely the result of intensive hunting pressures particularly in the recent past. In contrast, at the landscape scale chimpanzees showed a tendency to occur nearer villages in both dry and rainy seasons, suggesting that chimpanzees are able to find opportunities for feeding and nesting in areas highly frequented by people. When looking at the fine scale, chimpanzees in Caiquene–Cadique visited the villages but intensified the use of areas further away from them, showing some levels of risk avoidance. Chimpanzees also displayed a tendency to minimise the use of cultivated areas but used areas near roads more frequently. Chimpanzee home range use was also positively influenced by the spatiotemporal availability of ripe oil palm fruit, thus taking advantage of a dominant resource across both forest and the heterogeneous matrix. During the period of wild food scarcity, chimpanzees increased visits within the villages when orange, lime and papaya were available. Thus, when forest foods were scarce, risk avoidance was temporally overruled in favour of optimal foraging. Interview data with local people corroborated biological data and provided additional information on chimpanzee behaviour within villages. Based on local narratives, when foraging at the villages chimpanzees used different social groupings depending on the targeted resource, and behaved more boldly towards women and children during close interactions. My data emphasise the importance of using different spatial scale approaches and further highlight chimpanzee resilience and flexibility in human-dominated landscapes where people remain willing to share the space with them.



## Acknowledgements

First, I would like to thank my supervisors, Professor Catherine Hill, Dr. Kimberley Hockings and Professor Vincent Nijman for their guidance and support. Kate, your encouragement and mentorship throughout my PhD has been incredible. May your words of wisdom always be with me in all the future (life and work) adventures to come. Kim, you're an inspiration machine. Thank you for showing me the chimp way, both in the UK and in Cantanhez, and for always believing in me. Bring on the next project! Vincent, thank you for inspiring my interest in modelling, this was great fun! I would also like to thank Professor Amélia Frazão-Moreira for sharing her advice and knowledge about Guinea-Bissau, *muito obrigadu*. I am also grateful to Andrew Walmsley for teaching us how to climb trees safely, and to Dr. Matthew Silk for commenting on my chapter and providing advice on Bayesian modelling. I thank my examiners Professor Russell Hill and Dr. Giuseppe Donati for the great discussion during my viva and for their useful comments and recommendations.

For financial support, I thank Oxford Brookes University, the Mohamed bin Zayed Species Conservation Fund, Primate Society of Great Britain, International Primatological Society, Conservation International/Global Wildlife Conservation Primate Action Fund/Ms. Constance Roosevelt and Primate Conservation Inc. I am very grateful to the Instituto da Biodiversidade e das Areas Protegidas (IBAP) for their logistical support and permissions to conduct my research in Guinea-Bissau, specifically Dr. Alfredo Simão da Silva, Aissa Regalla, Dr. Justino Biaí, Dr. Abílio Rachid Said and *pape de dari* Queba Quecuta. To the Cadique Régulo Mamadu Camará and village representatives in Cantanhez, thank you for your support and for giving me permission to work in your forests. A big thank you also goes to the people who kindly gave me permission to set up camera traps in their orchards.

This thesis would have never materialised if it weren't for the hard work and commitment of my research team in Cantanhez: Iaia Tawél Camará, Mamadu Paulo Cassamá, Djibi Indjai, and Braima McIntosh Vieira. Thank you for showing me that anything is possible with a perfect team, and for teaching me so much about the chimps in Cantanhez. Iaia, *makina, bu ka ta kansa* – from fieldwork-day one to day 405, and then on your own to day 628. Thank you for your Olympic perseverance and for being an awesome accomplice.

Mamadu Paulo, the man of wisdom, thank you for guiding us always, me through the chimp trails and us all through the intricacies of life. A big thank you also goes to the awesome community guards and collaborators across Cantanhez who helped us in the forests. To all of you guys a massive *inuali*!

I will always be grateful to the many amazing people I've met and lived with in Cantanhez: Sale Camará, Nalu Indjai, Satu Indjai, Satan Cassamá, Abubacar Cassamá, Mansata Djallo, Duturna Djallo, Satu Cobe, Fatu Cande, Idrissa Indjai, Braima Indjai, Samba Djuma, Satu Serra, Abubacar Serra, Sadjo Djallo, Mbalo Djassi, Aua, Alimato, Adiato, Bebe, Mariama (3x), Fatim, Binta, Zoia, Fule, Seni, Kindo and Lama amongst many others. Mariama and Mamadu Djallo, thank you for your amazing support in Dulombi. Sadjo, thank you for unsuccessfully teaching me how to cook *warga*, and most of all thank you for dumping Zhou with me, the most precious gift I could ever be forced to receive. Mansata, *diarama* sister, partner in giggles and tears, you taught me more in the last three years than any school I've been to. Sorry for dumping Zhou with you, though we both know he's the luckiest to have you (and your *nene*, Saliu, Tomane, Alessandro and Fatumata).

Huge thanks go to Joana Bessa, for being the first to guide me in Guinea-Bissau before the PhD thing started and for being an amazing friend from then on, *ndiaaraaama*! I'm also grateful to you and Dr. Rosa Sá for saving my life twice. A big big thank you to Aimee, Chloë, Lydia and Sarah for your relentless support and the fun times during my write up. Chloë, yes, our competition was great, and what came out of it majestic. Aimee, thank you for the countless hours working together in the office, and for the much-needed mad adventures in-between!

To my family in Switzerland: my mum, dad and brother Ale, thank you for putting up with me. I will always be grateful for your incredible support, love and encouragement throughout my life. Thank you *zia* Livia, for being a source of inspiration ever since I was little. My Locarno crew: Nau, Isabel, Bullo, Arsu, Elin, Nahia and Liam, you guys are awesome – may we keep the goa, mountain and river fun going for many decades to come!

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## List of abbreviations

|      |                                                    |
|------|----------------------------------------------------|
| AIC  | Akaike's information criterion                     |
| DBH  | Diameter at breast height                          |
| DIC  | Deviance information criterion                     |
| CI   | Confidence intervals/Credible intervals            |
| CRT  | Cantanhez research team (led by K Hockings)        |
| FAI  | Food availability index                            |
| IBAP | Instituto da Biodiversidade e das Areas Protegidas |
| INLA | Integrated Nested Laplace Approximation            |
| IUCN | International Union for Conservation of Nature     |
| Kr   | Kriyol                                             |
| ML   | Maximum likelihood                                 |
| NP   | National Park                                      |
| NDVI | Normalised Difference Vegetation Index             |
| PL   | Penalised likelihood                               |
| RDF  | Relative detection frequency                       |
| SD   | Standard deviation                                 |
| SE   | Standard error                                     |



## CHAPTER 1

# Introduction



## 1.1 Shared landscapes

### 1.1.1 Humans as ecological engineers

Humans are the world's top ecological engineers, influencing abiotic and biotic factors across our planet (Chapin III et al. 2011; Lewis and Maslin 2015), shaping the structure of landscapes and biodiversity communities (Newbold et al. 2015). The majority of Earth's terrestrial surface today is impacted by humans to varying degrees (Ellis and Ramankutty 2008). Based on empirical data, Ellis and Ramankutty (2008) identified eighteen *anthropogenic biomes*, consisting of heterogeneous landscape mosaics of various types of land uses and human population densities, from urban areas to remote forests. The authors proposed the concept of anthropogenic biomes to highlight how contemporary ecosystem dynamics are almost never disconnected from humans, and that ecologists should explicitly take this into account in their research frameworks (Boivin et al. 2016; Ellis and Ramankutty 2008).

Anthropogenic landscapes are intrinsically complex environments. The myriad of ways in which human societies, groups and individuals organise and utilise the space and resources can affect the ecosystem in numerous ways (Western 2001). At the global scale, pervasive habitat loss and overexploitation since the 1950s are clearly having deleterious effects on biodiversity (Dirzo et al. 2014; Dobson et al. 2006; Ripple et al. 2016). About a third of the world's vertebrate taxa are estimated to be undergoing population declines and geographical range contractions (Ceballos et al. 2017). Humans are directly altering biodiversity community assemblages, indirectly changing interspecific interactions and ecosystem dynamics (Ripple and Beschta 2012). Direct and indirect effects of human activities will differ across localities, depending on the scale and type of activities, as well as species resilience to change. The species that are able to persist or even thrive in anthropogenic environments must undergo a shift in their ecological behaviour; from relying exclusively on wild resources to taking advantage of human or human-modified space for food and shelter. Many anthropogenic environments still retain significant biodiversity, particularly where smaller-scale human land uses are intertwined with natural habitats and where hunting pressure is low (Ehlers Smith et al. 2018; Estrada et al. 2012; Heinicke et al. 2019; Schroth et al. 2004). These types of shared landscapes offer the opportunity to uncover a multitude of human-wildlife interactions and co-occurrence mechanisms, as well as highlighting

patterns of behavioural and ecological flexibility in wildlife (Candolin and Wong 2012; Chazdon et al. 2009; Hockings et al. 2015).

### 1.1.2 Primates in shared landscapes

Nonhuman primates represent one of the most diverse taxonomic groups of terrestrial mammals, including at least 504 species belonging to 80 genera, (Estrada et al. 2017; Galán-Acedo et al. 2019a; ITIS 2019). Primates are present in nine out of 14 of the world's terrestrial biomes (Olson et al. 2001), from mangroves (e.g. lemurs in Madagascar) and semi-arid deserts (e.g. hamadryas baboons *Papio hamadryas* in Yemen) to temperate coniferous and broadleaf forests on snowy mountains (e.g. Yunnan snub-nosed monkeys *Rhinopithecus bieti* in China), as well as across tropical and subtropical forests and savannahs where most taxa are found (Al-Safadi 1994; Cui et al. 2006; Gardner 2016; Nowak 2019; Rowe and Myers 2016). Some species, such as chimpanzees (*Pan troglodytes*), are socio-ecologically equipped to inhabit multiple ecological biomes including arid savannas where they thermoregulate in natural caves (Pruetz 2007), coastal forest-mangroves (K Hockings unpubl. data; this thesis) as well as tropical lowland and montane rainforests (e.g. Morgan and Sanz 2006; Stanford and Nkurunungi 2003). The majority of primate geographical distributions overlap with anthropogenic biomes, most of which are croplands (Ellis and Ramankutty 2008; Estrada et al. 2012). Over half of the extant primate species are threatened with extinction mainly due to large-scale agriculture and hunting (Estrada et al. 2017; IUCN 2019). Subsistence agriculture and agro-forest systems impact a large proportion of primates, and the effects of habitat change within these landscapes vary across contexts and species (e.g. Estrada et al. 2012; McLennan et al. 2017; Schwitter et al. 2011). In heterogeneous cropland mosaics primates have shown diverse adaptive behaviours, from exploiting arboreal fences as corridors (Chacón and Harvey 2006; Nekaris et al. 2017) to using agricultural plantations for feeding, traveling and resting (for a review: Estrada et al. 2012). Some primates behave more cryptically when feeding on crops (Wallace and Hill 2012), others increase group cohesion and cooperation to deal with increased exposure to risks (Hockings 2007; Hockings et al. 2006, 2012; Oxley 2019).

Wildlife persistence in human-modified environments depends on landscape permeability, impacting the ability of animals to disperse and explore areas outside their home range. By

exploiting different parts of the agriculture-forest interface, primates decrease reliance on remnant patches (Estrada et al. 2012; Galán-Acedo et al. 2019b; McLennan et al. 2017). However, to be able to disperse across the matrix primates must also face increased potential risks associated with exposure to humans, including hunting and/or retaliatory aggressive behaviour by people in response to crop or livestock damage (Hill and Webber 2010; Hockings and McLennan 2016; Ripple et al. 2016). These risks are often species-specific and lay along a dynamic continuum, where at one end primates that are considered as ‘pests’ and are also commonly consumed for meat and at the other end species are protected by cultural beliefs, social norms or strict law enforcement and/or that seem to bear little costs to human livelihoods (Hill and Webber 2010). Therefore, in general terms co-existence capacity in agricultural mosaics largely depends on the landscape matrix providing enough or alternative resources including food and structural connectivity, the species’ socioecological responses, and the ultimate willingness of people to share the space and resources with them. The great diversity of primate adaptive behaviours and the various ways in which humans interact with and behave towards primates provide opportunities to uncover fascinating insights into human-wildlife co-occurrence dynamics.

## **1.2 Research approaches in human-modified landscapes**

### **1.2.1 Zooming in: from landscape to local scale (and vice versa)**

Research at different spatial scales can reveal different aspects of a studied phenomenon. Ecological studies at the population scale help identify environmental and interspecific elements that regulate species distribution and abundance (e.g. Ehlers Smith et al. 2019; Farris et al. 2014). Population data can be incorporated into range-wide (meta)population distribution models (Heinicke et al. 2019), for example to understand environmental determinants of migration and extinction dynamics (Gilpin 2012; Hanski 1998). Recently, primate ecologists have begun highlighting the scientific need for a landscape approach in (meta)population studies (Arroyo-Rodríguez and Fahrig 2014; Galán-Acedo et al. 2019b). In the context of shared environments, a landscape perspective consists of a spatially explicit approach that takes into account the heterogeneous matrix as well as the remnant patches. This approach allows us to incorporate the effects of the structural complexities of the

landscape, and not only habitat loss, to draw inferences on species responses to habitat fragmentation (Arroyo-Rodríguez and Fahrig 2014; Fahrig et al. 2019; Wiens et al. 1993).

Landscape-level perspectives can generate further questions which may be better addressed using fine-scale approaches. An example would be if we were looking to measure animal responses in relation to resource availability; if key resources were required to be finely measured *in situ* other than via remote sensing (e.g. fruit availability for frugivores vs. grassland land cover for grazers), small scale studies would demand substantially less sampling effort. Importantly, prior information gathered through case studies plays a key role in informing and formulating hypotheses for population-level studies, for example to select sampling areas and covariates relevant to the ecology and social behaviour of the species of interest. In essence, combining a landscape-scale approach with ‘focal-group’ studies provides us with the opportunity to quantify population dynamics and reveal socioecological mechanisms that may help explain those large-scale patterns, particularly within complex and fast-changing environments.

### **1.2.2 Incorporating social sciences to understand co-occurrence dynamics**

Understanding the complexities of human-wildlife interactions require a cross-disciplinary approach (Hill et al. 2017; Parathian et al. 2018; Setchell et al. 2017). Data from social sciences can reveal important socio-political and cultural contexts influencing human perceptions and behaviours towards wildlife (Hill et al. 2017; Rust et al. 2017; Sousa et al. 2017). Information from people living in proximity with wildlife can also provide additional elements to understanding species behaviours, including habitat and resource use (Sousa et al. 2014; Starr et al. 2011) as well as behavioural responses to encounters with humans. Social science can also highlight human concerns over sharing space with wildlife, which have important implications for long-term coexistence and the development of effective conservation policy (Hill and Wallace 2012; Hill and Webber 2010; Hockings and McLennan 2016).

### 1.3 Study aims

The main goal of this thesis was to understand how humans and primates share the space in a forest-agriculture-village mosaic in southern Guinea-Bissau. My aims were to (i) identify environmental and anthropogenic factors influencing the spatial occurrence of seven sympatric primates across the heterogeneous landscape in central Cantanhez National Park (NP), and (ii) examine how chimpanzees balance between optimal foraging and risk mitigation strategies throughout the year within their human-dominated home range.

This thesis complements previous work on primate responses to heterogeneous landscapes (Galán-Acedo et al. 2019b) and chimpanzee ecology and behaviour in anthropogenic environments (Garriga et al. 2019; Hockings 2007; McLennan 2010; Oxley 2019). This was the first study to investigate an unhabituated primate community across different spatial scales within a human-dominated environment. In addition, I used the *landscape of fear* framework (Gaynor et al. 2019; Laundré et al. 2001) which has been employed to examine predator-primate relationships (Burnham and Riordan 2012; Coleman and Hill 2014; Emerson et al. 2011; Willems and Hill 2009), but rarely human-primate interactions (but see Nowak et al. 2016; Oxley 2019). This is the first study to make use of the *landscape of fear* concept in the context of human-chimpanzee interactions.

The applied side of this research assessed the effectiveness of arboreal and terrestrial camera traps to identify mechanisms of co-existence between people and primates in anthropogenic environments. Furthermore, I wanted to examine how information from people living in close proximity to chimpanzees contributes to our understanding of chimpanzee behaviour, and how local people's knowledge and experiences can be incorporated into conservation management strategies that help increase co-existence capacity.

## 1.4 Thesis structure

Chapter 2 presents an overview of the study area, study species and methods.

Chapter 3 describes the landscape in central Cantanhez NP based on remote sensing analysis and presents the structural characteristics and species composition of different habitats based on vegetation surveys. Additionally, Chapter 3 provides details of availability of chimpanzee wild and cultivated foods.

In Part 1 (Chapters 4 and 5) I use a landscape-scale, camera trap approach typically applied to carnivore and mammal community research (Carter et al. 2012; Khorozyan et al. 2014; Oriol-Cotterill et al. 2015; Valeix et al. 2009). I draw inferences using occupancy models, an established method in population ecology (Bailey et al. 2014). Chapter 4 focuses on arboreal primates testing the efficacy of arboreal camera traps in agro-forest mosaics. In Chapter 5 I use terrestrial camera traps to examine anthropogenic factors affecting the temporal and spatial occurrence and activity patterns of four primate taxa.

In Part 2 (Chapters 6 and 7) I use a cross-disciplinary approach to examine chimpanzee responses to a human-specific *landscape of fear* at Caiquene–Cadique. In Chapter 6 I employ spatiotemporal modelling with INLA, a novel approach for Bayesian modelling approximation (Blangiardo and Cameletti 2015), to identify risk-related and resource factors affecting the chimpanzee intensity of space use within their home range across a full year. In Chapter 7 I use social sciences methods (Newing 2010) to unravel people’s perceptions of chimpanzee risk-taking behaviour and foraging strategies at the villages, whilst highlighting some concerns over living in close proximity to chimpanzees at this site.

In Chapter 8 I summarise my results and discuss the implications and opportunities for long-term co-existence between humans and primates in Cantanhez NP. I also provide recommendations for future research on primates in anthropogenic landscapes.

## CHAPTER 2

### Study area, study species and overview of methods



## 2.1 Study area

### 2.1.1 Location, climate and habitat

#### *Guinea-Bissau: climate*

Situated along the West African Atlantic coast, Guinea-Bissau includes 36,125 km<sup>2</sup> of National territory of which 78% consists of terrestrial land including the 88 Bijagós islands. Guinea-Bissau lies within the Guinean forest-savannah mosaics, a biodiverse ecoregion buffering the Guinean moist forests in the south and the West Sudanian savanna in the north (Olson et al. 2001). The climate in Guinea-Bissau is characterised by a rainy season from mid-May to the end of October and a long dry season from November to mid-May (Figure 2.1). During the 2017 rainy season the average monthly rainfall in central Cantanhez NP was 391.8 mm (range: 92.7–662.9 mm, total: 2350.5 mm), corresponding to 172.5 mm above the 1991–2016 national average (World Bank 2019). The dry season is characterised by a lack of rainfall and higher temperature fluctuations. In July 2017 – July 2018 January and May were the coldest and hottest months, respectively.

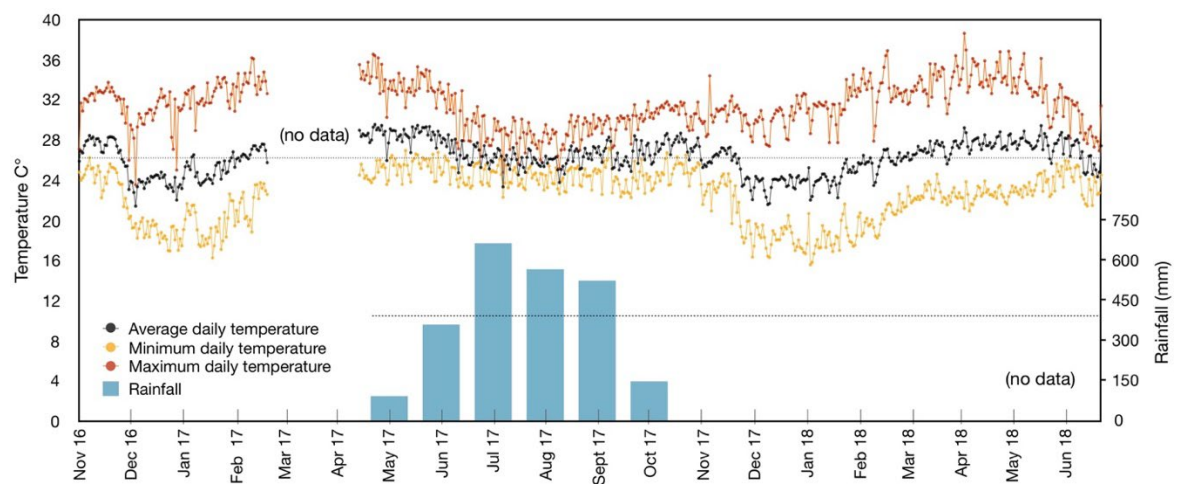


**Figure 2.1**

Climatic data from central Cantanhez NP during the study period (recorded from 15 November 2016 until 6 July 2018) showing daily mean, minimum and maximum temperature, and total monthly rainfall. Dotted lines represent annual average temperature (7 July 2017 – 6 July 2018) and rainfall (May – October 2017). Missing data include temperature (6 March – 23 April 2017) and rainfall (May and June 2018).

### *Cantanhez National Park*

At present, 16% and 10% of the terrestrial and marine territory of Guinea-Bissau lays within Protected Areas. Cantanhez National Park (NP, N11° 14.287' W15° 02.281') is located in the Tombali region in the south of the country bordering Guinea-Conakry (Figure 2.2). The park consists of a 1067 km<sup>2</sup> landscape covering the Cubucaré peninsula, which is enclosed by two estuaries, Rio Cacine and Rio Cumbidja. The landscape in Cantanhez NP is characterized by a mosaic of coastal sub-humid forest patches, mangroves, savannah grassland, woodland and agriculture, including mostly cashew orchards, shifting cultivation upland fields and mangrove swamp rice fields. In Chapter 3 I provide details about the landscape and vegetation structure in central Cantanhez NP. A network of roads and c. 200 villages and settlements are present across the park. At the time of this study, only small roads were present (c. 6m-wide the larger roads) and most of them were in poor conditions. The majority of traffic consisted of people traveling on foot, bicycles and motorbikes. Four-by-four vehicles, trucks and more rarely cars would also be used across the park. Trucks transporting goods to and from Bissau via the north of the park were also often used by local people as a mode of public transport. Due to the road conditions, particularly in the rainy season vehicles would often get stuck. In 2018 with funds from the European Union, efforts to improve the roads began and as of February 2020, the main road dissecting the north of the park (Guiledje to Bedanda) consisted of a 10-15m-wide gravel road. Renovation of the main road section in the central-southern part of Cantanhez NP began in 2019. This road will consist of a smaller version of that in the north (Q Quecuta, pers. Comm.).

The study area in Chapters 4 and 5 (Part 1) consisted of the central part of Cantanhez NP, whereas in Chapters 6 and 7 (Part 2) I focused on one site within my study area (Caiquene–Cadique).

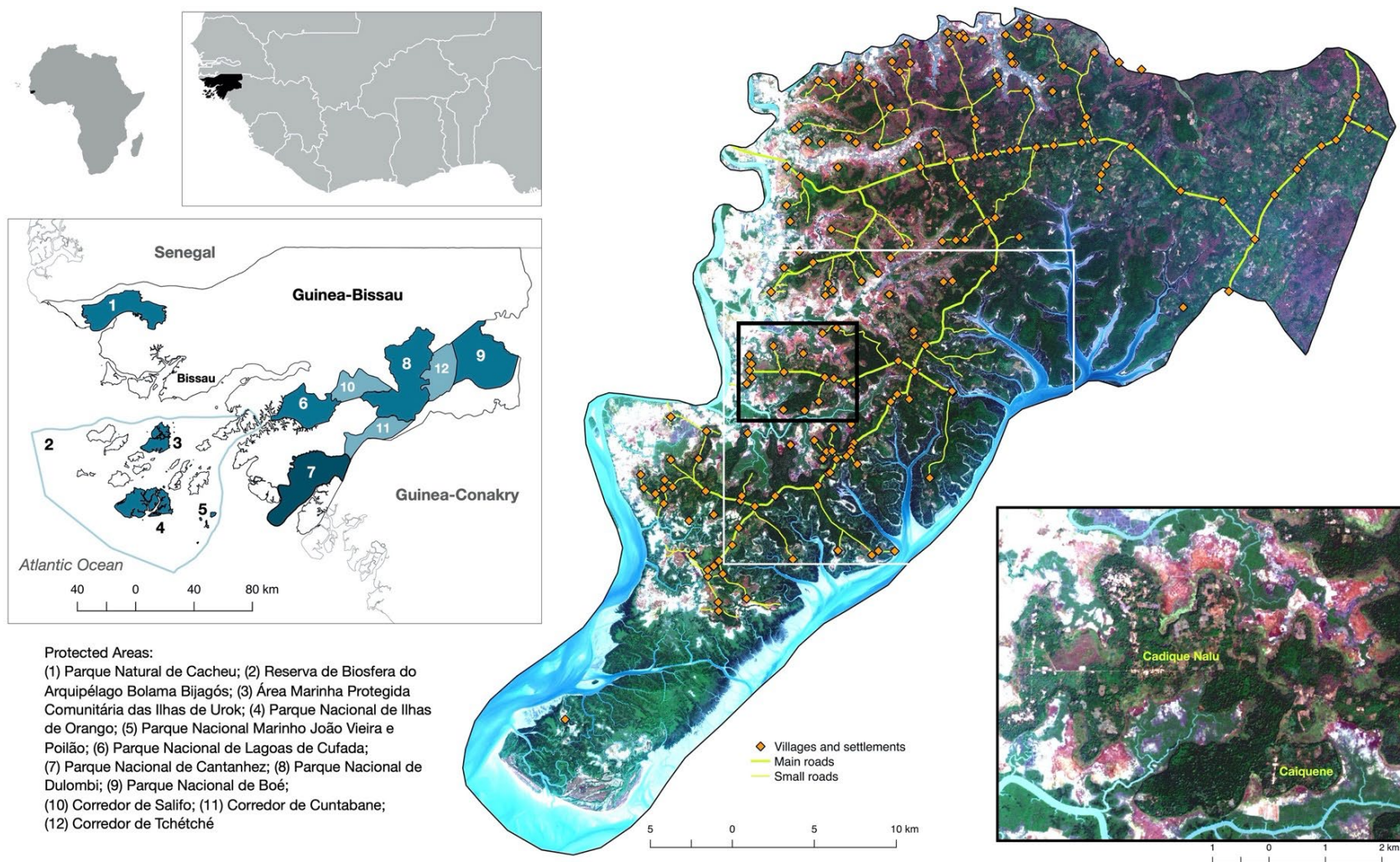


**Figure 2.2**

Map and location of Cantanhez National Park, showing villages and roads within the park. The white line at the centre of the park indicates the study area for Chapters 4 and 5; the detail of Caiquene-Cadique represents the study area for Chapters 6 and 7. Satellite imagery was downloaded from Sentinel Hub (imagery date: 25<sup>th</sup> January 2017).

### 2.1.2 People

Cantanhez was officially gazetted as a National Park in 2011 under the management of IBAP (Instituto da Biodiversidade e das Áreas Protegidas), the autonomous governmental institute with the mandate of managing biodiversity and Protected Areas in Guinea-Bissau. The park is managed following the IUCN Category V model for Protected Areas (IUCN 2016), including 14 formally protected forest patches as well as zones allocated to sustainable human/agricultural development. The central part of the Cubucaré peninsula, which includes the protected forests, is traditionally and legally regarded as the homeland of the Nalu people, the first ethnic group to colonise this area (Parathian et al. 2018). Nalu chiefs, as well as representatives from various ethnic groups inhabiting villages close to the protected forests, participate in the management of the park through meetings with IBAP park staff.

About 25,000 people across c. 200 villages and settlements are present inside Cantanhez NP, including mainly Nalu, Balanta, Fula, Sussu and Mandinga, but also Tanda, Pepel, Bijagos and Djakanka among others. The majority of people in Cantanhez NP are subsistence farmers practicing shifting agriculture, which includes mainly groundnuts (*Arachis hypogaea*) and rice (*Oryza glaberrima*, upland varieties). Maize (*Zea mays*), sugar cane (*Saccharum officinarum*), pigeon pea (*Cajanus cajan*) and cassava (*Manihot esculenta*) are also grown in shifting cultivation fields. Mango (*Mangifera indica*), orange (*Citrus sinensis*), lime (*Citrus auratifolia*), baobab (*Adansonia digitata*) and papaya (*Carica papaya*) are commonly grown within or bordering the villages. Mango and baobab are also present in abandoned villages. Mangrove swamp rice (*O. glaberrima*, mangrove swamp varieties) is cultivated along the buffer between mangrove forests and the forest edges. Importantly, farmers increasingly grow cash crop cashew orchards (*Anacardium occidentale*), which are prevalent across Cantanhez NP (cashew orchards account for c. 9% of the terrestrial land use in the central part of the park, Chapter 3). Following governmental incentives and the liberation of trade, in the 1990s cashew nut farming increased sharply across the country including Tombali (Havik et al. 2018; Temudo et al. 2015; Temudo and Abrantes 2014). The period of cashew crop expansion also coincided with an outbreak of an unknown disease that wiped out banana (*Musa* spp.) plantations across the Cubucaré peninsula (A Frazão-Moreira, pers. obs). At present, cashew represents the main source of financial income for Bissau-Guinean rural farmers and about 90% of the national export revenues (Havik et al.

2018). Cashew is increasingly sown in land used for shifting cultivation during the groundnuts crop growing period, replacing the fallow stages and increasing further demand for agricultural land (A Frazão–Moreira, pers. Comm.).

In addition to farming, local people in Cantanhez NP practice fishing and livestock keeping, as well as harvesting forest resources particularly oil palm and bushmeat. Hunting of certain species, including rodents, wild pigs and duikers is legal within agricultural zones; however, it is also frequently carried out inside protected forests. Despite being legally protected, monkeys are commonly hunted for bushmeat.

Untarmacked roads are present throughout the park. At the time of my fieldwork roads in Cantanhez NP were relatively small (from c. 8m wide in the north to 3-5m wide in the central part of the park). Road traffic included mostly people travelling on foot or bicycles, as well as motorbikes and occasionally trucks and 4x4 vehicles.

## **2.2 Study species**

My study species consist of the seven primates inhabiting central Cantanhez NP, including six diurnal and one nocturnal species (Table 2.1). Three primates, namely Western chimpanzees, Temminck's red colobus and king colobus are classified as threatened by the IUCN Red List of Threatened Species (IUCN 2019). In Part 1 of this thesis (Chapters 4 and 5) I present research on all seven taxa, whereas in Part 2 (Chapters 6 and 7) I will focus on western chimpanzees.

**Table 2.1**

Primate species present in central Cantanhez NP.

| Substrate use   | Activity | Common name            | Scientific name                       | Adult body weight (kg) | Diet                                                                         | Hunted in CNP?  | IUCN Status          |
|-----------------|----------|------------------------|---------------------------------------|------------------------|------------------------------------------------------------------------------|-----------------|----------------------|
| Semiterrestrial | ☀        | Western chimpanzee     | <i>Pan troglodytes verus</i>          | ♀ 47 / ♂ 60            | Omnivorous, ripe fruit specialist, plus insects, animal prey, roots, flowers | No <sup>1</sup> | EN (CR) <sup>2</sup> |
|                 |          | Guinea baboon          | <i>Papio papio</i>                    | ♀ 12 / ♂ 23            | Omnivorous, incl. crabs, insects, small animal prey, seeds, roots, fruit     | Yes             | NT                   |
|                 |          | Green monkey           | <i>Chlorocebus sabaeus</i>            | ♀ 3.3 / ♂ 5.3          | Omnivorous, incl. crabs, insects, seeds and fruit                            | Yes             | LC                   |
| Arboreal        | ☾        | Campbell's monkey      | <i>Cercopithecus campbelli</i>        | ♀ 2.7 / ♂ 4.5          | Frugivorous mainly, plus insects and flowers                                 | Yes             | LC                   |
|                 |          | Temminck's red colobus | <i>Piliocolobus badius temminckii</i> | ♀ 5.2 / ♂ 6.5          | Folivorous-frugivorous                                                       | Yes             | EN (CR) <sup>3</sup> |
|                 |          | King colobus           | <i>Colobus polykomos</i>              | ♀ 0.3 / ♂ 9.9          | Folivorous, plus seeds and unripe fruits                                     | Yes             | VU (EN) <sup>4</sup> |
|                 |          | Demidoff's galago      | <i>Galagoideus demidoff</i>           | ♀♂ 0.06                | Mainly insectivorous, plus fruit and gum                                     | No              | LC                   |

<sup>1</sup>Although chimpanzees in Cantanhez NP are not hunted for bushmeat, they may sometimes be killed over competition of cultivated foods (oranges in particular) and are accidentally caught in rope snares set up for other animals. See Category 1.2 and 2.1 in Williamson (2018).

<sup>2</sup>Endangered species, Critically Endangered subspecies.

<sup>3</sup>Listed as an Endangered species on the 2008 IUCN Red List assessment but will be updated to a Critically Endangered subspecies based on the 2016 assessment (C Schwitzer, pers. Comm.).

<sup>4</sup>Listed as Vulnerable on the 2008 IUCN Red List assessment but will be updated to Endangered based on the 2016 assessment (C Schwitzer, pers. Comm.).

Sources: Adie (1996); Davies and Oates (1994); Galán-Acedo et al. (2019); Horrocks (1986); Jungers and Susman (1984); Smith and Jungers (1997).

## **2.3 Data collection**

To achieve my research aims I combined methods from both biological and social sciences. These included camera trap surveys, vegetation plots, phenological monitoring as well as participant observation and interviews with local people. To maximise the camera trap photographic capture of all primate species, I used terrestrial and arboreal camera traps. In addition to the above methods, throughout the study period I used GPS to record primate presence (from direct observations, vocalisations and signs), human activity (e.g. signs in the forest, roads and paths) and to gather habitat type ground truth data for Chapter 3.

### **2.3.1 Study period and fieldwork team**

The overall period of fieldwork was between October 2016 and July 2018. For Chapter 4 and 5, I deployed camera traps between October 2016 and March 2017, coinciding with the first half of the 6-month long dry season. The second camera trap deployment period, coinciding with the rainy season, was conducted between July and October 2017 (Chapter 5 and partially Chapter 6). The full-year monitoring of chimpanzees in Caiquene–Cadique (Chapter 6) included camera trap data from July 2017 until July 2018. Participant observation was carried out throughout the fieldwork period and semi-structured interviews with local people were conducted between September and November 2017.

The fieldwork team included one to five local field assistants and myself. The field assistants included professional field guides Iaia Tawél Camará, who worked full-time during the entire study period, and Mamadu Paulo Cassamá, who worked full-time in October 2016 – February 2017. Community forest guard (now IBAP Park guard) Braima McIntosh Vieira was employed in October – November 2016. Community forest guard (now IBAP Park guard) Djibi Abu Indjai was employed part time throughout the study period. The team also comprised 12 additional community forest guards who were employed when working in their respective villages/forests. Full-time field assistants were paid a fixed monthly salary, part-time community forest guards were paid a daily salary.

### **2.3.2 Ethical approval**

This research involving wild unhabituated primates was non-invasive and complied with the ethics guidelines detailed by the Association for the Study of Animal Behaviour (UK) and to the legal requirements of Guinea-Bissau in which the research was conducted. The research was conducted on protected species in Cantanhez NP and permission was obtained from IBAP. Research permission was also obtained from local authorities (see more details below). The human part of this research, including interviews and management of camera trap data including people was fully approved by the University Research Ethics Committee at Oxford Brookes University (see Appendix 2.1 for letter of approval).

### **2.3.3 Camera trapping in anthropogenic habitats: informing people**

A total of 32 villages are present within my study area. Talking to and obtaining permission from local people to work in their forest and non-forest areas was crucial for developing good working relationships. Before starting data collection, I consulted with the two regional chiefs (*Régulos*) whose areas of jurisdiction included several villages and forests. I presented the research objectives and sought permission to conduct research within their areas of jurisdiction. In addition, I asked permission from local people in each village, which was usually done as work progressed and before entering forests. My fieldwork team and I talked about the objectives of my research to the village chiefs or committee members, including women, present on the day we visited. While research with the use of camera traps was previously conducted at two forest sites (2013 – 2015, K Hockings, unpubl. data), the majority of people we talked to were unfamiliar with camera traps. We explained how camera traps worked (heat-motion sensor) and sometimes showed the equipment and examples of camera trap images. As well as describing my research objectives, we emphasised that camera traps were used with the purpose of conducting research on animals, particularly primates, and if people were to be photographed, images would not be shown to anyone and would only be reviewed and managed by me. In several instances people offered information about specific locations or paths that animals were known to use, whether in forest, mangroves or orchards. Once camera traps were deployed, my team and I informed people about the approximate whereabouts of the cameras. All camera traps in human land uses (orchards, by cultivated fields and villages) were deployed with permission and

involvement from the farmers. Farmers would normally be present during camera set ups. We ensured that farmers were aware that people would be recorded on cameras frequently and that we expected farmers to go on with their business as usual. Again, I emphasised that camera trap data would be kept entirely anonymous.

#### **2.3.4 Study design Part 1: landscape**

The sampling design for Part 1 followed a landscape approach with sampling points spread across forest fragments and the heterogeneous matrix (Galán-Acedo et al. 2019b). I followed an occupancy modelling-based survey design, which involves a number of independent points sampled over a period of time (MacKenzie 2006). Similar to other survey-based sampling methods (e.g. distance sampling Buckland et al., 2005), occupancy modelling accounts for imperfect detection, which is the problem when a species is not recorded even though it is present. Occupancy enables one to model both occupancy ( $\psi$ ) and detection probability ( $p$ ), with the possibility to incorporate covariates (MacKenzie et al. 2002). Ideally, for a camera trap-based occupancy study,  $\geq 1800$  camera trap days (i.e. the sum of number of days for each active camera) locations are needed (Rovero et al. 2013). To select sampling sites, prior to fieldwork I used QGIS to place a grid over my study area. The grid comprised 2 km<sup>2</sup> cells with each cell containing one sampling point. I transferred the sampling points into Garmin BaseCamp<sup>TM</sup> and downloaded the latest BirdsEye satellite imagery covering my study area. I discarded sampling points that fell onto rivers and permanently flooded mangrove areas. I then uploaded the map and sampling points in a GPS (Garmin GPSMAP 64s). Additional details on camera trap sampling across the study area are provided in Chapters 4 and 5.

#### **2.3.5 Vegetation plot data for Part 1 occupancy models**

To generate covariates that described the local vegetation structure for Part 1 occupancy models, I used circular plots measuring 314 m<sup>2</sup> around each camera trap (i.e. a 10 m radius). Terrestrial camera trap vegetation plots (N = 65) were measured considering the camera trap as the centre of the plot. For the arboreal camera traps, I selected sites located  $\geq 30$  m from the terrestrial camera traps and measured vegetation plots (N = 34) considering the camera

trap side of the trunk of the tree where the device was set up as the centre of the plot. Vegetation data for six arboreal camera trap sites were taken from the nearest terrestrial camera trap vegetation plot (i.e. within 30 m from the arboreal site). The total number of plots included in covariate data for occupancy models was 99, equivalent to 31,086 m<sup>2</sup>.

Within each plot I measured all trees and lianas with diameter at breast height (DBH) equal or above 10 cm, and recorded DBH, tree height (with the help of a range finder) and tree and liana species. At the centre and four extremities of each plot I measured canopy cover using a densitometer. In addition, at each plot I assigned a score for degree of *human impact* based on the type and proportion of human vegetation modification within the plot:

0 = no human impact, i.e. there are no signs of vegetation modification by humans;

1 = 1–25% of the plot is impacted by humans, i.e. the plot contains signs of vegetation modification that affect less than 25% of the total vegetation, for example cut branches or <5cm DBH tree stumps;

2 = 25–50% of the plot is affected, i.e. human signs have likely affected 25-50% of the area within the plot, for example caused by cutting of >5cm DBH trees, or including a cultivated tree in regenerating forest (>10 years old), but where the majority of 10cm DBH vegetation is composed by unmodified wild tree species;

3 = 50-75% of the plot is affected, i.e. as above, but including either a larger number of tree stumps or more than one species of cultivated tree, and where 25-49% of the >10cm DBH tree composition comprises unmodified wild species;

4 = 75-100% of the plot is affected, i.e. at least 75% of the >10cm DBH consist of cultivated trees, for example an orchard.

### **2.3.6 Study design Part 2: local scale**

The study design for Chapter 6 was specifically selected to monitor one chimpanzee community continuously for 12 months. Based on previous work (Bessa et al. 2015, Hockings unpubl. data) and information during my fieldwork (including recce walks in areas identified by local informants), the home range of the Caiquene–Cadique chimpanzee

community is about 16 km<sup>2</sup> including one forest block and a heterogeneous matrix. Camera trap site selection was based on maximising detection of chimpanzees (i.e. choosing sites frequently used), maintaining a relatively even distribution of sampling points (N = 21) and representing areas of different habitat types and anthropogenic gradients (mangroves, forest, agriculture and village). In practical terms, this meant using the BirdsEye map as reference to select sampling areas across the home range, and discuss possible chimpanzee locations with my field assistants (ITC and DI, who have extensive knowledge and research experience on this specific chimpanzee community, e.g. Bessa et al. 2015; Hockings and Sousa 2012; Hockings et al. 2020). At chimpanzee locations I therefore checked the GPS map to select deployment sites that were at least 500 m apart.

### **2.3.7 Camera trap set ups in the field**

I used Bushnell Trophy Cam HD Aggressor Low-glow (2015 and 2016 editions) and No-glow (2017 edition). I set up terrestrial camera traps within old growth forest, regenerating forest, forest edge, mangroves, woodland, agricultural fields and orchards. To access camera trap locations, we travelled by mountain bike on unpaved roads, and then walked on human and animal paths and along the forest-mangrove or savanna edges (Plate 2.1). We kept vegetation cutting to a minimum by using the least resistance parts of the forest. Some vegetation types and landscape features such as forest, mangrove, areas recently cleared for agriculture and villages were discernible using the BirdsEye imagery on GPS. However due to the heterogenic, quickly-changing characteristics of the landscape (e.g. shifting agriculture), it was often difficult to predict the type of vegetation accurately at the fine scale. In some cases, the point fell onto abandoned or new agricultural fields, which lacked large tree trunks for placing a camera. Additionally, inside the forest there were instances where the thick low vegetation surrounding the GPS point made it inaccessible. We therefore searched around the point and selected the nearest appropriate place, provided that we could maintain a set minimum distance to the nearest sampling point (1 km for Part 1 and 500 m for Part 2 studies). For example, in non-arboreal cultivated areas we searched for the nearest forest patch. We did not set up cameras in sacred forests.



## Plate 2.1

Camera trap set up in Cantanhez NP. Camera trap sites within forest blocks were often accessed by walking on the mangrove mudflats along the forest edge (top image). During set ups (bottom left), the position of the camera trap was checked for appropriate height, angle and light conditions (bottom right).

Camera traps should be placed in a way that maximises the probabilities to record targeted species (O’Connell et al. 2010). For terrestrial camera traps (Chapter 5 and Chapter 6) we searched for chimpanzee paths and/or small human paths in forests. In orchards we searched for chimpanzee entry/exit paths along the border with forest or shrubs. In Caiquene–Cadique field assistants were particularly knowledgeable of chimpanzee paths or feeding locations. Often chimpanzee signs were present near human paths, particularly in forest edges where people collect oil palm kernels and chimpanzees use the palms to feed and build nests. In those cases, we mounted the camera targeting the human path assuming from the signs that chimpanzees use it too. If no clear animal trail was present, we chose to point the camera towards patches with relatively low density of undergrowth vegetation that included other animal signs such as feeding traces, footprints or animal stools. On average, we set up three terrestrial cameras per day. We mounted terrestrial cameras at an average height of 0.57 m, SD  $\pm 0.15$  (average camera trap height in forest: 0.53 m  $\pm 0.11$ ; mangrove: 0.94 m  $\pm 0.15$ ; orchard: 0.53 m  $\pm 0.04$ ).

For arboreal camera traps (Chapter 4) we chose arboreal locations that included the following characteristics: (i) presented signs of arboreal primate activity such as smoother branch/trunk surfaces and/or feeding traces, (ii) included trees with horizontal or slanting branches connecting to the canopy, and (iii) trees that could be climbed, either with or without climbing equipment. Targeted branches/trunks also had to include relatively large ( $\geq 15$  cm DBH) vertical surfaces such as branches or trunks to mount the cameras. These vertical surfaces had to be within 10 m distance of the target (the camera trap infrared sensor range is c. 15 m). Average camera trap height was 9.1 m, SD  $\pm 2.79$  (average camera trap height in forest: 9.7 m  $\pm 2.56$ ; forest-mangrove edge: 5.5 m  $\pm 0.87$ ; orchard 6.2 m  $\pm 1.83$ ).

Camera traps were programmed to take 3 pictures with a 10s interval and the sensor’s sensitivity set to ‘high’. I used 32 and 16 GB Class 10 SD cards with 8 AA Phillips Alkaline batteries.

## **2.4 Camera trap data management**

Camera traps were checked every month and data were retrieved every one to four months depending on the memory status of the SD card, as well as availability of spare SD cards following data upload into a computer. Data were backed up into three external hard drives (i.e. three copies). I organised camera trap images into camera trap site folders. I inspected images manually and renamed the image files adding “–species ID” to the original file names (e.g. –chimpanzee). I duplicated all primate images and placed copies into separate species folders for each camera trap site. To extract metadata and generate descriptive statistics, including the records table, number of independent events for each species and detection histories I used the R package CAMTRAPR (Niedballa et al. 2017; R Core Team 2016). This R package greatly facilitated management of a relatively large camera trap dataset (approximately 2 TB of data, totalling over 600,000 image files excluding species copies).

## **2.5 Data analysis**

### **2.5.1 Overview**

All statistical analyses except Pearson’s correlations were performed using various R packages (R Core Team 2016). In Chapters 4 and 5 I ran occupancy models (MacKenzie et al. 2006) using the UNMARKED R package (Fiske and Chandler 2011). In Chapter 6 I fitted Bayesian spatiotemporal models using the R-INLA R package (Blangiardo et al. 2013). Additional details on statistical analyses are provided in each Chapter. Below I describe analysis of vegetation plots to generate two covariates for Part 1 occupancy models.

### **2.5.2 Principal Component Analysis for Part 1 vegetation covariates**

Data from the 99 circular vegetation plots (described in Section 2.3.5 above) generated six variables: stem density, mean DBH, mean tree height, canopy cover, human influence score and Shannon diversity index. I used a principal component analysis (PCA) to reduce the six variables into fewer, orthogonal predictors for occupancy modelling (Part 1 Chapters 4 and 5). I transformed the vegetation variables into z-scores and used the *PCA* function in the

FACTOMINER package in R (Lê et al. 2008; R Core Team 2017). PCA extracted two components (PC's) which had eigenvalues  $>1$  (1.97 and 1.54) and retained 58.5% of the sample's variance (Table 2.2). PC1 was positively loaded by species diversity (Shannon index  $H$ ), canopy cover and tree density and negatively loaded by human-influence score. Mean DBH and vegetation height positively loaded on PC2. Figure 2.3 provides a scatterplot of PCA results.

**Table 2.2**

Percentage of variance of extracted principal components and component loadings of vegetation variables.

| Component | % of variance | Factor                | Component loading |
|-----------|---------------|-----------------------|-------------------|
| PC1       | 32.9          | Shannon diversity $H$ | 0.582             |
|           |               | Canopy cover          | 0.738             |
|           |               | Human influence       | -0.790            |
|           |               | Tree density          | 0.590             |
| PC2       | 25.6          | Mean DBH              | 0.858             |
|           |               | Mean tree height      | 0.871             |

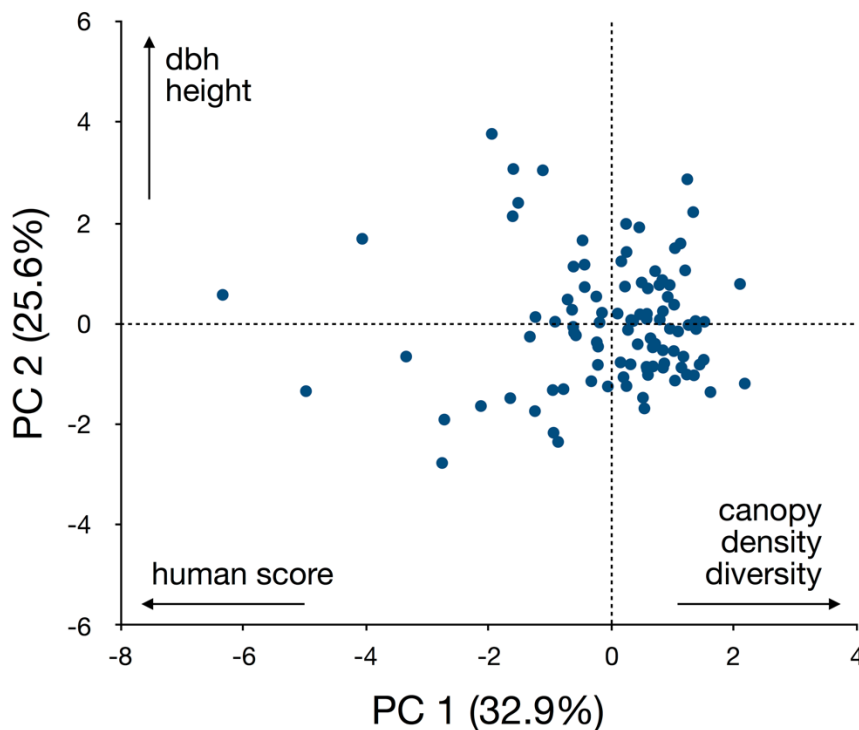


**Figure 2.3**

Principal component scores of vegetation variables measured using plots at my camera trap sites in Cantanhez National Park ( $N_{\text{plots}} = 99$ ). Values in brackets show percentage of variance retained by each component.



## CHAPTER 3

# Landscape structure and food availability across a heterogeneous forest-agricultural mosaic



## 3.1 Introduction

### 3.1.1 Forest-agricultural landscape mosaics

The majority of the world's terrestrial land surface has been modified by human activity (Döbert et al. 2014; Song et al. 2018; Vitousek et al. 1997). Deforestation and forest fragmentation are particularly affecting the tropics where the majority of terrestrial biodiversity is found (Taubert et al. 2018; Wright 2005). Most forest is converted through agricultural expansion, which varies in scale: from large-scale commercial plantations to subsistence or semi-subsistence rural agriculture such as shifting cultivation (Koh et al. 2011; Perfecto and Vandermeer 2008). Internationally driven commercial agriculture is one the major cause of forest loss and degradation (Curtis et al. 2018; Foley et al. 2011; Hansen et al. 2013). In contrast to industrial agriculture, the relationship between small-scale shifting cultivation with forest loss is more complex (Temudo et al. 2015). Many agro-forest systems support significant wildlife populations in the tropics (Estrada et al. 2012; Heinicke et al. 2019; Mandal and Shankar Raman 2016). Consequently, ecologists are increasingly highlighting the conservation value of such systems (Bersacola et al. 2018; Döbert et al. 2014; Hockings and McLennan 2019; Mandal and Shankar Raman 2016; Perfecto and Vandermeer 2008).

Understanding the matrix surrounding forest patches is crucial to evaluate the mechanisms that enable species persistence in fragmented landscapes (Laurance 2008; Perfecto and Vandermeer 2008; Prevedello and Vieira 2010). In the absence of hunting and physical barriers, certain types of matrices allow terrestrial species to migrate or frequently travel across habitat fragments (Moraes et al. 2018), particularly those that structurally resemble the 'natural' habitat (Anderson et al. 2007; Ruffell et al. 2017). In addition, land use heterogeneity within the matrix has been found to decrease isolation between forest fragments (Bender and Fahrig 2005). A mosaic of agricultural crops, fallow, young growth forest and forest plantations will create more corridor opportunities compared to single land use matrices. Thus, rather than focusing solely on single forest fragments, scientists must consider the landscape structure as a whole (including forest remnants and the surrounding matrix) to understand patterns of biodiversity abundance, distribution and persistence (Galán-Acedo et al. 2019b; Prevedello and Vieira 2010). At the large scale, a combination of remote sensing, ground truth data and knowledge of *in situ* land use types allows us to

quantify the landscape structure, i.e. the size and proportion of habitat types across a determined study area (Giri 2012). Measures for landscape connectivity and heterogeneity are crucial for developing population-level management strategies for wildlife inhabiting human-impacted landscapes (Fahrig et al. 2011).

### **3.1.2 Distribution and availability of food sources in heterogeneous agro-forest landscapes**

Forest fragmentation alters vegetation structure and the distribution and availability of fruit sources (Cordeiro and Howe 2001; McLennan and Plumptre 2012; Worman and Chapman 2006). The majority of tropical forest trees depend on animals for seed dispersal and favourable micro-climates for recruitment (Cordeiro and Howe 2001). The cascading effects of deforestation, increased light and edge effect as well as the loss of large seed dispersers reduces the availability of large, fruit-bearing trees in favour of pioneer and edge plant species such as lianas (Cordeiro and Howe 2001; Laurance et al. 2000, 2011; Magrach et al. 2014; McLennan and Plumptre 2012; Saunders et al. 1991). These effects are clearly severe in forest areas cleared for monoculture. In agro-forest habitats, vegetation structure can retain similar characteristics to forests and retain relatively high plant diversity (Rembold et al. 2017; Tynsong and Tiwari 2010). For example, in Jambi Province, Sumatra, plant species diversity was significantly higher in forest compared to plantations and mixed forest-rubber cultivation, but the latter agro-forest land use had similar tree densities to forests and retained intermediate values of plant diversity (Rembold et al. 2017).

Certain wild trees can persist in tropical agro-forest mosaics due to their resistance to fire (used in forest clearing in shifting agriculture) and light, as well as due to local farmers choosing to keep them in their cultivated fields for shade and/or as fruit sources. One such example is the oil palm (*Elaeis guineensis*), native to west and central Africa (Swaine 1992). In Bossou, Republic of Guinea, oil palm stems are present across cultivated areas and fallow at higher densities compared to forest habitats (Bryson-Morrison et al. 2016). In southern Guinea-Bissau, shifting cultivation farmers maintain a diverse array of wild trees in their cultivated fields including oil palms, *Ceiba pentandra* and *Parinari excelsa* (Temudo et al. 2015). Fruits of oil palm and *P. excelsa* are widely consumed by local people (Hockings et al. 2020), whereas *C. pentandra* is mainly used for shade. Coincidentally, these trees are also

important food sources for chimpanzees (*Pan troglodytes verus*) living in Cantanhez NP (Bessa et al. 2015). Taking into account the distribution and availability of wild food sources across the heterogeneous matrix, as well as within the forest fragments, is therefore crucial to enable more accurate inferences of wildlife landscape use.

In addition to the presence of wild food sources in the human-impacted matrix, human land uses such as fruit orchards or home gardens may offer alternative feeding opportunities to wildlife, particularly ecologically and behaviourally flexible taxa such as primates (Pozo-Montuy et al. 2011, 2013). Information on the spatiotemporal availability of human foods consumed by sympatric wildlife is relevant when studying the spatial ecology of wild taxa inhabiting anthropogenic environments (e.g. Bryson-Morrison et al. 2016; 2017; Rey 1995). The spatial distribution and availability of cultivars across the agro-forest landscape may differ by crop species and type (e.g. Lawrence et al. 1998). For example, certain fruit trees may be grown only close to villages because they are mostly used for home consumption or require more complex maintenance such as weeding, guarding, and higher sunlight (Havik et al. 2018). Other crops may require more space or are cultivated more extensively, particularly those of higher economic value such as cashew (*Anacardium occidentale*) in Guinea-Bissau (Temudo and Abrantes 2014).

As in the case with wild fruits, the availability of cultivars in agro-forest landscapes fluctuates over space and time (Carvalho et al. 2015; Hockings et al. 2009; McMullin et al. 2019). Understanding the spatiotemporal relationships between wild and cultivated food availability has important implications for human-wildlife coexistence. During periods of wild food scarcity certain crops may play an important nutritional role for sympatric wildlife (e.g. chimpanzees at Bossou, Guinea: Hockings et al. 2009; 2010; and Bulindi, Uganda: McLennan 2013). Wildlife may access more often and/or spend more time in human land uses or in proximity to humans during periods of wild scarcity in search for human food sources such as crops (Hockings et al. 2009; 2010). Some of these cultivated fallback foods may be available year-round, for example cassava (*Manihot esculenta*) consumed by chimpanzees when wild and cultivated foods are scarce in Bossou, Guinea (Hockings et al. 2010). Other crops may be seasonal and/or their availability peak during periods of wild food scarcity. In small-scale agro-forest systems, such crops may be much more vulnerable to depletion or significant loss as a result of frequent feeding by sympatric wildlife (Costa et al. 2017).

### 3.1.3 Aims and hypotheses

In this Chapter, I aim to quantify the landscape characteristics and temporal patterns of wild and cultivated resource availability in the agro-forest landscape of Cantanhez NP, Guinea-Bissau. Specifically, I:

1. Measure and describe the landscape structure, i.e. the availability and distribution of land cover types, in central Cantanhez NP (study area in Part 1) and Caiquene–Cadique (study site in Part 2) based on land classification analysis of satellite imagery;
2. Compare the vegetation structure and tree species composition across the main habitat types in Caiquene–Cadique using vegetation plots, and;
3. Examine annual patterns of wild and cultivated chimpanzee food availability in Caiquene–Cadique using plots and 12 months of phenological monitoring.

I test the following hypotheses:

| Hypothesis                                                                                                                          | Prediction                                                                                                                                                                                                                                                                             |
|-------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1. The landscape in Cantanhez NP is characterised by high structural heterogeneity.                                                 | 1.1 My study area will display a diverse landscape mosaic composed of different habitat types including forest, mangroves, woodland and grassland, as well as a high prevalence of agriculture including orchards and shifting cultivation fields intertwined with ‘natural’ habitats. |
| 2. The vegetation structure and tree species composition differ across habitat types.                                               | 2.1 Density of $\geq 10$ cm trees will be higher in forest and orchards compared to fallow, shifting cultivation fields and grassland;<br>2.2 Species diversity index will be higher in forest compared to other habitat types.                                                        |
| 3. The availability of wild fruit except for oil palm is higher in protected forest patches compared to the human-dominated matrix. | 3.1 Monthly oil palm fruit availability will be similar inside and outside the forest block;<br>3.2 Monthly ripe wild fruit availability scores will be higher within the main forest block in Caiquene–Cadique compared to the matrix.                                                |
| 4. The availability of some cultivars peak during periods of wild fruit scarcity.                                                   | 4.1 The ripe fruit availability score of certain cultivars will negatively correlate with that of wild fruit.                                                                                                                                                                          |

## 3.2 Methods

### 3.2.1 Study area

My study area comprises the central part of Cantanhez National Park (NP), located in the Tombali Region in southern Guinea–Bissau. The focal study site in this Chapter and Part 2 of this thesis consists of the home range of the Caiquene–Cadique chimpanzee community, which is located within the broader study area. Please refer to Chapter 2 for more details regarding Cantanhez NP and Caiquene–Cadique.

### 3.2.2 Data collection

#### *Ground truth data for land classification analysis*

To map and measure the landscape composition of my study area I used a supervised land classification analysis of satellite images (Congedo 2016). Land classification analysis is a widely used approach to measure landscape composition, quantify forest cover and compare land use changes over time (e.g. tropical: Koh et al. 2011; Vaglio Laurin et al. 2016; temperate: Immitzer et al. 2016; and urban systems: Congedo and Munafò 2014). This approach can be employed at the global (Gibbs et al. 2010; Taubert et al. 2018), regional (Walker et al. 2010; Wright and Wimberly 2013) and fine scale (Immitzer et al. 2016). Satellite images are multispectral georeferenced rasters composed of several layers (spectral bands). Each spectral band has a defined wavelength ( $\mu\text{m}$ ) range and spatial pixel resolution (e.g. 10 m x 10 m). Each pixel contains a spectral signature which varies across surface types (e.g. water, vegetation, soil) due to differences in reflected radiation. A supervised classification requires a number of representative samples for each land use type, which are used to train the classification algorithm. I gathered representative samples *in situ* (ground truth samples), as well as selecting samples of clearly distinguishable land classes (e.g. water and mangroves) remotely, i.e. by inspecting the satellite image. During the first five and a half months of fieldwork (October 2016 – March 2017) I collected a total of 500 georeferenced samples describing the habitat types across my study area (c. 180 km<sup>2</sup>). The georeferenced locations included secondary old growth forest (N = 80), young growth forest including fallow (N = 48), palm groves (N = 31), woodland (N = 13), grassland (N = 30), mangroves (N = 4), mangrove mudflats (N = 2), cashew orchards (N = 155), other orchards

(N = 9), open forest (N = 23), shifting cultivation fields (N = 99), mangrove rice fields (N = 6). The 500 sampling points were imported into QGIS and used as ground truth reference to select training polygons (more details in data analysis below).

### *Vegetation plots*

To gather data on vegetation characteristics in Caiquene–Cadique, I used 525 vegetation plots each measuring 10 m x 20 m. Plots were spread across 21 sampling locations across the landscape, each measuring 125,600 m<sup>2</sup> and containing 25 plots (Figure 3.1). The 21 sampling locations corresponded to 200 m radius areas surrounding the 21 camera traps established to monitor the Caiquene–Cadique chimpanzee community (Chapters 6 and 7). The GPS coordinates of plots were randomly generated using the research tool ‘Random points inside polygon’ on QGIS, setting 50 m as a minimum distance between plots. Upon inspection of the map including the generated sampling points and aerial imagery, I deleted 52 plots that were located in inaccessible areas, including those in flooded mangroves and river estuaries. Excluding additional plots removed during fieldwork (i.e. those located in flooded mangroves, lakes and sacred forests), the total number of plots was 453, corresponding to 90,600 m<sup>2</sup> or 9.06 ha of sampled area (average N plots for each of the 21 sampling locations: 21.6, SD  $\pm 4.5$ , range 10–25). Seven of the 21 sampling locations were within the Caiquene–Cadique main forest block, eleven were located across the matrix and three sampling locations partially covered the forest block and the matrix. Sampled habitat types included dense and secondary forest (N plots = 225), fallow (N = 31), mangroves (N = 14), grassland (N = 74), orchards (N = 58), shifting cultivation fields (N = 27), abandoned villages (N = 5), woodland (N = 2), mangrove rice fields (N = 6) and mudflats (N = 11).

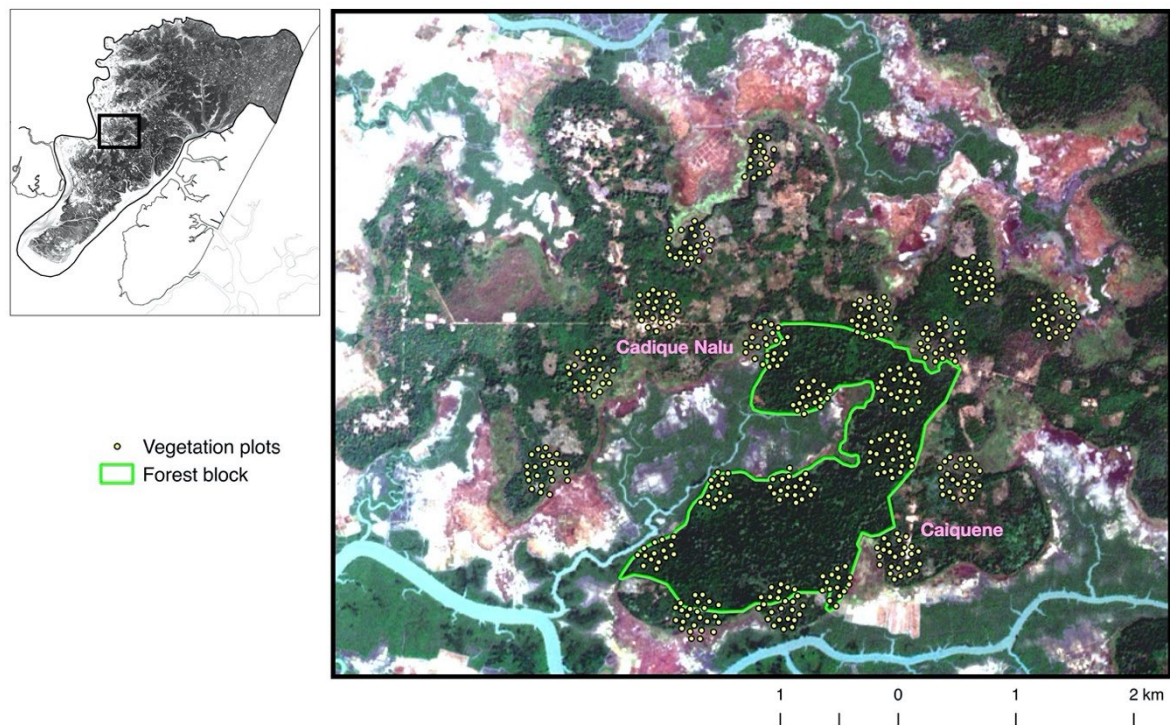


**Figure 3.1**

Map of Caiquene–Cadique showing the location of the 453 vegetation plots and the perimeters of the continuous forest block. Satellite imagery downloaded from Sentinel Hub (imagery date: 25th January 2017).

At each plot, my research field assistant (Iaia Tawél Camará) and I measured all trees, lianas and climbers that had a diameter at breast height (DBH) equal or larger than 10 cm. Data were collected on plant DBH, height of the tree to the nearest 1 m (with the aid of a laser range finder), and plant species name, which was initially identified in a local language (Kriyol, Nalu or Sussu). Tawél Camará has extensive knowledge of local plants demonstrated during previous studies (Bessa et al. 2015; Catarino et al. 2020; Hockings et al. 2020; Parathian et al. 2018). Latin names were subsequently identified following a comprehensive list of plant species found in Guinea-Bissau which includes common names in local languages (Catarino et al. 2008). In addition, I cross-checked common and scientific names using a list of plant species collated using plot data from Caiquene–Cadique (Bessa et al. 2015; Hockings et al. 2020). This additional list includes the common names in local languages and all corresponding plant specimens (N=157) are stored in the herbarium of the Environmental Anthropology and Behavioural Ecology Laboratory – Centre for Research in Anthropology, Lisbon, Portugal. Information from this list was later published in a field

guide of human and chimpanzee plant use in Cantanhez (Catarino et al. 2020). Density of each species was calculated as the number of identified stems divided by the total sampled area in hectares (9.06 ha). I compared vegetation structure, species diversity (using Shannon Index  $H$ , e.g. Morris et al. 2014) and composition of top ten species across habitats using habitat-level averages.

### *Phenology*

To monitor phenology the research team established two monitoring trails (one wild and one cultivated). I selected 17 species known to be consumed by chimpanzees in Caiquene–Cadique (Bessa et al. 2015), of which eleven were wild tree species and six were cultivated trees (Table 3.1). Ten of the eleven wild species were identified as the most important food sources for chimpanzees in Caiquene–Cadique (Bessa et al. 2015). The six cultivated species represent the most commonly grown fruit trees in my study area. We selected and tagged eight to ten individuals per species, except for *Mangifera indica* for which we selected ten individuals for two varieties (mango *de tera* and *Sierra Leon*, kr). We selected trees that were considered mature based on their DBH size. Monitoring was conducted by FAs twice per month; once at the beginning of the month (1<sup>st</sup> or 2<sup>nd</sup> day) and once in the middle of the month (14<sup>th</sup> – 16<sup>th</sup> day). We recorded a score for amount of new leaves, flowers, unripe fruit and ripe fruit based on their relative cover in the crown: 0 = absent, 1 = 1–25% cover, 2 = 26–50% cover, 3 = 51–75% cover and 4 = 76–100% cover (Hockings et al. 2012; McLennan 2013). Wild food trees were monitored from the 1<sup>st</sup> of March 2017 until the 1<sup>st</sup> of July 2018. Cultivated food trees were monitored from the 15<sup>th</sup> of July 2017 until the 1<sup>st</sup> of July 2018.

**Table 3.1**

Chimpanzee food tree species (11 wild and 6 cultivated) monitored for phenology. Species selection was based on feeding ecology data collected in Caiquene–Cadique in 2013 (Bessa et al. 2015). Density of adult trees was calculated from 453 plots.

| Family           | Species                       | N individuals | Min. DBH adults (cm) <sup>a</sup> | Mean DBH monitored (cm) | Density in plots (stems/ha) | Mean DBH in plots (cm) | Local name (kr)                    |
|------------------|-------------------------------|---------------|-----------------------------------|-------------------------|-----------------------------|------------------------|------------------------------------|
| Leguminosae      | <i>Dialium guineense</i>      | 10            | 10                                | 50.61 (±26.14)          | 12.25                       | 23.01 (±13.83)         | <i>Veludo</i>                      |
| Palmae           | <i>Elaeis guineensis</i>      | 10            | na <sup>b</sup>                   | 42.42 (±6.44)           | 14.46                       | 37.54 (±11.31)         | <i>Palmeira</i>                    |
| Bombacaceae      | <i>Ceiba pentandra</i>        | 10            | 30                                | 133.31 (±49.47)         | 0.99                        | 66.05 (±34.64)         | <i>Poilon</i>                      |
| Moraceae         | <i>Treculia africana</i>      | 10            | 20                                | 64.87 (±22.49)          | 0.77                        | 34.06 (±11.88)         | <i>Mantchambe</i>                  |
| Chrysobalanaceae | <i>Parinari excelsa</i>       | 10            | 20                                | 89.17 (±21.42)          | 1.77                        | 54.71 (±32.78)         | <i>Mampataz</i>                    |
| Apocynaceae      | <i>Saba senegalensis</i>      | 10            | 10 <sup>c</sup>                   | 8.66 (±5.27)            | 0.11                        | 11.3                   | <i>Foli elefante</i>               |
| Anacardiaceae    | <i>Spondias mombin</i>        | 10            | 10                                | 44.30 (±20.35)          | 1.21                        | 16.22 (±4.94)          | <i>Mandipli</i>                    |
| Leguminosae      | <i>Detarium senegalense</i>   | 10            | 15                                | 43.69 (±18.84)          | 0.55                        | 49.72 (±32.57)         | <i>Mambodi</i>                     |
| Apocynaceae      | <i>Landolphia heudelotii</i>  | 10            | 10 <sup>c</sup>                   | 5.06 (±1.56)            | 0.11                        | 10.35                  | <i>Foli macaco</i>                 |
| Moraceae         | <i>Ficus sur</i>              | 10            | 20                                | 58.34 (±21.63)          | 0.77                        | 31.19 (±5.45)          | <i>Figuera tonkinjá</i>            |
| Annonaceae       | <i>Uvaria chamae</i>          | 10            | 10 <sup>c</sup>                   | 5.45 (±1.53)            | 1.43                        | 13.05 (±1.83)          | <i>Banana santchu</i>              |
| Anacardiaceae    | <i>Anacardium occidentale</i> | 10            | 10                                | 22.99 (± 7.77)          | 21.96                       | 18.61 (±6.39)          | <i>Cadjú</i>                       |
| Bombacaceae      | <i>Adansonia digitata</i>     | 8             | 60                                | 105.89 (±14.07)         | 0.22                        | 104.72 (±34.21)        | <i>Cabaceira</i>                   |
| Anacardiaceae    | <i>Mangifera indica</i>       | 20            | 20                                | 87.25 (±28.70)          | 2.21                        | 66.92 (±29.80)         | <i>Mango de tera / Sierra Leon</i> |
| Rutaceae         | <i>Citrus sinensis</i>        | 10            | 15                                | 36.75 (±10.80)          | 1.21                        | 28.94 (±13.48)         | <i>Limão de tera</i>               |
| Rutaceae         | <i>Citrus aurantifolia</i>    | 10            | 4                                 | 18.98 (±10.90)          | 0.66                        | 20.21 (±18.78)         | <i>Larandja</i>                    |
| Caricaceae       | <i>Carica papaya</i>          | 10            | 10                                | 21.43 (±4.26)           | 0.44                        | 23.71 (±3.87)          | <i>Papaya</i>                      |

<sup>a</sup> Taken from McLennan (2010), Sun et al. (1996), Saw et al. (1991) and based on personal observations during fieldwork.

<sup>b</sup> Minimum adult tree based on height >5m due to younger palms having larger DBH compared to adult trees.

<sup>c</sup> Measured equal or above the reported DBH but smaller stems can also fruit.

### 3.2.3 Data analysis

#### *Land classification analysis*

I performed a land classification analysis of my study area using the Semi-Automatic Classification plug-in on QGIS (Congedo 2016; QGIS Development Team 2018). This plug-in allows QGIS users to perform supervised land cover classification using the spectral signature of material (e.g. vegetation, water, rocks) included in a satellite image (Congedo 2016). In pixel-based supervised classification, the classification algorithm uses the spectral signature of training sites, which are areas composed by a set of pixels belonging to different land use classes (Butt et al. 2015; Richards 2013). These areas can be selected using ground-truth references or by visual interpretation of aerial or satellite imagery. The same analysis can be performed using ArcGIS with the Spatial Analyst extension, however the main advantage of QGIS is that it is an open-source, free programme.

I used 10m resolution Sentinel-2 multi-spectral satellite imagery, available from the European Space Agency (<https://scihub.copernicus.eu>). I selected one image from January 2017, which coincided with my arboreal and terrestrial camera trap survey period during the dry season (image ID: S2A\_MSIL1C\_20170125T112331\_N0204\_R037\_T28PDT\_20170125T113357). For the analysis, I used 10 spectral bands (bands 2–8, 8A, 11, 12). I converted raw digital numbers of the satellite image into top-of-atmosphere reflectance values (Butt et al. 2015; Congedo 2016). Using the 500 representative sampling points collected during fieldwork, as well as by visually inspecting the map, I created 478 training sites belonging to 13 different habitat classes (Table 3.2). I ran the analysis using the Minimum Distance algorithm (Richards 2013; Congedo 2016).

**Table 3.2**

Details of the signature list used for the land classification analysis.

| Macroclass            | Class                                       | Details                                                                                                                                                                       | N of training samples |
|-----------------------|---------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------|
| Woody vegetation      | Dense forest                                | Dense old growth secondary forest                                                                                                                                             | 67                    |
|                       | Regenerating forest                         | Old growth and young growth forest, forest fallow, forest edge                                                                                                                | 105                   |
|                       | Mangroves                                   | Mangroves                                                                                                                                                                     | 69                    |
|                       | Palm groves                                 | Palm-dominated habitats, often present along the forest edges                                                                                                                 | 40                    |
|                       | Woodland                                    | Savannah woodland, often associated with grassland                                                                                                                            | 33                    |
|                       | Open forest                                 | Forest characterised by large (>30 cm DBH) upper canopy wild trees, occasionally including some cultivated tree species in low-mid canopy (e.g. in abandoned villages)        | 7                     |
|                       | Orchard                                     | Mostly cashew orchard, but also including orange, mango, guava orchards                                                                                                       | 60                    |
| Herbaceous vegetation | Grassland                                   | Savannah grassland and areas dominated by grassy vegetation                                                                                                                   | 20                    |
| Bare soil             | Shifting cultivation field ( <i>lugar</i> ) | Areas used for shifting cultivation, including upland rice, peanuts, cassava and other cultivar foods that were harvested during the study period                             | 24                    |
|                       | Bare soil                                   | Bare soil including roads, football pitches                                                                                                                                   | 10                    |
|                       | Mangrove mudflats                           | Mangrove mudflats, also including areas where mangrove rice is cultivated ( <i>bulanyas</i> , harvested during the study period therefore including no herbaceous vegetation) | 20                    |
| Built-up              | Village                                     | Villages (only the largest villages were used in the signature list)                                                                                                          | 4                     |
| Water                 | Water                                       | River estuaries, sea                                                                                                                                                          | 19                    |

I vectorised the resulting classification raster image using the ‘polygonize’ tool on QGIS. Palm groves mainly occurred along the forest edges and mixed forest was present in small patches in association with anthropogenic land uses. Because of their thin/small shape and/or patchy distribution, palm groves and mixed forests were difficult to discern in the overall resulting map. I therefore grouped palm groves, open forest and regenerating forest land classes into one class (mixed forest) to simplify visual representation. Similarly, bare soil, village and mangrove mudflats were grouped into one class (no vegetation). The perimeter of my study area was determined using a buffer of 5 km around each camera trap established

for occupancy modelling (Chapters 4–5), clipped by the limits of the park. Similarly for Caiquene–Cadique, which represents the area of one chimpanzee community (Bessa et al. 2015), I established a 1 km buffer around the camera traps that were established for chimpanzee monitoring (Chapters 6–7). This area also corresponded with the locations of vegetation plots presented in this Chapter (Figure 3.1). For both my overall study area and Caiquene–Cadique, I vectorised the land classification raster to calculate the area (in km<sup>2</sup>) for each land class. I calculated the size of the eleven forest blocks within my study area which are formally designated as protected (IBAP undated) by summing the total area of forest classes within the perimeters of each protected forest block.

### *Food availability*

I calculated the monthly food availability index ( $F_m$ ) for the selected wild and cultivated chimpanzee food species using the following formula:

$$F_m = \sum_{k=1}^n F_k \times D_k \times S_k$$

where  $F_k$  is the mean score of ripe fruit of monitored individuals in species  $k$  in month  $m$ ,  $D_k$  represents the overall density of adult trees in species  $k$  measured in plots, and  $S_k$  is the overall mean DBH of adult trees in species  $k$  measured in plots (McLennan 2013). The reproductive size threshold of adult trees was selected based on previous studies (McLennan 2010; Sun et al. 1996) and from personal observations during fieldwork (Table 3.1).

I compared monthly food availability across the year between seasons. I defined the dry season as the period including the month of November until and including the month of April, and the rainy season from and including the month of May until the end of October. I compared temporal fluctuations in oil palm fruit availability with other wild fruit availability ( $N$  species = 10) using Pearson correlation. To test Predictions 3.1 and 3.2 I compared ripe wild fruit and ripe oil palm fruit availability between areas inside the Caiquene–Cadique forest block and areas across the matrix. The forest block was defined as the continuous

protected forest comprising the Caiquene protected forest and the part of Cadique located south of the road (i.e. excluding the fragmented patches north of the road, Figure 3.1). This comparison was made using the average tree density and DBH of adult food trees from seven sampling areas inside the forest block (N plots = 130, average N plots per sampling site = 18.6, SD  $\pm 4.0$ ) and eleven sampling areas across the matrix (N plots = 248, average N plots per sampling site = 22.5  $\pm 4.4$ ). Three sampling areas (which included a total of 75 plots) were discarded because some plots fell inside the block (N = 18) and others (N = 57) were located outside or it was ambiguous. I visually examined temporal patterns of cultivated food availability, and identified the cultivars that showed a peak during months of wild food scarcity. To test Prediction 4.1, I then correlated the cumulative availability of selected cultivars against wild food availability using a Pearson correlation. For all Pearson correlations I used twice-a-month food availability scores (N = 24) instead of monthly averages. All data were normally distributed (checked using Kolmogorov–Smirnov test).

### 3.3 Results

#### 3.3.1 Landscape structure across central Cantanhez NP and within Caiquene–Cadique

The result of the land classification analysis for my study area is shown in Figure 3.2. Woodland and cashew orchards were sometimes misclassified as one another due to having similar structural characteristics. To provide more conservative estimates, I therefore excluded woodland as a forest habitat sub-type when comparing forest cover. Together, forest habitats (including dense forest, regenerating forest, palm groves and open forest) accounted for 149.1 km<sup>2</sup> or 36.4% of the study area excluding water (Table 3.3). Mangroves were the single most dominating vegetation type, covering 22.2% of the land. Woodland and grassland accounted for 14.2%. Orchards (most of which were cashew) and cultivated fields (*lugar*, defined as ‘active’ shifting cultivation fields, i.e. excluding fallow), accounted for 11.7% of the land use. In Caiquene–Cadique, forest (again comprising dense forest, regenerating forest, open forest and palm groves) covered 5.32 km<sup>2</sup> and dominated 28.7% of the area. Agricultural land uses and grassland were proportionally more dominant in Caiquene–Cadique compared to the rest of the overall study area (+9.6% and +8.6%, respectively).

**Table 3.3**

Size and proportion of land cover types across the study area and in Caiquene–Cadique.

| Land use            | Study area              |                | Caiquene–Cadique        |                | Proportional difference |
|---------------------|-------------------------|----------------|-------------------------|----------------|-------------------------|
|                     | Size (km <sup>2</sup> ) | % <sup>a</sup> | Size (km <sup>2</sup> ) | % <sup>a</sup> |                         |
| Dense forest        | 43.9                    | 10.7           | 0.97                    | 5.3            | –                       |
| Regenerating forest | 70.5                    | 17.2           | 2.32                    | 12.5           | –                       |
| Palm groves         | 29.8                    | 7.3            | 1.62                    | 8.8            | +                       |
| Open forest         | 4.9                     | 1.2            | 0.41                    | 2.2            | +                       |
| Woodland            | 24.6                    | 6.0            | 1.57                    | 8.5            | +                       |
| Mangroves           | 91.2                    | 22.2           | 0.86                    | 4.6            | –                       |
| Grassland           | 33.7                    | 8.2            | 3.11                    | 16.8           | +                       |
| Orchard             | 36.7                    | 9.0            | 2.7                     | 14.5           | +                       |
| Cultivated field    | 11.2                    | 2.7            | 1.25                    | 6.7            | +                       |
| No vegetation       | 63.5                    | 15.5           | 3.74                    | 20.2           | +                       |
| (Water)             | (12.3)                  |                | (0.31)                  |                |                         |

<sup>a</sup> Percentage values exclude water

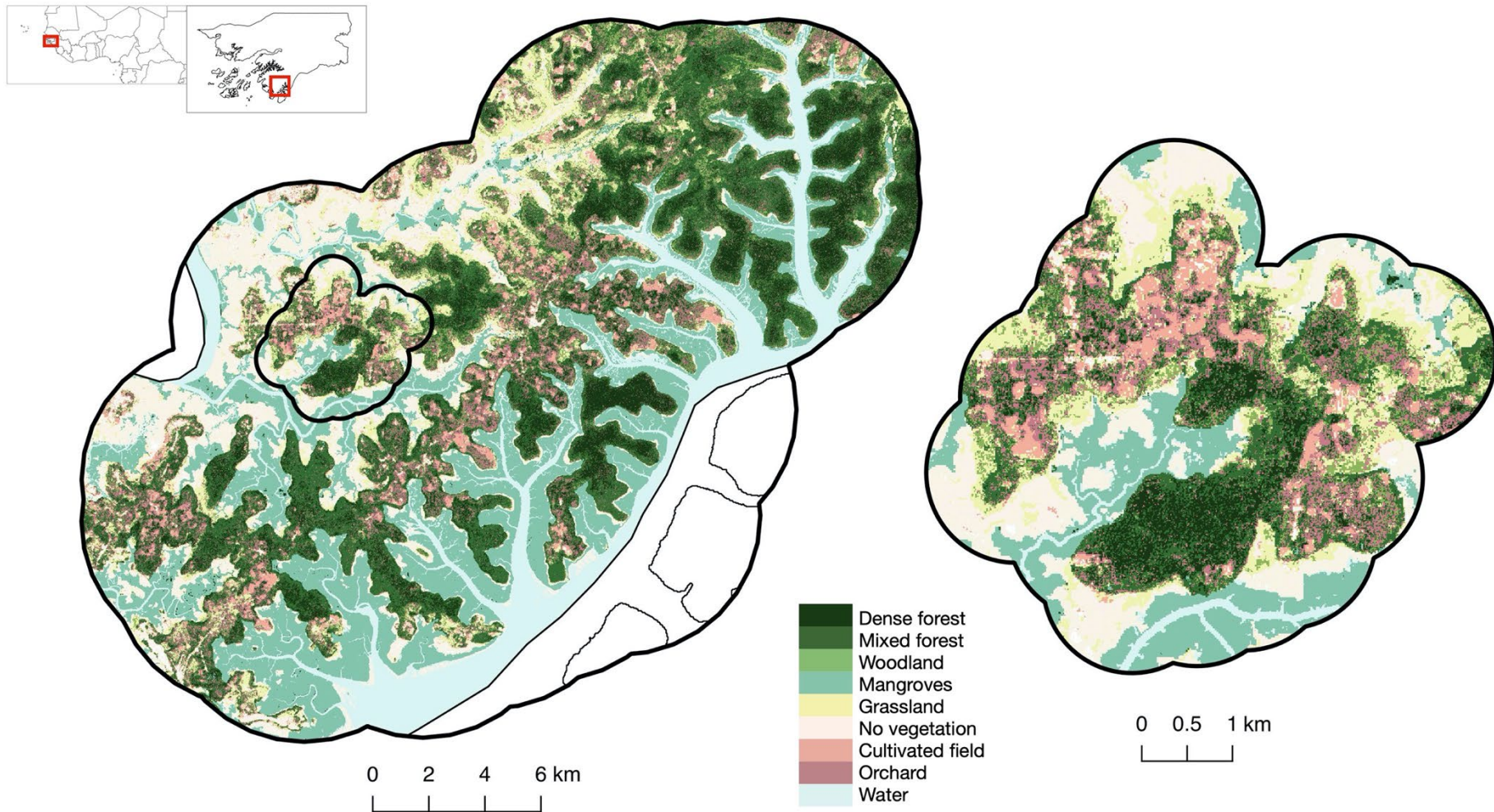


**Figure 3.2**

Result of the land use classification analysis of my study area in Cantanhez National Park, showing the detail of Caiquene–Cadique, where phenology and vegetation plots were collected for this chapter. Mixed forest includes regenerating forest (secondary forest and fallow), palm groves and open forest. Orchards are mainly cashew plantations, and ‘no vegetation’ includes bare soil, mudflats and villages.

### *Size of protected forests*

The total extent of forest (including habitat sub-types: dense forest, secondary regenerating forest, palm groves and open forest) within the fourteen formally protected forests was 81.35 km<sup>2</sup> (Figure 3.3). Excluding Cunha forest, which is outside my study area, the 13 protected forests accounted for 54% of the forest cover across the measured study area. Of the fourteen protected forest blocks, the average forest size was 5.81 km<sup>2</sup> SD  $\pm$ 8.64, ranging from 0.47 km<sup>2</sup> in Capicada in the south to 36.4 km<sup>2</sup> in Amindara in the north. Nine of the fourteen forest blocks were less than 5 km<sup>2</sup>. Amindara was over three times larger than Cambeque (10.63 km<sup>2</sup>), the second largest and about six times the average forest size. The size of Canamine and Cafatche forests combined (11.63 km<sup>2</sup>), which are divided by a small road, was similar to that of Cambeque. Within the protected zone, the extent of the forest in Caiquene and Cadique was 4.06 km<sup>2</sup>.

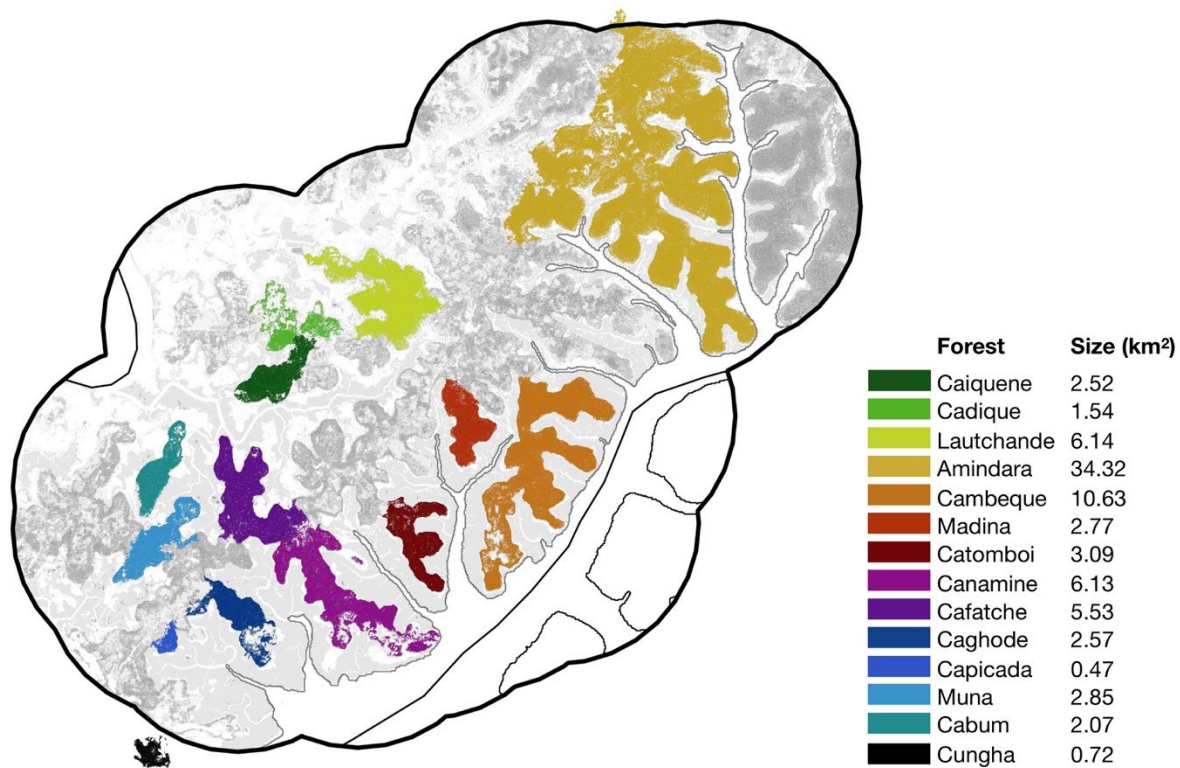


**Figure 3.3**

Extent of the forest cover for the 14 protected forest blocks in Cantanhez NP based on land classification analysis using Sentinel 2 data from January 2017. Dense forest, young and old growth secondary forest, palm groves, open forest and forest fallow are included in the measured forest extent. Cunha forest (the small forest shown in black) lays just outside my study area.

### 3.3.2 Vegetation structure and composition in Caiquene–Cadique

Structural characteristics and species diversity varied across habitat types (Table 3.4). Forest included the highest number of tree species overall, and mean Shannon diversity index  $H$  was similar to that of abandoned villages. Mangrove forests were dominated by *Avicennia germinans* and *Rhizophora* species. Tree density was highest in orchards and comparable values were found in forest, mangroves and abandoned villages. Shifting cultivation fields had the lowest tree density and showed largest mean DBH and tree height.

**Table 3.4**

Mean vegetation attributes across sampled habitat types. Total N of plots = 434 out of total N of plots = 453; nineteen plots were not included here due to belonging to other habitat types including mangrove rice fields, woodland and mudflats. In bold are the highest values for each measured attribute.

| Habitat                 | Mean density<br>(stems/ha) | Mean DBH<br>(cm)         | Mean height<br>(m)      | N of<br>species | Mean Shannon<br>index ( $H$ ) |
|-------------------------|----------------------------|--------------------------|-------------------------|-----------------|-------------------------------|
| Forest $N=225$          | 204.67 $\pm$ 126.11        | 25.46 $\pm$ 11.02        | 11.55 $\pm$ 4.04        | 90              | 0.854 $\pm$ 0.57              |
| Abandoned village $N=5$ | 180.00 $\pm$ 90.83         | 33.39 $\pm$ 18.60        | 14.62 $\pm$ 6.02        | 12              | <b>0.861</b> $\pm$ 0.56       |
| Orchard $N=58$          | <b>248.28</b> $\pm$ 125.29 | 27.57 $\pm$ 19.12        | 8.34 $\pm$ 3.99         | 36              | 0.441 $\pm$ 0.53              |
| Grassland $N=74$        | 39.87 $\pm$ 96.15          | 29.63 $\pm$ 10.06        | 9.28 $\pm$ 3.00         | 11              | 0.083 $\pm$ 0.25              |
| Fallow $N=31$           | 79.03 $\pm$ 80.39          | 27.61 $\pm$ 22.16        | 8.78 $\pm$ 4.66         | 26              | 0.314 $\pm$ 0.54              |
| Cultivated field $N=27$ | 25.93 $\pm$ 68.46          | <b>55.96</b> $\pm$ 24.86 | <b>17.20</b> $\pm$ 8.88 | 9               | 0.073 $\pm$ 0.26              |
| Mangrove $N=14$         | 189.29 $\pm$ 52.55         | 17.07 $\pm$ 3.82         | 6.78 $\pm$ 1.86         | 2               | 0                             |

Of the 453 sampled vegetation plots, 344 included  $\geq 10$  cm DBH trees and lianas and 109 either included no woody vegetation (e.g. in grassland or cultivated field) or only included small stems ( $< 10$  cm DBH, e.g. in fallow). From the 344 plots I recorded a total of 1443 stems that belonged to 35 Families comprising 107 species. Of the total 107 species, 20 were unknown. See Appendix 3.1 for a complete list of species recorded in this study. The identified trees included 98 wild species and 10 cultivated species. The most common tree species was cashew (*Anacardium occidentale*), with an overall density of 21.96 stems/ha ( $N_{\text{stems}} = 199$  across 453 sampled plots). The second most common species was oil palm (*Elaeis guineensis*), occurring at a density of 14.46 stems/ha ( $N_{\text{stems}} = 132$ ), followed by *Ricinus dendron heudelotii* (density = 13.91 stems/ha,  $N_{\text{stems}} = 126$ ) and *Dialium guineense* (density = 12.25 stems/ha,  $N_{\text{stems}} = 111$ ). Across habitat types there were differences in species composition regarding the ten most common tree species (Table 3.5). Cashew trees dominated orchards, but wild species were also present particularly oil palm and kola-

*malgos* (kr, *Carapa procera*), which are extensively used by local people. The ten most common  $\geq 10$  cm DBH trees in shifting cultivation fields were all wild species, only four of which were included in the top ten trees within fallow fields (oil palm, *Borassus aethiopum* and *Albizia* spp.).

**Table 3.5**

The most common species present in forest, orchard, grassland, fallow and cultivated fields (*lugar*) in Caiquene–Cadique. Data were collected using 453 randomly generated sampling plots of which 344 included  $\geq 10$  cm DBH stems. Stem density presented here was calculated as the number of stems divided by the area sampled within each habitat.

| Habitat <sup>a</sup> | #  | Family         | Species                          | Density (stems/ha) | Wild or cultivated |
|----------------------|----|----------------|----------------------------------|--------------------|--------------------|
| Forest               | 1  | Euphorbiaceae  | <i>Ricinodendron heudelotii</i>  | 26.00              | wild               |
|                      | 2  | Fabaceae/Leg.  | <i>Dialium guineense</i>         | 23.78              | wild               |
|                      | 3  | Palmae         | <i>Elaeis guineensis</i>         | 17.56              | wild               |
|                      | 4  | Meliaceae      | <i>Trichilia prieuriana</i>      | 8.00               | wild               |
|                      | 5  | Fabaceae/Leg.  | <i>Albizia adianthifolia</i>     | 6.89               | wild               |
|                      | 6  | Meliaceae      | <i>Carapa procera</i>            | 6.89               | wild               |
|                      | 7  | Sapindaceae    | <i>Lecaniodiscus cupanioides</i> | 6.89               | wild               |
|                      | 8  | Turneraceae    | <i>Trema guineensis</i>          | 5.11               | wild               |
|                      | 9  | Sapotaceae     | <i>Malacantha alnifolia</i>      | 4.89               | wild               |
|                      | 10 | Sapotaceae     | <i>Synsepalum pobeguianum</i>    | 4.67               | wild               |
| Orchard              | 1  | Anacardiaceae  | <i>Anacardium occidentale</i>    | 168.97             | cultivated         |
|                      | 2  | Palmae         | <i>Elaeis guineensis</i>         | 11.21              | wild               |
|                      | 3  | Anacardiaceae  | <i>Mangifera indica</i>          | 10.34              | cultivated         |
|                      | 4  | Rutaceae       | <i>Citrus sinensis</i>           | 8.62               | cultivated         |
|                      | 5  | Rutaceae       | <i>Citrus aurantifolia</i>       | 5.17               | cultivated         |
|                      | 6  | Meliaceae      | <i>Carapa procera</i>            | 4.31               | wild               |
|                      | 7  | Moraceae       | <i>Ficus</i> sp.                 | 4.31               | wild               |
|                      | 8  | Euphorbiaceae  | <i>Ricinodendron heudelotii</i>  | 3.45               | wild               |
|                      | 9  | Caricaceae     | <i>Carica papaya</i>             | 3.45               | cultivated         |
|                      | 10 | Sterculiaceae  | <i>Cola nitida</i>               | 2.59               | cultivated         |
| Grassland            | 1  | Combretaceae   | <i>Terminalia macroptera</i>     | 15.54              | wild               |
|                      | 2  | Palmae         | <i>Borassus aethiopum</i>        | 9.46               | wild               |
|                      | 3  | Palmae         | <i>Elaeis guineensis</i>         | 8.78               | wild               |
|                      | 4  | Fabaceae/Leg.  | <i>Albizia</i> sp.               | 1.35               | wild               |
|                      | 5  | Fabaceae/Leg.  | <i>Albizia adianthifolia</i>     | 0.68               | wild               |
|                      | 6  | Euphorbiaceae  | <i>Anthostema senegalense</i>    | 0.68               | wild               |
|                      | 7  | Fabaceae/Leg.  | <i>Cassia sieberiana</i>         | 0.68               | wild               |
|                      | 8  | Fabaceae/Leg.  | <i>Piliostigma thonningii</i>    | 0.68               | wild               |
|                      | 9  | Euphorbiaceae  | <i>Alchornea cordifolia</i>      | 0.68               | wild               |
|                      | 10 | Asclepiadaceae | <i>Calotropis procera</i>        | 0.68               | wild               |
| Fallow               | 1  | Palmae         | <i>Borassus aethiopum</i>        | 9.68               | wild               |
|                      | 2  | Palmae         | <i>Elaeis guineensis</i>         | 8.06               | wild               |
|                      | 3  | Fabaceae/Leg.  | <i>Albizia</i> sp.               | 8.06               | wild               |

| Habitat <sup>a</sup> | #  | Family           | Species                         | Density<br>(stems/ha) | Wild or<br>cultivated |
|----------------------|----|------------------|---------------------------------|-----------------------|-----------------------|
|                      | 4  | Euphorbiaceae    | <i>Ricinodendron heudelotii</i> | 6.45                  | wild                  |
|                      | 5  | Fabaceae/Leg.    | <i>Albizia adianthifolia</i>    | 4.84                  | wild                  |
|                      | 6  | Fabaceae/Leg.    | <i>Cassia sieberiana</i>        | 3.23                  | wild                  |
|                      | 7  | Anacardiaceae    | <i>Anacardium occidentale</i>   | 3.23                  | cultivated            |
|                      | 8  | Bombacaceae      | <i>Ceiba pentandra</i>          | 3.23                  | wild                  |
|                      | 9  | Apocynaceae      | <i>Alstonia congensis</i>       | 3.23                  | wild                  |
|                      | 10 | Moraceae         | <i>Antiaris toxicaria</i>       | 3.23                  | wild                  |
| Cultivated field     | 1  | Chrysobalanaceae | <i>Neocarya macrophylla</i>     | 7.41                  | wild                  |
|                      | 2  | Palmae           | <i>Borassus aethiopum</i>       | 5.56                  | wild                  |
|                      | 3  | Palmae           | <i>Elaeis guineensis</i>        | 1.85                  | wild                  |
|                      | 4  | Fabaceae/Leg.    | <i>Albizia sp.</i>              | 1.85                  | wild                  |
|                      | 5  | Fabaceae/Leg.    | <i>Albizia adianthifolia</i>    | 1.85                  | wild                  |
|                      | 6  | Meliaceae        | <i>Carapa procera</i>           | 1.85                  | wild                  |
|                      | 7  | Fabaceae/Leg.    | <i>Dialium guineense</i>        | 1.85                  | wild                  |
|                      | 8  | Fabaceae/Leg.    | <i>Parkia biglobosa</i>         | 1.85                  | wild                  |
|                      | 9  | Chrysobalanaceae | <i>Parinari excelsa</i>         | 1.85                  | wild                  |

<sup>a</sup>N of plots per habitat: forest = 225, orchard = 58, grassland = 74, fallow = 31, cultivated field = 27.

### 3.3.3 Patterns of wild and cultivated food availability in Caiquene–Cadique

When excluding oil palm fruit and flowers, the availability of ten wild ripe fruit species was similar between dry and rainy seasons (53.3% and 46.7% respectively, Figure 3.4a). During the dry season, 78.4% of wild ripe fruit was available during the second half of the season (February, March and April 2018). Fluctuations in ripe oil palm fruit availability were not positively associated with those of other wild fruit (Pearson correlation:  $r = 0.3427$ ,  $N = 24$ ,  $P = 0.101$ ). Including oil palm, chimpanzee wild fruit availability was higher in the rainy season (68.4%) compared to the dry season (31.6%; Figure 3.4b). However, during the rainy season the majority of the measured available ripe wild fruit (81.3%) consisted of oil palm fruit, whereas in the dry season oil palm fruit accounted for 53.7% of the available ripe wild fruit. Including all wild species, the period of lowest wild fruit availability was between October and January. Except for oil palm fruit and flowers, which were available across all months, only *Uvaria chamae* was available in October; in November only ripe fruit of *Detarium senegalense* was present, and in December–January ripe fruits of *D. senegalense* and *Parinari excelsa* were available.

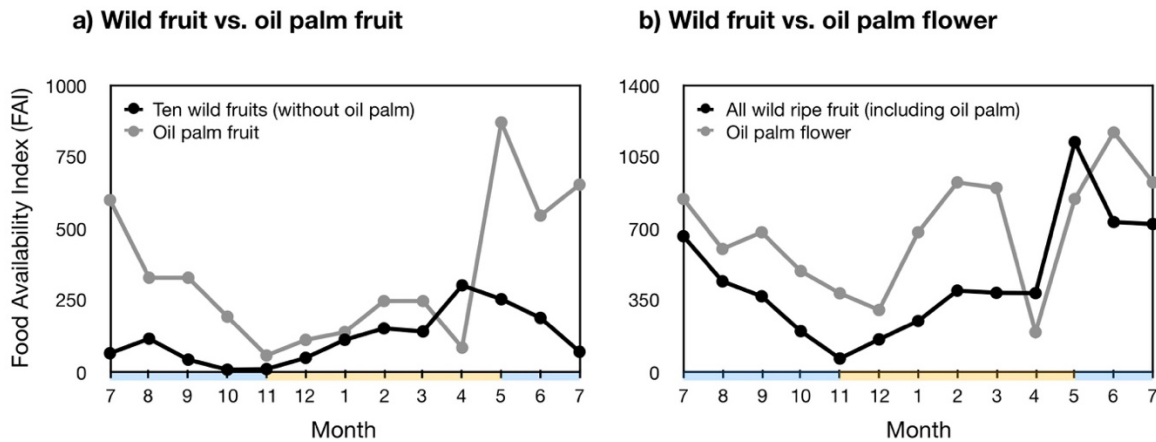


**Figure 3.4**

Overall monthly variation in wild food availability (FAI) between July 2017 and July 2018 in Caiquene–Cadique, Cantanhez NP. Graphs show scores of (a) ten wild fruit species compared to oil palm fruit, and (b) all wild fruit including oil palm compared to oil palm flower, another important chimpanzee food (Bessa et al. 2015). Blue colour shows rainy season months and yellow represents the dry season.

I compared averages of wild food availability inside and outside the forest block, which included the agriculture-forest-village matrix (see Figure 3.1 for a map including the forest block). Variations in FAI across areas were based on differences in mean adult tree density and DBH from seven areas within the forest block and eleven areas outside the main block. When excluding oil palm, wild ripe fruit availability was higher within the forest block compared to the heterogeneous matrix (Figure 3.5a). In contrast, oil palm fruit availability was nearly identical (Figure 3.5b), due to similar means in oil palm tree density and DBH within and outside the forest block (mean tree density and DBH respectively, inside forest block: 10.4 stems/ha and 27.1 cm; and across the outside matrix: 10.6 stems/ha and 33.7 cm).

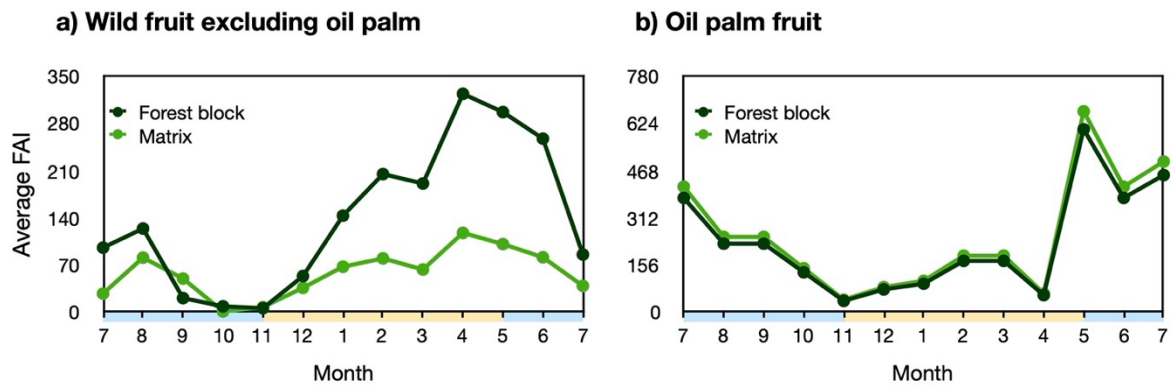


**Figure 3.5**

Comparison between wild food availability inside and outside the Caiquene–Cadique forest block between July 2017 and July 2018. (a) average availability of wild ripe fruit except oil palm and (b) ripe oil palm fruit availability. Blue colour shows rainy season months and yellow represents the dry season.

Cultivated food availability was highest between March and July 2018, which coincided with the cashew and mango ripe fruit peak availability periods (Figure 3.6). During this period, cashew represented on average 70.7% (range 41.4 – 91.4%) of the total available cultivated ripe fruit. May was the month with the highest cultivated ripe fruit availability due mostly to cashew and mango. Baobab fruit was available throughout the dry season. Papaya and orange fruit availability peaked in December, coinciding with the beginning of the dry season. Lime fruit availability peaked twice during the study period, in November 2017 and once again in July 2018. Therefore, the cultivated foods that peaked during the period of wild food scarcity were orange, lime and papaya, which correspond to the cultivated foods that were recorded inside the villages. The overall availability of ripe wild fruit (including oil palm) significantly negatively correlated with the combined availability of village foods (orange, lime and papaya, Pearson correlation:  $r = -0.489$ ,  $N = 24$ ,  $P = 0.01532$ , Figure 3.7).

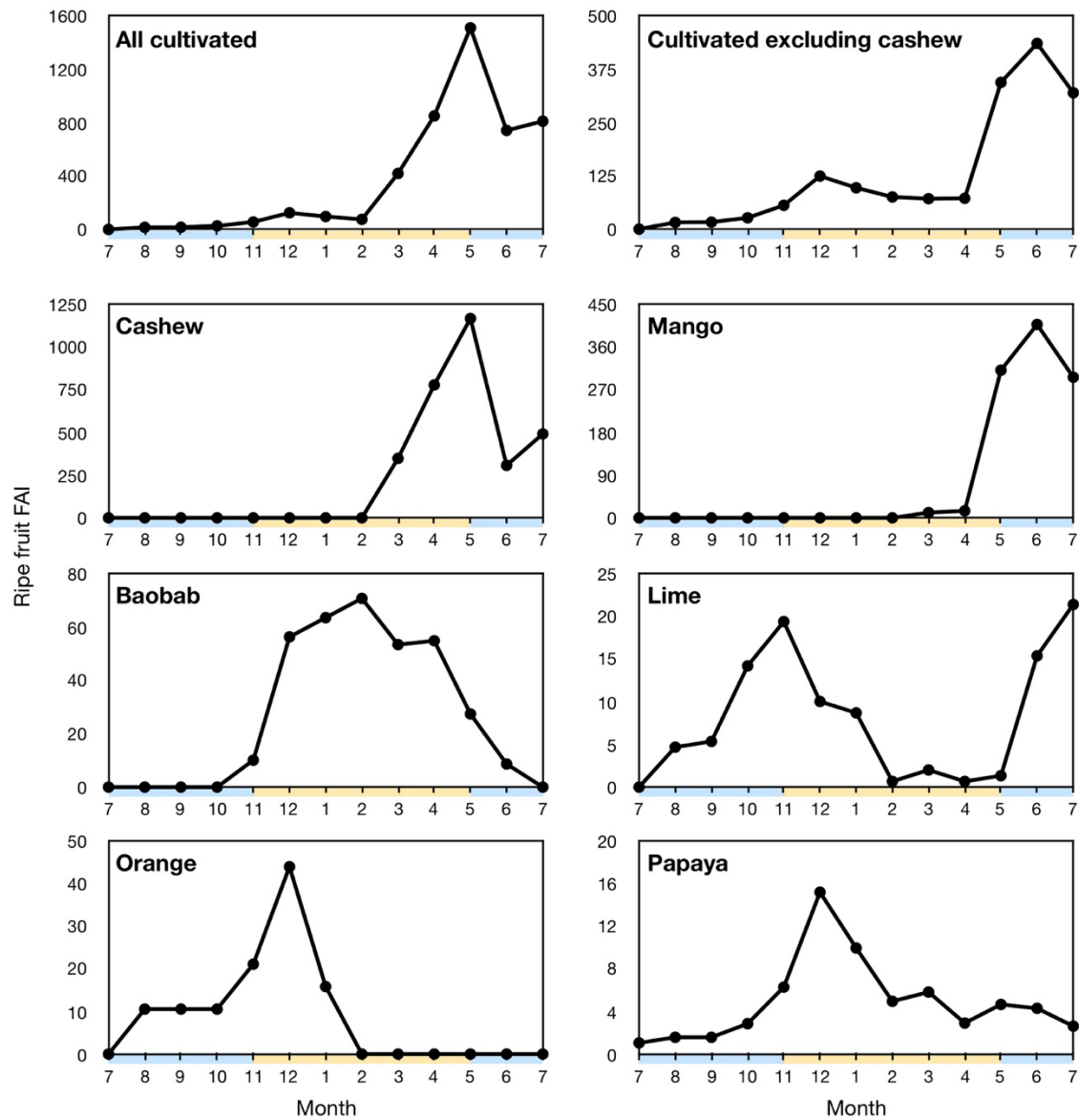


**Figure 3.6**

Monthly variation in cultivated ripe fruit availability in Caiquene–Cadique between July 2017 and July 2018. Blue colour shows rainy season months and yellow represents the dry season.

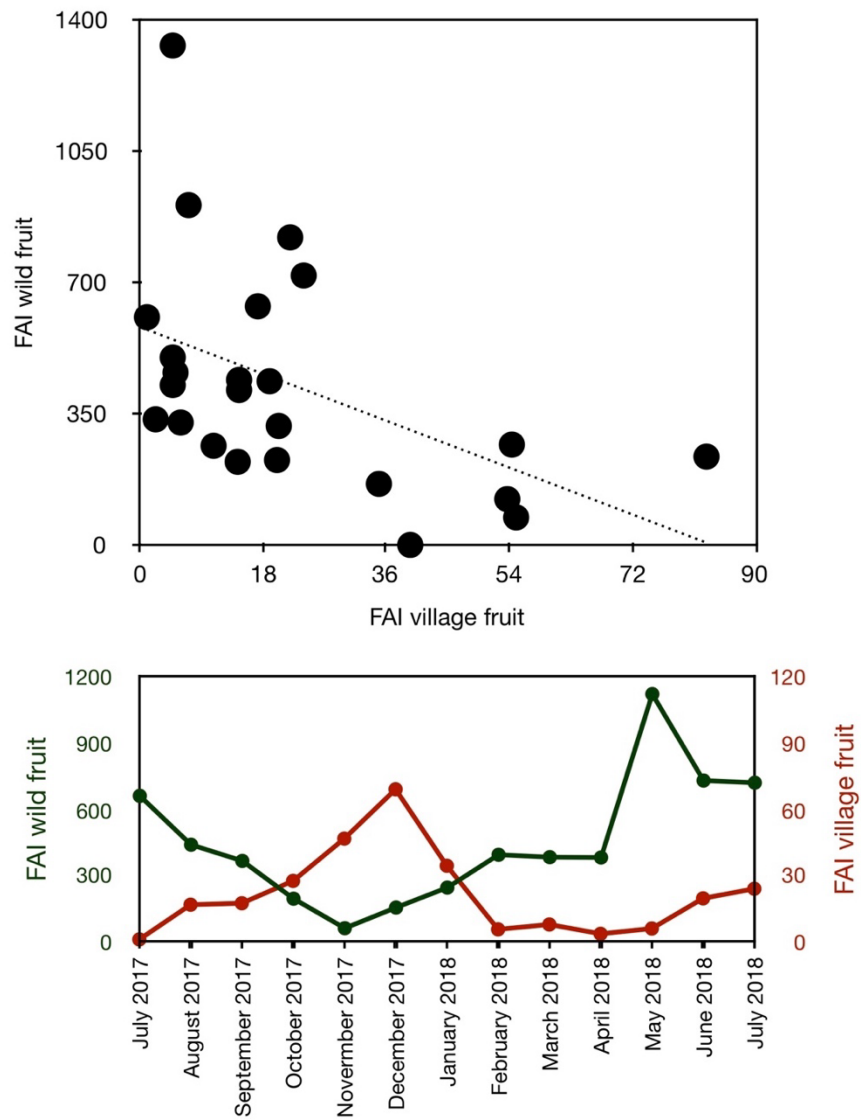


**Figure 3.7**

Negative relationship between availability of ripe wild fruit and cumulative availability of village foods (orange, lime and papaya) between July 2017 and July 2018. Data points in scatter plots represent 24 sampling points corresponding to phenology monitoring periods (twice per month).

### 3.4 Discussion

#### *Landscape composition*

As shown in my results, the landscape in central Cantanhez is characterised by a heterogeneous mosaic of habitats, and except for the higher prevalence of remnant forest blocks, presents similarities with other mangrove-coastal areas across Guinea-Bissau, Guinea and Sierra Leone (Global Forest Watch 2019). Compared to country-wide estimates in Guinea-Bissau, my study area contains proportionally more mangroves and much less savannah-woodland, which accounted for approximately 10% and 50% of the land cover in 2007, respectively (Oom et al. 2009). Forest cover was nearly 10% higher in my study area compared to country wide (Oom et al. 2009). Although these comparisons should be interpreted with caution due to different classification analyses (e.g. different data source, spatial resolution and vegetation types included in ‘forest’ classes), proportionally larger amounts of forest cover in Cantanhez are not surprising. The thirteen formally protected forest blocks within my study area accounted for just over a half of the forest cover across the measured landscape. These results indicate a large amount of forest across the matrix, albeit highly fragmented and intertwined with cultivated areas. Remnant forest edges are often found along the perimeters of fragments cleared for agriculture. In addition to fallow and orchards, forest edges may act as corridors for some wildlife including chimpanzees. However, these potential corridors may not be sufficient to facilitate optimal dispersal of forest-dependent arboreal species such as colobines (*Colobus polykomos* and *Piliocolobus badius temminckii*) (Minhós et al. 2016). The dominance of mangroves across the landscape and bordering forest blocks is likely to play a key role for travel and dispersal of ground-dwelling (and hunted, therefore cryptic) taxa such as Guinea baboons (*Papio papio*), green monkeys (*Chlorocebus sabaeus*) and African forest buffalos (*Syncerus caffer nanus*) (Hughes 1992).

#### *Vegetation structure*

As expected, forest and orchards showed higher stem density compared to fallow, grassland and cultivated fields. Forests, including mixed forest in abandoned villages, had a higher Shannon diversity index compared to matrix habitats. Orchards and fallows had comparable diversity indices which were higher compared to grassland, cultivated fields and mangroves.

A previous study found high wild species diversity of regenerating seedling and coppicing in cashew orchards, particularly within those that replaced forest and bordered grassland and forest habitats (Sousa et al. 2015). Except for six cultivated trees, the majority of wild trees in orchards were oil palms, *C. procera* and *Ficus* spp. all of which are used by local people. Seeds of *C. procera* are used to extract medicinal oil across West Africa including at my study site. The prevalence of wild oil palms across all habitat types shows that this tree is distributed throughout the landscape including across the matrix. Many of the orchards are present near remnants of forest edges (Figure 3.2), which are typically dominated by oil palms, likely explaining the tendency for oil palms to (naturally) occur within these land uses. All of the top ten stems found in cultivated areas were wild trees. Consistent with previous findings (Temudo et al. 2015), remnant stems of *C. pentandra*, *P. excelsa*, *B. aethiopum* and oil palms occurred in shifting cultivation fields, explaining the large mean DBH observed within the *lugares*. Except for *Albizia adianthifolia* and *C. procera*, all of the top species found in cultivated areas in my study have previously been recorded as chimpanzee foods at this site (Hockings unpubl. data).

### *Food availability*

Availability of wild and cultivated chimpanzee foods fluctuated across the year. Monthly patterns of wild food availability for the eleven species I measured slightly differed to those of 37 species measured in 2013 by Bessa et al. (2015). Wild fruit availability in 2013 peaked in March, whereas in my study the highest peak was in May. Scarcity of eleven chimpanzee wild foods in this study was recorded between October and January, which corresponds to the months not sampled in the 2013 study (Bessa et al. 2015). In Cantanhez NP, oil palms are more abundant along forest edges and rarely occur in the forest interior (K Hockings unpubl. data). Due to oil palm fruit being extensively used by local people, palm-dominated forest edges do not tend to be cleared for agriculture and oil palm stems within agricultural fields do not tend to be felled. In both forest and cultivated areas, Nalu people in Caiquene and Cadique Nalu mark oil palms that include unripe or small quantities of fruit to discourage people from overexploiting or damaging the palms (J Bessa unpubl. data). Stem density and mean DBH of oil palms in the matrix were comparable to the forest block, therefore, supporting prediction 3.1, oil palm fruit availability was nearly identical inside and outside the protected forest. Consistent with Prediction 3.2, the availability of wild fruit was higher

within the forest block compared to the heterogeneous matrix. However, during the period of lower wild fruit availability between August and January, FAI scores in the matrix were comparable to those of forest. This is also the period when orange, lime and papaya become abundant, corroborating Hypothesis 4 that some cultivars peak when wild foods are scarce. Therefore, albeit a riskier and patchier environment, the matrix may offer chimpanzees important foraging opportunities during periods of wild food scarcity including additional wild resources and alternative ones (cultivated foods).

In summary, for this Chapter I measured the landscape characteristics across my study area, describing the land cover heterogeneity, the vegetation structure across habitat types and patterns of wild and cultivated food availability. In Chapters 4 and 5 I use the land classification analysis to measure two covariates for occupancy models. An important limitation of this study was the difficulty to discriminate between fallow and forest land classes, as well as orchards and woodland/secondary forest. From *in situ* observations and ground truthing the visual representation of the landscape appears relatively accurate, but actual land cover measurements should be interpreted with caution. Therefore, the land use cover around camera trap sites measured for occupancy model covariates will be inspected carefully and compared to ground truth information to maximise full accuracy (for example by removing ‘orchard’ misclassified single pixels around cameras within forest blocks). Information on wild and cultivated food availability presented in this Chapter are used to develop one of the research hypotheses in Chapter 6. Orange, lime and papaya were exclusively recorded within villages and their cumulative availability showed an inverse relationship with that of wild food. Therefore, village foods are used as a proxy for testing whether chimpanzees increase risk-taking behaviour when wild foods are scarce. Chapters 6 and 7 examine this in detail through a complementary bio-social approach.

Part 1

Primate distributions in a shared landscape



## CHAPTER 4

### Arboreal primates in agro-forest landscape mosaics: exploring patterns of occurrence using arboreal camera traps



## 4.1 Introduction

In human-modified, rapidly changing environments, wildlife populations are increasingly faced with less predictable landscapes and limited preferred habitat. Across Europe, most of the areas where emblematic species occur, e.g. grey wolf (*Canis lupus*) and brown bear (*Ursus arctos*), are within 1 km from the nearest transport infrastructure (Torres et al. 2016). To persist in human-dominated environments the resident wildlife needs to find new ways to maintain fitness whilst minimising increased risks of being killed or injured. For example, wildlife will adjust their spatiotemporal activity patterns to minimise collisions with vehicles and/or direct contact with humans (Dowding et al. 2010; Gaynor et al. 2018; Oriol-Cotterill et al. 2015; Theuerkauf et al. 2003). The scale of behavioural adjustments will depend on the species ecological plasticity as well as the environmental context, including the levels and types of habitat modification and the presence of human activities that pose increased mortality risks. If mortality risks are low, some species will exploit human land uses to obtain foods (Hockings and McLennan 2012; Wallace and Hill 2012); whereas if risks of persecution exceed potential benefits of acquiring supplementary resources, wildlife will restrict their ranging to areas less frequented by people (Basille et al. 2009; Foster et al. 2010).

Tropical rainforests are characterised by a diverse vegetation composition which provide a great variety of structural pathways, accommodating the ecological and locomotory requirements of a wide range of taxa (Terborgh 1992). Animals that largely rely on the unique characteristics of tropical forests, such as arboreal wildlife, tend to be more vulnerable to habitat change compared to terrestrial or semi-terrestrial species. Even amongst arboreal taxa, variations in sensitivity to forest alteration do exist. Previous studies have linked these to diet, sleeping site requirements and the degree of arboreality (Laurance 1990) and the capacity to travel across the surrounding matrix (Laurance and Laurance 1999). Arboreal primates can be flexible and shift to terrestrial travel and activity to deal with forest fragmentation (Galat-Luong and Galat 2005; Mourthé et al. 2007). Although arboreal wildlife may sometimes exploit areas outside forest blocks (e.g. Anderson et al. 2007), long-term consequences of poor habitat connectivity such as loss of genetic diversity (Lancaster et al. 2011; Minhós et al. 2016) and occupancy reduction (Arroyo-Rodríguez et al. 2008) may still occur. Some matrix habitats may provide enough connectivity (Anderson et al. 2007; Smith-Ramirez et al. 2010), others may represent significant barriers (Rodríguez-

Cabal et al. 2007). Landscape permeability may be further reduced due to predation risks including hunting by humans. A landscape approach can help identify habitat and anthropogenic factors that pose constraints on the spatial occurrence of arboreal taxa because it takes into account elements outside the forest patches (Anderson et al. 2007; Galán-Acedo et al. 2019b; Pozo-Montuy et al. 2011). Landscape elements may include villages or other areas where risks of hunting by humans is higher, as well as types of matrices that may impact the ability of a species to disperse.

To obtain inferences of wildlife responses to anthropogenic influences at the landscape scale scientists often use survey-based techniques. Camera traps have been used extensively to study wildlife populations across a wide variety of environments and species assemblages (e.g. Brazilian wolf [*Chrysocyon brachyurus*] and foxes [*Dusicyon* spp.] in grassland: Jácomo et al., 2004; tiger [*Panthera tigris*] and leopard [*Panthera pardus*] in Bhutanese mountains: Wang & Macdonald, 2009; forest antelopes in South African coastal forest-agricultural mosaics: Ehlers Smith et al., 2019). Camera traps have been employed to gather data for various purposes and analytical frameworks, including exploring species activity patterns (Azlan and Sharma 2006; Cheyne and Macdonald 2011), providing indicators of abundance (Howe et al. 2018; Tichon et al. 2016), modelling patterns of species occurrence (Hearn et al. 2016; Rich et al. 2016; Steenweg et al. 2016; Tobler et al. 2015), examining interspecific interactions (Carter et al. 2012; Sollmann et al. 2012) and recording behaviour of unhabituated animals (Boyer-Onti and Pruetz 2014). In the past decade, scientists have begun exploring ways to take camera traps to higher vegetation strata, and discussing the possible effectiveness of arboreal camera traps for monitoring taxa in the canopy (Gregory et al. 2014; Méndez-Carvajal 2014; Oliveira-Santos et al. 2008a; Olson et al. 2012; Whitworth et al. 2016). However, it is only recently that survey-scale, quantitative analytical methods have been tested for the first time using data from arboreal camera traps (Bowler et al. 2017; Moore et al. 2020). Considering that the majority of primate species spend most of their time in the canopy, this new methodological technique has the potential to contribute significantly to our knowledge of primate ecology. In Majjuna-Kichwa, a lowland rainforest in Peru, Bowler et al. (2017) found that arboreal camera traps required less survey effort compared to line transects; arboreal camera traps took three weeks to be deployed, compared to line transects which took two months to cut. The authors successfully employed arboreal camera trap-based occupancy models on 18 arboreal species including nine primates.

#### 4.1.1 Aims and hypotheses

In this Chapter I present the first study to date that incorporates the arboreal camera trap-occupancy models approach within the context of human-dominated agro-forest mosaics. The aims of this study are to: (1) test arboreal camera traps in agro-forest mosaic and; (2) identify environmental and anthropogenic factors affecting distribution of arboreal primates in a human-dominated landscape. I compare camera trapping efficiency of terrestrial and arboreal surveys for seven primate species. This arboreal versus terrestrial camera trap comparative approach has not been employed to date. To identify patterns of primate occurrence, I use data generated from arboreal camera traps to fit occupancy models of four arboreal primate species: Temminck's red colobus, king colobus, Campbell's monkey, and Demidoff's galago.

I test the following hypotheses:

| Hypothesis                                                                                                                                                                                                                                                                                                                            | Prediction                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1. Arboreal camera traps are more effective for gathering data on arboreal primates compared to terrestrial camera traps.                                                                                                                                                                                                             | 1.1 Detection frequencies of arboreal primates will be higher when using arboreal camera traps compared to terrestrial camera traps;<br><br>1.2 Naïve occupancy of arboreal primates will be higher for arboreal camera traps compared to terrestrial cameras.                                                                                                                                                                                                                                                             |
| 2. Arboreal primates prefer higher quality forest and show sensitivity to anthropogenic influence in agro-forest landscapes. Specifically:<br><br>(i) The degree of arboreality predicts preference for higher quality habitat, and;<br><br>(ii) Low relative distribution is associated with sensitivity to anthropogenic influence. | 2.1 Occupancy probability of primates that were rarely detected on the ground (i.e. less than 20% of total number of independent detections are from terrestrial cameras) will be positively associated with measures of habitat quality (vegetation structure, and/or amount of forest cover);<br><br>2.2 Proximity to village and/or amount of human land use will negatively affect occupancy probability of primates with restricted distributions (i.e. primates that have an estimated occupancy probability <0.50). |

## **4.2 Methods**

### **4.2.1 Study area**

I collected data across a 180km<sup>2</sup> area within the southern part of Cantanhez NP (Figure 4.1). My study area included 32 villages and comprised the majority of the remaining coastal forests (12 forests out of c. 16 forest blocks in Cantanhez NP including the 14 formally protected ones), as well as mangroves, savannah and agriculture (mainly shifting cultivation and cashew orchards). See Chapter 2 and 3 for additional details.

### **4.2.2 Data collection**

I collected data between 17 October 2016 and 5 March 2017. We deployed camera traps (Bushnell Trophy Cam HD Aggressor Low-glow) using a two-array system. The first array (17 October – 15 December 2016) included 20 arboreal camera traps, the second array (26 December 2016 – 5 March 2017) comprised 20 arboreal camera traps. Two arboreal cameras malfunctioned, therefore the final number of arboreal camera sampling sites were 38, totalling 1922 arboreal camera trap days. During the same period, we deployed terrestrial camera traps overlapping the same study area: 33 camera trap sites for the first array and 32 camera trap sites for the second array. Two terrestrial cameras were stolen and one malfunctioned, resulting to 62 terrestrial camera trap sites totalling 3113 terrestrial camera trap days.

One of the assumptions of single-season occupancy modelling is population closure, meaning that there is no change in the state of occupancy (for example due to migration or immigration) within the sampled period (MacKenzie et al. 2006). The duration of my study period (140 days) was similar to previous studies that employed occupancy modelling on primate species (e.g. c. four months: Rovero et al. 2014; seven months: Kalan et al. 2013). Considering the slow reproductive rate of my study species (e.g. the interbirth intervals of Temminck's red colobus is over 24 months [Kingdon et al. 2013]), the territoriality of primates and the survey being conducted during the dry season only, the assumption of population closure should have been satisfied. Another assumption of occupancy is that sampling points require to be independent from one another (MacKenzie et al. 2006). A systematic survey grid with regularly spaced sampling points is typically employed in

camera trap-based survey studies (Ahumada et al. 2011; Rovero et al. 2014). My camera trap spacing was adapted from the Team Network standardised guidelines, in which the authors advise to place one sampling point at the centre of every other 1 km<sup>2</sup> squared cell (TEAM Network 2008). Prior to data collection, I therefore placed regularly spaced points every 1.41 km on the map of the study area. However, due to the heterogeneous characteristics of the landscape in Cantanhez NP, it was often not possible to deploy a camera trap at the exact pre-established location (Chapter 2). I ensured that a minimum distance of 1 km was maintained between sampling sites. This minimum distance was selected to account for independence (the home ranges of Temminck's red colobus and king colobus are approximately 0.24 km<sup>2</sup> and 0.36 km<sup>2</sup>, respectively [Dasilva 1989; Starin 1991]), to allow for some flexibility in a complex habitat mosaic ( $\pm 0.4$  km from originally planned spacing) and to maximise the probability of detecting primates that were present. The average nearest-neighbour distance between sampling points was 1.45 km SD $\pm$ 0.37 for arboreal camera traps and 1.30 km SD $\pm$ 0.21 for terrestrial camera traps.

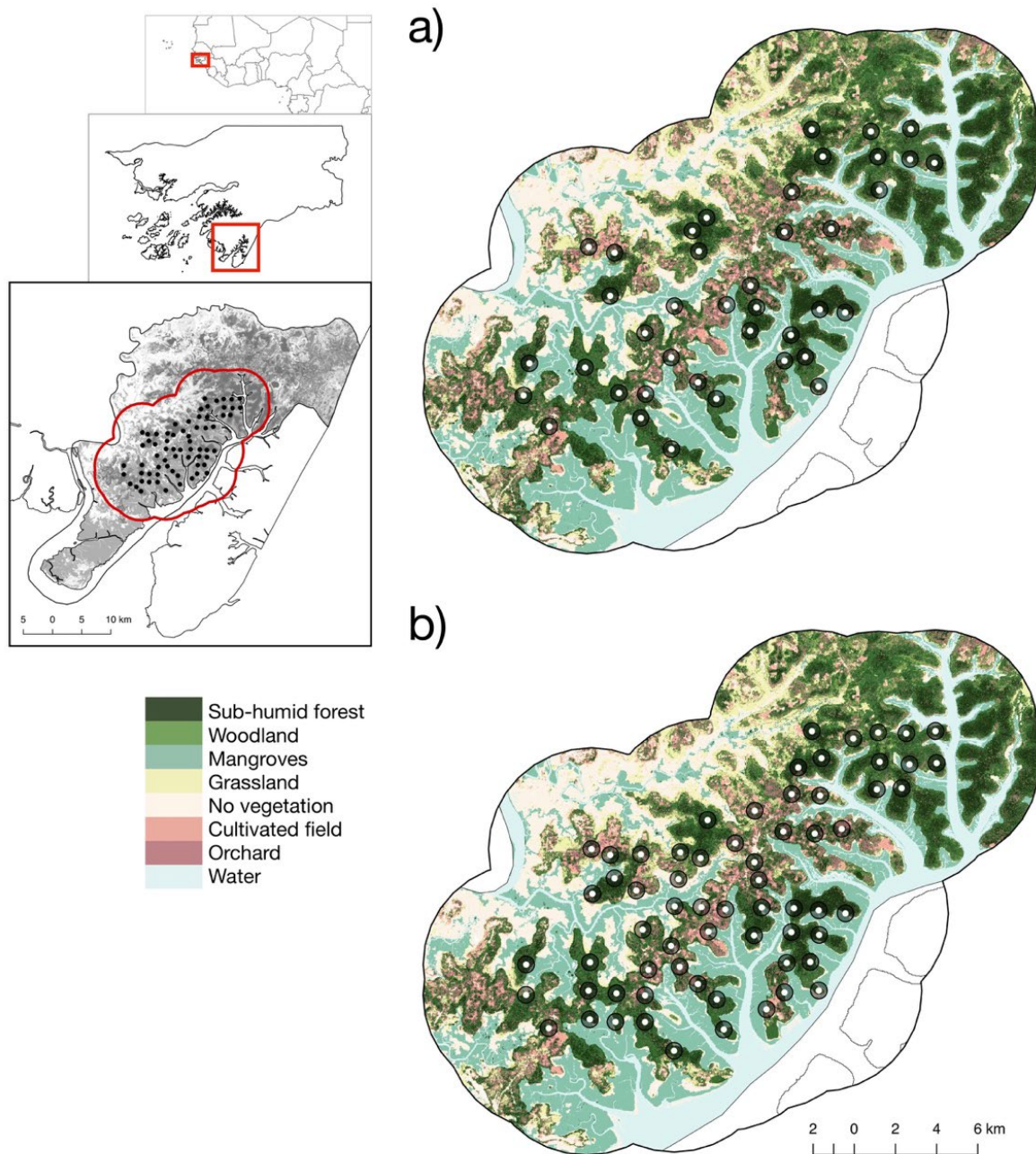


**Figure 4.1**

Map and location of Cantanhez National Park, Guinea-Bissau, showing the survey grid of (a) arboreal camera traps and (b) terrestrial camera traps deployed using a two-array system between October 2016 and March 2017.

Arboreal camera traps were deployed within forest (N = 27), forest-mangrove edge (N = 6) and open forest-orchards (N = 7). Research assistants Iaia Tawél Camará and Braima McIntosh Vieira climbed trees using the doubled-rope technique (DDRT) or when deemed safe and possible, free climbing (e.g. when the presence of several lianas and branches allowed field assistants to climb confidently). For the DDRT, we used a 36 m long 11.7 mm diameter tree climbing rope (Poison HI-VI with splice). Draped over a branch, the rope was connected with a friction hitch climber set up (which included a DMM Hitch Climber, two DMM Ultra O Locksafe carabiners and a prusik chord). This system allows for self-belaying, i.e. the climber is able to ascend and descend without the assistance of another climber. To ease climbing, we used a foot ascender (CT Quick Step R). For the arboreal sites, we chose relatively large trees ( $\geq 15$  cm DBH) that showed signs of primate activity (e.g. feeding traces, smoother bark) and presented horizontal or slanting surfaces that connected to the rest of the canopy. In addition, the chosen target (e.g. horizontal branch), had to be within 10 m from the camera trap. Average camera trap height was 9.1 m (range 5 – 15 m). Terrestrial camera traps were deployed within forest, mangroves, woodland, orchards and regenerating forest patches by cultivated areas. Terrestrial and arboreal cameras were programmed to record 3 consecutive 8MP images at a 10s interval. I used 32GB Class 10 SD cards with 8 AA Phillips Alkaline batteries. Arboreal camera traps were set up during the same period as the terrestrial camera traps.

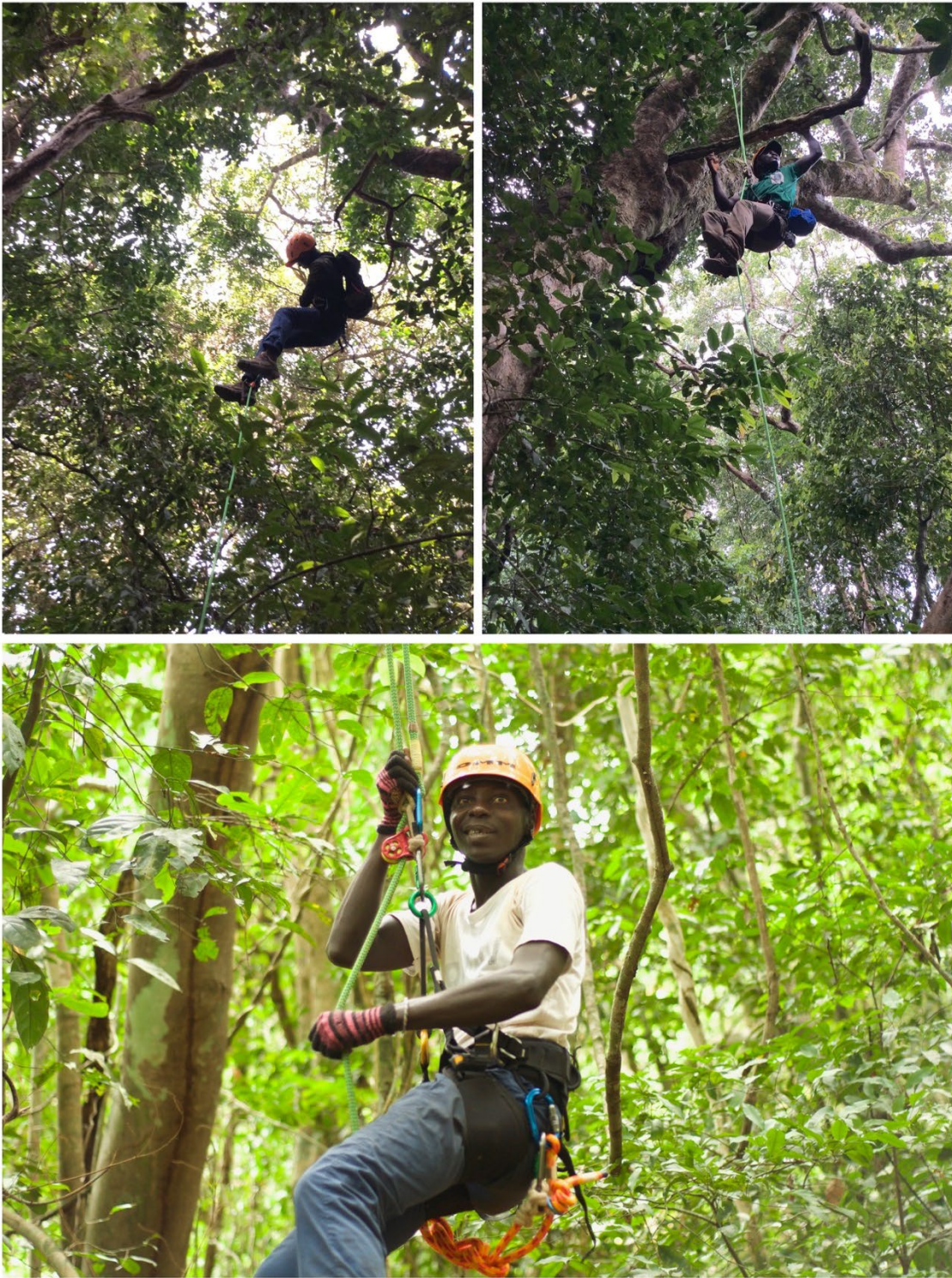


**Plate 4.1**

Arboreal camera trap set up in Cantanhez NP. Iaia Tawél Camará (top left and bottom images) and Braima McIntosh Vieira (top right) ascending trees using the doubled-rope technique.

### 4.2.3 Data analysis

Occupancy modelling allows us to infer ecological processes of species interactions and species responses to human-induced habitat modification using survey data. This is achieved by fitting models with covariates that are thought to affect the probability of occurrence (represented by the occupancy parameter  $\Psi$ ) of one or multiple species of interest (MacKenzie et al. 2006). Covariates are incorporated into the model via a logistic function (MacKenzie et al. 2002). Importantly, occupancy modelling accounts for imperfect detection, i.e. when the species of interest is actually present at a site but remains undetected, by estimating the probability of detection  $p$  using data from survey repetitions at each sampling point (MacKenzie et al. 2002; Royle et al. 2005; Zeller et al. 2011). Thus, occupancy is particularly useful for identifying abiotic and biotic constraints on species presence (including human-mediated effects) and is increasingly used as an alternative measure to abundance (typically density) to monitor population trends over time.

#### *Data management*

For details on the data management, image metadata extraction and dataset see Section 2.4 in Chapter 2. The arboreal and terrestrial datasets were treated separately. For each species I calculated the number of independent events, setting 60 minutes as the minimum time difference between photographs or sequences of photographs. This 1-hour interval is typically used in population survey studies (e.g. Garriga et al. 2019; Rovero and Marshall 2009; Rovero et al. 2014). To compare detection efficiency between arboreal and terrestrial camera traps, I selected sites that included an arboreal and a terrestrial camera trap within 200 m from one another, which resulted in a total of 23 'matching' camera trap sites. For the occupancy models, each sampling occasion consisted of seven camera trap days (Table 4.1).

**Table 4.1**

Sampling dates and number of occasions for each dataset for occupancy models.

| Arboreal species  | 1 <sup>st</sup> Array | 2 <sup>nd</sup> Array | N of occasions |
|-------------------|-----------------------|-----------------------|----------------|
| Red colobus       | 14 Nov – 18 Dec 2016  | 16 Jan – 19 Feb 2017  | 5              |
| King colobus      | 24 Oct – 18 Dec 2016  | 16 Jan – 19 Feb 2017  | 8              |
| Campbell's monkey | 24 Oct – 18 Dec 2016  | 16 Jan – 19 Feb 2017  | 8              |
| Demidoff's galago | 24 Oct – 18 Dec 2016  | 16 Jan – 19 Feb 2017  | 8              |

## *Covariates*

The models included a total of seven covariates (Table 4.2). I generated vegetation structure covariates using 314 m<sup>2</sup> plots around each camera trap, measuring all trees and lianas above 10 cm DBH, canopy cover and assigning a score of human influence based on the type and extent of vegetation alteration attributed to humans. To reduce the set of vegetation plot variables ( $N = 6$ ) into fewer orthogonal covariates I performed a principal component analysis (PCA). PC1 was negatively loaded by human influence and positively loaded by stem density, tree species diversity and canopy cover. PC2 was positively loaded by mean DBH and tree height. Together the PC scores explained 58.5% of the sample variance. Additional details on the PCA are provided in Sections 2.3.5 and 2.5.2 of Chapter 2.

I measured additional covariates that described the structure of the matrix and provided indices of anthropogenic impact using remote sensing on QGIS (Table 4.2). Using a land classification analysis (Chapter 3), I measured the relative amount of forest cover (covariate ‘forest’) and human land use (covariate ‘anthro’) within 400m from each camera trap site (hereafter referred to as ‘land use sampling plots’). I manually reviewed each land use sampling plot to discard misclassified pixels based on ground truthing data collected during camera set ups. For example, in forest areas where human land uses were known to be absent, I discarded single pixels of orchards, which were most commonly misclassified with woodland and secondary forests. This was particularly evident in forest blocks. Other covariates measured included distance to the nearest palm-dominated forest edge (covariate ‘palms’). I considered forest edges as the edge of forest blocks as well as the remnant forest strips, which are visible in aerial imagery and in the land classification map. They typically appear as a distinctive outer shell of converted forest patches. I initially considered three additional covariates that provided a measure of human influence, including distance to the nearest village, road and cultivated area. However, due to significant correlations amongst them ( $r^2 = 0.5 - 0.71$ , all  $P$ -values  $< 0.001$ ), I chose to exclude roads (which are untarmacked in Cantanhez NP) and cultivated areas and keep distance to the nearest village (covariate ‘village’), which provides a stronger measure for human presence and associated activities that may influence primate occurrence. Prior to analysis all covariates were standardised with a mean of 0 and standard deviation of 1.

**Table 4.2**

Summary of the covariates used in arboreal camera trap occupancy models.

| Covariate                                          | ID      | Type   | Description                                                                                                                                                                                                                                                |
|----------------------------------------------------|---------|--------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Camera height                                      | camht   | $p$    | Measured during camera set up. Height of camera above the ground (m).                                                                                                                                                                                      |
| Principal Component 1                              | PC1     | $\Psi$ | Measured using 314 m <sup>2</sup> vegetation plots around each camera trap. Principal Component positively loaded by tree density, canopy cover and Shannon diversity index and negatively loaded by human impact score.                                   |
| Principal Component 2                              | PC2     | $\Psi$ | Measured using 314 m <sup>2</sup> vegetation plots around each camera trap. Principal Component positively loaded by mean DBH and mean tree height.                                                                                                        |
| Forest Area                                        | forest  | $\Psi$ | Amount of forest land class (m <sup>2</sup> ) within 400 m from the camera trap site, measured from a land classification analysis. Forest land class included old secondary sub-humid forest, young secondary forest, oil palm dominated edges, woodland. |
| Anthropogenic Area                                 | anthro  | $\Psi$ | Amount of human land use (m <sup>2</sup> ) within 400 m from the camera trap site, measured from a land classification analysis. Human land use included cultivated areas and villages.                                                                    |
| Distance to nearest oil palm-dominated forest edge | palms   | $\Psi$ | Linear distance to the nearest forest edge dominated by oil palms, including the remaining forest edge in cleared fragments. Measured from satellite imagery and using ground truthing.                                                                    |
| Minimum distance to village                        | village | $\Psi$ | Linear distance to the nearest village (>10 households) or settlement (<10 households)                                                                                                                                                                     |

*Model selection*

I ran single species, single season occupancy models for four arboreal primates, namely Temminck's red colobus, king colobus, Campbell's monkey and Demidoff's galago. Firstly, for each species I compared two models for detection probability parameter  $p$  keeping the occupancy parameter  $\Psi$  constant: the first model included no covariates, i.e. representing the null model  $\Psi(.) p(.)$ , and the second model included detection probability as a function of camera trap height ( $\Psi(.) p(\text{camht})$ ). I selected the best model for detection probability based on the lowest Akaike's Information Criterion (AIC) value, and subsequently fitted occupancy probability on the best detection model as a function of covariates (MacKenzie 2006). I first fitted a full model (including all six covariates) and performed stepwise removal of covariates that contributed the least at predicting occupancy probability. Due to low sample size for detections of colobines, several models for Temminck's red colobus and king colobus that included more than two occupancy covariates failed to converge.

Therefore, for these two species, in addition to the detection models I considered 21 models that included single occupancy covariates and all possible combinations of two covariates. Again, model selection was based on the models' AIC values. Akaike's weights represent an additional method for model selection; a pair of models can be compared by dividing their Akaike's weights (Wagenmakers and Farrell 2004). Models with relatively large Akaike's weights can all be considered as possible candidates. Hereafter, I define the *best model* as the model with lowest AIC value, and *top models* as the models with their corresponding Akaike's weight equal or larger than 0.10.

When the number of sites and/or observations are small and detection probabilities are low, maximum likelihood (ML) models may produce biased estimates for occupancy probability (Welsh et al. 2013). This bias is evident when boundary estimates are generated, i.e. estimates that are very close to 0 or 1 (Hutchinson et al. 2015; MacKenzie et al. 2002; Welsh et al. 2013). The penalised likelihood methods for occupancy models developed by Hutchinson et al. (2015) are a way to improve parameter estimates from datasets that are constrained by small sample sizes (e.g. number of detections, sampling sites and/or survey repeats). For each ML top model, I applied the penalised likelihood method's ridge regularisation, which consists of adding a penalty term to the likelihood of the model to shrink the estimates towards zero, reducing their variance. A five-fold cross-validation was used to choose the penalty term value for each model (Hutchinson et al. 2015). For each species I selected the best penalised likelihood (PL) model based on the AIC value. The mean and standard errors of maximum likelihood and penalised likelihood estimates are presented and compared in the results.

Prior to analysis, I z-transformed all covariates, where the mean is 0 and the standard deviation is 1. I fitted occupancy models using the *occu* and *occuPEN* functions (maximum likelihood and penalised likelihood models, respectively) of the package UNMARKED (Fiske and Chandler 2011) in R version 3.4.2 (R Core Team, 2016). Models were selected using the Akaike's Information Criterion (AIC), where the lowest values represent best models (MacKenzie 2006). To assess model fit, for each best maximum likelihood model ( $N = 4$ ) I ran a chi-square goodness-of-fit test based on 1000 bootstrapped samples using the *mb.gof.test* function in the package AICCMODAVG (Mazerolle 2017).

## 4.3 Results

### 4.3.1 Arboreal camera trapping efficiency

During the four-month sampling period (18 October 2016 – 22 February 2017), arboreal and terrestrial camera traps respectively recorded a total of 56,703 and 70,062 images, of which 5595 and 8484 included primates. The dataset comprised a total of 1370 independent events of primates, of which 716 were from arboreal camera traps and 654 were from terrestrial camera traps (Table 4.3). Terrestrial camera traps recorded five primate species; arboreal camera traps detected all seven species including two not recorded by terrestrial camera traps, i.e. king colobus and Demidoff's galago. The four arboreal species, including Temminck's red colobus, king colobus, Demidoff's galago and Campbell's monkey, were more frequently detected by arboreal camera traps. Conversely, the three semi-terrestrial species, namely western chimpanzee, green monkey and Guinea baboon, were more frequently recorded by terrestrial camera traps. Campbell's monkey was the most detected species overall, with the highest naïve occupancy for both arboreal and terrestrial sites. However, the number of detections of green monkey from terrestrial camera traps was lower relative to that of arboreal camera traps when comparing between matching camera trap sites only, i.e. including only sites where both arboreal and terrestrial cameras were deployed. A selection of images recorded using arboreal camera traps are presented in Appendix 4.1.

**Table 4.3**

Number of independent events and naïve occupancy  $\Psi$  of primate species detected by arboreal and terrestrial camera traps in Cantanhez NP. Values in bold represent data from the 23 matching arboreal/terrestrial camera trap sites.

| Species           | N of independent events |            |             |            | Naïve $\Psi$ |           |             |           |
|-------------------|-------------------------|------------|-------------|------------|--------------|-----------|-------------|-----------|
|                   | arboreal                |            | terrestrial |            | arboreal     |           | terrestrial |           |
| Red colobus       | 14                      | <b>10</b>  | 2           | <b>0</b>   | 26           | <b>30</b> | 2           | <b>0</b>  |
| King colobus      | 19                      | <b>14</b>  | –           | –          | 16           | <b>22</b> | –           | –         |
| Demidoff's galago | 46                      | <b>25</b>  | –           | –          | 24           | <b>22</b> | –           | –         |
| Campbell's monkey | 598                     | <b>347</b> | 267         | <b>135</b> | 79           | <b>83</b> | 63          | <b>57</b> |
| Chimpanzee        | 5                       | <b>3</b>   | 221         | <b>74</b>  | 13           | <b>13</b> | 53          | <b>65</b> |
| Green monkey      | 31                      | <b>30</b>  | 103         | <b>17</b>  | 13           | <b>17</b> | 29          | <b>30</b> |
| Guinea baboon     | 3                       | <b>1</b>   | 61          | <b>13</b>  | 8            | <b>4</b>  | 32          | <b>26</b> |

Naïve occupancy is the proportion (%) of sites with at least one detection.

### 4.3.2 Occupancy models from arboreal camera traps

#### Model selection

Camera trap height was a predictor of detection probability for three of the four primate species (Table 4.4, see Appendix 4.2 for full list of models). Distance to the nearest village predicted occupancy probability in eleven of the 17 top models. Amount of forest habitat, Principal Component 2 and minimum distance to palm-dominated forest edge were included as predictors for occupancy in four models. Principal Component 1 was included in three top models and amount of anthropogenic land use was included in one top model.

**Table 4.4**

List of maximum likelihood occupancy models ( $w_i > 0.10$ ) considered for the penalised likelihood method. Models are compared to the null model  $\Psi(.)p(.)$  and are ranked using the Akaike's Information Criterion (AIC).  $K$ : number of parameters;  $\Delta AIC$ : deltaAIC;  $w_i$ : Akaike's weights. Full list of models shown in Appendix 4.2.

| Species           | # | Model                                         | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|-------------------|---|-----------------------------------------------|-----|--------|--------------|-------|
| Red colobus       | 1 | $\Psi(\text{palms, PC1})p(\text{camht})$      | 5   | 82.94  | 0.00         | 0.32  |
|                   | 2 | $\Psi(\text{palms, PC2})p(\text{camht})$      | 5   | 82.99  | 0.04         | 0.31  |
|                   | 3 | $\Psi(\text{palms, village})p(\text{camht})$  | 5   | 85.16  | 2.21         | 0.10  |
|                   |   | $\Psi(.)p(.)$                                 | 2   | 97.35  | 14.41        | 0.00  |
| King colobus      | 1 | $\Psi(\text{village})p(\text{camht})$         | 4   | 89.58  | 0.00         | 0.29  |
|                   | 2 | $\Psi(\text{village, forest})p(\text{camht})$ | 5   | 91.17  | 1.58         | 0.13  |
|                   | 3 | $\Psi(\text{village, palms})p(\text{camht})$  | 5   | 91.50  | 1.92         | 0.11  |
|                   | 4 | $\Psi(\text{village, PC1})p(\text{camht})$    | 5   | 91.51  | 1.92         | 0.11  |
|                   | 5 | $\Psi(\text{village, PC2})p(\text{camht})$    | 5   | 91.54  | 1.96         | 0.11  |
|                   | 6 | $\Psi(\text{village, anthro})p(\text{camht})$ | 5   | 91.57  | 1.99         | 0.11  |
|                   |   | $\Psi(.)p(.)$                                 | 2   | 97.14  | 7.56         | 0.01  |
| Campbell's monkey | 1 | $\Psi(.)p(\text{camht})$                      | 3   | 277.78 | 0.00         | 0.20  |
|                   | 2 | $\Psi(\text{village})p(\text{camht})$         | 4   | 278.38 | 0.60         | 0.15  |
|                   | 3 | $\Psi(\text{PC2})p(\text{camht})$             | 4   | 278.50 | 0.72         | 0.14  |
|                   | 4 | $\Psi(\text{PC1})p(\text{camht})$             | 4   | 278.99 | 1.21         | 0.11  |
|                   |   | $\Psi(.)p(.)$                                 | 2   | 283.07 | 18.94        | 0.00  |
| Demidoff's galago | 1 | $\Psi(\text{forest, village})p(.)$            | 4   | 117.29 | 0.00         | 0.31  |
|                   | 2 | $\Psi(\text{forest, village, PC2})p(.)$       | 5   | 118.46 | 1.17         | 0.17  |
|                   | 3 | $\Psi(\text{village})p(.)$                    | 3   | 119.21 | 1.92         | 0.12  |
|                   | 4 | $\Psi(\text{forest})p(.)$                     | 3   | 119.39 | 2.11         | 0.11  |
|                   |   | $\Psi(.)p(.)$                                 | 2   | 121.27 | 13.77        | 0.00  |

PC1: Principal Component 1 from vegetation attributes of 340m<sup>2</sup> vegetation plot surrounding the camera trap site (positively correlated with tree density, canopy cover and species diversity  $H$ , negatively correlated with human influence level); PC2: Principal Component 2 (positively correlated with mean DBH and vegetation height); village: distance to the nearest village; palms: distance to palm groves (forest edge of original forest fragments); forest: relative amount of forest cover within 400m of camera trap site; anthro: relative amount of human land use cover within 400m of camera trap site (including village, cultivated area and orchard); camht: camera trap height.

The chi-square goodness of fit test based on 1000 bootstrapped samples revealed statistical non-significance in all best (i.e. #1 based on AIC) maximum likelihood models, therefore providing no evidence of lack of fit (Temminck's red colobus:  $\hat{c} = 0.604$ ,  $P = 0.782$ ; king colobus:  $\hat{c} = 0.865$ ,  $P = 0.559$ ; Campbell's monkey:  $\hat{c} = 1.244$ ,  $P = 0.071$ ; Demidoff's galago:  $\hat{c} = 0.495$ ,  $P = 0.884$ ).

I ran the penalised maximum likelihood method on the 17 top models and ranked them according to their AIC values (Table 4.5). The second top maximum likelihood model for Temminck's red colobus showed the best fit using the penalised method. Therefore, the best model using the penalised method for this species included distance to the nearest palm groves and PC2. Best penalised likelihood models for king colobus, Campbell's monkey and Demidoff's galago were the same as those fitted using the maximum likelihood method.

**Table 4.5**

Model selection for penalised likelihood method. Models are ranked based on the AIC value.  $\lambda$ : chosen penalty weight based on k-fold cross-validation.

| Species           | # | Model                                          | $K$ | $\lambda$ | AIC    | $\Delta$ AIC |
|-------------------|---|------------------------------------------------|-----|-----------|--------|--------------|
| Red colobus       | 1 | $\Psi(\text{palms, PC2}) p(\text{camht})$      | 5   | 0.0625    | 86.42  | 0.00         |
|                   | 2 | $\Psi(\text{palms, village}) p(\text{camht})$  | 5   | 0.5000    | 91.23  | 4.81         |
|                   | 3 | $\Psi(\text{palms, PC1}) p(\text{camht})$      | 5   | 0.5000    | 91.35  | 4.93         |
| King colobus      | 1 | $\Psi(\text{village}) p(\text{camht})$         | 4   | 0.5000    | 90.73  | 0.00         |
|                   | 2 | $\Psi(\text{village, forest}) p(\text{camht})$ | 5   | 0.5000    | 92.45  | 1.72         |
|                   | 3 | $\Psi(\text{village, palms}) p(\text{camht})$  | 5   | 1.0000    | 93.44  | 2.71         |
|                   | 4 | $\Psi(\text{village, anthro}) p(\text{camht})$ | 5   | 1.0000    | 93.58  | 2.85         |
|                   | 5 | $\Psi(\text{village, PC1}) p(\text{camht})$    | 5   | 1.0000    | 93.59  | 2.86         |
|                   | 6 | $\Psi(\text{village, PC2}) p(\text{camht})$    | 5   | 1.0000    | 93.63  | 2.90         |
| Campbell's monkey | 1 | $\Psi(.) p(\text{camht})$                      | 3   | 16.000    | 279.86 | 0.00         |
|                   | 2 | $\Psi(\text{PC2}) p(\text{camht})$             | 4   | 16.000    | 281.55 | 1.69         |
|                   | 3 | $\Psi(\text{village}) p(\text{camht})$         | 4   | 16.000    | 281.57 | 1.70         |
|                   | 4 | $\Psi(\text{PC1}) p(\text{camht})$             | 4   | 16.000    | 281.68 | 1.81         |
| Demidoff's galago | 1 | $\Psi(\text{forest, village}) p(.)$            | 4   | 1.0000    | 118.66 | 0.00         |
|                   | 2 | $\Psi(\text{village}) p(.)$                    | 3   | 1.0000    | 119.78 | 1.12         |
|                   | 3 | $\Psi(\text{forest}) p(.)$                     | 3   | 1.0000    | 120.02 | 1.36         |
|                   | 4 | $\Psi(\text{forest, village, PC2}) p(.)$       | 5   | 2.0000    | 120.80 | 2.14         |

For all best models the standard errors of the parameters' intercepts and covariate beta coefficients were highly reduced in the penalised likelihood method (Table 4.6, see text below for  $\beta$  standard errors). In addition, the maximum likelihood method generated

boundary estimates for occupancy probability of Temminck's red colobus. For king colobus and Demidoff's galago the penalised likelihood method generated similar estimates and standard errors compared to the maximum likelihood models. Thus, the penalised likelihood method was deemed more accurate to obtain more reliable inferences and was selected hereafter.

**Table 4.6**

Comparison of estimates between the maximum likelihood and penalised likelihood models. Values in brackets represent  $\pm$ SE.

| Type | Species  | Model                                     | $\Psi$ Intercept | mean $\Psi$ | $p$ Intercept  | mean $p$    |
|------|----------|-------------------------------------------|------------------|-------------|----------------|-------------|
| ML   | Red col  | $\Psi(\text{palms, PC1}) p(\text{camht})$ | 4.880 (10.100)   | 1.00 (0.00) | -2.270 (0.352) | 0.09 (0.03) |
|      | King col | $\Psi(\text{village}) p(\text{camht})$    | -1.850 (0.618)   | 0.14 (0.07) | -0.386 (0.352) | 0.41 (0.09) |
|      | Campbell | $\Psi(.) p(\text{camht})$                 | 1.700 (0.456)    | 0.85 (0.06) | 0.701 (0.158)  | 0.67 (0.04) |
|      | Galago   | $\Psi(\text{forest, village}) p(.)$       | -1.298 (0.526)   | 0.22 (0.10) | -0.672 (0.316) | 0.34 (0.07) |
| PL   | Red col  | $\Psi(\text{palms, PC2}) p(\text{camht})$ | 0.768 (0.015)    | 0.68 (0.23) | -2.200 (0.005) | 0.10 (0.03) |
|      | King col | $\Psi(\text{village}) p(\text{camht})$    | -1.760 (0.009)   | 0.15 (0.08) | -0.395 (0.004) | 0.40 (0.07) |
|      | Campbell | $\Psi(.) p(\text{camht})$                 | 1.690 (0.015)    | 0.85 (0.14) | 0.698 (0.004)  | 0.67 (0.06) |
|      | Galago   | $\Psi(\text{forest, village}) p(.)$       | -1.160 (0.008)   | 0.24 (0.10) | -0.664 (0.006) | 0.34 (0.10) |

ML = Maximum likelihood, PL = Penalised Likelihood

### *Mean estimates*

The penalised likelihood models generated mean estimates for occupancy probabilities of king colobus, Campbell's monkey and Demidoff's galago that were comparable to their naïve occupancy, with a difference of  $-0.008$ ,  $+0.06$  and  $+0.003$ , respectively. The detection probabilities of these three species were relatively high, particularly for Campbell's monkey. With a low detection probability, Temminck's red colobus showed a much higher mean occupancy probability relative to the naïve occupancy ( $+0.417$ ).

### *Effects of covariates*

Camera trap height positively predicted detection probability of Temminck's red colobus (beta coefficient  $\beta = 1.040 \pm 0.006$ ) and Campbell's monkey ( $\beta = 0.304 \pm 0.003$ ) and negatively predicted that of king colobus ( $\beta = -0.775 \pm 0.009$ ). Occupancy probability of

Temminck's red colobus increased with decreasing distance from the nearest oil palm-dominated forest edge (beta coefficient  $\beta = -3.701$ , SE  $\pm 0.011$ ; Figure 4.2). Principal Component 2, which represented mean tree DBH and height, positively predicted occupancy probability of Temminck's red colobus ( $\beta = 2.585 \pm 0.018$ ). Therefore, occupancy probability of Temminck's red colobus is highest in areas dominated by large, tall trees and close to forest edge dominated by oil palms. Occupancy probability of king colobus was positively influenced by distance to the nearest village ( $\beta = 1.190 \pm 0.007$ ) as was that of Demidoff's galago ( $\beta = 0.726 \pm 0.005$ ). Additionally, for Demidoff's galago, the amount of forest surrounding the camera trap site positively predicted occupancy probability ( $\beta = 0.736 \pm 0.005$ ).

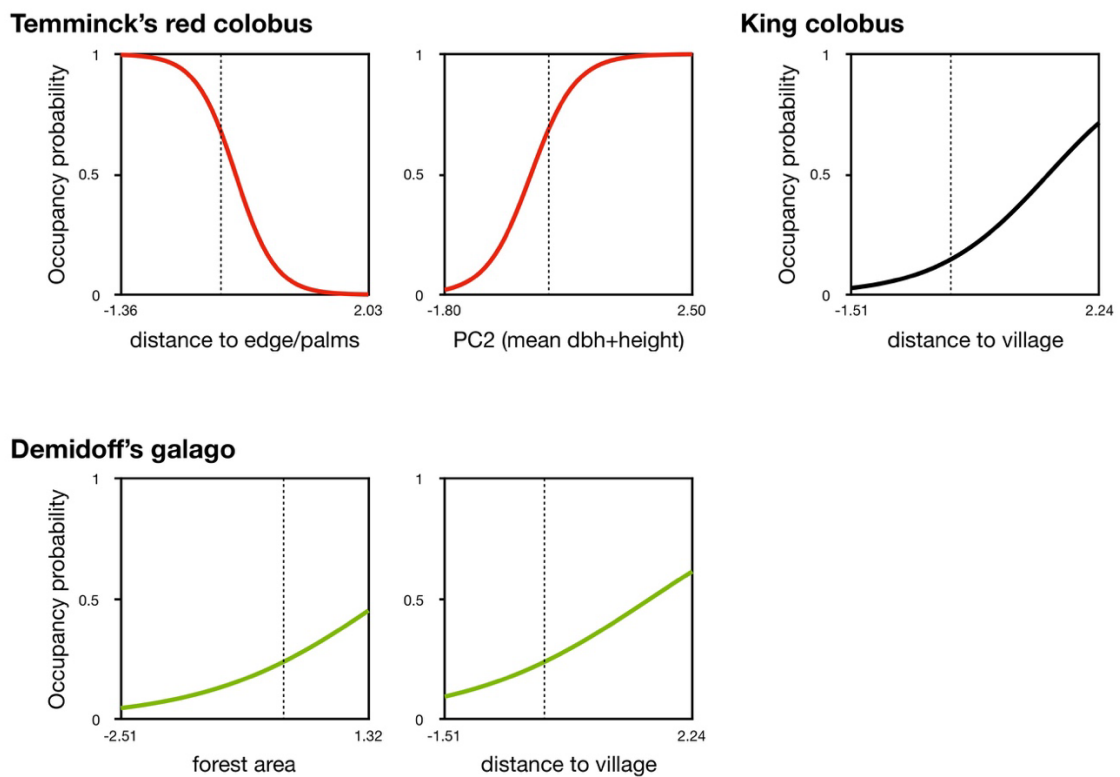


**Figure 4.2**

Effect of covariates on occupancy probabilities of Temminck's red colobus, king colobus and Demidoff's galagos estimated using arboreal camera traps in Cantanhez NP. Mean values are showed by the dotted line.

## 4.4 Discussion

In this Chapter I compared the efficiency of arboreal camera traps in relation to terrestrial camera traps and fitted occupancy models to identify factors affecting the distribution of arboreal primates in an agro-forest landscape mosaic. Despite being an established method in population ecology, occupancy studies are still relatively rare in primatology (Arroyo-Rodríguez et al. 2008; Galán-Acedo et al. 2019b; Guillera-Aroita et al. 2010; Hallam et al. 2016; Kalan et al. 2015; Neilson et al. 2013). This was the first study to combine arboreal camera traps with occupancy models to investigate primate community responses to anthropogenic activities in a heterogeneous forest-agricultural landscape mosaic. A terrestrial/arboreal camera trap occupancy modelling approach can be extended to the multitude of anthropogenic landscapes where primates occur (Estrada et al. 2012; McLennan et al. 2017), improving our understanding of landscape-scale effects on primate communities (Galán-Acedo et al. 2019b).

### 4.4.1 Arboreal camera trap efficiency

*Hypothesis 1: Arboreal camera traps are more effective for gathering data on arboreal primates compared to terrestrial camera traps.*

Arboreal camera traps detected all four arboreal primate species including two that were not recorded by terrestrial camera traps (king colobus and Demidoff's galago). Arboreal camera trap detection frequencies and naïve occupancy of arboreal primates were higher compared to terrestrial camera traps, supporting my first hypothesis. Arboreal camera trap detections of semi-terrestrial chimpanzees and baboons were inadequate for carrying out analysis. The degree of terrestriality in chimpanzees varies greatly across sites. For example, in the semi-arid savannah environments of Fongoli, Senegal, chimpanzees nearly always travel on the ground (Pruetz and Herzog 2017). In contrast at Bossou, Republic of Guinea, although chimpanzees tend to move terrestrially they generally spend more time in the canopy, and increase their terrestrial activities during warmer months (Takemoto 2004). Takemoto (2004) suggested that because local temperatures tend to increase with canopy height, during warmer months chimpanzees are able to minimise their thermoregulation by becoming more terrestrial. However, in Cantanhez the daily average temperature during the first half of the dry season, which coincided with the time of our surveys, are typically lower compared to

the rest of the year (see Chapter 2). While my results suggest that in Cantanhez chimpanzees are highly terrestrial, the comparatively low detection frequencies from arboreal cameras may also have been influenced by camera positioning, particularly when selecting the focal trees/branches. While we attempted to obtain equal chances of capturing all arboreal primates including chimpanzees on camera, our primary concern was to maximise the detection of species less likely to be captured by terrestrial cameras, i.e. arboreal monkeys. Additionally, large, climbable chimpanzee fruiting trees (Bessa et al. 2015) were often unavailable at or around sampling sites. We therefore had to select localities based on monkey signs (smoothened surfaces, colobine faeces) and/or vegetation structure alone (presence of connecting branches, lianas). Importantly, baboons and chimpanzees mostly travel on the ground which likely explains the difference in capture rates between datasets. Testing the efficiency of transects, terrestrial and arboreal cameras for primate surveys in Nyungwe NP, Rwanda, Moore et al. (2020) obtained contrasting results between species. Chimpanzees were more likely to be detected by terrestrial camera traps, mona monkeys (*Cercopithecus mona*) were more often detected by arboreal camera traps. Detection frequencies of Angolan colobus (*Colobus angolensis*) from both arboreal and terrestrial camera traps were lower compared to those from transect surveys (Moore et al. 2020). In Cantanhez NP detection rates of colobine monkeys were relatively low, possibly due to camera positioning (see below).

#### *Camera trap height as a function of detection probability*

For three of the four arboreal species, camera trap height predicted their detection probabilities. Detection probabilities of Campbell's monkey and Temminck's red colobus correlated positively with height of the camera from the ground. The high detection probability estimates of Campbell's monkey, and the relatively low beta coefficient for camera trap height, suggests that camera positioning was within the correct range of canopy strata used by this species. Similarly, at Abuko Nature Reserve, The Gambia, Campbell's monkeys were most commonly observed in mid-strata (defined as 10-15 m at that site) (Gunderson 1977). At the same Gambian site, Temminck's red colobus mostly occupied mid to upper canopy strata (10-25m), and frequently came to the ground to feed (Gunderson 1977). In Fathala, Senegal, this species was also often observed traveling, playing and feeding on the ground (Galat-Luong and Galat 2005). In Cantanhez NP, at average camera

trap heights (9 m), detection probabilities of Temminck's red colobus were still very low (0.10), highlighting a stronger arboreal tendency of this primate at this site. My results indicate that in Cantanhez NP camera traps should be placed above the height range of our cameras to increase detection of this species. Considering that the average vegetation height around camera trap sites was 12.4 m (SD  $\pm 2.7$ , Chapter 2), increasing the height of the camera would have meant choosing parts of the forest with taller vegetation, therefore (i) decreasing the availability of sampling sites, (ii) considerably increasing time-consuming searching and deploying efforts and (iii) possibly having to opt for an alternative sampling design to a systematic survey grid. Surprisingly, camera trap height showed a negative relationship with detection probability of king colobus. These results suggest that king colobus preferably use lower strata, which appears unrealistic considering the high arboreal tendency of this primate and that it is relatively common to observe mixed groups of king colobus and Temminck's red colobus high in the canopy (E Bersacola pers. obs.). In a Peruvian rainforest arboreal camera traps were deployed at a range of 16–30 m and camera trap height positively correlated with detection of all species (Bowler et al. 2017). Placing more camera traps at 20 m and above may actually increase detection of king colobus, which would make the relationship between the parameter and covariate more ecologically realistic.

### *Model fit and accuracy*

All Goodness of Fit tests of the best models showed high  $P$  values except for that of Campbell's monkey which approached significance. Standard errors of parameters following the penalised likelihood method were all less than 0.10 except for those of mean occupancy of Temminck's red colobus ( $\pm 0.23$ ) and Campbell's monkey ( $\pm 0.14$ ). Estimates were therefore less accurate for these two species compared to those of king colobus and Demidoff's galago. Large standard errors for occupancy of Temminck's red colobus is likely due to the very low detection probabilities. A larger number of camera trap sampling sites deployed at the same time will likely increase the accuracy of occupancy and detection estimates (MacKenzie 2006). Trade-offs should be considered between an optimal survey effort and cost-efficiency. In my case, the penalised likelihood method (Hutchinson et al. 2015) worked well for improving accuracy of beta coefficients. Increasing the number of

sampling sites to 50-60 and deploying camera traps in a single array will likely result to more robust estimates.

This study provides evidence that arboreal camera traps can be employed to model occupancy of arboreal primates in agro-forest mosaics, although my results reveal logistical complexities when targeting multiple primates using arboreal camera traps. In ideal terms, a larger number of camera traps should be placed across various canopy strata (including terrestrial, mid-strata and in upper canopy) if the objectives of the study are to maximise detection of all primates. A modelling approach that takes into account spatial autocorrelation would be more appropriate in this case (e.g. Bayesian approach), as it would allow researchers to be more flexible when selecting optimal locations of camera deployment in agro-forest mosaics without the concerns of independence between sampling sites.

#### **4.4.2 Spatial ecology of arboreal primates in an agro-forest landscape**

*Hypothesis 2: Arboreal primates prefer higher quality forest and show sensitivity to anthropogenic influence in agro-forest landscapes*

Colobine monkeys include large amounts of leaves in their diet, with the proportion of young and mature leaves varying across species and populations. However, colobines also depend on seeds, unripe and ripe fruit, buds and/or flowers, and have been found to be selective feeders, i.e. feeding on specific resources in disproportionately higher quantities relative to their availability (Chapman and Chapman 1999; Dasilva 1994; Davies and Oates 1994; Harris 2006; Struhsaker 2010). In Kibale, Uganda, guerezas (*Colobus guereza*) frequently experience intra-group competition to access clumped resources (Harris 2006). These studies clearly show that colobines do not simply rely on low-quality abundant foods. Therefore, the availability of important food-bearing stems is expected to have an impact on the behaviour of colobines, including on their abundance and spatial occurrence. Previous studies have found that availability of food (measured as cumulative DBH/basal area of food tree species) was positively associated with density of Ugandan red colobus (*Piliocolobus tephrosceles*) (Chapman et al. 2006; Chapman and Chapman 1999). On Borneo, red langurs

(*Presbytis rubicunda*) occurred at high densities in a mixed-swamp habitat where availability of large ( $\geq 20$  cm DBH) preferred food trees was high (70 stems/ha), and were absent from a forest sub-class that had lower availability of large preferred food trees (26.7 stems/ha) (Ehlers-Smith and Ehlers-Smith 2013). In my study, tree height and DBH size (PC2) positively predicted occupancy probability of Temminck's red colobus, supporting Prediction 2.1. Large, tall trees such as *Dialium guineense*, *Ficus* spp., *Parinari excelsa*, and *Albizia* spp. were identified as major food sources for Temminck's red colobus in The Gambia (Gunderson 1977). In Cantanhez NP, large red colobus food trees (*D. guineense*, *Albizia* spp. and *Ficus* spp.) are present across the landscape, including human land uses such as orchards and cultivated areas, although their availability is higher within the forest (Chapter 3). Compared to smaller stems, large trees produce more leaves, flowers and fruit, as well as providing more vertical substrate and arboreal pathways to hide and escape potential predators including hunters. According to my models, occupancy of Temminck's red colobus increased with proximity to palm-dominated forest edges. These are present across much of the landscape including the matrix outside the larger forests (Chapter 3). However, the majority (78%) of forest edges measured in this study were those associated with forest blocks (Figure 4.1). Forest edges may provide diverse feeding opportunities including access to adjacent land uses (e.g. orchards and mangroves which are also used (pers. obs.; Gunderson, 1977; Galat-Luong & Galat, 2005; K Hockings unpubl. data) and forest trees commonly present near forest edges including *D. guineense* (E Bersacola unpubl. data).

King colobus live in smaller group sizes compared to other colobus species (e.g. 5-20 individuals compared to 8-70 individuals in Western red colobus) (Davies and Oates 1994; Galat and Galat Luong 1985). King colobus tend to occur at lower densities compared to red colobus in continuous forest (Galat and Galat Luong 1985). King colobus were previously described as rare in Guinea-Bissau (Limoges, 1989) and appear to have a fragmented distribution (Bersacola et al. 2018). My results reveal a restricted spatial occurrence of king colobus in Cantanhez NP driven by a spatial avoidance of areas most intensively used by people: mean occupancy probability of king colobus in Cantanhez NP was very low ( $0.15 \pm 0.08$ ) and consistent with Prediction 2.2, proximity to villages negatively affected occupancy probability of king colobus. Average distance to village was 1.5 km and model predictions showed that beyond 2.5 km from a village king colobus occupancy probabilities

were  $>0.50$ . The restricted availability of space for king colobus in Cantanhez NP as a result of the presence of villages suggests low population numbers of this species. Genetic data of king colobus from Cantanhez showed a negative relationship between isolation-by-distance and genetic diversity (Minhós et al., 2016). Heavy hunting of this rare species contributed to the local extinction in some areas and their overall decline (Minhós et al. 2013). My results corroborate previous research demonstrating significant spatial constraints imposed by human activities on king colobus (Bersacola et al. 2018; Minhós et al. 2016; Minhós et al. 2013). The other human-related covariate ('anthro') negatively correlated with occupancy but was only included in the fourth top model (Table 4.5). King colobus were observed in agricultural areas in Dulombi NP, Guinea-Bissau (Bersacola et al. 2018) and Cantanhez NP (E Bersacola pers. obs). Although cultivated areas may pose certain constraints, king colobus are more sensitive to human presence *per se*. This is likely the result of severe hunting pressure reducing the population numbers and altering the monkeys' behaviour (i.e. increase crypticity and human-avoidance).

Consistent with Predictions 2.1 and 2.2, occupancy probabilities of Demidoff's galagos were positively influenced by forest cover and negatively affected by proximity to the nearest village. In Angola, high densities of this species were recorded in humid and gallery forests compared to more open habitats such as savannah and miombo woodlands (Bersacola et al. 2015). The same study identified the density of undergrowth vegetation and canopy cover as predictors of Demidoff's galagos abundance (Bersacola et al. 2015). Although remnant forest edges, shrubs and fallow may provide suitable vegetation, in this study arboreal camera traps were all placed above the typical canopy stratum used by Demidoff's galagos (i.e. below 5 m). The generally more open habitats near villages are likely to limit the spatial occurrence of this primate. Although they are likely to occur in patchily distributed remnants across the matrix, forest blocks are likely to provide a more suitable environment for this nocturnal primate.

Campbell's monkeys were frequently recorded on the ground. Unlike those of strictly arboreal primates, the best model of Campbell's monkeys included no covariates for the occupancy parameter. Estimates of occupancy probabilities of this primate were high, indicating that Campbell's monkeys are widespread across Cantanhez NP. The amount of anthropogenic land use was not included in any of the top models, and this species was commonly observed near agricultural areas, occasionally feeding on available cultivated

fruit (E Bersacola unpubl. data). These results provide further support for Hypothesis 2. Campbell's monkeys are likely to be better able to adapt to the matrix compared to the other three arboreal primates, at least partially due to their locomotory flexibility. At Taï National Park, Ivory Coast, Campbell's monkeys avoid food competition with other guenons by using the lowest strata in the canopy (Buzzard 2006). In Cantanhez NP Campbell's monkeys are the only guenon, but may occasionally be temporally displaced by chimpanzees, baboons and humans. Despite their abundance, Campbell's monkeys are the primate most commonly hunted (Minhós et al. 2013; E Bersacola unpubl. data). It is possible that in human parts of the habitat (such as cultivated fields, orchards and areas near villages) the monkeys switch between terrestrial and arboreal locomotion to access feeding patches and escape potential attacks by humans or dogs. The combined ecological flexibility and lack of arboreal primate competitors may explain why this species is relatively common and widespread in Cantanhez NP.

### *Conclusions*

In this Chapter, I demonstrated the usefulness of arboreal camera traps for modelling occupancy of arboreal taxa in agro-forest mosaics. The main limitation of this study was the survey effort required to obtain robust estimates on all arboreal primates. Specifically, the number of camera trap sampling sites and the range of substrate heights. Future camera trap studies on Temminck's red colobus and king colobus should increase the number of sampling locations to at least 50 and the average height of camera traps to at least 20 m above the ground. Despite these limitations, I was able to model occupancy and identify environmental and anthropogenic constraints on the occurrence of arboreal primates for the first time in this type of landscape using an arboreal camera trap approach. My occupancy models provided support for Hypothesis 2, that habitat quality plays an important role in the occurrence of arboreal primates. In the agro-forest landscape of Cantanhez NP, occupancy of Temminck's red colobus was mediated by tall vegetation and large stems, which likely provide key structural support and feeding sources. The spatial occurrence of the two rare arboreal primate species (king colobus and Demidoff's galago) was negatively mediated by the presence of villages. The limited distribution of king colobus across Cantanhez NP is likely the consequence of heavy hunting pressure. In the final Chapter I will discuss the implications of my results for the conservation of colobine monkeys in this region.

## CHAPTER 5

### Seasonal variation in primate occupancy and activity patterns in a heterogeneous, human-dominated landscape



## 5.1 Introduction

Species distributions are the result of interactions with abiotic and biotic components, as well as the species' ability for dispersal (Wisz et al. 2013). At the local scale, animal spatial organisation is shaped by the distribution of resources and interspecific interactions (Cowlshaw 1997; Heithaus and Dill 2002; Hughes et al. 1994; Valeix et al. 2009). For example, to maximise foraging efficiency animals may select habitats in relation to food availability (Bryson-Morrison et al. 2017; Furuichi et al. 2001), and/or seasonally shift across different parts of their home range accordingly (Schreier 2010; Vedder 1984). While meeting ecological requirements is essential to maintain long-term fitness, the presence of potential competitors and predators can strongly influence spatial organisation. Species that occupy similar ecological niches are able to coexist by exploiting resources at different times, maximising dietary diversity, increasing consumption of food that is more available, and/or by spatial partitioning, i.e. using different habitats or parts of the same habitat (Sexton et al. 2017). Coexistence also depends on habitat availability and population abundance of sympatric taxa (Chesson 2000; Holt 2009). Where predators are present prey species must balance foraging success with reducing the risks of predation, for example by selecting habitats that provide better protection or escape opportunities (Rodríguez et al. 2001; Wirsing et al. 2007), increasing vigilance (Creel et al. 2014), changing group size and cohesion (Schreier and Swedell 2012), and/or adjusting temporal activity patterns (Tambling et al. 2015). The risk of predation can sometimes be the main determinant of prey spatial distribution (Cowlshaw 1997; Fortin et al. 2009; Willems and Hill 2009), and may differ between similar prey taxa sharing the same landscape and predators (Coleman and Hill 2014; Willems and Hill 2009).

Anthropogenic activities are having a profound impact on global biodiversity (Pimm et al. 2014). Deforestation, forest degradation and fragmentation due to habitat conversion into agriculture are one of the major causes for the decline of tropical biodiversity (Estrada et al. 2017; Gibson et al. 2011; Newbold et al. 2015). Forest fragmentation leads to higher tree mortality and a decrease in the availability of large trees (Laurance et al. 2011; Saunders et al. 1991), changing the distribution and availability of wild resources particularly fruit. To persist in fragmented landscapes, animals need to find effective ways to access the redistributed resources, which largely depends on the species' ability to use the surrounding

matrix (Anderson et al. 2007). Species with greater ecological niche breadth may respond better to habitat alteration compared to specialists (e.g. in birds, rodents, bats, amphibians and butterflies: Julliard et al. 2004; Swihart et al. 2006; Warren et al. 2001). Frugivorous species will face longer periods of food scarcity as large fruit-bearing trees become scarcer in fragmented habitats (Laurance et al. 2011; Saunders et al. 1991). However, studies have also shown no link between degree of specialisation and vulnerability to extinction (Brashares 2003). Species that show high social and behavioural plasticity can adjust relatively quickly to new environmental conditions (Koirala et al. 2016; McLennan et al. 2017; Nowak and Lee 2013; Šálek et al. 2015). Some human land uses such as small-scale agriculture may offer alternative foraging opportunities particularly for omnivores and frugivores in the form of cultivated foods. However, exposure to humans may be risky for certain taxa if they are targeted for meat (Cullen et al. 2001; Linder and Oates 2011; Naughton-Treves et al. 2003; Ripple et al. 2016) and/or killed or scared away by people attempting to protect crops and livestock (Gusset et al. 2009; Hockings 2016; John et al. 2018; Meijaard et al. 2011; Osborn and Hill 2005; Woodroffe and Ginsberg 1998). Within human-dominated landscapes, behaviourally flexible, larger species with slow life histories may be more vulnerable to direct persecution by humans, rather than the indirect effects of fragmentation (Owens and Bennett 2000). Thus, anthropogenic activities impose new conditions that are likely to alter the wildlife's attempts to balance between meeting nutritional requirements, decreasing competition and minimising mortality risks.

Primates are found across a great diversity of ecosystems and different species are often co-occurring, particularly in tropical rainforests (Schreier et al. 2009). To avoid interspecific competition, primates may use fine-scale partitioning across space both horizontally and vertically (Bersacola et al. 2015; Buzzard 2006; Schreier et al. 2009). However, the effects of human activities on primate interspecific niche partitioning are still unclear, despite the majority of taxa inhabiting human-impacted environments (Hockings et al. 2015; McLennan et al. 2017). Primates often display high adaptability to novel environments due to their cognitive complexity and socioecological flexibility (Nowak and Lee 2013). Some primates are intrinsically more susceptible than others to habitat fragmentation and alteration, in particular arboreal species that rely on continuous vegetation for traveling, foraging and sleeping (Anzures-Dadda and Manson 2007; Cheyne 2011; Chapter 4). Small home range size and high levels of frugivory may also increase primate vulnerability to forest

fragmentation (Boyle and Smith 2010). Although certain ecological traits may help predict a species' capacity to persist in fragmented landscapes, behavioural flexibility can play an even greater role (Nowak and Lee 2013). Behavioural adjustments in primates include increasing terrestriality (Galat and Galat-Luong 1976; Mourthé et al. 2007), exploiting introduced food resources such as feeding on human crops or exotic plants (Bicca-Marques and Calegario-Marques 1994; Eppley et al. 2015; Hockings and McLennan 2012), using the surrounding matrix and/or roads for accessing resources including sleeping sites (Anderson et al. 2007; Hockings et al. 2006), and changing spatiotemporal activity patterns, for example by moving into new, undisturbed habitats (Nowak 2012), or increasing activity at night (Donati et al. 2016; Krief et al. 2014).

Agroforest ecosystems can provide alternative resources to primates, but the ability of primates to persist in these new environments largely depends on the species' behavioural flexibility, the type of land-use surrounding the forest fragments, and whether primates are persecuted or hunted (Estrada et al. 2012; Hill and Webber 2010; McLennan et al. 2017; Regmi et al. 2013). For example, chimpanzees have a broadly omnivorous diet, comprising a great diversity of plant and animal foods (Bogart and Pruetz 2011; McGrew 1983; Morgan and Sanz 2006; Watts et al. 2012a; Watts and Mitani 2002). However, they are considered ripe fruit specialists as they pursue a fruit-dominated diet even when fruit is scarce (Watts et al. 2012b; Wrangham et al. 1998). Chimpanzees exhibit flexible fission-fusion social organisation which allows them to respond to fruit scarcity quickly by adjusting their foraging grouping patterns (Lehmann et al. 2007; Tutin and Fernandez 1993). Moreover, chimpanzees display high behavioural flexibility in anthropogenic habitats (Hockings et al. 2006; McCarthy et al. 2017; McLennan and Hockings 2014). At Bossou, Guinea, Western chimpanzees (*P. t. verus*) increase crop foraging during periods of wild fruit scarcity (Hockings et al. 2009), and increase party cohesiveness when foraging in cultivated areas (Hockings et al. 2012). These findings suggest that chimpanzees are able to maintain an optimal foraging strategy throughout the year by exploiting cultivated resources and respond to increased potential risks presented by humans by modifying their social behaviour. Due to the capacity of modifying their behaviour in response to environmental change, as well as the presence of local taboos over chimpanzee hunting, the majority of Western chimpanzees are still present outside protected areas (Heinicke et al. 2019). In contrast, where primates are consumed as bushmeat, the costs of poaching can quickly overtake any benefits

associated with increased foraging opportunities in agricultural areas. Baboons (*Papio* spp.) are omnivorous and ecologically flexible; they are found in most environments including deserts and rainforests, and can easily adapt to modified environments by exploiting human resources (Hill 2000). Across Africa baboons are often perceived as a highly destructive species (Hill 2000; Hill and Webber 2010; Limoges 1989; McLennan et al. 2012; Mormile and Hill 2017) and in West Africa, they are also commonly hunted for meat (Ferreira da Silva et al. 2014; Minhós et al. 2013). The Guinea baboon (*P. papio*) is the most vulnerable of the *Papio* species and is believed to have suffered a 20-25% reduction in geographical range since the 1980's (Oates et al. 2008) as a result of bushmeat hunting (Ferreira da Silva et al. 2014) and regulatory advocacy for lethal management methods (at least in Guinea-Bissau: Limoges 1989). In Guinea-Bissau, Guinea baboons are believed to be locally extirpated from several localities (Ferreira da Silva et al. 2014; E Bersacola unpubl. data), and are rarely seen in human areas compared to baboons in eastern and southern Africa (E Bersacola, pers. obs). Historical and contemporary human behaviours towards primates must be taken into account when examining the mechanisms of co-existence across different spatiotemporal scales.

### **5.1.1 Aims and hypotheses**

For this Chapter, I examine primate spatiotemporal occurrence in the heterogeneous, human-dominated landscape of Cantanhez NP. First, I examine patterns of co-occurrence amongst semi-terrestrial primates based on their naïve occupancy across camera trap sites. Using a camera trap-based occupancy framework (MacKenzie et al. 2002), I then identify environmental and anthropogenic factors affecting the spatial distribution of four primate taxa: chimpanzees, Guinea baboons, green monkey and Campbell's monkey. Finally, I compare primate daily activity patterns between two space gradients across the heterogeneous mosaic: one representing the forest and a second defined as 'anthropogenic'.

Occupancy models have previously been used to assess the potential for the long-term monitoring of primate populations (Guillera-Arroita et al. 2010; Hallam et al. 2016; Keane et al. 2012), to identify primate ecological requirements (Arroyo-Rodríguez et al. 2008; Neilson et al. 2013), and to examine predator-primate interactions (Farris et al. 2014). However, camera trap-based approaches to examine species spatiotemporal responses at the

landscape scale in anthropogenic environments remain rare in primatology (Galán-Acedo et al. 2019b; Garriga et al. 2019). Camera traps have the advantage of enabling scientists to make socioecological inferences without influencing the behaviour of the study animals, as well as detecting elusive hunted species (Boyer-Ontl and Pruetz 2014; O’Connell et al. 2010), and carnivore research has long taken advantage of this method in landscape-scale studies (Carter et al. 2012, 2015; Khorozyan et al. 2014; Schuette et al. 2013; Wang et al. 2015). For example, Carter and colleagues (2012) found high spatial and low temporal overlap between tigers (*Panthera tigris*) and humans in south-central Nepal, suggesting that tigers adjust their temporal activity patterns to minimise direct encounters with people. In Santa Cruz, California, Wang and colleagues (2015) investigated whether a predator’s temporal activity influenced that of one another, and whether human influence had any effect on the predators’ temporal activities. They found that predators made temporal adjustments to avoid humans, and that human presence decreased temporal segregation between predators (Wang et al. 2015).

As a potential predator and dominant competitor of wildlife, humans are likely to impact the spatial distribution of sympatric primates, particularly those targeted for hunting (Donati et al. 2016). Humans, other apes and monkeys shifted to diurnal activity from early nocturnal ancestors (Ross 2000). Unlike carnivores that evolved to be mainly nocturnal or cathemeral (Wu et al. 2018), apes and monkeys share the same temporal niche with humans. Consequently, temporal overlap between people and primates will be much higher compared to that between humans and carnivores. However, peaks of primate activity in anthropogenic areas may differ to those in forest patches where human presence is likely to be discontinuous. Additionally, as in the case for some carnivores (Wang et al. 2015), temporal overlap between primate taxa may increase within human land uses due to a limited availability of ‘undisturbed’ time.

For this chapter, I test the following hypotheses:

| Hypothesis                                                                                                                                     | Prediction                                                                                                                                                                                                                                                                                                                                                                   |
|------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1. Semi-terrestrial primates show some degree of spatial partition across the heterogeneous landscape.                                         | <p>1.1 The majority of camera trap sites (&gt;50%) include up to one of the four semi-terrestrial primates.</p> <p>1.2 The naïve occupancy of one or more semi-terrestrial primates will not overlap with that of another.</p> <p>1.3 Occupancy probabilities of the four semi-terrestrial primates are predicted by different combinations of environmental covariates.</p> |
| 2. Patterns of spatial occurrence of primates are seasonally flexible in human-dominated agro-forest landscapes.                               | <p>2.1. Occupancy will be driven by different covariates between dry and rainy season, and/or:</p> <p>2.2. Covariates will have different effects in the dry and rainy seasons.</p>                                                                                                                                                                                          |
| 3. Primates targeted for bushmeat spatially avoid humans (primate response: spatial avoidance of risk).                                        | <p>3.1 Occupancy probabilities of hunted primates (diurnal primates except chimpanzees) will be negatively influenced by anthropogenic covariates.</p>                                                                                                                                                                                                                       |
| 4. Human activities alter the activity patterns of primates due to constituting potential risk (primate response: temporal avoidance of risk). | <p>4.1 Activity patterns will significantly differ between forest and anthropogenic areas;</p> <p>4.2 Temporal overlap amongst primates will be higher in anthropogenic areas compared to forest due to limited amount of ‘risk-free’ time.</p>                                                                                                                              |

## 5.2 Methods

### 5.2.1 Study area and study species

I selected my study area in the southern part of the park, comprising 12 protected forests and 32 villages, covering a 180 km<sup>2</sup> area (Figure 5.1). The landscape is characterised by forest-mangrove-savannah-agriculture-village heterogeneous mosaic. Much of the land converted into agriculture consists of cashew plantations and shifting cultivation. Remnant forest edges dominated by oil palms (*Elaeis guineensis*) are often present along cultivated areas. Chapter 3 provides more details about the landscape structure in Cantanhez NP. Seven primate species are present, of which four are semi-terrestrial (see Section 2.2 Chapter 2). See Section 2.1 in Chapter 2 for more information.

### 5.2.2 Data collection

To examine seasonal differences in primate spatial occurrence and temporal activity I gathered data between October 2016 and November 2017, covering two separate periods in both dry and rainy seasons. During the dry season (October 2016 – March 2017) I used 65 camera trap sampling sites using a two-array system: the first array (October – December 2016) comprised 33 camera trap sites, and the second array (December 2016 – March 2017) comprised 32 camera trap sites. For the rainy season (July – October 2017) I repeated the survey using 51 camera trap sampling sites, deployed all at once. During the dry season two cameras were stolen and one malfunctioned, and during the rainy season one camera was stolen. In summary, during the dry season there were 62 camera trap sites totalling 3113 camera trap days, and in the rainy season there were 50 camera trap sites totalling 4415 camera trap days.

I set up camera traps across old growth coastal forest, young growth forest, palm-dominated forest edges, mangrove edges, woodland, abandoned villages and orchards (cashew, orange-mixed). The minimum distance between camera trap sites was 1 km and the average nearest-neighbour distance between sites was 1.30 km SD±0.21 in the dry season and 1.30 km SD±0.24 in the rainy season. See Section 2.3 in Chapter 2 for additional information.

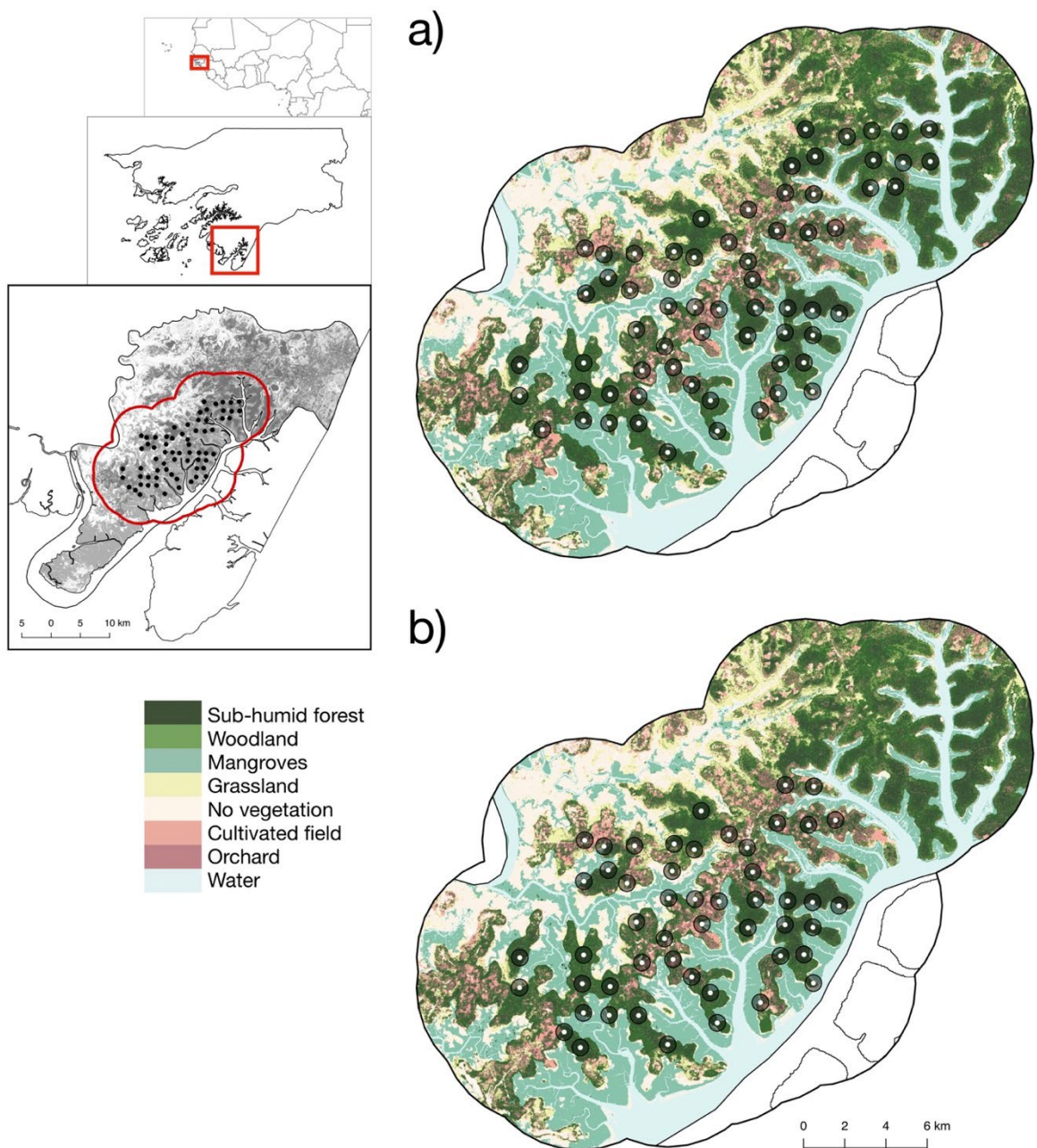


**Figure 5.1**

Map and location of the study area showing the camera trap survey sites in Cantanhez NP deployed during (a) the dry season (Oct 2016 – March 2017) and (b) the rainy season (July – October 2017).

### 5.2.3 Data analysis

#### *Data management*

I used the R package CAMTRAPR to extract image metadata, generate descriptive statistics and species detection histories for subsequent analyses of occupancy modelling (Niedballa et al. 2017; R Core Team 2016). I set 60 minutes as the minimum time interval separating independent detections and calculated the relative frequency (also known as Relative Abundance Index, (Jenks et al. 2011) for each species dividing the total number of independent detections by the total number of camera trap days and multiplying by 100. For the detection histories, each sampling occasion constituted a 7-day period. Detection histories included eight sampling occasions for the dry season survey (24 October 2015 – 28 February 2017), and eleven for the rainy season (27 July – 12 October 2017). For more information see Section 2.4 in Chapter 2.

#### *Covariates*

The models included a total of eight covariates (Table 5.1). PC1 and PC2 were generated using 314 m<sup>2</sup> circular vegetation plots around each camera trap site (Chapter 2). PC1 was negatively loaded by human influence and positively loaded by stem density, tree species diversity and canopy cover. PC2 was positively loaded by mean DBH and tree height. See Section 2.5.2 in Chapter 2 for additional details. Other covariates measured remotely included those used in Chapter 4 as well as distance to the nearest mangroves (covariate ‘mangr’), an important habitat for green monkeys (Galat and Galat-Luong 1976; Nowak 2012). Again, I included relative amount of forest cover ('forest'). Chimpanzees in Cantanhez NP extensively use wild oil palms for nesting (Sousa et al. 2011) as well as feeding (fruit, flower and pith, Bessa et al. 2015). I therefore included distance to the nearest palm-dominated forest edge (covariate ‘palms’), due to the importance of oil palms in the diet and nesting behaviour of chimpanzees in Cantanhez NP and elsewhere (Humle and Matsuzawa 2004). Other primates are also commonly seen on oil palms and are known to feed on the fruit. Human-related covariates consisted of distance to the nearest village ('village') and relative amount of human land use ('anthro'), which includes agricultural fields (orchards and shifting cultivation) and village areas. Chimpanzees at Cantanhez NP are reported to feed on cultivated foods including cashew, orange, mango and papaya (Bessa et al. 2015;

Hockings and Sousa 2012; Parathian et al. 2018). Orange, mango and papaya are present within villages, whereas cashew orchards dominate the agricultural matrix (Chapter 3). Farmers report that baboons and green monkeys feed on groundnut and rice, which are grown in the shifting cultivation fields.

**Table 5.1**

Covariates included in occupancy models. All covariates were standardised to z scores prior to analysis.

| Group                | Covariate | Description                                                                                                                                                                   |
|----------------------|-----------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Vegetation structure | PC1       | Vegetation composition within 10m from the camera trap site. Positively loaded by tree density, canopy cover, tree species diversity and negatively loaded by human influence |
|                      | PC2       | Vegetation composition within 10m from the camera trap site. Positively loaded by mean DBH and vegetation height                                                              |
| Landscape structure  | forest    | Relative amount of forest cover within 400m from the camera trap                                                                                                              |
|                      | mangr     | Minimum distance to the nearest mangrove (km)                                                                                                                                 |
|                      | palms     | Minimum distance to the nearest forest edge (or remaining forest edge of converted forests) dominated by oil palm groves (km)                                                 |
| Anthropogenic        | village   | Minimum distance to the nearest village (km)                                                                                                                                  |
|                      | anthro    | Relative amount of human land use (village and cultivated field) within 400m from the camera trap                                                                             |

### *Model selection*

I used the *occu* function in the R package UNMARKED to run single season occupancy models (Fiske and Chandler 2011; MacKenzie et al. 2006) of chimpanzees, baboons, green monkeys and Campbell's monkeys. I initially considered multi-season occupancy models (MacKenzie et al. 2003) using the *colex* function, also available in UNMARKED. However, the number of comparable surveys sites between the dry and the rainy seasons (i.e. repeated sites,  $N=48$ ), appeared too low to generate accurate estimates of seasonal changes in occupancy. The poor accuracy was shown by high standard errors of beta coefficients ( $\beta \pm SE$ ), large 95% CI's of the covariates' estimates for colonisation and extinction ( $\gamma$  and  $\epsilon$  parameters), and lack of fit (e.g. chi-square goodness of fit test for the best chimpanzee *colex* model, based on 1000 bootstrapped samples:  $\hat{c} = 2.03$ ,  $P = 0.013$ , indicating lack of fit). I therefore chose to run single-season models separately for each season, which allowed us to obtain estimates of two parameters (occupancy  $\Psi$  and detection  $p$ ) for both dry and rainy

seasons and identify seasonal variations in the influence of covariates. I ranked models based on the Akaike's information criterion (AIC) and Akaike's weight. To assess model fit, I used a chi-square goodness-of-fit test based on 1000 bootstrapped samples using the *mb.gof.test* function in the package AICCMODAVG (Mazerolle 2017). All *P*-values of best models were not significant, indicating no evidence of lack of fit. I used the function *predict* in the UNMARKED package to generate predictions of detection and occupancy probabilities of top models. I then plotted the obtained predictions to show relationships with covariates.

### *Activity patterns*

I compared diel activity patterns between land uses that are intensively used by people and those less frequently used by people. I defined camera trap sites placed inside or within 200m distance from a human land use (i.e. village or cultivated area) as 'anthropogenic', and sites further than 200m from a human land use (i.e. secondary forest, mangrove, woodland) as 'forest'. Therefore, in the dry season 36 sites were within forest and 26 sites were within anthropogenic areas. In the rainy season, the number of anthropogenic areas remained the same, whereas forest areas were reduced to 24 sites. Like for occupancy models, I extracted camera trap image metadata using the R package CAMTRAPR (Niedballa et al. 2016). I used the R package OVERLAP (Meredith and Ridout 2018) to estimate kernel density of time-of-day activity for chimpanzees, baboons, green monkeys and Campbell's monkeys in anthropogenic and forest habitats. I converted times into radians to calculate kernel density functions and coefficients of overlap ( $\Delta$ ), i.e. the amount of temporal overlap between species pairs. Using OVERLAP, for each species I calculated the optimal bandwidth for kernel density using the *getBandWidth* function with smoothing parameter  $\kappa = 3$  (Ridout and Linkie 2009), and fitted the von Mises kernel density using the *densityFit* function with a length of 200 sample points. To test for significant differences in the circular distribution of diel activity between anthropogenic and forest habitats I performed a Watson's test for homogeneity using the *watson.two.test* function in the R package CIRCULAR (Lund et al. 2017). Using the package OVERLAP, I compared temporal overlap between species in forest versus anthropogenic areas using the coefficient of overlap  $\hat{\Delta}_1$  for small sample sizes ( $N < 50$ ) and  $\hat{\Delta}_4$  for large sample size, as described in Ridout and Linkie (2009), and obtained 95% confidence intervals using 1000 bootstrap samples. Activity plots were generated using the *radial.plot* function in the R package PLOTRIX (Lemon 2006).

## 5.3 Results

I recorded a total of 1761 independent detections of terrestrial or semi-terrestrial primates, 652 of which were recorded in the dry season and 1109 in the rainy season. Campbell's monkeys had the highest number of detections and proportion of sites occupied (naïve occupancy), followed by chimpanzees (Table 5.2). Terrestrial camera traps also recorded Temminck's red colobus and king colobus, two primates that are largely arboreal, but independent detections were low ( $N = 10$  in total) precluding any further analysis (see Chapter 4 for analysis of arboreal camera trap data). Chimpanzee detection frequencies and naïve occupancy were similar between seasons. While in the rainy season detection frequencies were higher, in this period naïve occupancy of baboons more than halved. A selection of terrestrial camera trap images is presented in Appendix 5.1.

**Table 5.2**

Relative detection frequency (N of independent events/100 camera trap nights), naïve occupancy and N of independent events in forest and anthropogenic areas in the dry and rainy seasons.

|                   | Detection frequency |       | Naïve occupancy |       | IE, forest |       | IE, anthro |       |
|-------------------|---------------------|-------|-----------------|-------|------------|-------|------------|-------|
|                   | Dry                 | Rainy | Dry             | Rainy | Dry        | Rainy | Dry        | Rainy |
| Chimpanzee        | 7.10                | 7.11  | 53%             | 50%   | 144        | 134   | 77         | 180   |
| Baboon            | 1.96                | 2.49  | 32%             | 12%   | 59         | 110   | 2          | —     |
| Green monkey      | 3.31                | 4.01  | 29%             | 40%   | 33         | 76    | 70         | 101   |
| Campbell's monkey | 8.58                | 11.51 | 62%             | 78%   | 194        | 314   | 73         | 194   |

IE = independent events, anthro = anthropogenic

### 5.3.1. Primate co-occurrence at the fine scale

Eighty-nine percent and 94% of the total camera trap sites in the dry and rainy season, respectively, included at least one detected primate species. Of the occupied sites, 68% and 64% included two to four species in the dry and rainy season, respectively. The majority of sites occupied included two detected primate species (41% in the dry season and 43% in the rainy season). Twenty-three percent and 19% of occupied sites included three primate species detected in the dry and rainy season, respectively. Campbell's monkeys were the species that had the highest spatial overlap with other primates, occupying 58–100% of sites

where another species was detected (Figure 5.2). For example, in the dry season, Campbell's monkeys were recorded in 75% of the total sites where baboons were detected. In the rainy season, Campbell's monkeys occupied all recorded baboon sites. Chimpanzees occupied 50% of baboon sites in both seasons. Chimpanzees occupied 61% of green monkey sites in the dry season, and 55% in the rainy season. Chimpanzees occupied 49 and 55% of Campbell's monkey sites in the dry and rainy season, respectively. Green monkeys and baboons were the species pair that showed the highest spatial segregation; green monkeys occupied 33–35% of baboon sites, and baboons occupied 9–39% of green monkey sites.

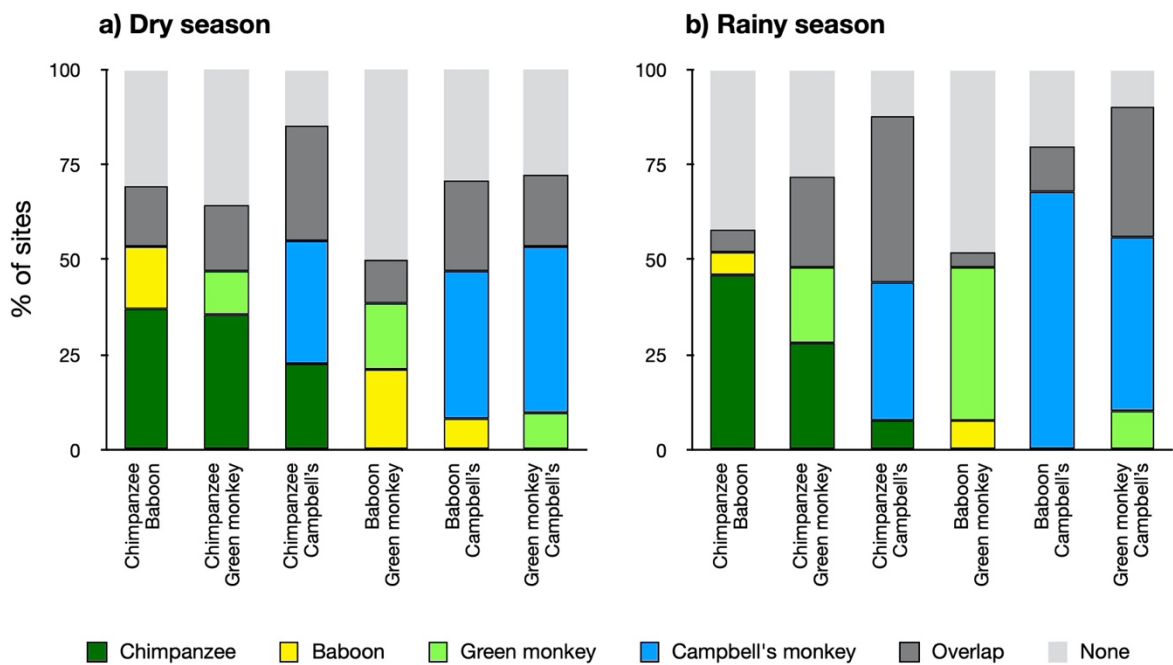


**Figure 5.2**

Co-occurrence of primates in Cantanhez NP during the (a) dry and (b) rainy seasons. Y axis is the percentage of sites where primates were detected, i.e. the naïve occupancy. In colour (red, yellow, green and blue) is the % of sites where only one the two species' pair was detected. Dark grey represents number of sites where both species were detected, light grey represents sites where none of the two species were detected.

### **5.3.2 Occupancy models: general patterns of detection and occupancy**

Single season occupancy modelling resulted in a total of 30 suitable models, i.e. with Akaike's weight of  $>0.10$ , including 13 dry season and 17 rainy season models (Table 5.3). The number of covariates included in top models ranged from two to eight. In general, detection probabilities of green monkeys and Campbell's monkeys were influenced by a larger number of covariates compared to the other two primates. Overall, occupancy probabilities of top models were more frequently influenced by environmental compared to anthropogenic covariates. Forest area and PC1 (which positively correlated with tree density, canopy cover and vegetation diversity and negatively correlated with human change) were the most important covariates for occupancy, occurring in 15 and 18 models, respectively. Distance to palm groves (palm-dominated forest edge) was also an important covariate for occupancy, present in 10 out of 30 top models. Distance to the nearest village and relative amount of human land use, i.e. the anthropogenic covariates considered in this analysis, influenced occupancy probabilities in seven and six out of the 30 top models, respectively. The full lists of models are available in Appendix 5.2.

**Table 5.3**

Best models of chimpanzees, baboons, green monkeys and Campbell's monkeys ( $w_i > 0.10$ ) compared to the null model  $\Psi(.)$   $p(.)$ . Models are ranked using the Akaike's Information Criterion (AIC).  $K$ : number of parameters;  $\Delta AIC$ : deltaAIC;  $w_i$ : Akaike's weights. Full list of models shown in Appendix 5.2.

| Species           | Season | # | Model                                                                            | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|-------------------|--------|---|----------------------------------------------------------------------------------|-----|--------|--------------|-------|
| Chimpanzee        | dry    | 1 | $\Psi(PC1, \text{village, palms}) p(PC1, PC2, \text{mangr})$                     | 8   | 379.55 | 0.00         | 0.30  |
|                   |        | 2 | $\Psi(PC1, \text{village}) p(PC1, PC2, \text{mangr})$                            | 7   | 380.29 | 0.73         | 0.20  |
|                   |        | 3 | $\Psi(PC1, \text{village, palms, forest}) p(PC1, PC2, \text{mangr})$             | 9   | 381.02 | 1.47         | 0.14  |
|                   |        | 4 | $\Psi(PC1) p(PC1, PC2, \text{mangr})$                                            | 6   | 381.70 | 2.14         | 0.10  |
|                   |        |   | $\Psi(.) p(.)$                                                                   | 2   | 407.56 | 28.01        |       |
|                   | rainy  | 1 | $\Psi(PC1, PC2, \text{village, palms}) p(PC2, \text{mangr, palms})$              | 9   | 405.39 | 0.00         | 0.15  |
|                   |        | 2 | $\Psi(PC1, PC2, \text{palms}) p(PC2, \text{mangr, palms})$                       | 8   | 405.83 | 0.44         | 0.12  |
|                   |        | 3 | $\Psi(PC2) p(PC2, \text{mangr, palms})$                                          | 6   | 405.83 | 0.44         | 0.12  |
|                   |        | 4 | $\Psi(PC2, \text{palms}) p(PC2, \text{mangr, palms})$                            | 7   | 405.98 | 0.59         | 0.11  |
|                   |        |   | $\Psi(.) p(.)$                                                                   | 2   | 411.19 | 5.8          |       |
| Baboon            | dry    | 1 | $\Psi(\text{forest, mangr}) p(\text{anthro, PC2})$                               | 6   | 223.24 | 0.00         | 0.29  |
|                   |        | 2 | $\Psi(\text{forest, mangr}) p(\text{anthro, mangr})$                             | 6   | 224.15 | 0.91         | 0.18  |
|                   |        | 3 | $\Psi(\text{forest, mangr}) p(\text{anthro, mangr, PC2})$                        | 7   | 224.22 | 0.98         | 0.18  |
|                   |        |   | $\Psi(.) p(.)$                                                                   | 2   | 250.01 | 26.77        |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   | rainy  | 1 | $\Psi(\text{anthro}) p(PC2, \text{forest})$                                      | 5   | 108.33 | 0.00         | 0.29  |
|                   |        | 2 | $\Psi(\text{anthro}) p(\text{forest})$                                           | 4   | 109.36 | 1.03         | 0.17  |
|                   |        | 3 | $\Psi(\text{forest, anthro}) p(PC2, \text{forest})$                              | 6   | 109.95 | 1.63         | 0.13  |
|                   |        | 4 | $\Psi(\text{palms, anthro}) p(PC2, \text{forest})$                               | 6   | 110.26 | 1.93         | 0.11  |
|                   |        | 5 | $\Psi(\text{mangr, palms, anthro}) p(PC2, \text{forest})$                        | 7   | 110.31 | 1.98         | 0.11  |
| Green monkey      | dry    | 1 | $\Psi(\text{forest}) p(PC1, \text{mangr, palms, forest})$                        | 7   | 220.04 | 0.00         | 0.11  |
|                   |        | 2 | $\Psi(.) p(\text{mangr, palms, forest})$                                         | 5   | 220.16 | 0.11         | 0.10  |
|                   |        | 3 | $\Psi(\text{forest}) p(\text{mangr, palms, forest})$                             | 6   | 220.27 | 0.22         | 0.10  |
|                   |        |   | $\Psi(.) p(.)$                                                                   | 2   | 240.45 | 20.41        |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   | rainy  | 1 | $\Psi(PC1, \text{palms}) p(PC2, PC1, \text{mangr, palms})$                       | 8   | 288.67 | 0.00         | 0.15  |
|                   |        | 2 | $\Psi(PC1) p(PC2, PC1, \text{mangr, palms})$                                     | 7   | 288.88 | 0.20         | 0.13  |
|                   |        | 3 | $\Psi(PC1, \text{palms}) p(PC2, PC1, \text{mangr, palms, forest})$               | 9   | 289.18 | 0.50         | 0.11  |
|                   |        | 4 | $\Psi(PC1) p(PC2, PC1, \text{mangr, palms, forest})$                             | 8   | 289.48 | 0.81         | 0.10  |
|                   |        |   | $\Psi(.) p(.)$                                                                   | 2   | 342.3  | 53.63        |       |
| Campbell's monkey | dry    | 1 | $\Psi(PC1, \text{village, forest}) p(PC1, \text{village, mangr, forest})$        | 9   | 427.23 | 0.00         | 0.13  |
|                   |        | 2 | $\Psi(PC1, \text{village, palms, forest}) p(PC1, \text{village, mangr, forest})$ | 10  | 427.62 | 0.39         | 0.10  |
|                   |        | 3 | $\Psi(PC1, \text{village, forest}) p(PC1, PC2, \text{village, mangr, forest})$   | 10  | 427.78 | 0.55         | 0.10  |
|                   |        |   | $\Psi(.) p(.)$                                                                   | 2   | 449.03 | 21.08        |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   | rainy  | 1 | $\Psi(PC1, \text{forest}) p(PC1, \text{village, palms, forest})$                 | 8   | 591.63 | 0.00         | 0.16  |
|                   |        | 2 | $\Psi(PC1, \text{forest}) p(PC1, \text{palms, forest})$                          | 7   | 592.01 | 0.38         | 0.13  |
|                   |        | 3 | $\Psi(PC1, \text{forest}) p(PC1, \text{palms, forest, village, anthro})$         | 9   | 592.29 | 0.65         | 0.11  |
|                   |        | 4 | $\Psi(PC1, \text{mangr, forest}) p(PC1, \text{village, palms, forest})$          | 9   | 592.35 | 0.71         | 0.11  |
|                   |        | 5 | $\Psi(PC1, \text{mangr, forest, anthro}) p(PC1, \text{village, palms, forest})$  | 10  | 592.40 | 0.77         | 0.11  |
|                   |        |   | $\Psi(.) p(.)$                                                                   | 2   | 602.3  | 10.67        |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   |        |   |                                                                                  |     |        |              |       |
|                   |        |   |                                                                                  |     |        |              |       |

PC1: Principal Component 1 from vegetation attributes of 340m<sup>2</sup> vegetation plot surrounding the camera trap site (positively correlated with tree density, canopy cover and species diversity H, negatively correlated with human influence level); PC2: Principal Component 2 (positively correlated with mean DBH and vegetation height); village: distance to the nearest village; palms: distance to palm groves (forest edge of original forest fragments); mangr: distance to nearest mangroves; forest: relative amount of forest cover within 400m of camera trap; anthro: relative amount of human land use cover within 400m of camera trap (including village, cultivated area and orchard).

### 5.3.3 Mean estimates: comparison with naïve occupancy and seasonal variation

Seasonal variation in occupancy probability varied across species (Table 5.4). Mean estimates of occupancy probabilities of baboons decreased in the rainy season, while those of green monkeys and Campbell's monkeys increased. In both seasons, mean occupancy probability estimates of chimpanzees were slightly higher compared to naïve occupancy (dry season naïve occupancy = 0.53, rainy season = 0.50), and detection probability estimates were lower in the rainy season. Compared to the dry season, mean estimates of occupancy probability of baboons decreased by 94.3% in the rainy season. In the dry season naïve occupancy of baboons was similar to the top model average estimates (0.32); in the rainy season the mean probability of occupancy was considerably lower than the naïve occupancy (0.12), dropping close to zero. Higher detection probabilities of baboons in the rainy season suggest that baboons intensified their activity within a much more limited space during this period. Mean occupancy probability of green monkeys doubled in the rainy season and was higher compared to naïve occupancy (0.29 and 0.4 for dry and rainy season, respectively). Campbell's monkeys were the most widely distributed primate, and mean estimates of occupancy probability increased slightly from the naïve occupancy in both periods (dry season naïve occupancy = 0.62, rainy season = 0.78).

**Table 5.4**

Mean estimates of occupancy and detection probabilities of best models for primate species in the dry and rainy seasons. Mean estimates are derived with covariates fixed at their mean values.

| Species      | Season | Model                                                           | $\Psi$ ( $\pm$ SE) | $p$ ( $\pm$ SE)    |
|--------------|--------|-----------------------------------------------------------------|--------------------|--------------------|
| Chimpanzee   | dry    | $\Psi$ (PC1, village, palms) $p$ (PC1, PC2, mangr)              | 0.55 ( $\pm$ 0.07) | 0.45 ( $\pm$ 0.04) |
|              | rainy  | $\Psi$ (PC1, PC2, village, palms) $p$ (PC2, mangr, palms)       | 0.52 ( $\pm$ 0.09) | 0.32 ( $\pm$ 0.03) |
| Baboon       | dry    | $\Psi$ (forest, mangr) $p$ (anthro, PC2)                        | 0.35 ( $\pm$ 0.12) | 0.11 ( $\pm$ 0.04) |
|              | rainy  | $\Psi$ (anthro) $p$ (PC2, forest)                               | 0.02 ( $\pm$ 0.04) | 0.58 ( $\pm$ 0.11) |
| Green monkey | dry    | $\Psi$ (forest) $p$ (PC1, mangr, palms, forest)                 | 0.40 ( $\pm$ 0.09) | 0.12 ( $\pm$ 0.05) |
|              | rainy  | $\Psi$ (PC1, palms) $p$ (PC2, PC1, mangr, palms)                | 0.82 ( $\pm$ 0.13) | 0.09 ( $\pm$ 0.03) |
| Campbell's   | dry    | $\Psi$ (PC1, village, forest) $p$ (PC1, village, mangr, forest) | 0.76 ( $\pm$ 0.08) | 0.40 ( $\pm$ 0.04) |
|              | rainy  | $\Psi$ (PC1, forest) $p$ (PC1, village, palms, forest)          | 0.84 ( $\pm$ 0.06) | 0.48 ( $\pm$ 0.03) |

#### 5.3.4 Effect of covariates on occupancy probabilities

Occupancy probability of chimpanzees in both seasons decreased with increasing distance to the nearest village, suggesting that in general chimpanzees showed an attraction to range closer to human settlements (beta coefficients  $\beta_{\text{dry}} = -0.575$ , SE  $\pm 0.31$ ;  $\beta_{\text{rainy}} = -0.564$ , SE  $\pm 0.39$ , Figure 5.3). During the dry season chimpanzee occupancy probability increased with distance from areas dominated by oil palm groves ( $\beta_{\text{dry}} = 0.504$ , SE  $\pm 0.32$ ), while in the rainy season this relationship shifted ( $\beta_{\text{rainy}} = -0.616$ , SE  $\pm 0.39$ ). PC1 had a positive influence of chimpanzee occupancy in both seasons ( $\beta_{\text{dry}} = 0.804$ , SE  $\pm 0.38$ ;  $\beta_{\text{rainy}} = 0.684$ , SE  $\pm 0.42$ ), and PC2 was a strong negative predictor of occupancy probability of chimpanzees during the rainy season ( $\beta_{\text{rainy}} = -0.749$ , SE  $\pm 0.38$ ).

In the dry season, occupancy probability of baboons was strongly positively associated with relative amount of forest cover ( $\beta_{\text{dry}} = 1.710$ , SE  $\pm 0.75$ ) and negatively associated with increasing distance from the nearest mangroves ( $\beta_{\text{dry}} = -1.750$ , SE  $\pm 0.68$ ). In the rainy season, relative amount of anthropogenic land use negatively influenced baboon occupancy ( $\beta_{\text{rainy}} = -3.290$ , SE  $\pm 2.00$ ). Forest cover was also a positive predictor of occupancy of Campbell's monkeys in both seasons ( $\beta_{\text{dry}} = 0.982$ , SE  $\pm 0.41$ ,  $\beta_{\text{rainy}} = 0.801$ , SE  $\pm 0.49$ ), and distance to the nearest village positively affected occupancy during the dry season ( $\beta_{\text{dry}} = 0.815$ , SE  $\pm 0.47$ ). In contrast with baboons and Campbell's monkeys, in the dry season occupancy of green monkeys was negatively correlated with forest cover ( $\beta_{\text{dry}} = -0.564$ , SE  $\pm 0.39$ ).

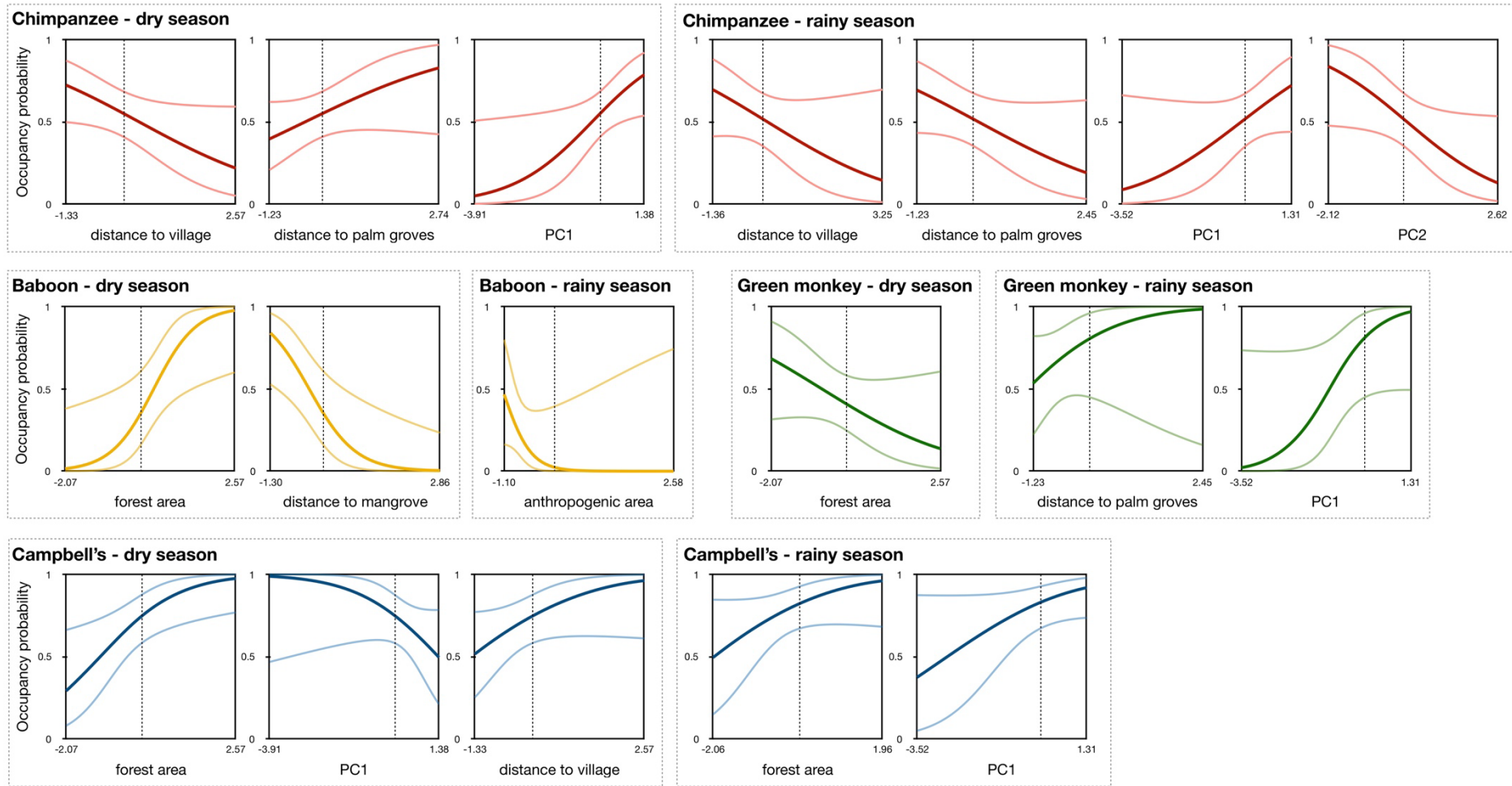


**Figure 5.3**

Effect of covariates on occupancy probability of chimpanzees, Guinea baboons, green monkeys and Campbell's monkeys in the dry and rainy season in Cantanhez NP. Lighter colour lines represent 95% CI. X axis are z-transformed values with the mean zero values represented by the dotted line.

### 5.3.5 Activity patterns

#### *Comparison of temporal activity between forest and anthropogenic areas*

Chimpanzees were active between 4h34 and 19h24 in the dry season and between 5h26 and 19h46 in the rainy season. Chimpanzee diel activity showed a bimodal pattern in both seasons, peaking in the morning, decreasing during the midday hours and peaking again in the afternoon (Figure 5.4). In both dry and rainy seasons, chimpanzee temporal activity significantly differed between forest and anthropogenic areas (Watson's Two-Sample test for Homogeneity, dry season:  $U^2 = 0.269$ ,  $P < 0.01$ ; rainy season:  $U^2 = 0.200$ ,  $P < 0.05$ ). In areas more frequently used by people, chimpanzees increased their activity in the afternoon, i.e. between 14h00 and 16h00 in the dry season and 13h00 and 15h00 in the rainy season. Diel activity of baboons within the forest showed a unimodal pattern, increasing in the afternoon. Baboons were only recorded twice in anthropogenic areas in the dry season. In the dry season, activity patterns of green monkeys significantly differed between forest and anthropogenic areas ( $U^2 = 0.431$ ,  $P < 0.001$ ), whereas for the rainy season I detected no significant difference ( $U^2 = 0.120$ ,  $P > 0.05$ ). During the dry season, within forest green monkeys maximised their activity between 11h00 and 12h00, whereas in anthropogenic areas activity was maintained between 9h00 and 16h00. In the rainy season activity of green monkeys was generally higher in the afternoon. Campbell's monkeys showed significant differences in activity patterns between forest and anthropogenic habitats in both seasons (dry season:  $U^2 = 1.162$ ,  $P < 0.001$ ; rainy season:  $U^2 = 0.348$ ,  $P < 0.01$ ). In the dry season Campbell's monkeys showed a single peak in their activity within forest habitats, between 12h30 and 14h30, whereas in human areas activity remained constant between 7h30 and 18h30. In the rainy season activity patterns of Campbell's monkeys showed a different pattern compared to the dry season. Within forests activity peaked in the morning at 8h00 and slowly decreased, whereas in anthropogenic areas activity of Campbell's monkeys was highest between 10h00 and 13h00.

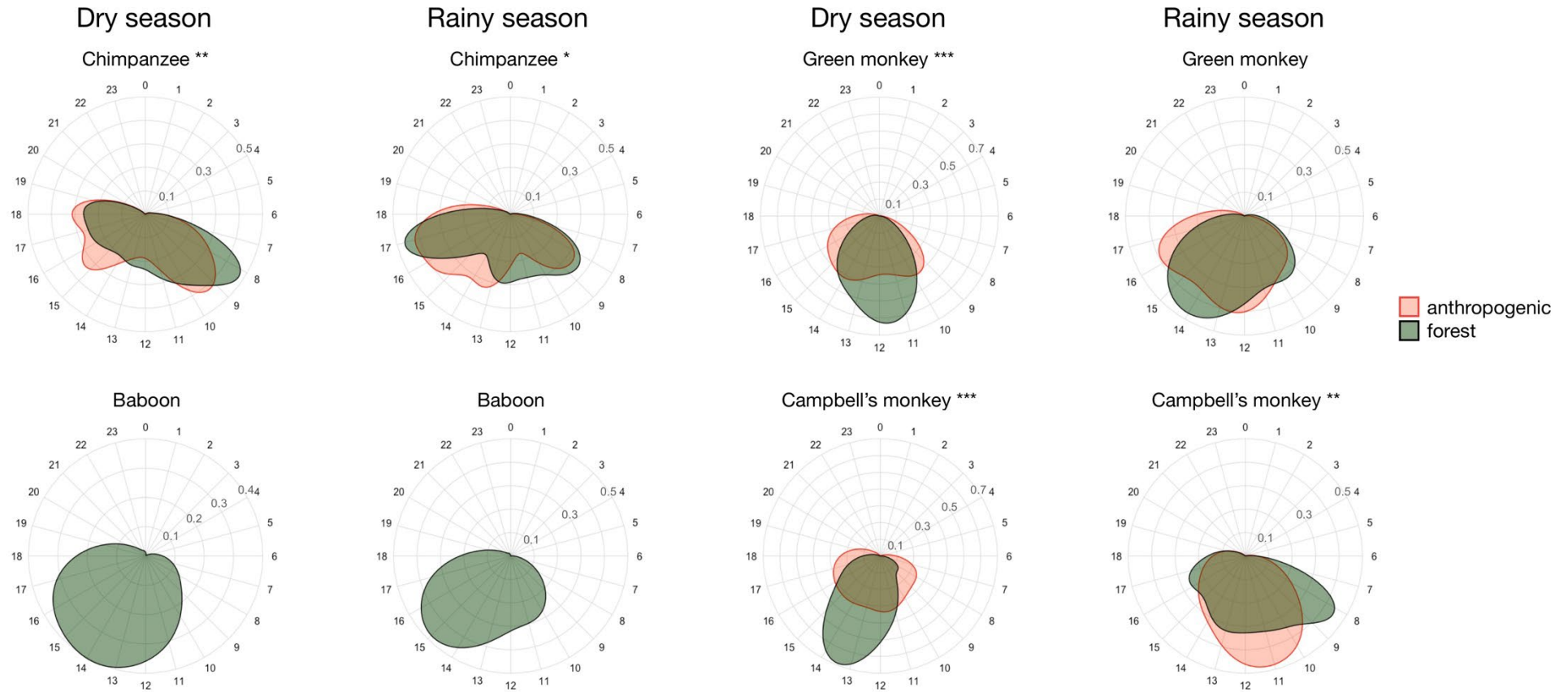


**Figure 5.4**

Activity patterns of chimpanzees, baboons, green monkeys and Campbell's monkeys in habitats of low (forest) and high (anthropogenic) human presence in the dry and rainy seasons. Radial axes represent kernel density of temporal activity. Asterix after species names represent statistical significance: \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

*Temporal overlap between primates across habitats*

In the dry season, temporal overlap between chimpanzees and the two monkey species (green monkeys and Campbell's monkey) increased by 15 and 22% respectively in anthropogenic areas compared to forest areas (Table 5.5). However, in the rainy season temporal overlap between chimpanzees and monkeys was similar across habitat types. Green monkeys and Campbell's monkeys consistently showed high temporal overlap, with over 80% overlap across seasons and habitats. Within forest sites, temporal overlap ( $\hat{\Delta}$ ) between chimpanzees and other primates had a tendency to be higher during the rainy season (79–85% overlap) compared to the dry season (62–75% overlap).

**Table 5.5**

Comparison of coefficients of overlap  $\hat{\Delta}$  between primate species pairs in forest and anthropogenic areas. Values in brackets represent 95% confidence intervals. Blank cells are given due to insufficient sample size for baboon detections in anthropogenic areas ( $N = 2$  in dry season,  $N = 0$  in rainy season). Bold values indicate  $\geq 15\%$  difference in temporal overlap between habitats with non-overlapping 95% confidence intervals.

| Species pair                    | Dry season              |                              |             | Rainy season          |                              |            |
|---------------------------------|-------------------------|------------------------------|-------------|-----------------------|------------------------------|------------|
|                                 | Forest $\hat{\Delta}$   | Anthropogenic $\hat{\Delta}$ | Difference  | Forest $\hat{\Delta}$ | Anthropogenic $\hat{\Delta}$ | Difference |
| Chimpanzee, baboon              | 0.75 (0.63–0.85)        |                              |             | 0.80 (0.71–0.88)      |                              |            |
| Chimpanzee, green monkey        | <b>0.64 (0.52–0.77)</b> | <b>0.79 (0.67–0.90)</b>      | <b>0.15</b> | 0.79 (0.69–0.89)      | 0.85 (0.75–0.92)             | 0.06       |
| Chimpanzee, Campbell's monkey   | <b>0.62 (0.53–0.71)</b> | <b>0.84 (0.73–0.93)</b>      | <b>0.22</b> | 0.85 (0.77–0.92)      | 0.77 (0.69–0.85)             | –0.08      |
| Baboon, green monkey            | 0.73 (0.56–0.87)        |                              |             | 0.86 (0.74–0.94)      |                              |            |
| Baboon, Campbell's monkey       | 0.78 (0.67–0.88)        |                              |             | 0.77 (0.68–0.86)      |                              |            |
| Green monkey, Campbell's monkey | 0.82 (0.68–0.83)        | 0.85 (0.74–0.93)             | 0.03        | 0.83 (0.73–0.91)      | 0.84 (0.77–0.93)             | 0.01       |

## 5.4 Discussion

In this Chapter I explored primate spatiotemporal dynamics as a measure of response to human activities employing methods typically established in carnivore research (e.g. Carter et al. 2012; Schuette et al. 2013; Wang et al. 2015). I used a camera trap-occupancy modelling approach on four primates inhabiting a forest-mangrove-village-agricultural landscape mosaic in Guinea-Bissau. The type of landscape in Cantanhez NP can be compared to rural areas across West Africa characterised by small-scale agricultural production and low forest resource extraction. This type of environment can often support rich biodiversity and include several species of primates (e.g. Bersacola et al. 2018; Brncic et al. 2015; Hockings et al. 2012; Parathian et al. 2018). In this Chapter and Chapter 4 I demonstrated the potential of camera traps to study primate communities in human-modified heterogeneous landscapes.

Species occurrence is influenced by the distribution of resources, particularly food, and protection from potential predators including humans, as well as the presence/absence of ecologically similar taxa. The low availability of undisturbed space in anthropogenic environments has been shown to alter interspecific interactions (Schuette et al. 2013; Tylianakis et al. 2008; Wang et al. 2015). A species' response to human presence and activities mainly depends on the species' ecology, behavioural flexibility and perceived risk of harm/predation by humans, which is largely the result of past and present human behaviour. Therefore, I expected that the primates in Cantanhez NP would show interspecific differences in their spatiotemporal distribution and responses to anthropogenic presence/activities. Below I discuss my results following the order of my hypotheses.

### 5.4.1 Spatial patterns of occurrence

*Hypothesis 1: Semi-terrestrial primates show some degree of spatial partition across the heterogeneous landscape*

The distribution of primates in Cantanhez NP overlapped at several locations and no species pair showed complete avoidance, contrasting with my first two predictions. The overall

combination and effects of environmental covariates on occupancy probability differed across chimpanzee, baboon, green monkey and Campbell's monkey (see summary in Table 5.6), indicating a tendency of these primates to exploit different parts of the heterogeneous landscape. Thus, my results indicate low levels of spatial partitioning of semi-terrestrial primates across Cantanhez NP.

**Table 5.6**

Summary of covariate relationships of best occupancy models for chimpanzees, baboons, green monkeys and Campbell's monkeys. + indicates positive relationship, – indicates negative relationship.

| Season | Species      | PC1 | PC2 | forest | mangr | palms | village | anthro |
|--------|--------------|-----|-----|--------|-------|-------|---------|--------|
| Dry    | Chimpanzee   | +   |     |        |       | +     | –       |        |
|        | Baboon       |     |     | +      | –     |       |         |        |
|        | Green monkey |     |     | –      |       |       |         |        |
|        | Campbell's   | –   |     | +      |       |       | +       |        |
| Rainy  | Chimpanzee   | +   | –   |        |       | –     | –       |        |
|        | Baboon       |     |     |        |       |       |         | –      |
|        | Green monkey | +   |     |        |       | +     |         |        |
|        | Campbell's   | +   |     | +      |       |       |         |        |

Campbell's monkeys overlapped most with other primate species, which is not surprising considering that this species was the most widely distributed across our study area. Baboons and green monkeys showed least spatial overlap. During the dry season forest cover had opposite effects on the occurrence of baboons and green monkeys. Mangrove forests are known to be an important habitat for green monkeys across West Africa (Bi et al. 2009; Galat and Galat-Luong 1976; Head et al. 2019). Although green monkeys in Cantanhez NP were detected within/near mangroves, the distance-to-mangrove covariate only influenced their detection probabilities but not occupancy. In contrast, for baboons the spatial distribution of mangroves had a strong effect on baboon occupancy probability in the dry season. Mangroves are the most abundant habitat type in central Cantanhez NP (Chapter 3). Difficult to access mangroves represent an important refuge habitat in human-dominated environments for several taxa including Guinea baboons (Nowak 2012, 2019). The seasonal occurrence of baboons in or near mangrove forests in Cantanhez NP may impose competitive constraints on green monkeys forcing them to choose other parts of the landscape.

*Hypothesis 2: Patterns of spatial occurrence of primates are seasonally flexible in human-dominated agro-forest landscapes*

Effects of covariates on occupancy probabilities varied between seasons for all primates, aligning with my second hypothesis. Different constraints or opportunities are likely to shape primate spatial occurrence in the dry and rainy seasons, including differences in food availability (e.g. Barton et al. 1992) and human activities (for possible anthropogenic effects, see discussion in the subsection below). During the dry season, chimpanzee occupancy increased further from oil palm-dominated forest edges, whereas in the rainy season this relationship shifted. Chimpanzees in Cantanhez NP preferentially use oil palms for nesting (Sousa et al. 2011; K Hockings unpubl. data). In Caiquene–Cadique (Cantanhez NP), oil palm nests accounted for 46% of the total number of nests followed by 31% of those on *Parinari excelsa* (K Hockings, unpubl. data). Fresh oil palm nests were more commonly observed in September, i.e. during the second half of the rainy season (K Hockings, unpubl. data). Oil palm fruit and flower are available throughout the year (Bessa et al. 2015; Chapter 3), and previous research found that chimpanzees in Caiquene–Cadique increased their intake of oil palm fruit and flower during the rainy season (Bessa et al. 2015). My results build on these findings to show that at the landscape scale, chimpanzees in Cantanhez NP tend to occur within or closer to oil palm-dominated forest edges in the rainy season.

*Hypothesis 3: Primates targeted for bushmeat spatially avoid humans (primate response: spatial avoidance of risk)*

Anthropogenic covariates considered in this study affected occupancy probability of primates differently, ranging from positive (chimpanzee), no effect (green monkey), moderate effect (Campbell's monkey) and negative effect (baboon). Baboons, green monkeys and Campbell's monkey are targeted for meat in Guinea-Bissau, including Cantanhez NP (Ferreira da Silva et al. 2014; Minhós et al. 2013). These species are therefore likely to perceive humans as potential predators. My models however show that human-mediated exposure of risk only had a significant effect on spatial distribution of baboons. This species showed the narrowest distribution compared to the other primates; in the dry season occupancy probability was moderately low but in the rainy season it dropped close to zero. Higher baboon detection probabilities and their extremely low occupancy in the

rainy season indicate that baboons decrease their area of occurrence and intensify the use of undisturbed space during this period. Guinea baboons and green monkeys have been reported to feed on groundnuts and rice in Sierra Leone (Harding 1984) and Guinea-Bissau (E Bersacola, unpubl. data), which is sown and harvested during the rainy season. However, based on my occupancy models, baboons in Cantanhez NP showed a strong tendency to avoid human-dominated areas, especially during the rainy season. Forest and particularly flooded mangroves are the habitats that people frequent the least in Cantanhez NP. The high association of baboon occupancy with these habitats in the dry season may therefore indicate that baboons select habitats to reduce predation risk. The behaviour of baboons in Cantanhez NP shows a strong contrast with that of baboons at sites where they are not hunted (particularly across East and Southern Africa: e.g. Hill 2000; Mormile and Hill 2017).

Occupancy probability of Campbell's monkey in the dry season moderately increased with increased distance from villages, whereas in the rainy season spatial distribution of this species was not influenced by any anthropogenic covariate. In the rainy season PC1, which was negatively loaded by human influence score and positively loaded by tree density, canopy cover and tree species diversity, had a positive effect on occupancy of Campbell's monkey. In both seasons, this species' occurrence was positively influenced by amount of forest cover. Indeed, Campbell's monkeys are largely arboreal and associated with forest habitats across their range (Bersacola et al. 2018; Bourlière 1985; Schreier et al. 2009). Our results indicate that Campbell's monkeys in Cantanhez NP move on the ground in the vicinity or within anthropogenic areas where vegetation cover is present.

Chimpanzees and baboons showed the strongest and most contrasting response to anthropogenic variables. In both seasons, chimpanzees had a strong tendency to occur closer to villages. Although mango is also present in abandoned settlements, orange, papaya and mango are mostly grown within villages in Cantanhez NP, making villages particularly attractive areas to chimpanzees. Chimpanzees across tropical Africa are known to enter villages to forage on cultivated foods (Hockings et al. 2007, 2009; McLennan 2013). In Sebitoli (Uganda), proximity to forest edges bordering positively influenced distribution of East African chimpanzees (*Pan troglodytes schweinfurthii*) (Bortolamiol et al. 2016). Chimpanzees in Cantanhez NP are not targeted for bushmeat and retaliatory killings due to crop feeding are infrequent (Parathian et al. 2018). It is therefore likely that their perception

of humans as a potential predator is relatively low. Chapters 6 and 7 in this thesis will explore this question in more detail.

#### **5.4.2 Daily temporal patterns**

*Hypothesis 4: Human activities alter the activity patterns of primates due to constituting potential risk (primate response: temporal avoidance of risk)*

Animal circadian rhythms, or diel activity patterns, are constrained by the availability of daylight, darkness and semi-darkness hours as well as temperature (Bennie et al. 2014). The presence and the activity of sympatric taxa including humans, as well as the availability of food resources can also influence animal activity patterns (Cozzi et al. 2012; Ross 2000; Schuette et al. 2013). Temporal partitioning between taxa is associated with strategies to avoid food competition and/or predation (Hayward and Slotow 2009). Human activities have been shown to alter the temporal activity in wildlife (Gaynor et al. 2018) including lemurs (*Eulemur* spp.) (Donati et al. 2016), blue duikers (*Philantomba monticola*) (Ehlers Smith et al. 2019), brown bears (*Ursus arctos*) (Martin et al. 2010), puma (*Puma concolor*) coyote (*Canis latrans*) and bobcat (*Lynx rufus*) (Wang et al. 2015). To primates inhabiting agro-forest areas, human land uses may represent feeding areas where attractive, energy-rich cultivated food sources are available, as well as dominating areas surrounding forest fragments and corridors. The use of human land uses is often temporally constrained by the presence of humans, due to the risk of predation and/or competitive aggression. Thus, I expected that the primates' more limited choice of *when* to use human-dominated space compared to areas of low human presence to be reflected by differences in temporal activity patterns between the two habitat gradients and higher temporal overlap between primates in human-dominated areas.

In general, the difference of activity patterns between forest and anthropogenic areas was stronger in the dry season, which likely reflects the higher presence of people in cultivated areas. During the first half of the dry season people are often present in cashew orchards to cut and clear the overgrown vegetation before harvest. The second half of the rainy season (August-October) corresponds to the time after the cashew harvest, when the orchards are

left unattended. In July-August the presence of people in the cultivated fields is low, peaking again only during the rice and groundnut harvest in September-November.

Activity patterns of chimpanzees showed a bimodal shape in both forest and anthropogenic habitats. The significant difference in activity patterns between habitats was likely due to an earlier peak of activity in the afternoon in anthropogenic areas. In these areas, activity of green monkeys was also higher in the afternoon, as that of Campbell's monkeys in the dry season. The increase in activity from early afternoon may indicate a relatively consistent time window where people are absent from cultivated fields. Around Kibale NP, Uganda, chimpanzee sometimes crop feed after twilight to decrease detectability (Krief et al. 2014). In Cantanhez NP, chimpanzee nests are often found within or in very close proximity to orchards. In the dry season chimpanzee activity in human-dominated areas was still relatively high during twilight hours (around 19h00). It is probable that chimpanzees at Cantanhez NP are crop foraging in orchards during semi-darkness or dark hours.

Recent studies have found higher intraguild temporal niche overlap within human-dominated areas compared to undisturbed sites (Smith et al. 2018; Wang et al. 2015). My results partially align with these previous findings: during the dry season, temporal activity overlap between chimpanzee and monkeys was higher in human land uses compared to sites characterised by low human activity. In contrast, I found no difference in temporal overlap between these taxa during the rainy season and between green monkey and Campbell's monkey in both seasons. Again, these findings may highlight higher human activity in cultivated areas in the dry season, indicating that during this period, the availability of 'risk-free' time is more limited compared to the rainy season. At least in part, my results are consistent with my fourth hypothesis that human activities influence the daily activity patterns of primates in this agro-forest landscape.

## *Conclusions*

In this Chapter I found that primates in Cantanhez NP spatially overlap at the fine scale but their distribution is driven by different characteristics of the heterogeneous landscape. Chimpanzee occupancy models showed that at the landscape scale, their spatial occurrence was strongly influenced by the spatial distribution of landmarks associated with some of

their key food sources, specifically village foods and oil palms, and not by human avoidance. Baboons were the species most sensitive to human influence, highlighting predation risk as a strong factor driving their spatial occurrence. Differences in activity patterns between anthropogenic areas and forest habitats were stronger in the dry season, when people are more active in agricultural fields. This suggests that primates use temporal adjustments to avoid direct interactions with humans. In addition, during the dry season the temporal overlap between chimpanzees and two monkey species was higher in anthropogenic areas compared to forest, highlighting again that in the dry season the more intensive human presence in cultivated fields pose temporal constraints on primate use of human habitats.



## Part 2

# Chimpanzees and humans in a shared landscape of fear



## CHAPTER 6

Balancing strategies in human-influenced landscapes:  
chimpanzee spatiotemporal home range use predicted by  
risk and resource availability



## 6.1 Introduction

### 6.1.1 Predation risk and its role in shaping prey behaviour

Across ecosystems, animals use strategies to respond to perceived risks of attacks by sympatric predators (Brown et al. 1999). Risk-mitigation strategies against lethal and non-lethal attacks occur within the context of human–human (Pain 1997) and wildlife–human/prey–predator interactions (Ciuti, et al. 2012a; 2012b; Hockings et al. 2006; Willems and Hill 2009; Wirsing et al. 2007; Zuberbühler 2001). These anti-predator behaviours include long-term adjustments (e.g. spatiotemporal predator avoidance, forming larger group sizes), preparing for anticipated danger (e.g. increased vigilance, group cohesion) and responding to immediate threats (alarm calling, escape) (e.g. Creel et al. 2014; Gould and Sauther 2007; Hill and Lee 1998) and have important social and ecological consequences. At the population scale, spatiotemporal rearrangements in response to fear of predation may result in changes in community structure and trophic interactions (Creel et al. 2005; Fortin et al. 2005; Ripple and Beschta 2004; Suraci et al. 2016). Explicitly considering *fear* as an element shaping an animal’s decisions over habitat and resource use will enable a more comprehensive understanding of species interactions, including identifying effects and constraints that a species may impose on (one) another.

### 6.1.2 The landscape of fear concept

Introduced by Laundré et al. (2001), the ‘landscape of fear’ model is based on the idea that predation risk fluctuates across space and time, which results in spatial and temporal variations in prey perception of fear and behavioural adjustments. Prey species learn about spatiotemporal variations in risk through predation escapes, and the learnt fear shapes the prey’s decisions over where and when to feed and rest (Laundré et al. 2010). The concept relates to the ‘ecology of fear’ model (Brown et al. 1999), but explicitly adds a spatial component which creates an additional, abstract landscape of the perceived fear by prey (Laundré et al. 2001, 2010). Recently, Gaynor and colleagues (2019) redefined again the ‘landscape of fear’ as a “spatial variation in risk perception” (p. 11) that lays between the physical environment that influences it and the physical response displayed by prey. Therefore, to understand a landscape of fear one measures the physical landscape attributes (including habitat characteristics), and predator distribution and behaviour, and compares

them to the measured spatiotemporal response by prey related to home range use and/or behaviour (Gaynor et al. 2019). The prey's manifested response may mismatch the actual physical risks due to imperfect 'risk-assessments' and/or trade-offs with other survival activities such as feeding requirements (Gaynor et al. 2019).

### *Physical attributes of a landscape shaping animal perception of risk and response*

Predation risk varies through space and time due to spatial variations in landscape configuration and spatiotemporal variations in predator activity. Some habitats or landmarks may be more risky than others depending on the predator(s) behaviour, the opportunity for prey to detect it, prey social behaviour and mode of escape (Lima 1992). Habitats or parts of the landscape preferred by predators will be more dangerous due to higher risks of encounters (Creel et al. 2005), but patterns may temporally vary according to seasonal variations in landscape use by predators (Fortin et al. 2005). Open habitats increase visual exposure which may deter some species, particularly where the predator uses a chasing strategy (Creel et al. 2005). However where ambush predators are present, some prey species including giraffe (*Giraffa camelopardalis*) and chacma baboons (*Papio ursinus*) may actually prefer open areas due to higher chances of predator detection and escape (Hill and Weingrill 2007; Riginos and Grace 2008; Valeix et al. 2009). In addition, for animals with dynamic social groupings, forming larger group sizes may offset the increased risks of being detected in open habitats (Fortin et al. 2009).

Habitat selection driven by predator avoidance may be stronger in landscapes where multiple predators are present (Thaker et al. 2011). Home range use may be regulated by some sympatric predators but not others depending on predator and prey vertical space use. For example, at Lajuma, South Africa, intensity of space use by arboreal samango monkeys (*Cercopithecus mitis erythrarchus*) was influenced by eagles (Coleman and Hill 2014) whereas that of semiterrestrial vervet monkeys (*Chlorocebus aethiops pygerythrus*) was influenced by terrestrial leopards (*Panthera pardus*) and semiterrestrial chacma baboons (Willems and Hill 2009). In multi-predator landscapes, dominant predators may pose stronger selective pressure on prey (Thaker et al. 2011). Indeed, anthropogenic cues including villages, roads and cultivated fields, coupled with higher relative human density and activity can have a much greater effect than those of natural predators (Ciuti et al. 2012b;

Theuerkauf and Rouys 2008). The inclusion of humans as additional or alternative agents for anti-predator behaviour in the landscape of fear concept has increased over the recent years (Ciuti et al. 2012b; Clinchy et al. 2016; Nowak et al. 2016). However, considering the number of nonhuman primate populations living in human-impacted landscapes (Estrada et al. 2012; McKinney 2015), studies that explicitly include a human-influenced landscape of fear framework for this group of taxa remain rare (Nowak et al. 2016, 2017).

Different types of anthropogenic features and habitats are likely to be perceived differently by wildlife, and risk perceptions may vary across time according to types and fluctuations in intensity of human activities (Bonnot et al. 2013; Lone et al. 2014). For example, villages may represent a temporally continuous risk due to the continuous presence of people, with relatively high perceived risk during the daytime more or less equal across days and months. To exploit these habitats, wild animals must use short-term activity and behavioural anti-predator responses, for example through maximising activity at night, increasing vigilance and group cohesion. In contrast, perceived risks in cultivated areas will fluctuate throughout the year depending on agricultural cycles and the proximity to other anthropogenic features. An animal's response to perceived risks in agricultural areas will differ when cultivated foods are available. Despite the high peaks in risks associated for example with high human presence and crop guarding, animals will attempt to forage in cultivated areas to take advantage of the available foods, increasing foraging efficiency (Campbell-Smith et al. 2011; Hockings et al. 2009; McLennan 2013; Sukumar 1990). Thus, the potential risks of persecution or predation by humans may be outweighed by the benefits of accessing energy-rich foods when cultivated foods are available.

Anti-predator strategies increase the chances of surviving or avoiding attacks but depending on the response, they may also involve some energetic costs. Animals must balance between foraging efficiently and increasing safety. Fear of predation may cause species to avoid high quality feeding areas (Creel et al. 2005) or spend less time at a foraging site (Brown 1988; Brown et al. 1999), which would implicate foraging costs. Particularly in the case of conspicuous, ecologically flexible species, the hypothetical absence of *costs* associated with maximising safety (e.g. from hunting, physical injury), will be displayed by a lack of risk-related, spatiotemporal barriers, i.e. there will be no habitats or features that are completely avoided, including villages. In the absence of risk constraints, home range use will be strongly associated with the spatiotemporal distribution of food, including foraging

opportunities in agricultural areas. Chimpanzees, a socially, ecologically and behaviourally flexible species (Hockings et al. 2009; 2015; McLennan 2013; Tutin et al. 1997) are expected to decrease potential costs associated with predation risks through increased vigilance, social cohesion and cooperation (Hockings et al. 2006, 2012). A spatiotemporal approach that links home range use to variations in risk and resource availability allows us to identify ecological trade-offs.

### 6.1.3 Research aim and hypotheses

For this chapter, I measure chimpanzee spatiotemporal home range use considering the human-mediated risks and foraging opportunities in an agro-forest mosaic. In the absence of large-bodied, natural predators, in Caiquene–Cadique humans were assumed to constitute the main source of potential risk to chimpanzees. Local people in Cantanhez do not actively hunt chimpanzees primarily due to traditional taboos (Hockings and Sousa 2013; Parathian et al. 2018). However, anecdotal retaliatory killings and occasional aggression due to orange feeding have previously been reported. Across other sites where chimpanzees are not hunted, chimpanzees display significant social re-adjustments and different activity patterns in response to increased risks of exposure to humans (Hockings et al. 2006, 2012; Krief et al. 2014; Wilson et al. 2007).

I test the following hypotheses:

| Hypothesis                                                                                                                                                        | Prediction                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1. Humans and chimpanzees do not overlap in habitat selection and show a tendency to partition spatially at the site-scale (fine-scale spatial niche separation). | <p>1.1 On average, camera trap detection rates of chimpanzees will be considerably higher within the forest block compared to the agriculture-village matrix, with the opposite pattern for humans. This prediction will be tested with descriptive statistics comparing the means and variations (SDs) for each of the four groups' detection frequencies;</p> <p>1.2 There will be a negative correlation between the overall detection frequencies of chimpanzees and those of humans across the 21 sampled sites in Caiquene–Cadique.</p> |

2. The spatial and spatiotemporal variation in risk of direct interactions with humans modulates chimpanzee home range use (spatiotemporal anti-predator response).
  - 2.1 Distance to anthropogenic features in the landscape (villages, agriculture and/or roads) will positively predict intensity of space use by chimpanzees;
  - 2.2 Human camera trap detections will negatively predict intensity of space use by chimpanzees.
  
3. Spatiotemporal variation in resource availability modulates spatiotemporal variation of chimpanzee home range use (maximise foraging efficiency).
  - 3.1 The availability of important chimpanzee wild foods consumed in Caiquene–Cadique ([Bessa et al. 2015], ripe wild fruit, ripe oil palm fruit and/or oil palm flower), positively predicts intensity of space use by chimpanzees;
  - 3.2 The availability of cultivar fruit consumed by chimpanzees in Caiquene–Cadique ([Bessa et al. 2015], cashew, mango, baobab, orange, lime and/or papaya) positively influence intensity of space use by chimpanzees.
  
4. Chimpanzees will increase the use of high-risk areas when cultivated foods are available and wild foods are scarce (trade risk mitigation strategy in favour of foraging efficiency).
 

In Chapter 3 I found that the combined availability of cultivated fruits solely obtainable in villages (orange, lime and papaya) negatively correlated with the availability of chimpanzee wild fruits. This hypothesis can be tested if part of prediction 2.1 is true, i.e. if distance to the nearest village significantly positively predicted intensity of space use by chimpanzees, villages would modulate chimpanzee home range use and therefore represent high-risk areas that chimpanzees would normally choose to avoid. Therefore, the prediction for Hypothesis 4 would follow:

  - 4.1. Both distance to village and the availability of high-risk village cultivar foods (orange, lime and papaya) positively influence intensity of site use by chimpanzees.

The null hypothesis will be:

Throughout the year, chimpanzees select parts of their home range randomly. Therefore, camera trap detection rates will be similar throughout the sampling area and an intercept-only spatiotemporal model will be identified as the best model.

## **6.2 Methods**

### **6.2.1 Study area**

The study area consisted of the home range of the Caiquene–Cadique chimpanzee community, one of the approximately twelve chimpanzee communities present in Cantanhez National Park (CRT unpubl. data). The study area included three medium-sized villages (Caiquene, Cadique Nalu and Cadique Iala), five settlements (Abdaia, new Camada, Caras, new Butchifula and Crozamento de Caiquene), and four abandoned villages (old Camada, old Butchifula, Filac Bontche and old Caiquene). The vast majority of people living within the study area are Nalu, with Balanta, Fula and Djakanka also present. The main agricultural activities are shifting agriculture and cashew farming. The Caiquene–Cadique chimpanzee community consists of approximately 40 individuals (J Bessa and K Hockings, unpubl. data) ranging across a ~16 km<sup>2</sup> area. Their home range includes a main protected forest block that covers 3 km<sup>2</sup>, as well as mangroves, grassland and anthropogenic land uses. See Chapter 2 for more information on the study area. Previous studies found that primates living in fragmented landscapes can have multiple core areas within their home range (Campera et al. 2014; Vieira et al. 2019). Based on the heterogeneous characteristics of the landscape and opportunistic indirect observations (e.g. chimpanzee feeding traces, faeces), it is possible that this would also be the case for the Caiquene–Cadique chimpanzee community.

### **6.2.2 Data collection**

To collect data on chimpanzee space use across 12 months, between July 2017 and July 2018 I set up 21 camera traps within the home range of the Caiquene–Cadique chimpanzee community. I deployed camera traps at a minimum distance of 500 m between cameras (mean 652 m SD  $\pm 115$ , range 520 m – 918 m, Figure 6.1), pointing towards main chimpanzee paths within their home range. Camera trap sites were placed in areas characterised by different human activities (e.g. cultivated areas, near road, village, human/chimpanzee path in the forest). Cameras were set up to capture three consecutive photographs when triggered and remained active for 12 months.

To measure availability of wild and cultivated chimpanzee foods I used phenology trails and vegetation plots. I established two phenology trails, including a wild trail located inside the

main forest block and a cultivated trail located inside and around Cadique Nalu village. I monitored the most important wild ( $N = 12$ ) and cultivated ( $N = 7$ ) food tree species to this chimpanzee community following Bessa et al. (2015, see Chapter 3 for additional information). Every two weeks I assigned a 0–4 score for new leaves, flowers, unripe and ripe fruit of 8 to 10 individuals for each tree species. To quantify food availability, for each camera trap site I gathered data from 25 10x20 m vegetation plots within a 200 m radius. The length of the radius was chosen to maintain spatial independence between camera trap sites and provide an adequate representation of the availability of foods. Plot locations were established randomly using the research tool ‘Random points inside polygon’ on QGIS, setting 50 m as a minimum distance between plots. Plots that were located in flooded or inaccessible areas (usually mangroves) or sacred forest were discarded. The total number of plots was 454, giving a total sampled area of 90,800 m<sup>2</sup>. At each plot I recorded habitat type (forest, mangrove, orchard, grassland, cultivated field, village grounds, abandoned village), identified plant species and measured DBH of all trees ( $\geq 10$  cm) and lianas ( $\geq 5$  cm), and estimated tree height (to the nearest 0.5 m).

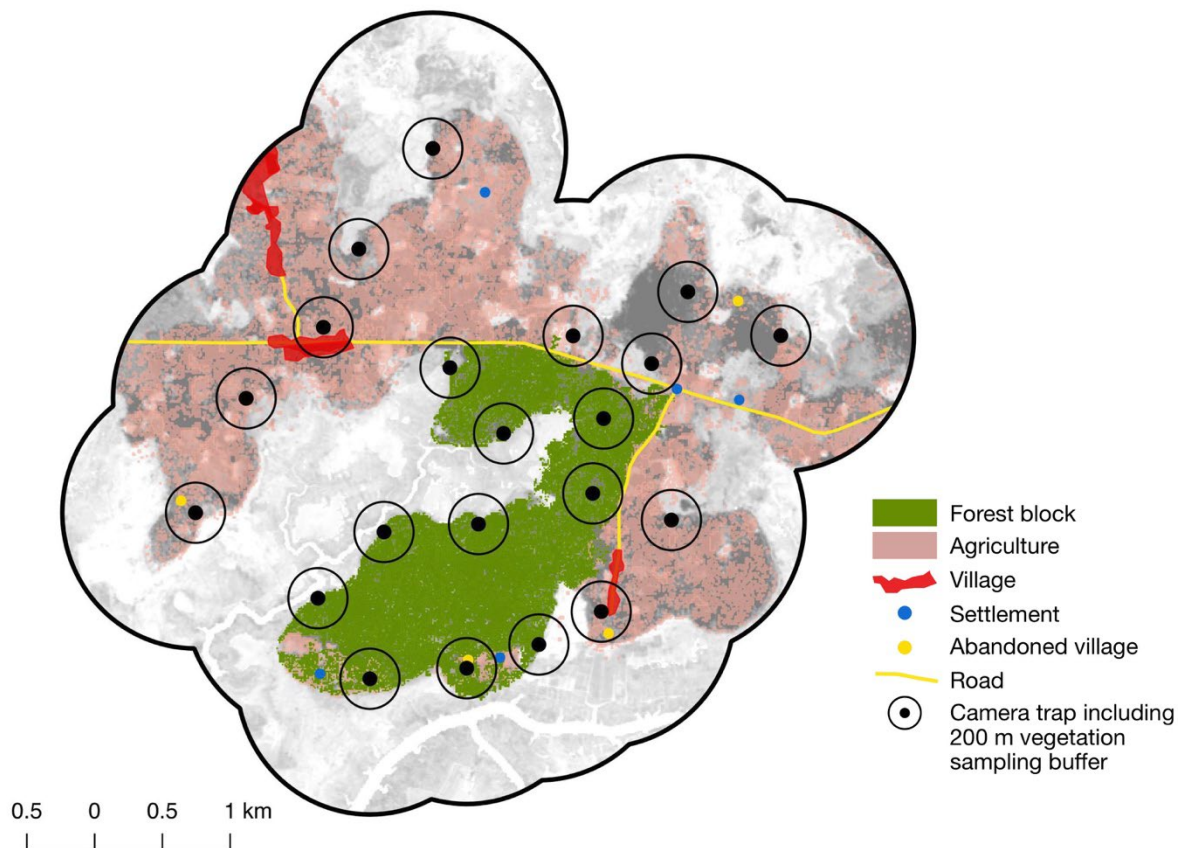


**Figure 6.1**

Map of Caiquene–Cadique showing the 21 camera trap chimpanzee monitoring sites, villages, settlements, abandoned villages, roads, agricultural areas and the continuous forest block. Grey scale indicates NDVI levels.

### 6.2.3 Data analysis

I calculated the number of independent events of chimpanzees and humans detected at the 21 camera trap sites. An event was considered independent from another event if the photograph or sequence of photographs were taken  $\geq 60$  minutes before and after another photograph. Previous studies have used different thresholds of elapsed time between images (e.g. 15 minutes to measure party size and composition in chimpanzees [McCarthy et al. 2018]). However, habitat use/occupancy studies have more commonly used 1-hour thresholds (e.g. including chimpanzees [Garriga et al. 2019; Mugerwa et al. 2013], ungulates [Tobler et al. 2009], and arboreal wildlife [Bowler et al. 2017]). I calculated the relative detection frequency (RDF) as the number of independent events divided by the camera trap effort (number of days) and multiplied by 100. Previous camera trap studies have used this measure and referred to it as the Relative Abundance Index (e.g. Jenks et al. 2011). I chose to refer to it as ‘RDF’ instead of ‘RAI’ to reflect a measure of site selection rather than abundance. To test my first hypothesis, that chimpanzees and humans show overall site and habitat partitioning, I tested for negative trends in chimpanzee and human RDF across sites using Pearson correlation. To see if site partitioning differed between forest and heterogeneous habitat, I also tested for correlation separately for the seven and 14 sites inside and outside the forest block.

#### *Spatiotemporal models: dataset preparation*

The 9<sup>th</sup> July 2017 – 5<sup>th</sup> July 2018 dataset was divided into 24 sampling occasions, i.e. two sampling occasions per calendar month. I chose to divide sampling occasions twice per month rather than every 15 days consistently to be able to match the twice-monthly phenological data collection. Due to calendar months varying in length (28 to 31 days), sampling occasions varied from 12 to 16 days (mean 15.1, SD  $\pm 0.9$ ). To select cut-off dates, I attempted to balance between consistency in occasion length and ensuring that the phenological sampling day fell approximately in the middle of the sampling occasion. For example, occasion 1 started on the 9<sup>th</sup> of July and ended on the 23<sup>rd</sup> of July (15 days), corresponding with phenological data collected on the 15<sup>th</sup> of July. Occasion 2 started on the 24<sup>th</sup> of July and ended on the 8<sup>th</sup> of August (16 days), matching the phenology data collected on the 1<sup>st</sup> of August. Due to camera malfunction, throughout the sampling period some

camera trap sites were inactive for parts or entire occasions. I set a minimum of seven active days per occasion, i.e. if a camera was active for fewer than seven days during an occasion I discarded it (i.e. entered “NA” in the dataset). The total number of occasions per camera trap site ranged from 17 to 24 (mean 21.5, SD  $\pm 2.3$ ).

#### *Spatiotemporal models: response variable*

I considered a measure of intensity of space use by chimpanzees as the response variable for the models. This measure consisted of the number of chimpanzee independent events at each camera trap site during each sampling occasion scaled to the number of camera trap active days. For example, if during sampling occasion 1, camera trap site ‘LF1’ included three independent detections of chimpanzees and cameras were continuously operational for 15 days, I calculated chimpanzee detection frequency for occasion 1 at site LF1 as:  $3/15 = 0.2$ .

#### *Spatiotemporal models: covariates*

I generated spatial and spatiotemporal covariates that described measures of exposure to potential human-related risk and the availability of important chimpanzee food sources. The spatial covariates, i.e. those that varied across space and did not vary across time, were all measures of exposure to risk and included: minimum linear distance to the nearest village (dist\_village), minimum linear distance to the nearest road (dist\_road), minimum linear distance to the nearest agricultural field (dist\_agriculture) and minimum nearest distance to the forest block (dist\_forest). If camera trap sites were located within the landscape feature(s), i.e. village/road/agriculture/forest block, I assigned a zero value for the Euclidian distance (i.e. 0 m). For sites located outside, I measured the Euclidian distance to the edge of the feature. A ‘village’ was defined as a permanent human settlement comprising at least ten households. Thus, based on previous censuses (Hockings et al. 2020), within the spatial range of this study’s chimpanzee community I included three villages, namely Cadique Nalu (29 households), Caiquene (15 households) and Cadique Iala (>10 households). I defined ‘roads’ as those that are accessible by car. It is important to point out that within this study area roads are relatively small (maximum ~5m wide), and in some areas they resemble more of a large path rather than a typical road. At the time of the study the roads were not tarmacked and vehicle traffic mainly comprised motorbikes, bicycles and people on foot.

The two roads included in this study were the road that runs from Iemberem to Cadique and its intersecting road to Caiquene. As chimpanzees will behave differently according to the level of exposure in human land uses, I distinguished between types of agriculture that have distinctive vegetation cover, i.e. shifting cultivation fields (*lugares*) and mangroves rice fields versus orchards. However, the variables ‘distance to orchard’ and ‘distance to cultivated field/mangrove rice’ were highly correlated ( $r = 0.90$ ,  $N = 21$ ,  $P < 0.00001$ ). I therefore merged the two covariates into one (dist\_agriculture), where the agricultural area nearest to camera trap sites included orchard (N sites = 15), shifting cultivation field (N sites = 5) and mangrove rice field (N sites = 1), bearing in mind that most cashew orchards were near cultivated fields and vice versa. I define the ‘forest block’ as the continuous protected forest located south of the Iemberem-Cadique road and west of the Caiquene road (see Figure 6.1 above) (IBAP undated).

The spatiotemporal covariates, i.e. those that varied both across space and time, included human detection frequency in camera traps (human\_det), availability of twelve most important chimpanzee wild foods (covariates palm\_fruit and other\_wild) and availability of six cultivar fruits (covariates cashew, mango+baobab and orange+lime+papaya). Food species were chosen based on those that were recorded as most commonly consumed by chimpanzees at this site (Bessa et al. 2015). To generate the food availability covariates, I calculated the food availability index (FAI) for the selected wild and cultivated chimpanzee food species using the following formula:

$$FAI_{s,t} = \sum_{k=1}^n F_k \times D_k \times S_k$$

where  $F_k$  is the mean score of ripe fruit of monitored individuals in species  $k$  in the sampling occasion  $t$ ,  $D_k$  represents the overall density of adult trees in species  $k$  measured in plots around camera trap site  $s$ , and  $S_k$  is the overall mean DBH of adult trees in species  $k$  measured in plots around camera trap site  $s$  (adapted from McLennan, 2013). Please see Chapter 3 for the minimum DBH of adult trees for each species. I considered the grouped wild and cultivated foods as two covariates and also considered them separately (Table 6.1). Below I provide the justification for the different groups of food covariates.

Orange, lime and papaya are typically grown in villages. A few *Citrus* sp. trees may be present in abandoned villages (e.g. in old Camada, old Caiquene and Butchifula). However, fruit productivity is much lower compared to that of trees in the village orchards, particularly for orange which requires regular maintenance (including adequate sunlight conditions and clearing of strangling climbers, Iaia Tawél Camará, pers. comm.). Oranges are considered more valuable than mango because they are harder to grow and maintain, as well as producing less fruit. Oranges and limes are sold in markets. Limes are also often made into and sold as juice. Papaya trees are typically grown by the cooking area at the back of houses within the village grounds. People that grow papaya usually keep one to four trees. Due to the spatial distribution strongly associated with village settings and low availability compared to other crops, I group orange, lime and papaya together as *potentially high risk cultivars*, i.e. cultivars that present the highest risks of direct interactions with people and human response/retaliation when targeted by chimpanzees (Hockings and McLennan 2012). In addition, the availability of these fruits coincided with the period of forest fruit scarcity (Chapter 3), allowing for testing Hypothesis 4, that chimpanzees increase exposure to risk when wild foods are scarce, temporally trading risk avoidance in favour of optimal foraging.

Mango and baobab are present in both villages and abandoned villages. Mango is occasionally present in cashew orchards outside the village (I identified one such orchard belonging to a farmer from Caiquene). In abandoned villages the density of mango trees tends to be lower relative to villages, but their individual productivity is comparable to that of individual trees present inside villages. Due to the availability of mango and baobab patchy areas across the landscape that are characterised by different levels of human exposure, I group these cultivars as *potentially medium/low risk cultivars*.

Cashew is the most abundant tree species across the sampled area, and the fruit availability of cashew is high compared to other crops (Chapter 3). For example, the FAI value of cashew during its peak month is 1116 compared to mango, the second most available cultivated fruit, which reaches a FAI value of 388 during its peak month (Chapter 3). Structurally, cashew orchards resemble a forest (mean DBH and height, Chapter 3). Cashew nuts represent between 25 and 33% of the total income for smallholder cashew farmers in Guinea-Bissau (Havik et al. 2018). Chimpanzees are known to feed on the ripe fruit and leave the nut intact, therefore presumably, risks of aggressive retaliation by humans due to chimpanzee crop feeding is much lower for cashew compared to other resources (Hockings and Sousa 2012).

Due to the high availability of cashew across the village-forest continuum and the resource partition between chimpanzee and humans, I used the FAI of cashew fruit as a separate covariate from all other crops and considered it a *potentially low/no risk cultivar*.

Oil palm is the second most abundant tree species across the study area (Chapter 3). Wild oil palms are most abundant along the forest edges and within the forest near the edge, close to the mangroves and/or grassland. Oil palm is one of the most important wild resources for local people. Oil palm fruit is used as an ingredient in the majority of local dishes. The oil (typically from the fruit but also from the kernel) is produced locally and often sold. The kernel is also used to produce soap, which is sold in markets. In general, men climb the palms to harvest the oil palm bunches, and women cook it or make products to sell. Women and children often help the climbers to transport the collected bunches to the village. In agricultural areas, oil palms are resistant to slash and burn fires and are present within the forest edge and sometimes within the orchards. Not all chimpanzee communities feed on oil palm resources if present (Humble and Matsuzawa 2004). However, at Caiquene–Cadique oil palm fruit and flowers were two of the most important wild chimpanzee foods (Bessa et al. 2015). They are consumed by chimpanzees throughout the year, and at the time of Bessa and colleagues’ (2015) study, oil palm fruit and flowers contributed to most of the chimpanzee diet in September, when other wild fruit availability was low. In addition, oil palms are the most common species of trees selected for nests by chimpanzees (Sousa et al. 2011). Due to the high availability of oil palm throughout the landscape, including in forest and human land uses, and the importance of this wild species for both chimpanzees and people, I separated oil palms from other important chimpanzee wild fruits and generated three covariates: FAI of oil palm fruit and flower combined, and separate FAI of oil palm fruit and FAI of oil palm flower, which were included in separate models (Table 6.1).

The covariate of the other wild fruit sources’ availability index included ten species: seven trees (*Dialium guineense*, *Spondias mombin*, *Parinari excelsa*, *Treculia africana*, *Ceiba pentandra*, *Ficus sur* and *Detarium senegalense*) and three liana/climbers (*Landolphia heudelotti*, *Saba senegalensis* and *Uvaria chamae*).

The human detection covariate was measured as the daily mean number of camera trap human independent events for each site, i.e. the total number of independent events in a sampling occasion scaled by the number of operational camera trap days during that

occasion. Human detections included researchers as there was no reason to believe the unhabituated chimpanzees would perceive us as different from other people. Again, the time threshold between consecutive photographs for independent events was 60 minutes. Human detection was therefore measured the same way as the chimpanzee response variable. Table 1 summarises the covariates considered in the spatiotemporal models.

**Table 6.1**

List of covariates considered for the spatiotemporal models for this study. Variation measured for the study period and type of inference.

| #   | Model covariates         | Code               | Variation      | Type                  |
|-----|--------------------------|--------------------|----------------|-----------------------|
| 1)  | Distance to village      | dist_village       | Spatial        | Risk                  |
| 2)  | Distance to road         | dist_road          | Spatial        | Risk                  |
| 3)  | Distance to agriculture  | dist_agriculture   | Spatial        | Risk                  |
| 4)  | Distance to forest block | dist_forest        | Spatial        | Risk                  |
| 5)  | Human detections         | human_det          | Spatiotemporal | Risk                  |
| 6)  | Oil palm fruit           | palm_fruit         | Spatiotemporal | Resource              |
| 7)  | Other wild fruits        | other_wild         | Spatiotemporal | Resource              |
| 8)  | Cashew                   | cashew             | Spatiotemporal | Low risk resource     |
| 9)  | Mango and baobab         | mango+baobab       | Spatiotemporal | Medium risk resources |
| 10) | Orange, lime and papaya  | orange+lime+papaya | Spatiotemporal | High risk resources   |

In addition to the covariates presented above, I experimentally fitted covariates that represented different groupings for resource availability. I considered all wild fruit combined (replacing covariates 6 and 7) and all cultivated food combined (instead of covariates 8, 9 and 10). I also tested the effects of combined oil palm fruit and flower availability (replacing covariate 6) and those of all cultivated fruits separate for each food type (i.e. separate mango, baobab, orange, lime and papaya replacing covariates 9 and 10).

#### 6.2.4 Fitting spatiotemporal models using INLA

To identify risk and resource factors that affect variations of chimpanzee ranging patterns across space and time, I employed Bayesian spatiotemporal modeling using the Integrated Nested Laplace Approximation (INLA) algorithm (Blangiardo et al. 2013; Blangiardo and Cameletti 2015; Martins et al. 2013; Rue et al. 2009). For the Bayesian inference, I fitted a Gaussian Markov Random Field (GMRF) autoregressive spatiotemporal model with a Stochastic Partial Differential Equations (SPDE) approach, following Cameletti et al.

(2013). This model accounts for spatial and temporal dependencies, which are a common occurrence in natural processes. For the statistical estimation of Bayesian models, INLA is a computationally efficient alternative to the more traditionally used Markov Chain Monte Carlo (MCMC) method. Since it was proposed ten years ago (Rue et al. 2009), INLA is becoming popular in spatial and spatiotemporal Bayesian modelling (Bakka et al. 2018; Blangiardo et al. 2013; Cameletti et al. 2013; Martins et al. 2013; Rue et al. 2017). INLA uses the Stochastic Partial Differentiation Equation (SPDE) approach to estimate the spatial autocorrelation through triangulation of the study area (Lindgren et al. 2011). Below I briefly describe the GMRF and SPDE and outline the components of the model used in this study.

### *The Gaussian Markov Random Field (GMRF)*

In mathematical terms, a *random field* consists of spatially georeferenced numbers that define a process. The Gaussian Field (GF) is the random field and its interaction with variables, i.e. the covariance function, that varies through space and time (Abrahamsens 1997). For example, in this study the random field would be represented by the variation in intensity of space use by chimpanzees within their home range, and the GF also involves the relationship of chimpanzee movements with the covariates (e.g. risk, resources). The GF is termed “Gaussian” because it refers to the Gaussian probability density functions of the covariates. One of the key aspects of any spatio-temporal processes that must be addressed in spatiotemporal modelling is that of autocorrelation. In the random field, the spatially georeferenced numbers are often assumed to be correlated in space and time, or to covary. In other words, measurements at neighbouring points are more related to one another than those at more distant points, and measurements taken at consecutive time points are more likely to depend on one another than time points measured with a larger time gap. The Matérn covariance function is a widely used approach to describe how the covariance between two measurements changes with their distance apart. Certain GFs with a Matérn covariance function can be represented as GMRFs, with the GMRF constructed using a particular SPDE (Lindgren et al. 2011). Representing a GF as a GMRF enables it to be described using a sparse matrix and considerably reduces the computational time required to estimate the covariance structure of the model. GMRF (also known as conditional autoregressions [CAR]) are already commonly used in spatiotemporal analysis, and the reduction

in computation time generated by incorporating the SPDE approach makes it possible to include more fine-scale spatial data over larger areas.

Using INLA, through the R package R-INLA, it is possible to fit spatiotemporal models incorporating the SPDE approach (Blangiardo et al. 2013). The triangulation mesh used in the SPDE approach is built using the R-INLA package function *inla.mesh.create.helper*, providing the study area sampling points and borders, and indicating the Euclidean distance of the limits from the study area borders, the absolute outer limits (to decrease edge effect), and their corresponding maximal edge lengths and minimal allowed vertex angles (Blangiardo et al. 2013; Cameletti et al. 2013). Figure 6.2 shows the triangulation mesh I created for the Caiquene–Cadique study area. See Appendix 6.1 for the R script codes. The mesh is then incorporated in the SPDE and the data structure necessary to run the model (See Appendix 6.1 for the full script).

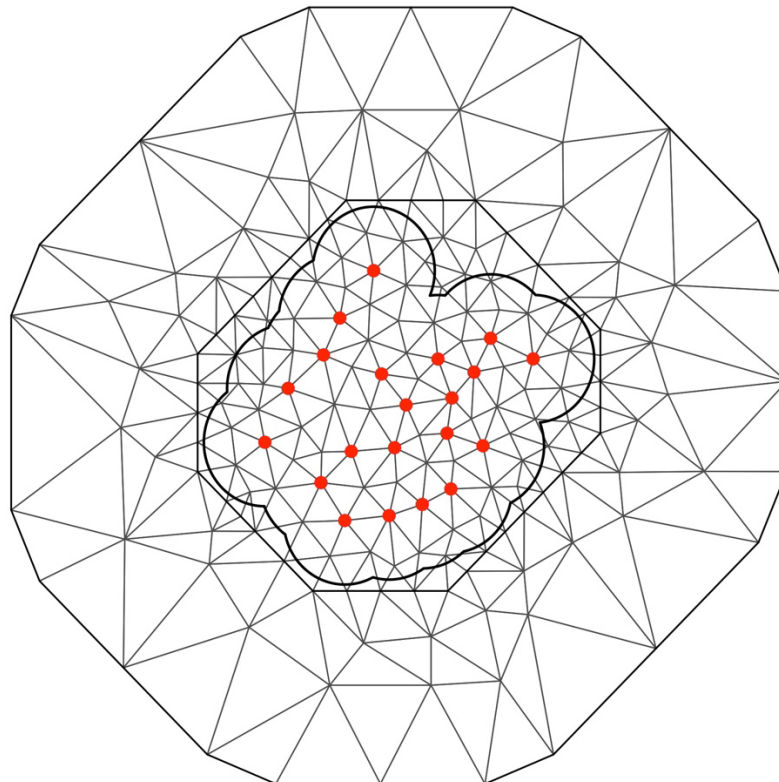


**Figure 6.2**

Triangulation mesh of the study area using 192 vertices. Red dots represent the 21 camera trap sampling sites.

### *Components of the spatiotemporal model*

The spatiotemporal GRMF-SPDE models follow a Bayesian hierarchical approach, and include the following layers: (1) the observed data, (2) the latent field and (3) the hyperparameters (Lindgren et al. 2011; Opitz 2017; Rue et al. 2009). Following Cameletti et al. (2013), the model is based on the following equation:

$$y(s_i, t) = z(s_i, t)\beta + \xi(s_i, t) + \varepsilon(s_i, t)$$

where  $y(s_i, t)$  is the spatiotemporal process that represents the Gaussian Field, which in this case is the distribution of chimpanzee intensity of space use measured by the relative chimpanzee detection frequency at camera trap site  $i = 1, \dots, 21$  located at site  $s_i$  during sampling occasion  $t = 1, \dots, 24$ . The vector of  $p$  covariates is written as  $z(s_i, t) = (z_1(s_i, t), \dots, z_p(s_i, t))$ .  $\beta = (\beta_1, \dots, \beta_p)$  represents the vector of the covariate coefficients. In addition,  $\xi(s_i, t)$  is the spatiotemporal GF that evolves over time following a first order autoregressive process AR(1) with coefficient  $a$ . In AR(1), the value at one time in space is dependent only on the preceding value in time. Lastly,  $\varepsilon(s_i, t)$  is the measurement error (see below for a summary). The R-INLA model results provide the posterior estimates of the latent random field, the beta coefficients of the covariates (the relationship) and the *hyperparameters*. The hyperparameters consist of the measurement error and the spatiotemporal dependencies given to the latent field. The hyperparameters are the following:

$\sigma_\varepsilon^2$  = measurement error variance: also referred to as nugget effect (Cressie and Wikle 2015). The measurement error corresponds to the difference between the observed value and the true value, i.e. a residual variance that is spatially and temporally uncorrelated.

$\sigma_\omega^2$  = the marginal variance of the GMRF (Lindgren et al. 2011);

$a$  = temporal autocorrelation coefficient of the AR(1);

$\rho$  = empirically-derived spatial autocorrelation: the Euclidean distance where the spatial correlation is close to null, i.e. where there is no more spatial correlation.

Cameletti et al. (2013) and Lindgen et al. (2011) provide detailed information on the concepts behind this type of model, including all relevant equations.

All models were run using the *inla* function in the R-INLA package in R (Blangiardo et al. 2013; R Core Team 2016). Due to occasional camera malfunctions, some NA's were generated in the dataset for human and chimpanzee detections. At present, INLA is not able to deal with missing covariates (<http://www.r-inla.org/faq#TOC-Can-INLA-deal-with-missing-covariates->). As I intended to use human detections as a covariate in the chimpanzee models, prior to running chimpanzee models I fitted a GF spatiotemporal model using human detections as response variable. The human model was fitted with the purpose to 'fill' the NAs in the dataset and included no covariates. I extracted the model's posterior means of the measured spatiotemporal field, which corresponded to the mean estimates measured at the 21 sites at each sampling occasion ( $N = 24$ ), totalling 504 values of which 51 were newly generated values from the missing observations. The posterior means and the corresponding observed data were highly correlated ( $r = 0.95$ ,  $N = 453$ ,  $P < 0.00001$ ) and were thus deemed suitable to be included as a covariate in the chimpanzee models. Posterior results including the hyperparameters of the human spatiotemporal model are available in Appendix 6.2. Response variables were  $\log(x+1)$  transformed and all covariates were mean centred and scaled (using a z-transformation) prior to analysis. A default Gaussian prior was used for all models (Cameletti et al. 2013). Model selection was based on the Deviance Information Criterion (DIC), the Akaike Information Criterion's equivalent for Bayesian models. I ran a model without covariates and a model including all covariates presented in Table 6.1. I gradually excluded covariates in a step-wise procedure to identify the model with the lowest DIC. In addition, I considered 21 models including eight exploratory covariates described at in the previous section. Model fit was based on the DIC value and the posterior density symmetry of the parameters showed by the equal mean, credible interval quantiles at 50% and the mode presented in Table 6.2 and showed Figure 6.4 of the results (Spiegelhalter et al. 2002). The significant impact of covariates was determined based on the 95% credible interval not overlapping with zero.

## 6.3 Results

### 6.3.1 Human-chimpanzee overlap

Between 9<sup>th</sup> July 2017 and 5<sup>th</sup> July 2018 I obtained a total of 356,745 images, of which 19,174 were of chimpanzees and 29,145 of humans. The total effort was 6722 camera trap days (average camera trap days per sampling site: 320.10 days, SD  $\pm 33.67$ , range 247 – 359 days). The total number of independent events was 1247 for chimpanzees and 1576 for humans. Chimpanzees were recorded in all 21 camera trap sampling sites but the number of independent events ( $N_{ie}$ ) varied greatly across sites (mean  $N_{ie} = 59.4$ , SD  $\pm 56.7$ ). The largest number of independent events was recorded at one forest-mangrove site ( $N_{ie} = 250$ ) and the site with the smallest number of chimpanzee records was at the forest edge by a mangrove rice farm ( $N_{ie} = 5$ ). Humans were recorded at all 21 sites (mean  $N_{ie} = 74.6$ , SD  $\pm 67.6$ ), with the number of independent events varying from 14 at a forest patch to 214 independent events inside an orange orchard by a village. At the seven sites within the Caiquene-Cadique continuous forest block, chimpanzee independent events ranged from 5 to 89, and human independent events ranged from 17 to 209. Both chimpanzee and humans showed large variation in site visits irrespective of habitat type. Within the forest block, the average relative detection frequency (RDF) of chimpanzees was 16.47 (SD  $\pm 9.71$ ), and humans was 19.11 (SD  $\pm 20.33$ ). Outside the forest block, average chimpanzee RDF was 19.02 (SD  $\pm 19.28$ ), and humans was 26.38 (SD  $\pm 22.99$ ). I found no correlation between the relative detection frequency (RDF) of chimpanzees and humans recorded during the twelve-month sampling period across the 21 sampling sites ( $R = -0.209$ ,  $N = 21$ ,  $P = 0.363$ , Figure 6.3). I considered that chimpanzee and human partitioning trends may differ inside the forest block and across the heterogeneous forest patch-agriculture-village mosaic. Again, I found no relationship between chimpanzee and human RDF across sites inside ( $r = 0.242$ ,  $N = 7$ ,  $P = 0.602$ ) nor outside the forest block ( $r = -0.326$ ,  $N = 14$ ,  $P = 0.255$ ).

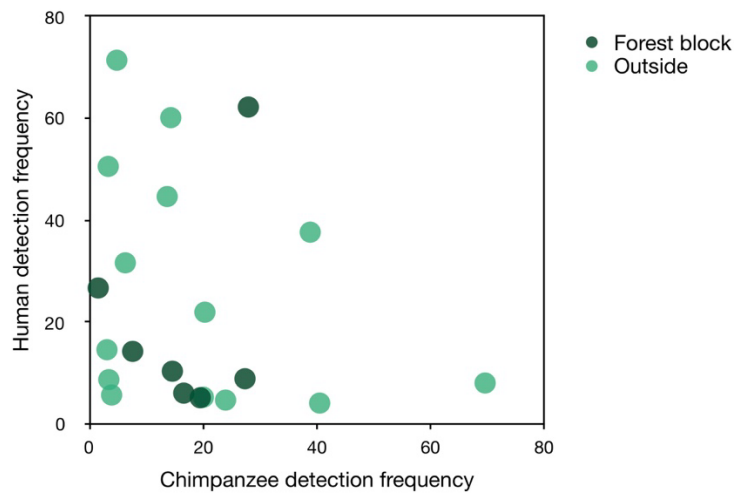


**Figure 6.3**

Comparison between chimpanzee and human relative detection frequency during the twelve-month sampling period across 21 camera trap sampling sites in Caiquene–Cadique.

Therefore, contrary to my first two predictions, I found no evidence for overall site or habitat partitioning between chimpanzees and humans across Caiquene–Cadique. Below I present the results of the spatiotemporal models (Hypotheses 2–4), which tested for the predictive power of spatial and spatiotemporal covariates related to human land use (villages, roads and agriculture) and activity (human detections), as well as the availability of important food sources on the intensity of site use by chimpanzees.

### 6.3.2 Spatiotemporal modelling

I ran a total of 36 models, including the full model, 13 additional models including fewer covariates, a model without covariates, i.e. comprising only the intercept and the spatiotemporal effects, and 21 models that included experimental covariates. See Appendix 6.3 for a full list of considered models. The model with the lowest Deviance Information Criterion (DIC), i.e. the model with the best fit selected as the best model, include eight covariates (Table 6.2). The spatial covariates with significant predictive power on chimpanzees' intensity of space use, i.e. those with 95% credible intervals not overlapping with zero, are *dist\_road* (beta coefficient  $\beta -0.09$ , SD  $\pm 0.02$ ), and *dist\_village* ( $\beta +0.08 \pm 0.02$ ). Based on these effects, within their home range Caiquene–Cadique chimpanzees intensify

the use of areas close to the small roads and away from the villages. The spatial covariate *dist\_agriculture* shows a strong predictive power for chimpanzee space use ( $\beta +0.03 \pm 0.02$ ), indicating a tendency of chimpanzees to avoid agricultural fields. Of the spatiotemporal covariates, the most important is *palm\_fruit* ( $\beta +0.02 \pm 0.01$ ), indicating that chimpanzee spatiotemporal home range use in Caiquene–Cadique was positively modulated by the availability of oil palm ripe fruit. Despite the 95% credible intervals of *mango+baobab* and *orange+lime+papaya* slightly overlapping with the zero value, the model that includes them has a considerably better fit compared to the model that exclude them ( $\Delta\text{DIC} = 39.35$ ). The effects of these covariates indicate a tendency of chimpanzees to intensify their activity in areas with lower availability of mango and baobab ( $\beta -0.01 \pm 0.01$ ), and higher availability of orange, lime and papaya ( $\beta +0.01 \pm 0.01$ ). The best model also includes the cumulative availability of important chimpanzee wild ripe fruit other than oil palm (*other\_wild*) and human detection frequency (*human\_det*). Despite the credible intervals of these two covariates encompassing the zero value at 50% and both covariate coefficients  $\beta = 0.00 \pm 0.01$ , excluding these two covariates from the model would reduce model fit ( $\Delta\text{DIC} = 23.7$ ). All posterior density means align with the credible interval quantiles at 50% and their mode (Table 6.2) and show symmetrical densities (Figure 6.4) indicating adequate fit between the best model’s parameters and the GMRF.

**Table 6.2**

Posterior mean of the intercept and covariate coefficients  $\beta$  for the best model, including standard deviations, credible interval quantiles and mode. Bold indicates significant predictive power of covariate. (Best model DIC = -876.183, compared to Intercept-only model DIC = -779.444,  $\Delta\text{DIC} = 96.7$ . See Appendix 6.3 for the full list.).

| Covariate                  | Mean          | $\pm\text{SD}$ | 2.5%          | 50%           | 97.5%         | Mode          |
|----------------------------|---------------|----------------|---------------|---------------|---------------|---------------|
| Intercept                  | 0.145         | 0.020          | 0.106         | 0.145         | 0.184         | 0.145         |
| <b>Distance to road</b>    | <b>-0.092</b> | <b>0.021</b>   | <b>-0.134</b> | <b>-0.092</b> | <b>-0.051</b> | <b>-0.092</b> |
| <b>Distance to village</b> | <b>0.077</b>  | <b>0.021</b>   | <b>0.036</b>  | <b>0.077</b>  | <b>0.119</b>  | <b>0.077</b>  |
| Distance to agriculture    | 0.032         | 0.018          | -0.003        | 0.032         | 0.066         | 0.032         |
| Human detections           | 0.001         | 0.013          | -0.025        | 0.001         | 0.026         | 0.000         |
| <b>Oil palm fruit</b>      | <b>0.019</b>  | <b>0.010</b>   | <b>0.000</b>  | <b>0.019</b>  | <b>0.038</b>  | <b>0.019</b>  |
| Other wild fruit           | 0.002         | 0.010          | -0.017        | 0.002         | 0.021         | 0.002         |
| Mango and baobab           | -0.014        | 0.012          | -0.037        | -0.014        | 0.010         | -0.014        |
| Orange, lime and papaya    | 0.012         | 0.012          | -0.012        | 0.012         | 0.035         | 0.012         |

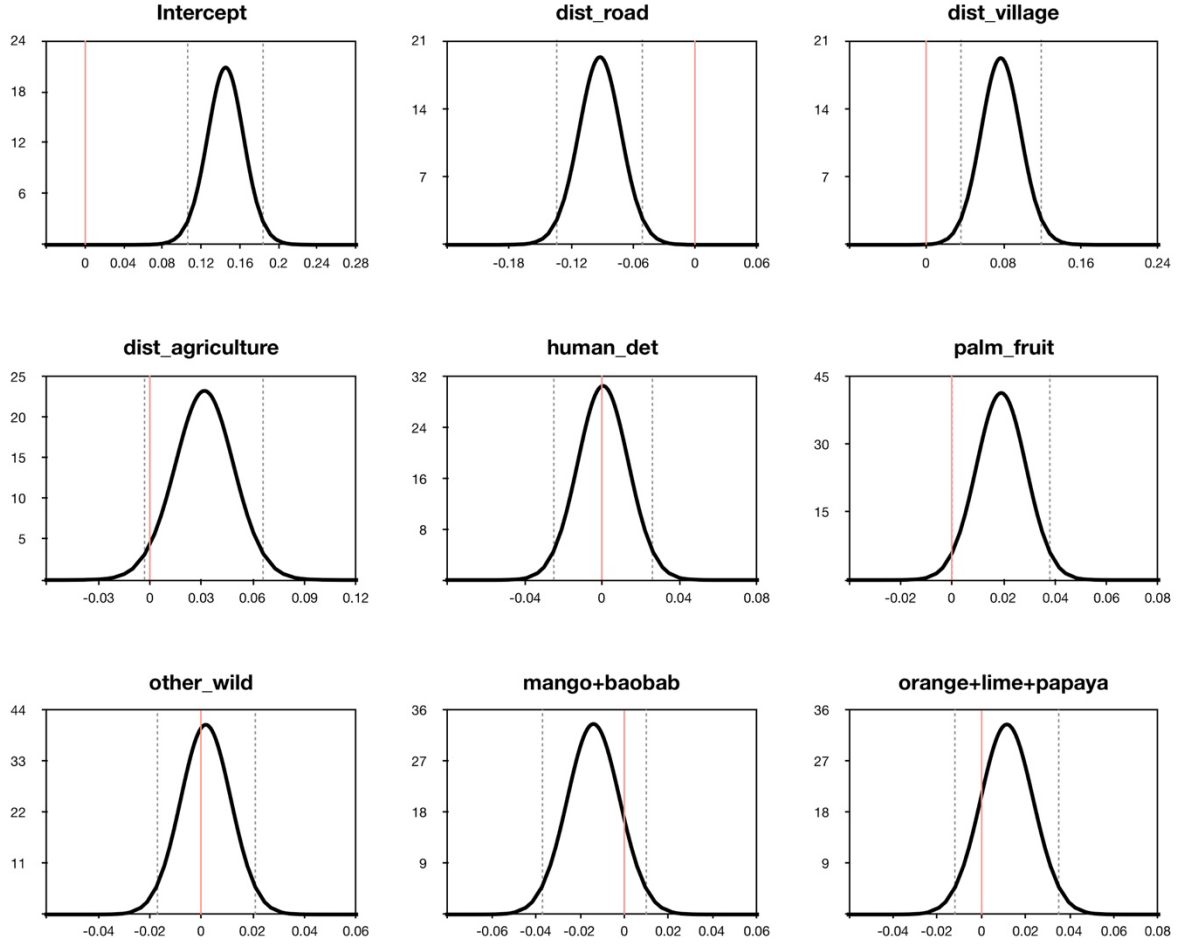


**Figure 6.4**

Marginal posterior density plots for the fixed effects of the model parameters. Pink line represents the zero value and dashed grey lines show 0.025 and 0.975 quantiles of credible intervals.

The hyperparameters of the best model (Table 6.3) show that the GMRF variance  $\sigma_{\omega}^2$  explains more of the spatial variation compared to the residual measurement error  $\sigma_{\epsilon}^2$ , therefore indicating that the spatial field is important. The empirically derived spatial correlation value  $\rho$  shows that at a distance of 616m the correlation is close to null, revealing that the spatial extent of the correlation was low. The minimum distance between camera trap sites was 520 m, a strong correlation between sampling sites was therefore unlikely. The value of the temporal correlation coefficient  $a$  indicates high temporal correlation, showing that in general, changes in intensity of space use by chimpanzees evolved relatively slowly over time (longer than two weeks).

**Table 6.3**

Posterior estimates of hyperparameters of best model showing means, standard deviations and credible interval quantiles.

| Parameter                | Mean   | ±SD     | 2.5%   | 50%    | 97.5%  |
|--------------------------|--------|---------|--------|--------|--------|
| $\sigma_{\varepsilon}^2$ | 0.0052 | ±0.0018 | 0.0025 | 0.0049 | 0.0094 |
| $\sigma_{\omega}^2$      | 0.0297 | ±0.0081 | 0.0177 | 0.0283 | 0.0492 |
| $a$                      | 0.7479 | ±0.0532 | 0.6311 | 0.7523 | 0.8391 |
| $\rho$                   | 615.97 | ±148.20 | 361.54 | 604.68 | 938.98 |

$\sigma_{\varepsilon}^2$  = measurement error of variance referred to as nugget effect (Cressie and Wikle 2015);  $\sigma_{\omega}^2$  = marginal variance of the Gaussian Markov Random Field (Lindgren et al. 2011);  $a$  = temporal autocorrelation coefficient AR(1);  $\rho$  = empirically derived spatial autocorrelation.

In summary, the best model shows that chimpanzee spatiotemporal home range use was driven by both risk of exposure to humans and opportunity to access food resources. At the spatial dimension, villages represented the most influential landscape feature for overall spatial avoidance by chimpanzees, supporting Prediction 2.1. Proximity to agriculture also negatively influenced chimpanzee frequency of site use and in contrast, roads/areas in proximity to roads were intensively used. Contrary to Prediction 2.2, human detections had no effects on spatiotemporal variation of chimpanzee site use. Supporting Prediction 3.1, ripe oil palm fruit availability positively impacted spatiotemporal variation in intensity of space use year-round. In contrast, the combined availability of other wild fruits showed no significant influence. Regarding important cultivated chimpanzee foods, the availability of ripe cashew fruit had no overall effect on chimpanzee intensity of space use and was not included in the best model. The availability of cultivars found in both village and abandoned villages (mango and baobab – *medium/low risk cultivars*) showed a negative relationship with the frequency of visits to a site. This suggests that chimpanzees showed a tendency to use areas characterised by low availability of ripe mango and baobab fruit more frequently than areas with high availability of ripe mango and baobab fruit. In contrast, the availability of cultivar foods mainly found within or by villages (orange, lime and papaya – *high risk cultivars*) had a positive relationship with chimpanzee frequency of visits supporting Prediction 3.2. The negative influence of village proximity on chimpanzee space use highlights villages as high risk areas; combined with the positive relationship of the response variable with the availability of village-fruits (orange, lime and papaya), the results of the model support Prediction 4.1.

### *Posterior estimates: prediction maps*

Heatmaps showing the posterior latent field during four sampling occasions are presented in Figure 6.5. During occasion 7 (9 – 23 October 2017), the highest values of chimpanzee intensity of space use were predicted at a forest/mangrove site that chimpanzees often used to access orchards south of Cadique Nalu (Figure 6.5a). This corresponds to the period where orange, lime and papaya become available and is just before the baobab ripe fruit season. During the same period, relatively high values were also predicted for the sites in the orange orchards within the two villages (Cadique Nalu and Caiquene). During occasion 15, which corresponded to the peak of baobab ripe fruit season (9 – 23 February 2018), highest relative values of chimpanzee space use were detected close to and within abandoned villages, in contrast to low values in the villages (Figure 6.5b). In February papaya was still available, but orange and lime were not (see Chapter 3 for FAI figures). Maps of posterior means for each of the 24 sampling occasions are presented in Appendix 6.5.

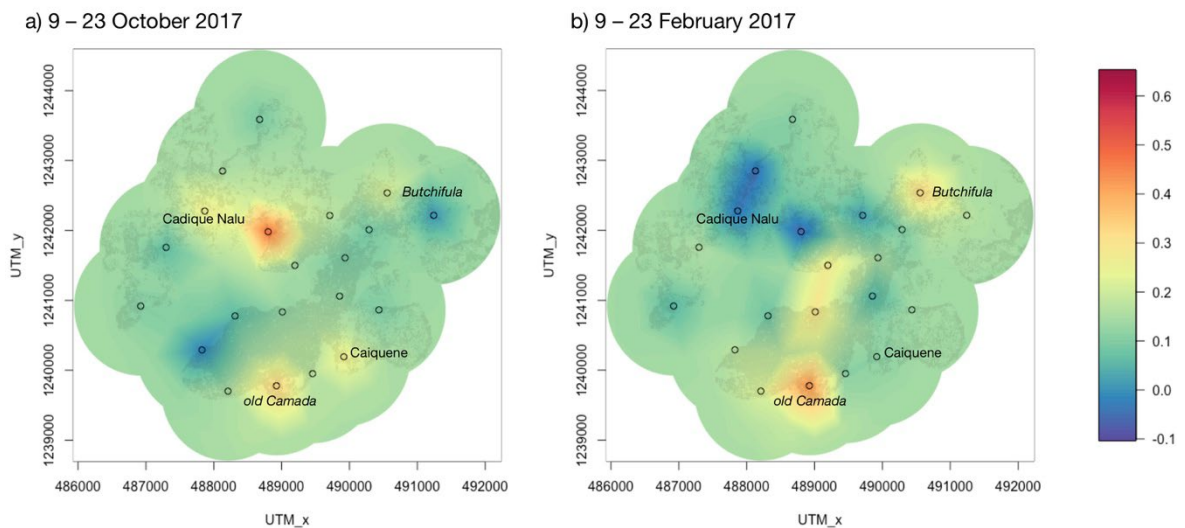


**Figure 6.5**

Maps of the posterior mean of chimpanzee intensity of space use in Caiquene–Cadique. Posterior mean is shown on the logarithmic scale during two periods: (a) at the beginning of orange, lime and papaya fruit season, which coincides with low wild fruit availability and (b) during the peak of the baobab fruit season. Maps show locations of villages (Cadique Nalu and Caiquene) and two important abandoned villages (old Camada and Butchifula). Shaded background represents forest vegetation.



### Plate 6.1

Chimpanzee feeding on orange fruit in Caiquene village in October 2017.



### Plate 6.2

Chimpanzees feeding terrestrially on baobab fruit near the abandoned village of Butchifula at the start of baobab season in November 2017.



### Plate 6.3

Chimpanzee transporting mango fruit at a forest site near a cashew/mango orchard in May 2018.



### Plate 6.4

Chimpanzees travelling through a cashew orchard in Cadique Nalu in April 2018. The adult male in front of the camera is seen carrying cashew fruit. During cashew season orchards are kept cleared by farmers for the harvest.

## 6.4 Discussion

The aim of this study was to quantify chimpanzee spatiotemporal home range use in a human-influenced landscape of fear, following a conceptual approach similar to previous research (e.g. including humans as potential ‘predators’ [Ciuti et al. 2012b; Støen et al. 2015; Tolon et al. 2009]; or exclusively nonhuman predators [Coleman and Hill 2014; Thaker et al. 2011; Willems and Hill 2009]). Specifically, I identified spatiotemporal factors that contribute to shaping risk-avoidance and foraging efficiency strategies of a West African chimpanzee community. I employed Bayesian GMRF spatiotemporal modelling using the INLA-SPDE method of approximation (Cameletti et al. 2013; Lindgren et al. 2011). To my knowledge, this was the first study to make use of this statistical approach for fine-scale, camera trap-based georeferenced data. I provided evidence in support of three of the four hypotheses (2–4), therefore rejecting the null hypothesis that chimpanzee spatiotemporal variation in space use within their home range is random. Below I discuss my results following the order of hypotheses. I also outline the study limitations and provide recommendations for future research using this methodological approach.

*Hypothesis 1: Humans and chimpanzees do not overlap in habitat selection and show a tendency to spatially partition at the site-scale (fine-scale spatial niche separation)*

At Caiquene–Cadique chimpanzees and humans were detected at the same camera trap sites and both used areas inside and outside the forest block. Overall detection frequencies between chimpanzees and humans showed no significant negative relationship, and I found no evidence for a strong spatial niche separation. I reject Hypothesis 1 and suggest that humans and chimpanzees co-occur at a fine spatial scale. Similarly tigers and humans in Nepal used the same locations across their study area including within the forest of Chitwan National Park and in a multi-use forest outside the park (Carter et al. 2012). In Hawf, Yemen, humans and several wildlife species use the same locations and the occupancy probability of some taxa including hyenas (*Hyaena hyaena*), honey badgers (*Mellivora capensis*) and wolves (*Canis lupus*) is positively predicted by human presence (Khorozyan et al. 2014). The authors proposed that the fine-scale co-occurrence was due to sharing the same water points across the landscape and that the presence of livestock and human leftovers constituted attractive food sources (Khorozyan et al. 2014). In Caiquene–Cadique, Hockings

et al. (2020) measured human and chimpanzee wild plant resource use and found a total of 46 shared species, including oil palm, figs (*Ficus* spp.), velvet tamarind (*Dialium guineense*) and saba (*Saba senegalensis*), which were intensively used by both humans and chimpanzees. Local people in Caiquene–Cadique exploit at least 142 wild plant resources (Hockings et al. 2020) and use forest trails for traveling and accessing fishing areas in the mangroves. Chimpanzees feed on at least 57 wild resources and ten cultivated foods (Bessa et al. 2015; Hockings and Sousa 2013; Hockings et al. 2020) and often travel on human forest-paths (E Bersacola, pers. obs.). Thus, the fine-scale co-occurrence between chimpanzees and humans in Caiquene–Cadique across multiple habitats is most likely associated with the high overlap in the use of trail networks and resources, including wild resources available in the forest block and both wild and cultivated resources available across the heterogeneous mosaic (Chapter 3). Despite the absence of negative correlation, my data show an upper limit for co-occurrence; there were no sites where both humans and chimpanzees had very high detection frequencies (i.e. of >40). This is expected considering the placement of camera trap in both forest and human habitats such as villages; in general, forests are occupied by fewer people compared to villages or agricultural areas. However, it may also suggest a tendency for chimpanzees to maximise the use of space where humans are less likely to visit.

*Hypothesis 2: The spatial and spatiotemporal variation in risk of direct interactions with humans modulates chimpanzee home range use (risk avoidance strategy)*

According to the spatiotemporal model chimpanzees showed spatial sensitivity to risk. My results support Hypothesis 2, that spatial variation in the risk of direct interactions with humans alters chimpanzee intensity of space use: chimpanzees employ a risk-avoidance strategy at a fine spatial scale. The spatial variation in risk was represented in the physical environment by human settlements that included at least 10 households (referred here as villages, N = 3 within the study area). Compared to other anthropogenic land uses, villages are characterised by the most intense levels of human activity in terms of number of people and temporal continuum. Although villages were sometimes accessed by the chimpanzees, they represented the highest risk-peaks within their home range and were mostly avoided. In contrast, at the landscape scale in Cantanhez, chimpanzees were more likely to occur closer to villages and settlements (Chapter 5), highlighting scale-dependent relationships. At

the landscape scale, where ape hunting is absent and the chimpanzees are tolerated by local people, the ecological benefit for chimpanzees to occur close to villages/cultivated areas may outweigh the potential risks (McLennan and Ganzhorn 2017; Rode et al. 2006). At the home range scale, chimpanzees are likely to increase the frequency of visits at villages only during specific periods (e.g. low wild fruit availability – Hypothesis 4), and generally maximise the use of space further from villages to reduce the risks of direct interactions with people. When entering “risky” villages in Caiquene–Cadique, chimpanzees will likely use behavioural strategies in response to the perceived risks, including increased vigilance and other anti-predator behaviour, food transport, different social grouping patterns and maximise activity at dusk/night (Hockings et al. 2007, 2012; Krief et al. 2014; Lindshield et al. 2017; Wilson et al. 2007). In Chapter 7 I construct a possible chimpanzee behavioural model at the Caiquene–Cadique village settings based on accounts from local people.

Distance to the nearest road negatively predicted chimpanzee intensity of space use, i.e. chimpanzees used areas near roads more frequently. Chimpanzees are known to cross roads regularly within their home ranges (Cibot et al. 2015; Hockings et al. 2006), although fatal collisions between chimpanzees and vehicles have previously been recorded at some sites (McLennan and Asiimwe 2016). Tarmacked and/or heavily trafficked roads particularly can represent high-risk landscape features that given the opportunity, wildlife may choose to avoid. For example, to minimise contact with roads, bobcats (*Lynx rufus*) establish their home ranges in parts of the landscape that contain fewer roads (Poessel et al. 2014). In contrast to my results, within an agricultural-swamp forest mosaic in Moyamba, Sierra Leone, chimpanzees significantly avoided untarmacked roads (Garriga et al. 2019). The polarizing results may be partially explained by the position of roads and by striking differences in amount of forest cover between the two sites: the vast majority of land use surrounding the roads in Moyamba consisted of shifting cultivation fields including cleared and fallow land (Garriga et al. 2019). In Caiquene–Cadique, one road intersects at approximately the centre of the chimpanzees’ home range and combined, the two roads run along ~1.8 km of the main forest block. The camera trap sites used in this study were spread relatively evenly across the known chimpanzees’ home range (Bessa et al. 2015; CRT, unpubl. data). Except for camera traps placed within villages, all camera traps were placed at least 110 m from the nearest road. The strong positive relationship of the covariate *dist\_road* with chimpanzee intensity of space use may actually indicate that roads happen to be present within the chimpanzees’ core range. Chimpanzees are frequently seen by local

people crossing these roads (Plate 6.5) and common chimpanzee crossing points are easily discerned along the road where shrubs are present (E Berascola, unpubl. data/pers. obs). Thus, at present the two roads in Caiquene–Cadique do not seem to pose significant spatial constraints on chimpanzee home range use, likely due to very low vehicle-traffic, relatively small width, lack of tarmac and sufficient amount of forest and shrub cover along the sides of the roads. However, chimpanzees will likely perceive some risk when crossing roads, employing behavioural responses such as waiting, scanning, running, group cohesion and social cooperation (Hockings et al. 2006). The associated risks may be perceived differently by different age and sex classes, with females and immatures crossing rapidly and adult males occupying guarding positions (K Hockings, pers. obs).



**Plate 6.5**

Chimpanzees and people on the road in Cadique. Bottom image photo credit: K Hockings

The best model showed that the spatiotemporal variation in human camera trap detections had no overall effect on chimpanzee detections. Therefore, I found no evidence for strong temporal avoidance of humans by chimpanzees. The lack of any overall positive or negative relationship-trends suggests some levels of temporal co-occurrence at the measured scale (c. two-week periods). Temporal co-occurrence is likely the result of chimpanzees and humans targeting the same areas when forest and/or cultivated resources are available. Chimpanzees may use some orchards more often when ripe cultivar fruit are available (e.g. orange: this Chapter), which would coincide with the harvesting periods when people are also present. Local people use wild resources more frequently when they are available (Hockings et al. 2020), perhaps harvesting in the same forest areas used by the chimpanzees. At other times, humans and chimpanzees may use separate parts of the landscape, which would explain the non-positive relationship between the human detection covariate and the chimpanzee response variable. For example, during the cashew fruiting season, local people may focus on cashew harvest and temporally abandon activities in the forest such as oil palm gathering and mangrove fishing (E Bersacola, unpubl. data). At certain times of the year agricultural areas may be used intensively by local people and avoided by chimpanzees (e.g. during slash and burn of cultivated fields and cleanings of cashew orchards). Indeed, the model also showed a strong positive effect of distance to agriculture on chimpanzee intensity of space use. In Chapter 7 I supplement this finding with data from interviews with local people to draw additional inferences on how the spatiotemporal variation in human activities in agricultural fields may impact chimpanzee home range use.

*Hypothesis 3: Spatiotemporal variation in resource availability modulates spatiotemporal variation of chimpanzee home range use (optimal foraging strategy)*

The results of the best model provided support for Hypothesis 3, that the spatiotemporal variation in resource availability shapes chimpanzee spatiotemporal variation in home range use. The availability of ripe oil palm fruit positively predicted chimpanzee frequencies of site use. These findings reiterate the ecological importance of oil palm for this chimpanzee community (Bessa et al. 2015; Sousa et al. 2011), supporting similar findings elsewhere (Goodall 1968; Hockings et al. 2009; Tutin et al. 1991; Yamakoshi 1998). Oil palms were the second-most abundant plant species across Caiquene–Cadique and oil palm fruit availability seasonal fluctuations coincided with the cumulative availability of ten other ripe

wild fruits (Chapter 3). November had the lowest availability of ripe oil palm fruit, coinciding with the period of wild foods scarcity (September – January, Chapter 3). In 2013 Bessa et al. (2015) recorded chimpanzees in Caiquene–Cadique consuming oil palm fruits and flowers throughout the year regardless of fruit availability. Therefore, oil palm fruit was considered as ‘staple’ food (Bessa et al. 2015). My results suggest a positive relationship between ripe oil palm fruit availability and its exploitation by chimpanzees at this site which would fit the definition of a ‘preferred–staple’ resource (McLennan 2013). I found no correlation between the availability of other wild fruit and chimpanzee space use. The inclusion of this covariate in the best model and its posterior distribution that nearly perfectly overlapped with the zero value suggests that the availability of some wild fruits may be positively associated with chimpanzee site use, whereas others may show a negative or neutral trend.

The availability of orange, lime and papaya fruit positively correlated with the response variable, providing further support for Hypothesis 3 (and see below Hypothesis 4). The negative relationship of mango and baobab availability may suggest that chimpanzees exploit these resources more often in areas where availability is comparatively low, preferring to use low-risk abandoned villages/orchards where they rarely encounter people (e.g. Bossou, Guinea: Hockings et al. 2009; Bafing, Mali: Duvall 2008). Indeed, if available, previous research has shown that animals often prefer to feed on the same resources in low rather than high risk areas (Lindshield et al. 2017; Nowak et al. 2016). Furthermore, chimpanzees may select mango and baobab areas intensively during lower availability periods (e.g. at the start or end of mango/baobab season). At Caiquene-Cadique, the beginning of the baobab season in November coincided with the period of lowest wild fruit availability (Chapter 3). Mango fruits on the other hand, appear to be targeted by chimpanzees regardless of wild fruit availability similar to other sites in West Africa (e.g. Bossou in Guinea, Hockings et al. 2009).

When available (March–July in Caiquene–Cadique), cashew pseudofruit is consumed by chimpanzee communities across Guinea-Bissau (Bessa et al. 2015; Carvalho et al. 2015; Hockings et al. 2009; Hockings and Sousa 2012). My models showed an orthogonal relationship between cashew fruit availability and chimpanzee home range use (Appendix 6.4) and the covariate was absent in the best model. The prevalence of cashew orchards across the landscape offers numerous locations where chimpanzees may choose to feed.

Consequently, representative data showing variation in chimpanzee use of cashew orchards will require a different sampling approach, for example using a much finer spatiotemporal scale, possibly solely focusing on cashew orchard versus another habitat use. Additionally, chimpanzees used cashew orchards to access foraging sites across the matrix throughout the year (E Bersacola, unpubl. data), with cashew availability scores ranging from zero during eight months of this study to >1000 during peak availability in April/May (Chapter 3). Thus, cashew orchard use by chimpanzees will unlikely be predicted by measures of cashew fruit availability alone. Other factors such as proximity to other feeding and/or nesting sites, undergrowth and forest/shrub cover may play equally important roles. When cashew is not being harvested or cleaned, cashew orchards show structurally similarities to forest or fallow habitats depending on the age of the orchard (Chapter 3, E Bersacola pers. obs.). In addition, some chimpanzee wild foods, such as fruits of *Salacia senegalensis*, are sometimes present in uncleared orchards (IT Camará/K Hockings/E Bersacola, pers. obs.).

*Hypothesis 4: Chimpanzees will increase the use of high-risk areas when cultivated foods are available and wild foods are scarce*

The strong positive effect of distance to village and the positive relationship of availability of orange, lime and papaya fruits combined suggest that when village food were available, chimpanzee avoidance of areas in or in proximity to villages was temporally overruled. Orange, lime and papaya were available when wild foods were scarcest (Chapter 3). My results indicate that the temporal increase in chimpanzee use of high-risk areas was driven by access to cultivars and low wild fruit availability, providing support for Hypothesis 4. For this study I used frequencies of chimpanzee site-use in relation to site-food availability as a proxy for resource use, rather than direct or indirect feeding observations. Incorporating an element of risk into the model allows us to weight the costs and benefits of site selection. If a habitat is generally avoided by an animal, but the availability of resources associated with that particular habitat increases the animal's visits, one can infer that the use of that habitat is largely driven by foraging necessity or opportunity. Studies on chimpanzee temporal dietary patterns showed higher crop foraging during periods of wild fruit scarcity (Bossou, Guinea: Hockings et al. 2009; Bulindi, Uganda: McLennan 2013; Kibale, Uganda (banana pith): Naughton-Treves et al. 1998), suggesting an element of 'response-to-necessity' to maintain a high amount of food in the diet. African elephants (*Loxodonta africana*) were

also found to exploit cultivated foods in periods of low wild food availability and nutritional quality (Osborn 2004; Rode et al. 2006). At other sites wildlife crop foraging is associated with food preference and increased opportunity rather than responding to a nutritional necessity (Campbell-Smith et al. 2011; Seiler and Robbins 2016; Sukumar 1990; Tweheyo et al. 2005). Some crops may represent ‘fallback’ foods, some will not: around Kibale, Uganda, chimpanzees consume some crops regardless of wild food availability but the frequency in banana pith feeding was negatively related to the availability of a key wild fruit (Naughton-Treves et al. 1998). Outside Budongo, Uganda, chimpanzees were reported feeding on sugar cane more frequently during wild and cultivated food shortages, whereas crop feeding reports of other foods were positively associated with overall fruit availability (Tweheyo et al. 2005). Chimpanzees at Caiquene–Cadique fed on cultivars when they were available (Bessa et al. 2015), including those within high and low risk areas. My study highlights that chimpanzees access high-risk orange, lime and papaya fruits in response to nutritional necessity rather than preference alone.

### *Conclusions*

The landscape of fear framework (Gaynor et al. 2019; Laundré et al. 2010) allows us to draw inferences on wildlife optimal foraging/predation risk trade-offs using spatially and spatiotemporally explicit modelling approaches (Coleman and Hill 2014; Willems and Hill 2009). In this study, I showed that chimpanzee intensity of space use within their home range is modulated by both anti-predator and optimal-foraging strategies. Chimpanzees in Caiquene–Cadique showed relatively low levels of spatial risk avoidance; only high human-activity landmarks (i.e. villages) negatively influenced intensity of site use, and to a lesser extent agricultural areas. Both villages and agricultural areas were not completely avoided, and perhaps more surprisingly, chimpanzee site use increased with increased proximity to roads. Chimpanzees intensified the use of space in accordance with ripe oil palm fruit availability, taking advantage of this highly available resource in their landscape. My results also showed that when crops were available and wild fruits were scarce, chimpanzees increased their exposure to potential risks, therefore trading off a spatial anti-predator strategy in favour of optimal foraging. In the next Chapter I include a theoretical model of chimpanzee behavioural strategies in the high-risk areas identified here (villages) based on interviews with local residents across Caiquene–Cadique.



## CHAPTER 7

# Understanding chimpanzee risk behaviour through local people's narratives



## 7.1 Introduction

Across the world, indigenous people possess local ecological knowledge developed through multi-generational connections with the environment (Menzies 2006). These linkages constitute intimate observations and experiences varying in type and scale: from the day-to-day use of resources and interactions with wildlife to the long-term witnessing of changes in ecological processes (Joa et al. 2018; Kutz and Tomaselli 2019). Ecological knowledge is passed and accumulated through generations using oral and/or written forms. Scientists are increasingly becoming aware of its value to corroborate scientific data and provide a more complete understanding of natural phenomena (Calheiros et al. 2000). Local ecological knowledge can help scientists gather information on wildlife presence, distribution, habitat use and preference, activity, diet and sociality (Ergete et al. 2018; Kutz and Tomaselli 2019; Mallory et al. 2006; Starr et al. 2011; Telfer and Garde 2006). For example, in northern Australia, Bininj people reported that the seasonal physical difference in fur condition of rock kangaroos (*Macropus* spp. and *Petrogale* spp.) was due to differences in their food availability, which complemented scientific findings (Telfer and Garde 2006). Indigenous people in northern Canada have known for generations that caribou (*Rangifer tarandus*) leaders play a crucial role in the migration of the herd, corroborating more recent scientific studies (Kutz and Tomaselli 2019). Several studies have also argued that by providing context to scientific findings local ecological knowledge can inform conservation management and can be actively incorporated to implement inclusive and locally-appropriate conservation approaches (Drew 2005; Kutz and Tomaselli 2019; Mallory et al. 2006).

Previous research indicated extensive ecological knowledge about chimpanzees by people living in Cantanhez NP (Parathian et al. 2018; Sousa et al. 2014). Local people were knowledgeable about chimpanzee selection of tree species for nesting as well as feeding sources, including wild and cultivated plant species and non-plant foods (Sousa et al. 2014). Although chimpanzees in Caiquene–Cadique encounter people regularly, the chimpanzee community is not habituated. Camera traps can gather indirect data allowing researchers to measure patterns of occupancy, activity and habitat use (Chapters 5 and 6; O’Connell et al. 2010). Through these quantitative measures, one can make inferences about environmental and anthropogenic constraints on the species of interest. However, to quantify behaviour in

response to risk, data through direct observations of habituated animals are necessary (e.g. Hockings et al. 2012). Typically, these behaviours are measured using scan and/or focal sampling (Hockings 2007; Oxley 2019). For example, in a forest-agricultural mosaic in Uganda, Oxley (2019) found that chimpanzees increased group size and the number of males when using the riskier agricultural-village matrix outside the forest. At Bossou, Guinea, when the risks of road-crossing increased, the alpha male was significantly more likely to cross the road in the last position, whereas the second and third ranking males usually led the group (Hockings et al. 2006). Interview data with local people may not provide quantitative measures of chimpanzee behaviour but qualitative analysis of local narratives about chimpanzees could highlight certain aspects of chimpanzee behaviour that help explain scientific (indirect) observations. Furthermore, such data can provide additional context to the human-chimpanzee interface, and might help us understand how people react to problematic chimpanzee behaviours such as attacks on local persons (Hockings and McLennan 2016; Sousa et al. 2017). This information is crucial to make informed conservation decisions.

To identify mechanisms that hinder or promote long-term coexistence in shared landscapes, it is necessary to understand the costs that humans and wildlife exert on each other using cross-disciplinary approaches. In shared landscapes, humans are typically the dominant species (Ciuti et al. 2012b) affecting wildlife in a number of ways including through competitive advantage over space and resources (Torres et al. 2016), direct persecution (top-down influence) and by altering habitats and the availability of wild resources (bottom-up influence) (Gandiwa 2013). However, wildlife can also pose certain threats to human wellbeing, both directly through lethal and non-lethal attacks and indirectly by killing livestock and damaging crops (Dunham et al. 2010; Hill 2000; Hockings and McLennan 2016; Loe and Röskft 2004; Packer et al. 2019; Wallace and Hill 2012). Therefore, biological data are required to predict wildlife responses to risks and to identify ecological constraints imposed by humans. In the same way, social science approaches offer an opportunity to highlight local people's livelihood and safety concerns over sharing the space with wildlife. Combining local knowledge and perceptions with biological data is crucial to develop locally-appropriate conservation programs that accommodate the needs of both humans and wildlife (Mallory et al. 2006).

### 7.1.1 Chapter aims

In this Chapter, I:

- (1) compare local reports of human resource use by chimpanzees to some of the findings presented in Chapter 6, specifically the effects of some spatial (agriculture) and temporal covariates (cultivated food availability), and;
- (2) examine local narratives of chimpanzee behaviour and interactions with people to (i) identify potential chimpanzee strategies in response to risk, and (ii) highlight human concerns.

In Chapter 6 I used spatiotemporal models to identify risk and resource factors influencing chimpanzee intensity of site use. To supplement model inferences based on indirect data from camera traps with relevant information about chimpanzee behaviour, I used semi-structured interviews and participatory observations with local people. I compared the effects of the anthropogenic covariates of the best model on the response variable with local reports about the chimpanzees' use of cultivated areas and resources. Of the covariates included in the spatiotemporal models, villages were the most spatially constraining element for chimpanzee space use. Specifically, proximity to villages negatively predicted intensity of space use by chimpanzees, suggesting that villages are perceived as the riskiest areas. However, villages were also identified by interview participants as the context where human-chimpanzee encounters occurred most frequently and at very close physical distance, specifically during orange and papaya season. Thus, to examine possible chimpanzee behavioural foraging strategies in response to risk and explore human perceptions and concerns, I focused on exploring local narratives of human-chimpanzee interactions in the village context.

## 7.2 Methods

### 7.2.1 Study area

Please refer to Chapter 3 or Chapter 6.

### 7.2.2 Interviews

I used participatory observation and conducted interviews with people living and working within the home range of the Caiquene–Cadique chimpanzee community. I carried out participatory observation between October 2016 and November 2017, and for one month in June 2018. Participant observation followed *moderate participation* as described by Musante (DeWalt) and DeWalt (2010). This involved living in a village throughout my fieldwork (fourteen months) sharing significant parts of my daily life with people other than my teammates, participating opportunistically in activities (e.g. harvesting cashew fruit, extracting palm oil, and collecting firewood), and conducting non-participant observation (e.g. harvesting oil palm fruit, fishing). Interviews were conducted between September and November 2017. I interviewed a total of 49 people, including 30 women and 19 men. Twenty-seven of the interviews were conducted in the villages of Cadique Nalu ( $n = 13$ ) and Caiquene ( $n = 14$ ). In addition, I conducted interviews with people in five smaller villages/settlements ( $n = 14$ ), and outside villages including with farmers in agricultural areas ( $n = 6$ ) and with oil palm harvesters in the forest ( $n = 2$ ). Women tend to be more continuously present in the village throughout the day than men, specifically by the village-orchard border where chimpanzees visit. This area is where the *fugon* (kr, a roof-covered outdoor kitchen) is typically located and where many daily household work and social activities are carried out. Therefore, two thirds of the interviews were conducted with women. Interview participants were Nalu ( $n = 32$ ), Balanta ( $n = 14$ ), Fula ( $n = 2$ ) and Djakanka ( $n = 1$ ). The interviews were relatively informal and followed a semi-structure format (Newing 2010). I asked participants about their use of land, including listing the number and type of agricultural fields they either owned or worked at. Follow-up questions included the timeline of agricultural cycles and corresponding work activities. The second part of the interview focussed on direct and indirect observations of chimpanzees. I asked participants to recall where and when they would observe chimpanzees and provide descriptions of chimpanzee behaviour, including about feeding events, accessing and using anthropogenic land uses. When recalling close interactions, I would ask about the

participant's and other people's perceptions and reactions, as well as chimpanzee reactions to people involved. Questions were also asked about the use of cultivated resources by other wildlife. When participants recalled a chimpanzee event we walked to the location where the observation/encounter took place and I recorded GPS coordinates. This was used to match responses with chimpanzee locations to aid analysis. For example, if a participant reported chimpanzees coming to feed at their papaya tree, I walked to the papaya tree and recorded the coordinates and made a note linking the point to the participant's observations. Papaya trees that were not used by chimpanzees according to participants were also recorded, although I only measured this within the participants' homes and not across the entire village. Likewise, if a baobab tree was present in a village and was visible from the participants' homes, I recorded GPS coordinates and noted whether chimpanzee were reported using it. I conducted all interviews in Kriyol (kr, first *lingua franca* in Guinea-Bissau). A field assistant (Iaia Tawél Camará) who also speaks Nalu and Sussu (the second *lingua franca* in this region), helped me with language and terms clarifications when required. Data were recorded in writing in Kriyol, including specific quoting when recalling chimpanzee encounters, with additional contextual or clarification notes in English or Italian (my first language). I translated relevant parts into English but kept most of the raw data in Kriyol due to sufficient levels of language fluency.

In Southeastern Guinea-Bissau local people distinguish between two different chimpanzees (Sousa et al. 2017). The 'simple' chimpanzees are perceived similarly to how other people including scientists view them, although in Cantanhez chimpanzees are also associated with cultural beliefs (Parathian et al. 2018; Sousa et al. 2014). In contrast, the 'dirty' chimpanzees consist of human individuals who temporally shape-shift into chimpanzees, usually with the intent of causing harm to another person (Sousa et al. 2017). In my study I believe that all local accounts referred to the 'simple' chimpanzees, as it was generally understood that I was a chimpanzee researcher interested in studying the 'normal' wildlife behaviour. However, particularly when informants recalled chimpanzee behaviour that was perceived as antagonistic towards humans, I took care to ensure that I interpreted the chimpanzee attribution correctly.

## 7.3 Results

### 7.3.1 Chimpanzee use of human resources and land: comparisons between model components and information from local people

The INLA spatiotemporal model in Chapter 6 showed that across the year, the Caiquene–Cadique chimpanzees use areas farther from the villages more intensively, suggesting that villages are generally avoided by chimpanzees. Albeit not statistically significant, the model also showed that intensity of space use by chimpanzees was positively associated with the combined fruit availability of orange, lime and papaya. Orange, lime and papaya were exclusively measured in village grounds, indicating that when these resources were available chimpanzees visited the villages more often than usual. The majority of people who own and/or live next to orange (100% of participants), lime (67%) and papaya (83%) trees observed chimpanzees using these resources (Table 7.1), providing support for this model component. The model also indicated a negative trend between the availability of mango and baobab fruits combined and intensity of space use by chimpanzees, despite a lack of statistical significance. Chimpanzees in Caiquene–Cadique use areas where mango and baobab fruit are available as they were recorded feeding on both resources by camera traps (in Chapter 6) and by indirect observations (E Bersacola, unpubl. data; Bessa et al. 2015). From the interviews, only 14% and 23% of participants who live by mango and baobab trees, respectively, reported chimpanzees using the trees inside the villages. Of the participants describing chimpanzee feeding on these resources, 58% and 85% of mango and baobab locations respectively represented areas outside villages, including abandoned villages and agricultural fields. Thus, both model and data from interviews suggest that chimpanzees use areas where mango and baobab ripe fruit are available but the intensity of use of these areas is disproportionate to their availability of fruit.

**Table 7.1**

Summary of chimpanzee resource use as reported by interview participants and locations where chimpanzees were reported feeding.

| Resource | N of participants observing chimpanzees using resource | Reported locations of chimpanzee feeding (N of reports) |               |                |         |
|----------|--------------------------------------------------------|---------------------------------------------------------|---------------|----------------|---------|
|          |                                                        | Large village                                           | Small village | Aband. village | Outside |
| Orange   | 22 (22)                                                | 21                                                      | NA            | 1              | NA      |
| Lime     | 5 (8)                                                  | 4                                                       | –             | 1              | NA      |
| Papaya   | 21 (25)                                                | 19                                                      | 2             | NA             | NA      |
| Mango    | 7 (37)                                                 | 5                                                       | –             | 6              | 1       |
| Baobab   | 10 (22)                                                | 5                                                       | –             | 7              | 2       |

Values in brackets represent the N of participants that either owned or lived by the cultivated resource at the time of my study. NA = resource not present at location type. Reported location values are independent from N of participants, i.e. each participant may have reported one or more locations

According to the best model, chimpanzees also showed a tendency to use areas farther from agriculture more intensively. Except for two orange orchards and one mangrove rice field, all agricultural patches measured for the distance-to-agriculture covariate were cashew orchards and shifting cultivation fields (*lugar/lugares*, kr). I was unable to separate distance to cashew orchards and distance to other cultivated areas into two covariates due to the high positive correlation. Thus, interpretation of this model component would have been relatively difficult without complementary data. Local people frequently described observing chimpanzees using cashew orchards across the landscape, including near and far from villages and settlements. In cashew orchards, chimpanzees were sometimes observed directly but their presence was also confirmed indirectly through feeding traces, such as cashew fruit wadges and broken branches. An informant stated that chimpanzees travel through cashew orchards throughout the year to access other habitats and resources, but indirect signs are fewer and more difficult to observe when cashew fruits are not available. In the *lugares* chimpanzees were reported to feed on sugar cane, hibiscus flower and pigeon pea by farmers who use these plants (N = 3). During my study the predominant crops in the *lugares* were peanut and to a much lesser extent rice. Local people commonly reported other wildlife feeding on peanut and rice, including baboons (*Papio papio*), Campbell's monkey (*Cercopithecus campbelli*), green monkeys (*Chlorocebus sabaeus*), red river hogs (*Potamochoerus porcus*), porcupines (*Hystrix cristata*), cane rats (*Thryonomys swinderianus*) and birds. However, chimpanzees were known to use forest edges along cultivated fields to access feeding locations and were heard in nearby forests by farmers working in their *lugar*. According to some participants, chimpanzees may avoid passing

directly through their *lugar* during times of intensive agricultural work. Information from local people therefore suggested that chimpanzees do use areas near/within agricultural fields to access wild and cultivated food resources, but tend to minimise proximity of agricultural areas during periods of intensive human activity. Based on information from farmers in Cadique and Caiquene, cashew orchards are typically cleaned between October and January for the nut harvest in March–July. *Lugares* are cleared right before and after the onset of the wet season (May–June), sowed in the rainy season (July–August) and the peanut and rice are harvested in September–November. Thus, the continuous alternation in type and intensity of human activities across the landscape is likely to explain the overall negative effect of proximity to agriculture on chimpanzee space use.

In summary, local people’s reports of chimpanzee habitat use supported and helped explain some of the model’s result components, which included the effects of the following covariates on the response variable: (1) ripe fruit availability of orange, lime and papaya, (2) ripe fruit availability of mango and baobab and (3) distance to nearest agricultural field.

### **7.3.2 Chimpanzee behavioural response to risk according to local people’s accounts**

The two villages included in my study area included orange orchards surrounding the village perimeters and papaya trees located irregularly along the village border, within back yards in proximity to people’s houses. According to local reports, chimpanzees showed different foraging strategies when exploiting oranges compared to papaya. When feeding on oranges, chimpanzees were generally described in the village orchards as being in large or small groups, including males and females carrying their offspring. Chimpanzees would feed on the oranges on site, and stay in the orchards either until the oranges were fully exploited or until the chimpanzees were chased away. In contrast, papaya trees would typically be accessed by one or two chimpanzee individuals at a time and the event would occur during a short time-frame; a ‘large’ chimpanzee would enter the village grounds, climb the tree, take one or two fruits and quickly transport the fruit away from the village. In some instances, during a papaya event people recalled hearing or observing the rest of the chimpanzee party ‘remaining’, ‘sitting’ or ‘waiting’ further back. Therefore based on local accounts, there appeared to be two distinctive spatial dimensions of risk for chimpanzees at the village

setting, manifesting in different foraging strategies (Figure 7.1). The first dimension of risk, represented in the environment by orange and lime orchards, is located in normally close proximity to the village where exposure to humans is high but direct interactions may not always arise immediately or at all. The second dimension, represented by the papaya trees, is located within the village back yards at the border with orchards or shrubs, where close encounters and interactions with people are almost always guaranteed.

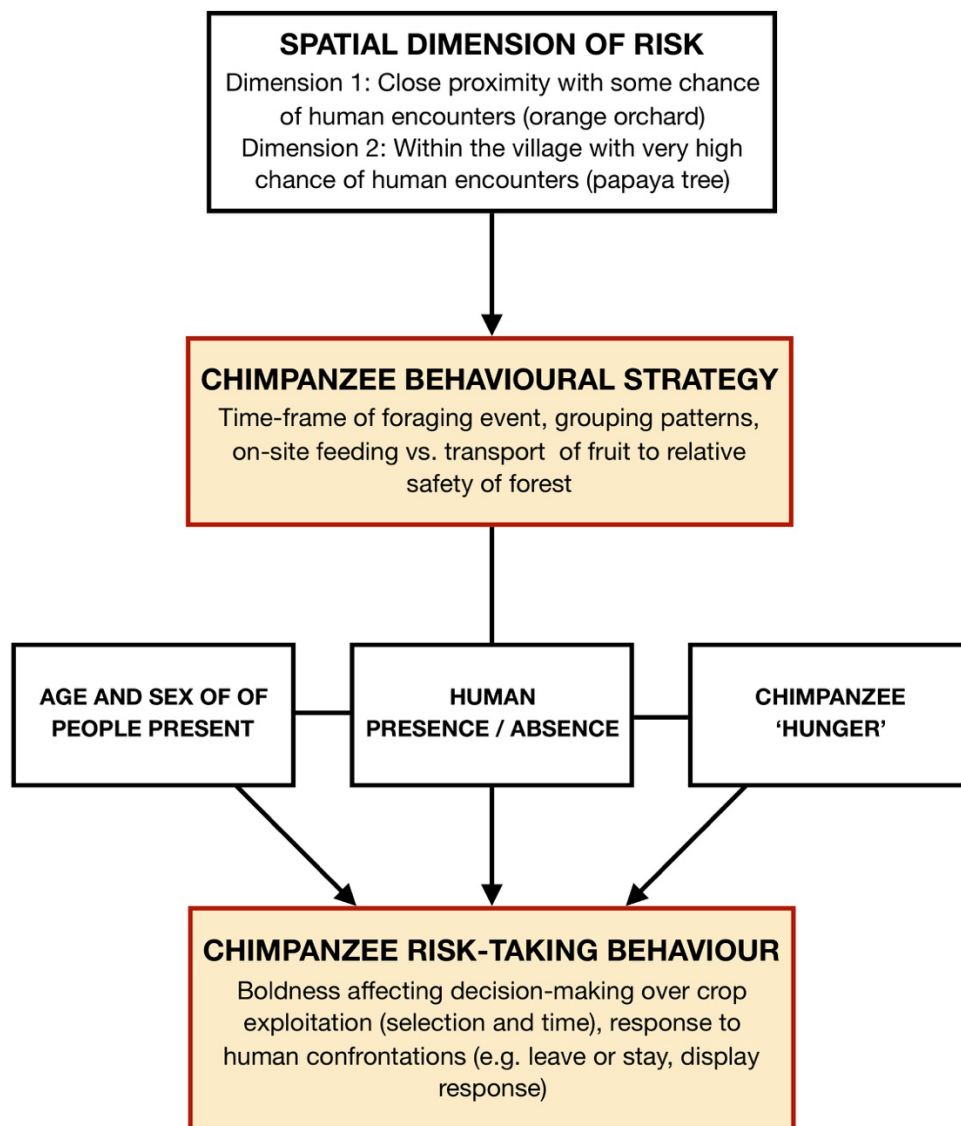


**Figure 7.1**

Chimpanzee behavioural model at the villages based on local people's narratives and perceptions.

In addition to the spatial dimensions, I identified three elements perceived by local people as factors influencing chimpanzee behaviour. These three elements were represented by the presence or absence of people, the different age and sex groups of people involved, and the perceived chimpanzees' state of 'hunger'.

Chimpanzees were often described as being aware of the people's presence in the village and behaving accordingly. As reported by several people, if people were in the village or back yard but not necessarily aware of the presence of the chimpanzees in proximity to the village, the chimpanzees would typically move and behave silently. For example, within orange orchards, people reported that chimpanzees would usually remain silent whilst feeding. Nearly all orchard owners complained that when chimpanzees remained undetected or when people were not present in the back yard chimpanzees would feed on oranges for a long time and in large quantities, consuming all available fruit. An informant noted that chimpanzees would only target the papaya if people in the village were 'distracted', implying that chimpanzees would observe people's movements or arrangements and choose the right opportunity to approach. Another participant said that chimpanzees never targeted their papaya because of the many people present, which would make them 'scared to come up' close to their house. One participant stated that when no one was present in the back yard and a chimpanzee took a papaya fruit, another chimpanzee would follow. Generally, chimpanzees would start vocalising loudly only when leaving the proximity of the village, once the targeted resources were obtained or consumed.

Chimpanzees were occasionally described as behaving more boldly when confronted by children and women compared to men. Chimpanzees were said to consume more cultivated resources in the absence of men, entering people's back yard to take papaya when only women were present, or to feed on papaya more heavily when children were left in the village alone. Moreover, chimpanzees would either refuse to run away when yelled at and/or chased by women or children, or they would remain close by waiting for a second opportunity to return. Some of the chimpanzee behaviours described by interviewees fit descriptions of agonistic behaviour at other chimpanzee research sites in Africa (e.g. McLennan and Hill 2010), including vocal intimidation and physical threat displays towards children and women in response to attempts to prevent the chimpanzees from taking the resources. The gender bias was more commonly expressed by women, whereas the fear for children's safety was relatively equal across women and men. However, the perceived bias

in chimpanzee fear toward people of different gender and age was not consistent across interview participants. A woman noted that when she or older children were present in the back yard, chimpanzees would not ‘dare’ to target the papaya. Although she mentioned that sometimes chimpanzees were scared of children and sometimes were not, she did not attribute the chimpanzee’s lack of fear to any gender differences.

In some narratives the chimpanzees’ manifestation of boldness was also perceived as a consequence of hunger: when hungry, the chimpanzees were careless and stubborn, refusing to run away upon being chased. Hunger was also used to explain chimpanzee behaviour that was interpreted as aggressive dominance displays towards the women and children who attempted to chase them away. The chimpanzees would ‘scare’ women or children until they would ‘run back home’. Hunger was implied as a factor increasing the chimpanzees’ determination to exploit the village resources, even when facing physical pain. One woman stated:

“They are hungry, if they are hungry they do not care. [...] My husband’s little brother did get to chase them. He was screaming with vigour [at the chimpanzees], like in a theatre play, holding a long branch going after them. If a chimpanzee held orange fruit, he would not leave the fruit behind. He would suffer with that pain.. even if the chimpanzee was beaten with a branch, he did not leave the orange fruit behind.”

In summary, by examining local people’s accounts of chimpanzee use of human resources and behaviour in village settings I identified elements that may contribute to shaping foraging strategies and risk-taking behaviour in this study’s chimpanzees. The first element consisted of two distinctive spatial dimensions, represented by orange orchards and papaya trees, which appeared to influence premeditated chimpanzee foraging strategies including grouping patterns, feeding on site versus transporting fruit off site and time-frame of foraging event. Three additional elements were identified based on some people’s perceived conditions that would influence chimpanzee boldness and risk-taking behaviour. Two of these elements were related to the circumstances of the foraging events, represented by the presence or absence of people and the gender or age of people involved in the interactions, which would influence chimpanzee decision-making over crop selection and obstinate behaviour upon being chased away. The perceived gender bias was nearly exclusively

expressed by women. The third element was associated with a perceived physical state of the chimpanzees: because of hunger, chimpanzee would be more careless, show impassivity towards pain and display bold or antagonistic behaviour towards women and children.

## **7.4 Discussion**

In this chapter, I showed that information from local people helped provide context and support to biological data collected using indirect methods. For example, local reports matched with the Chapter 6 model results in that chimpanzees appear to take advantage of mango and baobab resources outside villages more often compared to those within villages. Chimpanzees in Caiquene–Cadique are therefore likely to perceive abandoned villages as much less risky compared to villages. Indeed, abandoned villages are occasionally used by local people to gather mango, baobab and other resources when available, but are usually visited by far fewer people compared to other anthropogenic landmarks. These results corroborate previous research that primates will preferentially exploit human resources in low-risk areas (Duvall 2008; Hockings et al. 2009; Lindshield et al. 2017; Nowak et al. 2016). For example at Bossou, Guinea, mango fruit was only consumed in abandoned orchards even though mango fruits were available in the village (Hockings 2007; Hockings et al. 2009). At the same site, chimpanzees were more cohesive when feeding in active cultivated fields compared to the forest. However social cohesiveness did not differ between forest and abandoned fields, indicating that perceived risks when feeding on abandoned crops are similar to those in forest settings (Hockings et al. 2012). Although I was unable to directly observe these behavioural modifications at Caiquene–Cadique, local people's observations of chimpanzees in abandoned villages appear to suggest high frequency of chimpanzee use and relatively large group sizes when mango and baobab fruits are available. Both the spatiotemporal model and interview data suggest some level of cultivated field avoidance by chimpanzees. Some local participants suggested temporal fluctuations in chimpanzee avoidance of shifting cultivation areas are based on whether the land is temporally being used by people or not. These data support previous findings from Cadique and Caiquene (Sousa et al. 2014) by highlighting some local awareness of possible constraints imposed by humans on chimpanzees.

*Chimpanzee behavioural strategies: the spatial dimension that influences grouping patterns as identified in local narratives*

The local people's descriptions of chimpanzee behaviour at villages supports the theoretical concept that spatial variation in fear shapes behaviour (Laundré et al. 2010). The chimpanzee behavioural model based on local people's accounts (Figure 7.1) fits within the landscape of fear framework outlined by Gaynor and colleagues (2019). Distinctive dimensions involving different levels of risk of exposure to humans result in different levels of fear in chimpanzees, manifested as different chimpanzee anti-predator behavioural responses. The different foraging strategies according to the spatial dimensions (Figure 7.1) suggest a pre-determined adaptive response to anticipated risks by chimpanzees. Food size may also play a role in chimpanzee decisions to feed on site or transport food away. Papaya is larger compared to orange and takes much longer to consume, meaning that a chimpanzee does not need to make repeated visits as would be the case with smaller fruits. Transporting the papaya away will increase the chances that chimpanzees consume the whole fruit without interruption. However, chimpanzees have also been observed transporting orange away from the village into the nearby forest patches (J Bessa and E Bersacola, unpubl. data). Most of the fruit carried away from the village appeared to come from trees located closest to the village perimeters (J Bessa, pers. obs.). The spatial dimension associated with food transport behaviour would therefore mimic that of papaya. Consequently, chimpanzees seem to respond flexibly through the use of foraging strategies that are not strictly resource-specific but more influenced by the spatial risk context. The local descriptions of chimpanzee social groupings when obtaining papaya fruit in Caiquene–Cadique echo observations of papaya foraging elsewhere. At Bossou, Guinea, one adult individual, usually male, would enter the village to gather one or two papaya fruits and transport them back to the group (Hockings et al. 2007). It also remains unknown if chimpanzees at Caiquene–Cadique, share papaya fruit with conspecifics like at other sites (e.g. Bossou, Hockings et al. 2007).

*Contextual components influencing chimpanzee boldness*

Caiquene–Cadique chimpanzees seemed to behave silently when entering and exploiting village orchards, only becoming vocal when detected by people once resources were

depleted and/or when leaving the village. The perceived cryptic behaviour of chimpanzees in Caiquene–Cadique mirrors behavioural observations of various taxa, including chimpanzees, at other human-impacted sites. For example, at Kibale, Uganda, chimpanzees vocalised less frequently at the edge of the forest and within cultivated areas compared to inside the forest, where they displayed species-average calling frequencies (Wilson et al. 2007). In addition, chimpanzees in Caiquene–Cadique were described as taking advantage of people’s absence or lack of awareness of their presence to feed more heavily on cultivars in the village. Around Budongo, Uganda, part-time systematic crop guarding decreased chimpanzee crop feeding by 90% (Hill and Wallace 2012). At Bossou, Guinea, crop feeding on simple-sugar fruit including papaya, mandarin and orange within the village occurred more often when people were absent (Hockings 2007). In Caiquene–Cadique the perceived chimpanzee awareness about people’s gender and lack of vigilance in the village may reflect the people’s view of chimpanzees as ‘intelligent’ and ‘similar to humans’ (Costa et al. 2013).

Intimidating behaviour of chimpanzees towards women and children fitted previous descriptions of chimpanzee aggressive response towards people, including loud vocalisations and charging display (McLennan and Hill 2010). Previous research shows that compared to men, women tended to express more fear towards wildlife (Kaltenborn et al. 2006; Zinn and Pierce 2002) including chimpanzees (McLennan and Hill 2012). In Caiquene–Cadique several women suggested that chimpanzees take advantage of the absence of men and act more boldly around women. It is unknown whether chimpanzees can tell the difference between men and women, or whether men and women tend to behave differently when they encounter chimpanzees. It is possible that different behaviour towards chimpanzees by women and men will play some role in shaping the differences in chimpanzee perceptions of people of different genders. Concerns over children’s safety were shared by people of different gender identities. As reported in Bossou (Hockings 2007), in Cantanhez NP some people cut their papaya trees due to fear of chimpanzees harming their children when left unattended. Indeed, research at other sites has shown that children are more vulnerable than adults to chimpanzee attacks, with victims either alone or accompanied by women when an attack took place (Goodall 1986; Hockings et al. 2010; Hockings and McLennan 2016; McLennan and Hockings 2016; Wrangham et al. 2000). The recent chimpanzee attacks in Quinara Region, Guinea-Bissau involved unaccompanied children accessing *Saba senegalensis* fruit (unpubl. reports; Sousa et al. 2018). Across other regions

wildlife attacks follow similar patterns: unguarded children are much more likely to be attacked by European and North American carnivores (Penteriani et al. 2016). When attacks involve pumas (*Puma concolor*), children are over four times more likely to die if adults are not able to intervene (Mattson et al. 2011). Similarly to reports from Bossou, once men were able to intervene, the chimpanzees would normally flee (Hockings et al. 2010).

When chimpanzees were thought to be behaving recklessly when foraging for village foods and risking possible injury from people, this was explained as being a consequence of the animals being hungry. Local people associated chimpanzee hunger with the end of the rainy season and/or the period when oranges were available. This association matches phenological data on wild chimpanzee food availability (Chapter 3) as well as results in Chapter 6 (Hypothesis 4). It is unclear how much of the people's awareness of wild food scarcity and association with chimpanzee hunger was influenced by perceptions expressed by chimpanzee researchers and research assistants. However, at this site local people use many of the same wild resources consumed by chimpanzees (Hockings et al, in review), and have knowledge about chimpanzee wild diet (Sousa et al. 2014). Thus, local people are likely to be aware about temporal shortages in chimpanzee wild fruit availability, particularly those that are consumed more often by chimpanzees. Hunger was also associated with a readiness to 'fight' a person (women and children) over cultivated sources. This described behaviour coincides with patterns of reported aggressiveness in Bossou chimpanzees, where seven of the eleven recorded chimpanzee attacks on people occurred during periods of wild food scarcity and higher frequencies of cultivar feeding (Hockings et al. 2010).

People can sometimes associate behaviours of nonhuman animals to those of humans, projecting the same social norms and expectations (Hill and Webber 2010; Sousa et al. 2017). In Uganda, baboons (*P. anubis*) are often described as malicious rebels or enemies by farmers due to baboons being perceived as highly organised, capable of taking over the crop fields using military-like strategies and causing extensive and wasteful crop damage (Hill and Webber 2010). At the same site, chimpanzees and monkeys are described as 'disciplined' and 'honest' when they are perceived to take quantities of crop foods that are considered as fair by the farmers (Hill and Webber 2010). The anthropomorphism assigned to chimpanzees by local people in Caiquene–Cadique may also be interpreted as a

justification for chimpanzee behaviours that transgress social boundaries (i.e. bold and confrontational behaviour due to hunger in this case).

#### *Safety risks that chimpanzees impose on local people*

Wildlife are expected to try to avoid humans when perceived as potential physical danger. However, many wild species can also pose significant physical risks to people, notably big carnivores, but also other wildlife including venomous snakes, elephants (*Loxodonta africana*), crocodiles (*Crocodylus niloticus*) and hippos (*Hippopotamus amphibius*) (e.g. Dunham et al. 2010; Harrison and Gutiérrez 2016; Loe and Röskaf 2004). Although much more rarely, attacks by nonhuman primates have also been recorded (Hockings and McLennan 2016; McLennan and Hockings 2016). Most of the chimpanzee attacks on people occur in human-influenced landscapes where human-chimpanzee interactions and competition over food were relatively high (for a review see: Hockings and McLennan 2016). In extreme cases, chimpanzees targeted human children for consumption, a behaviour consistent with predation (Goodall 1986; Wrangham et al. 2000). Therefore fear of ‘predation’, including of lethal attacks and injuries, may not only concern wildlife but also people living alongside wildlife. It remains unclear how likely chimpanzees are to attack people, particularly children, at Caiquene-Cadique. However, when cultivars are available, close direct interactions are frequent and local people’s accounts suggest patterns of chimpanzee behaviour consistent with some degree of intimidation and aggression. The behaviour of chimpanzees in the villages during orange and papaya season is likely to cause stress and fear, particularly to women for their own safety and that of their children (Jadhav and Barua 2012).

#### *Implications for chimpanzee conservation*

Through indirect and direct cues, humans and wildlife continuously influence the behaviour of one another. Aggressive behaviour towards humans will result in an increase in fear and a likelihood of aggressive retaliatory behaviour towards wildlife (Hockings and McLennan 2016). In Guinea-Bissau, unprovoked attacks by chimpanzees are generally attributed to shape-shifted human individuals, rather than the ‘normal’ chimpanzees (Sousa et al. 2017;

2018). Aggressive behaviour towards people in Caiquene–Cadique was always explained by either the chimpanzees’ ‘hunger’, and/or as a response to people (particularly women and children) who attempted to ‘prevent them from eating or taking’ cultivated foods. On the one hand these perceptions indicate some level of tolerance and empathy towards chimpanzees which are crucial for enabling long-term human-chimpanzee coexistence in these shared landscapes. On the other hand, it remains unknown how many chimpanzee attacks go unreported due to attribution to witchcraft (Sousa et al. 2017; 2018), posing serious concerns over human wellbeing. In addition, attitudes towards (normal) chimpanzees may change, partly due to external influences including conflicts with conservation organisations or practitioners (e.g. Sousa et al. 2018; Temudo 2012) and partly due to chimpanzee aggressive behaviour (Hockings et al. 2014). The risk of antagonistic behaviour by both chimpanzee and humans is particularly high during orange and papaya season. In addition to concerns for personal safety, orange farmers reported severe crop losses and one farmer expressed a desire to retaliate: in one instance by harming the chimpanzee and another time by destroying the chimpanzees’ nests by the village so that they would stop sleeping close to his orchard. Retaliatory aggression towards chimpanzees can lead to serious or lethal injuries to the chimpanzees as well as the people involved when chimpanzees respond aggressively (e.g. Hockings et al. 2010; Sousa et al. 2018). Strategies to mitigate risks of chimpanzee attacks and human retaliatory responses will require working closely with local people to test alternative ways to manage village resources (Hill and Wallace 2012). Inclusive approaches to conservation will also help minimise conservation conflicts between the people sharing the landscape with chimpanzees and external conservation managers.



## CHAPTER 8

### Summary and conclusions



## 8.1 Summary

In this thesis I aimed to understand how a West African primate community responds to human activities in a human-dominated protected area in Guinea-Bissau. Using a landscape-scale approach, I sought to identify environmental and anthropogenic factors driving the spatial and spatiotemporal occurrence of seven primate taxa including Western chimpanzees, Guinea baboons, Temminck's red colobus, king colobus, green monkeys, Campbell's monkeys and Demidoff's galagos. Data from studies at various spatial scales can complement and inform one another, allowing for comprehensive interpretations of ecological phenomena. Focussing on chimpanzees, I 'zoomed-in' – from landscape to home range and finally to village – to reveal chimpanzee ecological strategies in anthropogenic landscapes at the population and community scales. To do this I used a cross-disciplinary approach. Biological data were used to obtain inferences of chimpanzee space use in relation to human activity and food availability, and chimpanzee socioecological strategies within the village dimension were inferred through local people's narratives.

### *Main results*

Chapter 3 focussed on describing the study area using remote sensing and habitat surveys. The landscape structure in central Cantanhez NP is extremely heterogeneous, characterised by mangroves, coastal secondary forests and regenerating forest patches interlaced with grassland as well as arboreal (cashew orchards) and mainly-non-arboreal (roads, villages, cultivated fields) human land uses. Some of the major wild fruit sources consumed by chimpanzees and people (Bessa et al. 2015; Hockings et al. 2020) as well as other primates (E Bersacola pers. obs) are more abundant within the forest block (e.g. *Dialium guineense*) but some are also found within the matrix (e.g. *Ficus* spp., *Ceiba pentandra*, *Parinari excelsa*). Oil palms (*Elaeis guineensis*) are equally abundant throughout the landscape including within agriculture and grassland, making the matrix rich in primate food sources albeit increased risks of physical exposure to and direct interactions with humans.

Part 1 (Chapters 4 and 5) focussed on primate distributions through the landscape. Across Cantanhez NP, some primates were more arboreal than others (upper canopy Temminck's red colobus vs. mid-canopy Campbell's monkey vs. semiterrestrial chimpanzees, Guinea

baboons and green monkeys). Additionally, occupancy of seven primate species was mediated by different combinations of environmental factors. Therefore, I concluded that in Cantanhez NP the seven primate taxa tend to occupy separate niches across horizontal and vertical axes. The spatial niche separation in Cantanhez NP is likely facilitated by the heterogeneity of the landscape (Bourlière 1985), with some areas providing key habitat and structural/feeding resources for certain species (e.g. large trees for Temminck's red colobus, forest for Demidoff's galago) or even refuge for others (mangroves for Guinea baboons). At the landscape scale, responses to anthropogenic factors (i.e. the presence of villages and other human land uses) ranged from negative (king colobus, Guinea baboons, Demidoff's galagos) to positive (chimpanzees). These varying responses are likely the consequences of different human behaviour towards primates (baboons and monkeys are hunted whereas chimpanzees are not) as well as interspecific differences in socioecological traits (wild resource selection and small group sizes in arboreal king colobus vs. wild and cultivated resource feeding and flexible fission-fusion social organisation in semiterrestrial chimpanzees). In summary, the spatial occurrence of primates across Cantanhez is mainly shaped by human predation risk for some primates (king colobus and Guinea baboons) and optimal foraging for others (chimpanzees).

Part 2 (Chapters 6 and 7) zoomed in. At the home range scale and across the year, chimpanzees balanced risk avoidance with maximising foraging efficiency. Chimpanzees in Caiquene–Cadique used areas near or within villages significantly less often compared to parts of their home range further away from these anthropogenic landmarks. Temporal fluctuations in human activities within cultivated areas likely contributed to a tendency to spatially avoid these areas during periods of high human activity. Chimpanzees frequently used areas in proximity to roads as they bordered forest, had low levels of human use, and provided opportunities to access resources across the matrix. The chimpanzees' spatial responses strongly suggest that their *landscape of fear* is driven by spatiotemporal variations in high intensity human space use. In addition, oil palm fruit availability positively influenced frequencies of site selection and importantly, the spatial avoidance of villages was temporally relaxed when wild foods were scarce. During this time chimpanzees more frequently entered the riskiest areas to forage on orange and papaya, and according to local narratives, used different grouping strategies when targeting oranges surrounding villages and papayas within people's backyards. While chimpanzees would feed on oranges in groups, papayas were taken by one or two particularly bold individuals and transported away

whilst the rest of the party ‘waited’ in the back. According to local perceptions, chimpanzees behaved more boldly when confronted with women and children as opposed to men, and particularly when they were hungry during periods of wild food scarcity which corresponded to when oranges were available.

## **8.2 Contribution to the literature**

### **8.2.1 Theoretical contribution**

This study provides a contribution to the broader theoretical and applied literature on the ability of wildlife to persist in the long-term in human-modified landscapes. Anthropogenic biomes, from urban areas to populated forests, now represent most of the terrestrial surface on Earth (Ellis and Ramankutty 2008). Within those human biomes lay a myriad of ecological contexts: different plant and animal communities, different human behaviour, climatic conditions and ecological processes (Hobbs et al. 2006). Including humans in ecological frameworks is crucial to understand how species are able to persist in changing environments (Miller and Hobbs 2002; Palmer et al. 2004). My results contribute to improving our understanding of the spatiotemporal occurrence of wildlife populations in human-modified landscapes by exploring dynamics of interspecific co-occurrence (e.g. Darmon et al. 2012; Kamilar and Ledogar 2011; Schreier 2010), assessing habitat/resource requirements and the effects of human activities (e.g. Basille et al. 2009; Carter et al. 2012; Khorozyan et al. 2014). In addition, my study adds to the theoretical frameworks of the landscape (or ecology) of fear (Brown et al. 1999; Laundré et al. 2001), specifically how wildlife balance feeding strategies with risk avoidance within a human-impacted home range (Coleman and Hill 2014; Cowlshaw 1997; Martin et al. 2010; Nowak et al. 2017; Willems and Hill 2009).

### **8.2.2 Applied contribution**

Terrestrial camera traps have been widely applied in ecology (O’Connell et al. 2010), with research covering numerous geographical areas and terrestrial biomes. The number of

published studies on camera traps increasingly progressed since the 1990s (e.g. total N = 1411 from a Web of Science search of words “camera traps” included in all fields, 25 July 2019). In contrast, at present only 6 published studies are available on arboreal camera trapping (Bowler et al. 2017; Gregory et al. 2014; Méndez-Carvajal 2014; Oliveira-Santos et al. 2008; Olson et al. 2012; Whitworth et al. 2016). Thus, the methodological designs and deployment techniques for ground-based camera traps are well established, whereas those for arboreal camera traps still require testing and adjusting, particularly considering the high variation of vegetation structures and multitude of above-ground pathways across forest types. My research provides the first methodological insights on arboreal camera trapping in human-dominated agro-forest landscapes.

Interdisciplinary approaches, specifically the inclusion of local perspectives and knowledge into quantitative biological research frameworks, allows us to explore opportunities and gather information for developing inclusive conservation (Apgar 2017; Mallory et al. 2006; Parathian et al. 2018). My research showed that information from local people living in proximity to wildlife can help us better understand aspects of wildlife behaviour and the habitat use of animals unhabituated to human observers. Information from local people provided context for and complemented findings from ecological models, and highlighted specific human-chimpanzee interactions that could hinder long-term coexistence. My study showed that local knowledge about wildlife behaviour can be as informative as ecological data to understand human-chimpanzee coexistence dynamics in shared landscapes. Conservation management practitioners will need to recognise local stakeholders, including women, as key assets for developing effective conservation plans and contributing in decision-making processes.

## **8.3 Conservation**

### **8.3.1 Implications of my results for primate conservation**

Through this research I identified different conservation-related issues facing primates in Cantanhez NP. Habitat loss represents the main driving force of terrestrial biodiversity decline across the globe (Newbold et al. 2015). In West Africa, bushmeat hunting

considerably exacerbates the effects of habitat loss for large and medium-sized wildlife including primates (Fa and Brown 2009; Minhós et al. 2013, 2016). In Cantanhez NP, my data show that the remaining forests and mangroves represent crucial refuge habitat particularly for Guinea baboons and the two colobine species. These primates are likely to rely on mangrove-forest edge areas for dispersal, maximising avoidance of potential hunters. Forest edge/mangrove areas are also likely to provide primates with key feeding resources as well as freshwater through small streams that flow out of the forest ground.

Conserving the remaining forest blocks is imperative to minimise potential conflicts between chimpanzees and people. At the landscape scale chimpanzees may find some ecological benefit from occupying areas relatively close to villages. However, my community-scale data show that chimpanzees do prefer to use areas away from high human activities and that wild fruit scarcity increases the chimpanzee's use of high-risk crops. Although papaya has little economic value to local people in Cantanhez NP, risks of close physical interactions between humans and chimpanzees during chimpanzee's acquisition of papaya are high. Oranges are valuable to farmers who grow them as a cash crop and are difficult to maintain. Consequently, chimpanzee orange foraging events often involve physical responses by people. Competition between people and chimpanzees over village foods, particularly orange, can lead eventually to potential retaliatory killings of chimpanzees (Halloran et al. 2014) and/or attacks of chimpanzees towards people particularly children (Hockings and McLennan 2016; McLennan and Hockings 2016). In fact, infrequent retaliatory killings of chimpanzees due to orange feeding have already been recorded in Cantanhez NP, as well as serious and fatal chimpanzee attacks on children elsewhere in Guinea-Bissau (E Bersacola unpubl. data). If wild resources were to become scarcer, such risky encounters and the likelihood of potentially serious consequences to both people and chimpanzees would increase, putting future prospects of co-existence at serious risk. Chimpanzees are an extremely flexible species, demonstrating socioecological and behavioural resilience and adaptability to habitat change (Hockings 2007; McLennan 2010; Oxley 2019; this thesis). However, frequent close interactions with sympatric humans are also likely to introduce new, invisible actors, adding a new layer of complexity to the human-chimpanzee interface. For example, some lethal disease outbreaks in nonhuman primate populations including chimpanzees have been previously linked to humans (Leendertz et al. 2006; Wolf et al. 2014). Several pathogens found in great ape populations are transmissible to humans and vice versa (Calvignac-Spencer et al. 2012).

### 8.3.2 Cantanhez National Park

Conservation in Cantanhez NP will require an inclusive approach (Bersacola et al. 2018; Hill et al. 2017; Parathian et al. 2018). Local ecological knowledge and people's concerns over sharing space with wildlife should play a determining role in conservation management to promote co-existence. Strategies will need to be developed with the full participation of local stakeholders including *high-risk crop* farmers (oranges in particular) and women representatives, as well as traditional authorities and the forest management committee currently involved in the park management. To minimise conservation conflicts at the village dimension, farmers and conservation planners could work together to come up with fine-scale solutions, including testing ways to increase crop protection (Hill and Wallace 2012), and consider spatial re-organisation of village resources, e.g. planting more papaya and other important foods in locations more rarely accessed by chimpanzees to minimise close direct interactions particularly involving women and children. Disease surveillance and outbreak response strategies, including from a local population perspective to improve public health and mitigate human-chimpanzee conflicts, should also be considered in conservation management (Hockings et al. Darwin project 26018: 2019-2022).

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## Appendices

- Appendix 2.1 Letter of ethical approval from the University Research Ethics Committee at Oxford Brookes University.
- Appendix 3.1 Complete list of species identified in 344 vegetation plots (68'800 m<sup>2</sup>) in Caiquene–Cadique, Cantanhez NP.
- Appendix 4.1 Selection of images captured using arboreal camera traps in Cantanhez NP.
- Appendix 4.2 Full list of arboreal camera trap maximum likelihood occupancy models.
- Appendix 5.1 Selection of images recorded using terrestrial camera traps in Cantanhez NP.
- Appendix 5.2 Full list of terrestrial camera trap maximum likelihood occupancy models.
- Appendix 6.1 R script of spatiotemporal models ran using R-INLA.
- Appendix 6.2 Details of the human spatiotemporal model ran to extract the human detection covariate for chimpanzee models.
- Appendix 6.3 List of chimpanzee spatiotemporal models considered for this study.
- Appendix 6.4 Posterior mean of the intercept and covariate coefficients  $\beta$  for full model, including standard deviations, credible intervals quantiles and mode.
- Appendix 6.5 Posterior mean of chimpanzee intensity of space use across 12 months. Each map represents a sampling occasion (N = 24).



## Appendix 2.1

Letter of ethical approval from the University Research Ethics Committee at Oxford Brookes University.



Professor Catherine Hill  
Director of Studies  
Department of Social Sciences  
Faculty of Humanities and Social Sciences  
Oxford Brookes University  
Headington Campus

28 June 2016

Dear Professor Hill

**UREC Registration No: 161018**

**Seeking human-wildlife coexistence: primate community response to anthropogenic activities and land transformation in Guinea-Bissau, West Africa**

Thank you for the email of 22 June 2016 outlining the response to the points raised in my previous letter about the PhD study of your research student Elena Bersacola and attaching the revised documents. I am pleased to inform you that, on this basis, I have given Chair's Approval for the study to begin.

The UREC approval period for this study is two years from the date of this letter, so 28 June 2018. If you need the approval to be extended please do contact me nearer the time of expiry.

Should the recruitment, methodology or data storage change from your original plans, or should any study participants experience adverse physical, psychological, social, legal or economic effects from the research, please inform me with full details as soon as possible.

Yours sincerely

A handwritten signature in blue ink, appearing to read "S Quinton", with a long horizontal flourish extending to the right.

Dr Sarah Quinton  
Chair of the University Research Ethics Committee

cc: Kimberley Hockings, Second Supervisor  
Elena Bersacola, Research Student  
Maja Cederberg, Research Ethics Officer  
Jill Organ, Research Degrees Team  
Louise Wood, UREC Administrator



### Appendix 3.1

Complete list of species identified in 344 vegetation plots (68'800 m<sup>2</sup>) in Caiquene–Cadique, Cantanhez NP.

| #  | Family                                       | Species                                   | wild or cultivated | Number of stems |
|----|----------------------------------------------|-------------------------------------------|--------------------|-----------------|
| 1  | Acanthaceae/Rhizophoraceae                   | <i>Avicennia germinans/Rhizophora</i> sp. | wild               | 55              |
| 2  | Anacardiaceae                                | <i>Anacardium occidentale</i>             | cultivated         | 199             |
| 3  | Anacardiaceae                                | <i>Mangifera indica</i>                   | cultivated         | 30              |
| 4  | Anacardiaceae                                | <i>Spondias mombin</i>                    | wild               | 11              |
| 5  | Annonaceae                                   | <i>Annona muricata</i>                    | cultivated         | 2               |
| 6  | Annonaceae                                   | <i>Monodora tenuifolia</i>                | wild               | 1               |
| 7  | Annonaceae                                   | <i>Uvaria chamae</i>                      | wild               | 13              |
| 8  | Annonaceae                                   | <i>Xylopia aethiopica</i>                 | wild               | 1               |
| 9  | Apocynaceae                                  | <i>Alstonia congensis</i>                 | wild               | 14              |
| 10 | Apocynaceae                                  | <i>Calotropis procera</i>                 | wild               | 1               |
| 11 | Apocynaceae                                  | <i>Holarrhena floribunda</i>              | wild               | 8               |
| 12 | Apocynaceae                                  | <i>Landolphia heudelotii</i>              | wild               | 1               |
| 13 | Apocynaceae                                  | <i>Landolphia hirsuta</i>                 | wild               | 5               |
| 14 | Apocynaceae                                  | <i>Rauvolfia vomitoria</i>                | wild               | 3               |
| 15 | Apocynaceae                                  | <i>Saba senegalensis</i>                  | wild               | 1               |
| 16 | Apocynaceae                                  | <i>Tabernaemontana africana</i>           | wild               | 5               |
| 17 | Arecaceae                                    | <i>Cocos nucifera</i>                     | cultivated         | 1               |
| 18 | Asteraceae                                   | <i>Aedesia glabra</i>                     | wild               | 19              |
| 19 | Bignoniaceae                                 | <i>Newbouldia laevis</i>                  | wild               | 1               |
| 20 | Caricaceae                                   | <i>Carica papaya</i>                      | cultivated         | 4               |
| 21 | Celastraceae                                 | <i>Salacia senegalensis</i>               | wild               | 14              |
| 22 | Chrysobalanaceae                             | <i>Neocarya macrophylla</i>               | wild               | 5               |
| 23 | Chrysobalanaceae                             | <i>Parinari excelsa</i>                   | wild               | 17              |
| 24 | Combretaceae                                 | <i>Combretum micranthum</i>               | wild               | 4               |
| 25 | Combretaceae                                 | <i>Terminalia macroptera</i>              | wild               | 25              |
| 26 | Convolvulaceae                               | <i>Calycobolus heudelotii</i>             | wild               | 2               |
| 27 | Ebenaceae                                    | <i>Diospyros heudelotii</i>               | wild               | 16              |
| 28 | Euphorbiaceae                                | <i>Alchornea cordifolia</i>               | wild               | 6               |
| 29 | Euphorbiaceae                                | <i>Anthostema senegalense</i>             | wild               | 24              |
| 30 | Euphorbiaceae                                | <i>Antidesma membranaceum</i>             | wild               | 1               |
| 31 | Euphorbiaceae                                | <i>Hymenocardia acida</i>                 | wild               | 1               |
| 32 | Euphorbiaceae                                | <i>Ricinodendron heudelotii</i>           | wild               | 126             |
| 33 | Gentianaceae                                 | <i>Anthocleista procera</i>               | wild               | 4               |
| 34 | Gramineae / Poaceae                          | <i>Paspalum scrobiculatum</i>             | wild               | 1               |
| 35 | Irvingiaceae                                 | <i>Klainedoxa gabonensis</i>              | wild               | 1               |
| 36 | Labiatae                                     | <i>Vitex doniana</i>                      | wild               | 1               |
| 37 | Leguminosae / Fabaceae -<br>Caesalpinioideae | <i>Cassia sieberiana</i>                  | wild               | 18              |
| 38 | Leguminosae / Fabaceae -<br>Caesalpinioideae | <i>Detarium senegalense</i>               | wild               | 5               |
| 39 | Leguminosae / Fabaceae -<br>Caesalpinioideae | <i>Dialium guineense</i>                  | wild               | 111             |
| 40 | Leguminosae / Fabaceae -<br>Caesalpinioideae | <i>Piliostigma thonningii</i>             | wild               | 2               |
| 41 | Leguminosae / Fabaceae -<br>Mimosoideae      | <i>Afzelia africana</i>                   | wild               | 2               |

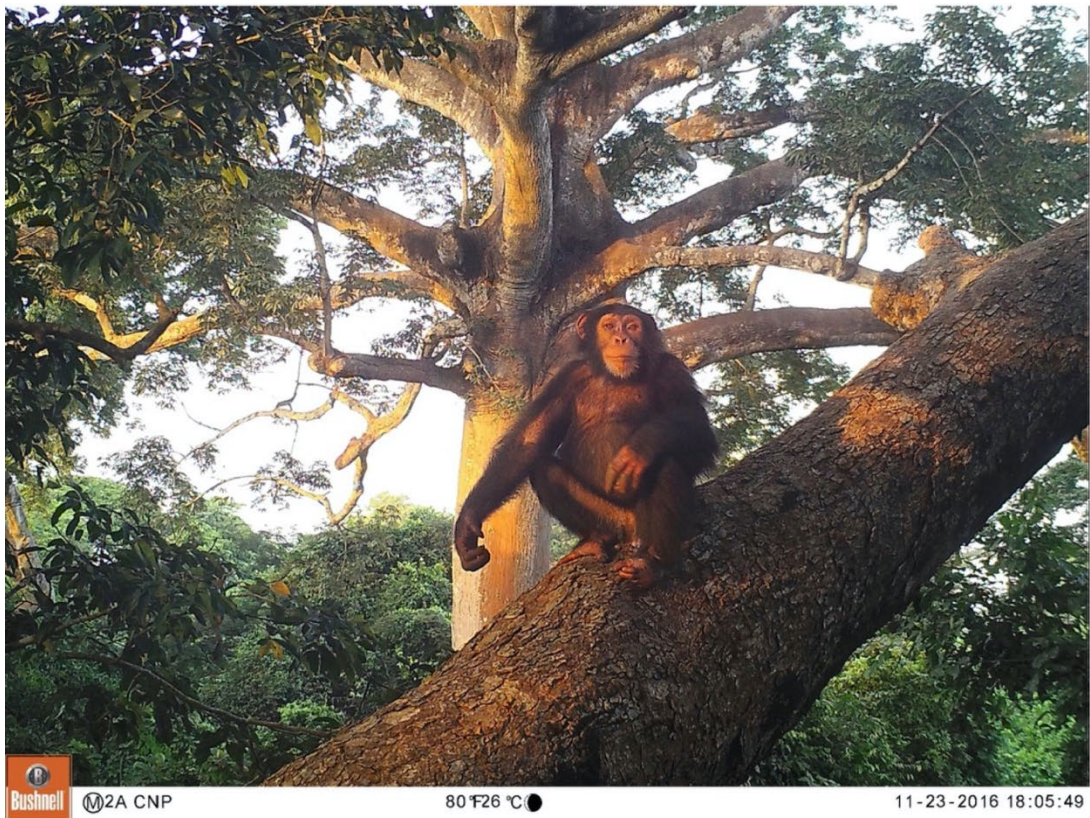
| #  | Family                                  | Species                          | wild or cultivated | Number of stems |
|----|-----------------------------------------|----------------------------------|--------------------|-----------------|
| 42 | Leguminosae / Fabaceae - Mimosoideae    | <i>Albizia adianthifolia</i>     | wild               | 37              |
| 43 | Leguminosae / Fabaceae - Mimosoideae    | <i>Albizia dinklagei</i>         | wild               | 2               |
| 44 | Leguminosae / Fabaceae - Mimosoideae    | <i>Albizia ferruginea</i>        | wild               | 5               |
| 45 | Leguminosae / Fabaceae - Mimosoideae    | <i>Albizia glaberrima</i>        | wild               | 6               |
| 46 | Leguminosae / Fabaceae - Mimosoideae    | <i>Albizia sp.</i>               | wild               | 18              |
| 47 | Leguminosae / Fabaceae - Mimosoideae    | <i>Albizia zygia</i>             | wild               | 4               |
| 48 | Leguminosae / Fabaceae - Mimosoideae    | <i>Dichrostachys cinerea</i>     | wild               | 2               |
| 49 | Leguminosae / Fabaceae - Mimosoideae    | <i>Parkia biglobosa</i>          | wild               | 3               |
| 50 | Leguminosae / Fabaceae - Mimosoideae    | <i>Prosopis africana</i>         | wild               | 2               |
| 51 | Leguminosae / Fabaceae - Papilionoideae | <i>Erythrina senegalensis</i>    | wild               | 3               |
| 52 | Leguminosae / Fabaceae - Papilionoideae | <i>Pterocarpus erinaceus</i>     | wild               | 20              |
| 53 | Malvaceae                               | <i>Adansonia digitata</i>        | cultivated         | 3               |
| 54 | Malvaceae                               | <i>Ceiba pentandra</i>           | wild               | 15              |
| 55 | Meliaceae                               | <i>Carapa procera</i>            | wild               | 40              |
| 56 | Meliaceae                               | <i>Trichilia monadelpha</i>      | wild               | 10              |
| 57 | Meliaceae                               | <i>Trichilia prieuriana</i>      | wild               | 37              |
| 58 | Menispermaceae                          | <i>Cissampelos mucronata</i>     | wild               | 1               |
| 59 | Moraceae                                | <i>Antiaris toxicaria</i>        | wild               | 5               |
| 60 | Moraceae                                | <i>Artocarpus altilis</i>        | wild               | 1               |
| 61 | Moraceae                                | <i>Artocarpus heterophyllus</i>  | wild               | 3               |
| 62 | Moraceae                                | <i>Ficus exasperata</i>          | wild               | 1               |
| 63 | Moraceae                                | <i>Ficus sp.</i>                 | wild               | 23              |
| 64 | Moraceae                                | <i>Ficus sur</i>                 | wild               | 14              |
| 65 | Moraceae                                | <i>Milicia regia</i>             | wild               | 17              |
| 66 | Moraceae                                | <i>Treculia africana</i>         | wild               | 10              |
| 67 | Myrtaceae                               | <i>Syzygium guineense</i>        | wild               | 6               |
| 68 | Olacaceae                               | <i>Strombosia pustulata</i>      | wild               | 1               |
| 69 | Palmae / Arecaceae                      | <i>Borassus aethiopum</i>        | wild               | 33              |
| 70 | Palmae / Arecaceae                      | <i>Elaeis guineensis</i>         | wild               | 132             |
| 71 | Passifloraceae                          | <i>Smeathmannia pubescens</i>    | wild               | 3               |
| 72 | Rhizophoraceae                          | <i>Anisophyllea laurina</i>      | wild               | 4               |
| 73 | Rubiaceae                               | <i>Craterispermum laurinum</i>   | wild               | 2               |
| 74 | Rubiaceae                               | <i>Hallea stipulosa</i>          | wild               | 1               |
| 75 | Rubiaceae                               | <i>Morinda geminata</i>          | wild               | 10              |
| 76 | Rubiaceae                               | <i>Sarcocephalus latifolius</i>  | wild               | 15              |
| 77 | Rutaceae                                | <i>Citrus aurantifolia</i>       | cultivated         | 6               |
| 78 | Rutaceae                                | <i>Citrus sinensis</i>           | cultivated         | 10              |
| 79 | Rutaceae                                | <i>Citrus sp.</i>                | cultivated         | 1               |
| 80 | Sapindaceae                             | <i>Allophylus africanus</i>      | wild               | 3               |
| 81 | Sapindaceae                             | <i>Lecaniodiscus cupanioides</i> | wild               | 33              |

| #   | Family        | Species                       | wild or cultivated | Number of stems |
|-----|---------------|-------------------------------|--------------------|-----------------|
| 82  | Sapotaceae    | <i>Malacantha alnifolia</i>   | wild               | 23              |
| 83  | Sapotaceae    | <i>Synsepalum pobeguianum</i> | wild               | 21              |
| 84  | Sterculiaceae | <i>Cola nitidia</i>           | cultivated         | 3               |
| 85  | Sterculiaceae | <i>Cola cordifolia</i>        | wild               | 1               |
| 86  | Sterculiaceae | <i>Sterculia tragacantha</i>  | wild               | 21              |
| 87  | Ulmaceae      | <i>Trema guineensis</i>       | wild               | 25              |
| 88  | Unknown       | Unknown (ID1)                 | wild               | 12              |
| 89  | Unknown       | Unknown (Balanta)             | wild               | 2               |
| 90  | Unknown       | Unknown (Candé)               | wild               | 2               |
| 91  | Unknown       | Unknown (disquere-mane)       | wild               | 1               |
| 92  | Unknown       | Unknown (Kabetundji)          | wild               | 1               |
| 93  | Unknown       | Unknown (kankansa)            | wild               | 2               |
| 94  | Unknown       | Unknown (lala)                | wild               | 1               |
| 95  | Unknown       | Unknown (Mafandji)            | wild               | 4               |
| 96  | Unknown       | Unknown (N'penca)             | wild               | 1               |
| 97  | Unknown       | Unknown (n'tchaf)             | wild               | 2               |
| 98  | Unknown       | Unknown (n'tchei)             | wild               | 2               |
| 99  | Unknown       | Unknown (N'ti-une)            | wild               | 1               |
| 100 | Unknown       | Unknown (n'tot)               | wild               | 3               |
| 101 | Unknown       | Unknown (po fino)             | wild               | 3               |
| 102 | Unknown       | Unknown (Po-de-lala)          | wild               | 1               |
| 103 | Unknown       | Unknown (saco)                | wild               | 2               |
| 104 | Unknown       | Unknown (tulindji/N'tat)      | wild               | 3               |
| 105 | Unknown       | Unknown (uri-fiké)            | wild               | 1               |
| 106 | Unknown       | Unknown (uri-uri)             | wild               | 1               |
| 107 | Unknown       | Unknown (vundo)               | wild               | 1               |



## Appendix 4.1

Selection of images captured using arboreal camera traps in Cantanhez NP.



A chimpanzee rests on a velvet tamarind tree for a quick look at the arboreal camera trap before moving on. A green monkey feeds on figs of *Ficus lutea* at the mangrove-forest edge.



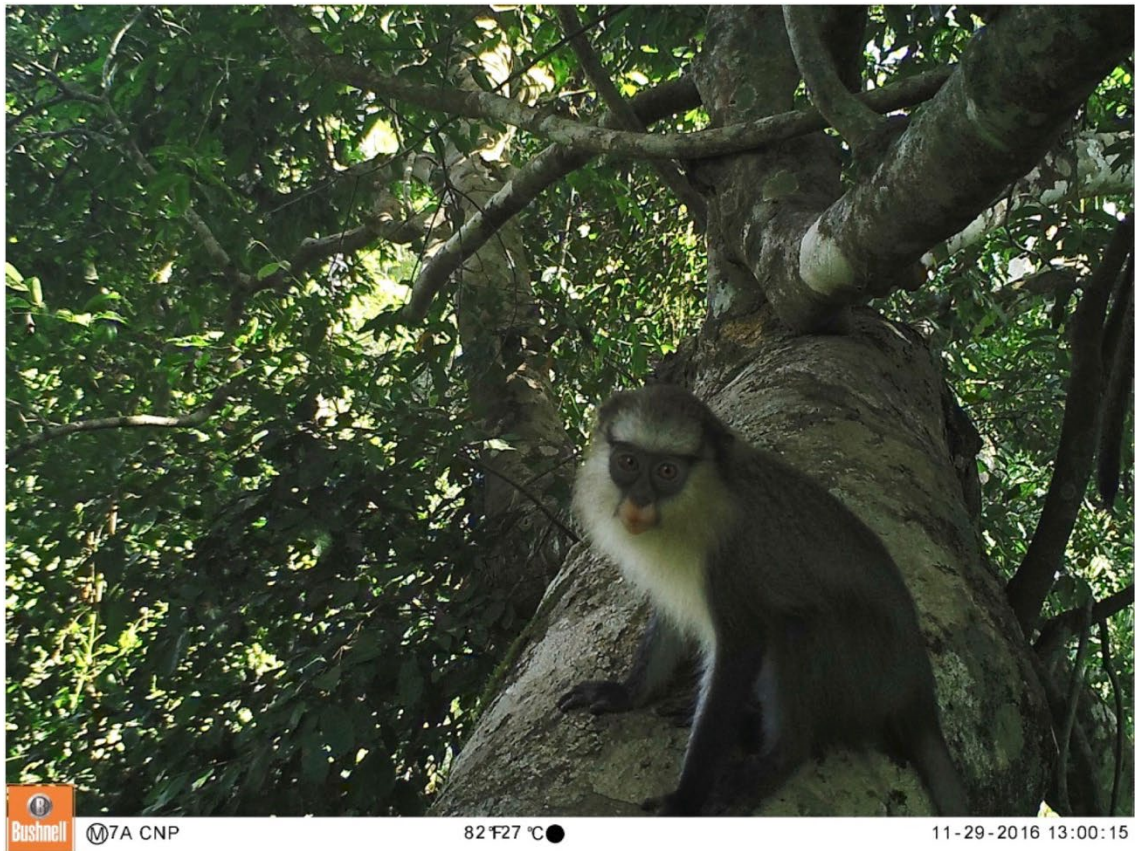
Temminck's red colobus and king colobus detected in two of the largest forest blocks in Cantanhez NP.



Green monkeys detected by a large *Ceiba pentandra* shown in the background. Within the largest forest block in Cantanhez NP, two juvenile Campbell's monkeys display curiosity for the camera trap.



A king colobus travels on top of an *Azelia africana* at the forest edge by the mangroves in the park's largest forest block. A Demidoff's galago detected in regenerating forest near an abandoned village.



A juvenile Campbell's monkey sits on a large *Pterocarpus santalinoides* tree near a freshwater source by the forest edge. A Temminck's red colobus on a velvet tamarind tree looks at the camera trap.



## Appendix 4.2

Full list of arboreal camera trap maximum likelihood occupancy models.

### Temminck's red colobus

| Model                                          | $K$ | AIC   | $\Delta$ AIC | $w_i$   |
|------------------------------------------------|-----|-------|--------------|---------|
| $\Psi(\text{palms, PC1}) p(\text{camht})$      | 5   | 82.94 | 0            | 0.31538 |
| $\Psi(\text{palms, PC2}) p(\text{camht})$      | 5   | 82.99 | 0.043        | 0.3087  |
| $\Psi(\text{palms, village}) p(\text{camht})$  | 5   | 85.16 | 2.214        | 0.10427 |
| $\Psi(\text{palms, forest}) p(\text{camht})$   | 5   | 85.49 | 2.546        | 0.08832 |
| $\Psi(\text{palms}) p(\text{camht})$           | 4   | 85.64 | 2.696        | 0.08191 |
| $\Psi(\text{anthro, palms}) p(\text{camht})$   | 5   | 87.11 | 4.163        | 0.03933 |
| $\Psi(\text{village, forest}) p(\text{camht})$ | 5   | 89.45 | 6.505        | 0.0122  |
| $\Psi(\text{forest}) p(\text{camht})$          | 4   | 89.47 | 6.524        | 0.01208 |
| $\Psi(\text{village}) p(\text{camht})$         | 4   | 90.59 | 7.649        | 0.00689 |
| $\Psi(\text{PC2, village}) p(\text{camht})$    | 5   | 90.64 | 7.698        | 0.00672 |
| $\Psi(\text{PC1, forest}) p(\text{camht})$     | 5   | 91.19 | 8.246        | 0.00511 |
| $\Psi(\text{PC1, village}) p(\text{camht})$    | 5   | 91.25 | 8.305        | 0.00496 |
| $\Psi(\text{anthro, forest}) p(\text{camht})$  | 5   | 91.64 | 8.7          | 0.00407 |
| $\Psi(\text{PC2, forest}) p(\text{camht})$     | 5   | 92.38 | 9.437        | 0.00282 |
| $\Psi(\text{PC1, anthro}) p(\text{camht})$     | 5   | 92.55 | 9.609        | 0.00258 |
| $\Psi(\text{PC2, anthro}) p(\text{camht})$     | 5   | 93.14 | 10.201       | 0.00192 |
| $\Psi(\text{anthro}) p(\text{camht})$          | 4   | 94.88 | 11.934       | 0.00081 |
| $\Psi(.) p(\text{camht})$                      | 3   | 95.64 | 12.699       | 0.00055 |
| $\Psi(\text{PC1}) p(\text{camht})$             | 4   | 96.47 | 13.529       | 0.00036 |
| $\Psi(\text{village, anthro}) p(\text{camht})$ | 5   | 96.49 | 13.544       | 0.00036 |
| $\Psi(\text{PC2}) p(\text{camht})$             | 4   | 97.16 | 14.218       | 0.00026 |
| $\Psi(.) p(.)$                                 | 2   | 97.35 | 14.409       | 0.00023 |
| $\Psi(\text{PC1, PC2}) p(\text{camht})$        | 5   | 97.98 | 15.037       | 0.00017 |

### King colobus

| Model                                          | $K$ | AIC   | $\Delta$ AIC | $w_i$  |
|------------------------------------------------|-----|-------|--------------|--------|
| $\Psi(\text{village}) p(\text{camht})$         | 4   | 89.58 | 0            | 0.29   |
| $\Psi(\text{village, forest}) p(\text{camht})$ | 5   | 91.17 | 1.58         | 0.13   |
| $\Psi(\text{village, palms}) p(\text{camht})$  | 5   | 91.5  | 1.92         | 0.11   |
| $\Psi(\text{PC1, village}) p(\text{camht})$    | 5   | 91.51 | 1.92         | 0.11   |
| $\Psi(\text{PC2, village}) p(\text{camht})$    | 5   | 91.54 | 1.96         | 0.11   |
| $\Psi(\text{village, anthro}) p(\text{camht})$ | 5   | 91.57 | 1.99         | 0.11   |
| $\Psi(\text{palms, forest}) p(\text{camht})$   | 5   | 95.72 | 6.14         | 0.01   |
| $\Psi(\text{anthro}) p(\text{camht})$          | 4   | 95.75 | 6.17         | 0.0134 |
| $\Psi(.) p(\text{camht})$                      | 3   | 95.81 | 6.23         | 0.013  |
| $\Psi(\text{PC2}) p(\text{camht})$             | 4   | 95.99 | 6.41         | 0.0119 |
| $\Psi(\text{palms}) p(\text{camht})$           | 4   | 96.23 | 6.65         | 0.0105 |
| $\Psi(\text{PC2, anthro}) p(\text{camht})$     | 5   | 96.35 | 6.77         | 0.0099 |
| $\Psi(\text{palms, anthro}) p(\text{camht})$   | 5   | 96.69 | 7.11         | 0.0084 |
| $\Psi(\text{PC2, palms}) p(\text{camht})$      | 5   | 96.71 | 7.13         | 0.0083 |

| Model                                         | $K$ | AIC   | $\Delta AIC$ | $w_i$  |
|-----------------------------------------------|-----|-------|--------------|--------|
| $\Psi(.) p(.)$                                | 2   | 97.14 | 7.56         | 0.0067 |
| $\Psi(\text{forest}) p(\text{camht})$         | 4   | 97.55 | 7.97         | 0.0055 |
| $\Psi(\text{PC1}) p(\text{camht})$            | 4   | 97.64 | 8.06         | 0.0052 |
| $\Psi(\text{PC1, anthro}) p(\text{camht})$    | 5   | 97.65 | 8.07         | 0.0052 |
| $\Psi(\text{forest, anthro}) p(\text{camht})$ | 5   | 97.73 | 8.14         | 0.005  |
| $\Psi(\text{PC2, forest}) p(\text{camht})$    | 5   | 97.75 | 8.17         | 0.0049 |
| $\Psi(\text{PC1, PC2}) p(\text{camht})$       | 5   | 97.95 | 8.37         | 0.0045 |
| $\Psi(\text{PC1, palms}) p(\text{camht})$     | 5   | 98.23 | 8.65         | 0.0039 |
| $\Psi(\text{PC1, forest}) p(\text{camht})$    | 5   | 99.38 | 9.8          | 0.0022 |

### Campbell's monkeys

| Model                                                                   | $K$ | AIC    | $\Delta AIC$ | $w_i$  |
|-------------------------------------------------------------------------|-----|--------|--------------|--------|
| $\Psi(.) p(\text{camht})$                                               | 3   | 277.78 | 0            | 0.1979 |
| $\Psi(\text{village}) p(\text{camht})$                                  | 4   | 278.38 | 0.6          | 0.1464 |
| $\Psi(\text{PC2}) p(\text{camht})$                                      | 4   | 278.5  | 0.72         | 0.1378 |
| $\Psi(\text{PC1}) p(\text{camht})$                                      | 4   | 278.99 | 1.21         | 0.1078 |
| $\Psi(\text{forest}) p(\text{camht})$                                   | 4   | 279.54 | 1.76         | 0.0821 |
| $\Psi(\text{anthro}) p(\text{camht})$                                   | 4   | 279.64 | 1.86         | 0.0779 |
| $\Psi(\text{palms}) p(\text{camht})$                                    | 4   | 279.78 | 2            | 0.0729 |
| $\Psi(\text{PC2, village}) p(\text{camht})$                             | 5   | 280.11 | 2.33         | 0.0616 |
| $\Psi(\text{village, anthro}) p(\text{camht})$                          | 5   | 280.21 | 2.43         | 0.0588 |
| $\Psi(\text{village, forest, anthro}) p(\text{camht})$                  | 6   | 281.91 | 4.14         | 0.025  |
| $\Psi(.) p(.)$                                                          | 2   | 283.07 | 5.3          | 0.014  |
| $\Psi(\text{PC1, village, forest, anthro}) p(\text{camht})$             | 7   | 283.45 | 5.67         | 0.0116 |
| $\Psi(\text{PC1, PC2, village, forest, anthro}) p(\text{camht})$        | 8   | 285.31 | 7.53         | 0.0046 |
| $\Psi(\text{PC1, PC2, village, palms, forest, anthro}) p(\text{camht})$ | 9   | 287.29 | 9.51         | 0.0017 |

### Demidoff's galagos

| Model                                            | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|--------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(\text{village, forest}) p(.)$              | 4   | 117.29 | 0            | 0.306 |
| $\Psi(\text{village, forest, PC2}) p(.)$         | 5   | 118.46 | 1.17         | 0.17  |
| $\Psi(\text{village}) p(.)$                      | 3   | 119.21 | 1.92         | 0.117 |
| $\Psi(\text{forest}) p(.)$                       | 3   | 119.39 | 2.11         | 0.107 |
| $\Psi(\text{anthro}) p(.)$                       | 3   | 120.21 | 2.92         | 0.071 |
| $\Psi(\text{PC2}) p(.)$                          | 3   | 120.32 | 3.03         | 0.067 |
| $\Psi(\text{village, forest, anthro, PC2}) p(.)$ | 6   | 120.43 | 3.14         | 0.064 |
| $\Psi(.) p(.)$                                   | 2   | 121.27 | 3.99         | 0.042 |
| $\Psi(.) p(\text{camht})$                        | 3   | 122.16 | 4.88         | 0.027 |
| $\Psi(\text{palms}) p(.)$                        | 3   | 123.25 | 5.96         | 0.016 |
| $\Psi(\text{PC1}) p(.)$                          | 3   | 123.27 | 5.99         | 0.015 |

## Appendix 5.1

Selection of images recorded using terrestrial camera traps in Cantanhez NP.



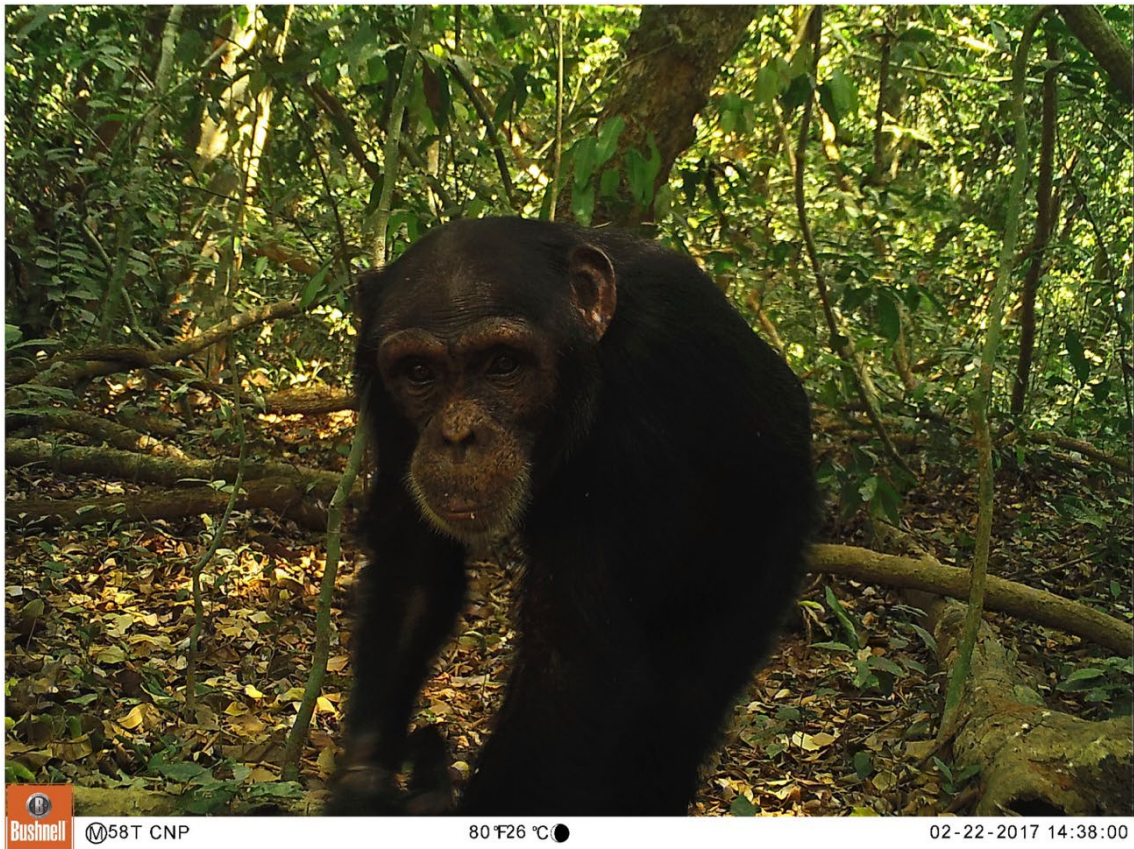
A female chimpanzee carrying her infant travels along the edge of a small forest patch by the mangroves. Within the largest forest block, a young Guinea baboon briefly stops looking at a camera trap before resuming with the rest of the group.



Guinea baboons feeding at a freshwater source by the edge of a forest block. A green monkey stands bipedally on wet mangrove floor near agricultural fields.



Chimpanzees sit within the overgrowth of a cashew orchard surrounded by agricultural farms, grassland and palm groves. Green monkeys feed on orange by a large fallow field.



A chimpanzee travels across an intersection of chimpanzee trails within a small forest patch in an area dominated by agriculture. A male Campbell's monkey lifts his tail in a remnant forest strip within an abandoned village.



Campbell's monkeys displaying vigilance at the open edge of a mangrove-forest area.



## Appendix 5.2

Full list of terrestrial camera trap maximum likelihood occupancy models.

### Chimpanzees – dry season detection probability models

| Model                                                        | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|--------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(.) p(PC1, PC2, mangr)$                                 | 5   | 383.73 | 0            | 0.50  |
| $\Psi(.) p(PC1, PC2, mangr, palms)$                          | 6   | 385.32 | 1.59         | 0.22  |
| $\Psi(.) p(PC1, PC2)$                                        | 4   | 386.18 | 2.45         | 0.15  |
| $\Psi(.) p(PC1, PC2, mangr, palms, anthro)$                  | 7   | 387.23 | 3.51         | 0.09  |
| $\Psi(.) p(PC1, PC2, mangr, palms, forest, anthro)$          | 8   | 389.14 | 5.41         | 0.03  |
| $\Psi(.) p(PC1, PC2, village, mangr, palms, forest, anthro)$ | 9   | 391.12 | 7.39         | 0.01  |
| $\Psi(.) p(anthro)$                                          | 3   | 397.73 | 14           | 0.00  |
| $\Psi(.) p(village, anthro)$                                 | 4   | 398.14 | 14.42        | 0.00  |
| $\Psi(.) p(dv)$                                              | 3   | 399.52 | 15.79        | 0.00  |
| $\Psi(.) p(PC1)$                                             | 3   | 400.07 | 16.34        | 0.00  |
| $\Psi(.) p(PC2)$                                             | 3   | 400.37 | 16.64        | 0.00  |
| $\Psi(.) p(mangr)$                                           | 3   | 406.21 | 22.49        | 0.00  |
| $\Psi(.) p(.)$                                               | 2   | 407.56 | 23.84        | 0.00  |
| $\Psi(.) p(forest)$                                          | 3   | 408.81 | 25.08        | 0.00  |
| $\Psi(.) p(palms)$                                           | 3   | 409.56 | 25.83        | 0.00  |

### Chimpanzees – dry season occupancy models

| Model                                                                      | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|----------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(PC1, village, palms) p(PC1, PC2, mangr)$                             | 8   | 379.55 | 0            | 0.30  |
| $\Psi(PC1, village) p(PC1, PC2, mangr)$                                    | 7   | 380.29 | 0.73         | 0.20  |
| $\Psi(PC1, village, palms, forest) p(PC1, PC2, mangr)$                     | 9   | 381.02 | 1.47         | 0.14  |
| $\Psi(PC1) p(PC1, PC2, mangr)$                                             | 6   | 381.7  | 2.14         | 0.10  |
| $\Psi(PC1, village, mangr, palms, forest) p(PC1, PC2, mangr)$              | 10  | 382.45 | 2.89         | 0.07  |
| $\Psi(palms) p(PC1, PC2, mangr)$                                           | 6   | 383.62 | 4.07         | 0.04  |
| $\Psi(village) p(PC1, PC2, mangr)$                                         | 6   | 383.93 | 4.38         | 0.03  |
| $\Psi(PC1, PC2, village, mangr, palms, forest) p(PC1, PC2, mangr)$         | 11  | 384.19 | 4.64         | 0.03  |
| $\Psi(mangr) p(PC1, PC2, mangr)$                                           | 6   | 384.21 | 4.65         | 0.03  |
| $\Psi(forest) p(PC1, PC2, mangr)$                                          | 6   | 385.24 | 5.69         | 0.02  |
| $\Psi(PC2) p(PC1, PC2, mangr)$                                             | 6   | 385.54 | 5.99         | 0.02  |
| $\Psi(anthro) p(PC1, PC2, mangr)$                                          | 6   | 385.62 | 6.07         | 0.01  |
| $\Psi(PC1, PC2, village, mangr, palms, forest, anthro) p(PC1, PC2, mangr)$ | 12  | 386.08 | 6.53         | 0.01  |
| $\Psi(.) p(.)$                                                             | 2   | 407.56 | 28.01        | 0.00  |

### Chimpanzees – rainy season detection probability models

| Model                                                                  | $K$ | AIC    | $\Delta AIC$ | $w_i$  |
|------------------------------------------------------------------------|-----|--------|--------------|--------|
| $\Psi(.) p(PC2, mangr, palms)$                                         | 5   | 406.38 | 0            | 0.23   |
| $\Psi(.) p(PC2, village, mangr, palms)$                                | 6   | 407.14 | 0.76         | 0.16   |
| $\Psi(.) p(PC2, village, mangr, palms, anthro)$                        | 7   | 407.22 | 0.85         | 0.1526 |
| $\Psi(.) p(PC2, mangr)$                                                | 4   | 407.33 | 0.95         | 0.1447 |
| $\Psi(.) p(PC2, village, mangr, palms, forest, anthro)$                | 8   | 408.34 | 1.96         | 0.0876 |
| $\Psi(.) p(PC2)$                                                       | 3   | 408.48 | 2.11         | 0.0813 |
| $\Psi(.) p(PC2, PC1, village, mangr, palms, forest, anthro)$           | 9   | 410.02 | 3.64         | 0.0378 |
| $\Psi(.) p(.)$                                                         | 2   | 411.19 | 4.81         | 0.021  |
| $\Psi(.) p(PC2, PC1, village, mangr, palms, forest, anthro, rainfall)$ | 10  | 411.89 | 5.51         | 0.0148 |
| $\Psi(.) p(palms)$                                                     | 3   | 412.11 | 5.73         | 0.0133 |
| $\Psi(.) p(mangr)$                                                     | 3   | 412.15 | 5.78         | 0.013  |
| $\Psi(.) p(anthro)$                                                    | 3   | 412.7  | 6.32         | 0.0099 |
| $\Psi(.) p(forest)$                                                    | 3   | 413.06 | 6.69         | 0.0082 |
| $\Psi(.) p(PC1)$                                                       | 3   | 413.18 | 6.8          | 0.0078 |
| $\Psi(.) p(village)$                                                   | 3   | 413.19 | 6.81         | 0.0077 |

### Chimpanzees – rainy season occupancy models

| Model                                                                        | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(PC1, PC2, village, palms) p(PC2, mangr, palms)$                        | 9   | 405.39 | 0            | 0.148 |
| $\Psi(PC1, PC2, palms) p(PC2, mangr, palms)$                                 | 8   | 405.83 | 0.44         | 0.119 |
| $\Psi(PC2) p(PC2, mangr, palms)$                                             | 6   | 405.83 | 0.44         | 0.119 |
| $\Psi(PC2, palms) p(PC2, mangr, palms)$                                      | 7   | 405.98 | 0.59         | 0.11  |
| $\Psi(.) p(PC2, mangr, palms)$                                               | 5   | 406.38 | 0.98         | 0.091 |
| $\Psi(PC1) p(PC2, mangr, palms)$                                             | 6   | 406.56 | 1.16         | 0.083 |
| $\Psi(PC1, PC2, village, mangr, palms) p(PC2, mangr, palms)$                 | 10  | 406.68 | 1.28         | 0.078 |
| $\Psi(palms) p(PC2, mangr, palms)$                                           | 6   | 407.48 | 2.09         | 0.052 |
| $\Psi(village) p(PC2, mangr, palms)$                                         | 6   | 407.63 | 2.23         | 0.049 |
| $\Psi(anthro) p(PC2, mangr, palms)$                                          | 6   | 408.25 | 2.85         | 0.036 |
| $\Psi(forest) p(PC2, mangr, palms)$                                          | 6   | 408.26 | 2.86         | 0.035 |
| $\Psi(mangr) p(PC2, mangr, palms)$                                           | 6   | 408.35 | 2.95         | 0.034 |
| $\Psi(PC1, PC2, village, mangr, palms, forest) p(PC2, mangr, palms)$         | 11  | 408.47 | 3.07         | 0.032 |
| $\Psi(PC1, PC2, village, mangr, palms, forest, anthro) p(PC2, mangr, palms)$ | 12  | 410.09 | 4.7          | 0.014 |

### Guinea baboons – dry season detection probability models

| Model                                                               | $K$ | AIC    | $\Delta$ AIC | $w_i$ |
|---------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(.) p(\text{PC2, mangr, anthro})$                              | 5   | 228.96 | 0            | 0.25  |
| $\Psi(.) p(\text{PC2, anthro})$                                     | 4   | 229.11 | 0.15         | 0.23  |
| $\Psi(.) p(\text{mangr, anthro})$                                   | 4   | 229.66 | 0.69         | 0.17  |
| $\Psi(.) p(\text{PC1, PC2, mangr, anthro})$                         | 6   | 229.86 | 0.89         | 0.16  |
| $\Psi(.) p(\text{PC1, PC2, mangr, forest, anthro})$                 | 7   | 230.77 | 1.8          | 0.10  |
| $\Psi(.) p(\text{PC1, PC2, village, mangr, forest, anthro})$        | 8   | 232.52 | 3.56         | 0.04  |
| $\Psi(.) p(\text{anthro})$                                          | 3   | 232.98 | 4.02         | 0.03  |
| $\Psi(.) p(\text{PC1, PC2, village, mangr, palms, forest, anthro})$ | 9   | 234.45 | 5.49         | 0.02  |
| $\Psi(.) p(\text{village})$                                         | 3   | 243.66 | 14.7         | 0.00  |
| $\Psi(.) p(\text{PCI})$                                             | 3   | 246.37 | 17.41        | 0.00  |
| $\Psi(.) p(\text{mangr})$                                           | 3   | 247.72 | 18.76        | 0.00  |
| $\Psi(.) p(.)$                                                      | 2   | 250.01 | 21.04        | 0.00  |
| $\Psi(.) p(\text{PC2})$                                             | 3   | 250.35 | 21.39        | 0.00  |
| $\Psi(.) p(\text{palms})$                                           | 3   | 250.53 | 21.56        | 0.00  |
| $\Psi(.) p(\text{forest})$                                          | 3   | 251.84 | 22.87        | 0.00  |

### Guinea baboons – dry season occupancy models

| Model                                                                                       | $K$ | AIC    | $\Delta$ AIC | $w_i$ |
|---------------------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(\text{mangr, forest}) p(\text{PC2, anthro})$                                          | 6   | 223.24 | 0            | 0.29  |
| $\Psi(\text{mangr, forest}) p(\text{mangr, anthro})$                                        | 6   | 224.15 | 0.91         | 0.18  |
| $\Psi(\text{mangr, forest}) p(\text{PC2, mangr, anthro})$                                   | 7   | 224.22 | 0.98         | 0.18  |
| $\Psi(\text{mangr, forest}) p(\text{PC1, PC2, mangr, anthro})$                              | 8   | 225.79 | 2.55         | 0.08  |
| $\Psi(\text{PC2, mangr, forest}) p(\text{PC2, mangr, anthro})$                              | 8   | 225.92 | 2.69         | 0.07  |
| $\Psi(\text{PC2, mangr, forest, anthro}) p(\text{PC2, mangr, anthro})$                      | 9   | 226.95 | 3.71         | 0.04  |
| $\Psi(\text{forest}) p(\text{PC2, mangr, anthro})$                                          | 6   | 227.47 | 4.24         | 0.03  |
| $\Psi(\text{mangr, forest}) p(\text{PC1, PC2, mangr, forest, anthro})$                      | 9   | 227.62 | 4.39         | 0.03  |
| $\Psi(\text{PC1, PC2, mangr, forest, anthro}) p(\text{PC2, mangr, anthro})$                 | 10  | 228.69 | 5.45         | 0.02  |
| $\Psi(.) p(\text{PC2, anthro, mangr})$                                                      | 5   | 228.96 | 5.73         | 0.02  |
| $\Psi(\text{anthro}) p(\text{PC2, mangr, anthro})$                                          | 6   | 229.77 | 6.53         | 0.01  |
| $\Psi(\text{mangr}) p(\text{PC2, mangr, anthro})$                                           | 6   | 230.26 | 7.02         | 0.01  |
| $\Psi(\text{PC1, PC2, mangr, palms, forest, anthro}) p(\text{PC2, mangr, anthro})$          | 11  | 230.45 | 7.21         | 0.01  |
| $\Psi(\text{palms}) p(\text{PC2, mangr, anthro})$                                           | 6   | 230.83 | 7.59         | 0.01  |
| $\Psi(\text{PC2}) p(\text{PC2, mangr, anthro})$                                             | 6   | 230.87 | 7.64         | 0.01  |
| $\Psi(\text{PC1}) p(\text{PC2, mangr, anthro})$                                             | 6   | 230.91 | 7.68         | 0.01  |
| $\Psi(\text{village}) p(\text{PC2, mangr, anthro})$                                         | 6   | 230.96 | 7.72         | 0.01  |
| $\Psi(\text{PC1, PC2, village, mangr, palms, forest, anthro}) p(\text{PC2, mangr, anthro})$ | 12  | 232.2  | 8.97         | 0.00  |

### Guinea baboons – rainy season detection probability models

| Model                                                                       | $K$ | AIC    | $\Delta AIC$ | $w_i$   |
|-----------------------------------------------------------------------------|-----|--------|--------------|---------|
| $\Psi(.) p(PC2, \text{forest})$                                             | 4   | 115.83 | 0            | 0.30647 |
| $\Psi(.) p(PC2, \text{forest}, \text{mangr})$                               | 5   | 116.56 | 0.74         | 0.21217 |
| $\Psi(.) p(\text{forest})$                                                  | 3   | 116.94 | 1.11         | 0.17553 |
| $\Psi(.) p(PC2, \text{forest}, \text{mangr}, \text{palms})$                 | 6   | 117.79 | 1.96         | 0.11497 |
| $\Psi(.) p(PC2)$                                                            | 3   | 118.15 | 2.32         | 0.09621 |
| $\Psi(.) p(PC2, \text{forest}, \text{mangr}, \text{palms}, \text{village})$ | 7   | 118.91 | 3.08         | 0.06554 |
| $\Psi(.) p(\text{mangr})$                                                   | 3   | 122.07 | 6.24         | 0.01351 |
| $\Psi(.) p(\text{palms})$                                                   | 3   | 123.06 | 7.24         | 0.00822 |
| $\Psi(.) p(\text{village})$                                                 | 3   | 123.98 | 8.15         | 0.0052  |
| $\Psi(.) p(\text{anthro})$                                                  | 3   | 127.4  | 11.57        | 0.00094 |
| $\Psi(.) p(.)$                                                              | 2   | 127.99 | 12.17        | 0.0007  |
| $\Psi(.) p(PC1)$                                                            | 3   | 129.95 | 14.12        | 0.00026 |

### Guinea baboons – rainy season occupancy models

| Model                                                                                                            | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|------------------------------------------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(\text{anthro}) p(PC2, \text{forest})$                                                                      | 5   | 108.33 | 0            | 0.29  |
| $\Psi(\text{anthro}) p(\text{forest})$                                                                           | 4   | 109.36 | 1.03         | 0.17  |
| $\Psi(\text{forest}, \text{anthro}) p(PC2, \text{forest})$                                                       | 6   | 109.95 | 1.62         | 0.13  |
| $\Psi(\text{palms}, \text{anthro}) p(PC2, \text{forest})$                                                        | 6   | 110.26 | 1.93         | 0.11  |
| $\Psi(\text{mangr}, \text{palms}, \text{anthro}) p(PC2, \text{forest})$                                          | 7   | 110.31 | 1.98         | 0.11  |
| $\Psi(\text{mangr}, \text{palms}, \text{forest}, \text{anthro}) p(PC2, \text{forest})$                           | 8   | 111.42 | 3.09         | 0.06  |
| $\Psi(PC2, \text{mangr}, \text{palms}, \text{forest}, \text{anthro}) p(PC2, \text{forest})$                      | 9   | 112.44 | 4.11         | 0.04  |
| $\Psi(PC1, PC2, \text{mangr}, \text{palms}, \text{forest}, \text{anthro}) p(PC2, \text{forest})$                 | 10  | 114.27 | 5.93         | 0.02  |
| $\Psi(\text{forest}) p(PC2, \text{forest})$                                                                      | 5   | 114.59 | 6.26         | 0.01  |
| $\Psi(\text{mangr}) p(PC2, \text{forest})$                                                                       | 5   | 115.26 | 6.93         | 0.01  |
| $\Psi(\text{forest}) p(\text{forest})$                                                                           | 4   | 115.88 | 7.55         | 0.01  |
| $\Psi(\text{village}) p(PC2, \text{forest})$                                                                     | 5   | 115.91 | 7.57         | 0.01  |
| $\Psi(PC1, PC2, \text{village}, \text{mangr}, \text{palms}, \text{forest}, \text{anthro}) p(PC2, \text{forest})$ | 11  | 116.14 | 7.81         | 0.01  |
| $\Psi(PC1) p(PC2, \text{forest})$                                                                                | 5   | 116.36 | 8.03         | 0.01  |
| $\Psi(\text{mangr}) p(\text{forest})$                                                                            | 4   | 116.36 | 8.03         | 0.01  |
| $\Psi(\text{village}) p(\text{forest})$                                                                          | 4   | 117.12 | 8.79         | 0.00  |
| $\Psi(PC2) p(PC2, \text{forest})$                                                                                | 5   | 117.46 | 9.13         | 0.00  |
| $\Psi(PC1) p(\text{forest})$                                                                                     | 4   | 117.48 | 9.15         | 0.00  |
| $\Psi(\text{palms}) p(PC2, \text{forest})$                                                                       | 5   | 117.72 | 9.39         | 0.00  |
| $\Psi(PC2) p(\text{forest})$                                                                                     | 4   | 118.45 | 10.11        | 0.00  |
| $\Psi(\text{palms}) p(\text{forest})$                                                                            | 4   | 118.83 | 10.5         | 0.00  |
| $\Psi(.) p(.)$                                                                                                   | 2   | 127.99 | 19.66        | 0.00  |

### Green monkeys – dry season detection probability models

| Model                                                               | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|---------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(.) p(\text{mangr, palms, forest})$                            | 5   | 220.16 | 0            | 0.31  |
| $\Psi(.) p(\text{PC1, mangr, palms, forest})$                       | 6   | 220.19 | 0.032        | 0.31  |
| $\Psi(.) p(\text{PC1, village, mangr, palms, forest})$              | 7   | 220.71 | 0.555        | 0.24  |
| $\Psi(.) p(\text{PC1, PC2, village, mangr, palms, forest})$         | 8   | 222.43 | 2.276        | 0.10  |
| $\Psi(.) p(\text{PC1, PC2, village, mangr, palms, forest, anthro})$ | 9   | 224.36 | 4.208        | 0.04  |
| $\Psi(.) p(\text{PC1, forest})$                                     | 4   | 232.37 | 12.216       | 0.00  |
| $\Psi(.) p(\text{palms, forest})$                                   | 4   | 234.37 | 14.215       | 0.00  |
| $\Psi(.) p(\text{PC1})$                                             | 3   | 234.78 | 14.629       | 0.00  |
| $\Psi(.) p(\text{forest})$                                          | 3   | 235.41 | 15.249       | 0.00  |
| $\Psi(.) p(\text{anthro})$                                          | 3   | 236.4  | 16.242       | 0.00  |
| $\Psi(.) p(\text{PC2})$                                             | 3   | 237.25 | 17.094       | 0.00  |
| $\Psi(.) p(\text{mangr})$                                           | 3   | 238.3  | 18.142       | 0.00  |
| $\Psi(.) p(.)$                                                      | 2   | 240.45 | 20.295       | 0.00  |
| $\Psi(.) p(\text{dv})$                                              | 3   | 241.77 | 21.619       | 0.00  |
| $\Psi(.) p(\text{palms})$                                           | 3   | 242.04 | 21.885       | 0.00  |

### Green monkeys – dry season occupancy models

| Model                                                                                         | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|-----------------------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(\text{forest}) p(\text{PC1, mangr, palms, forest})$                                     | 7   | 220.04 | 0            | 0.11  |
| $\Psi(.) p(\text{mangr, palms, forest})$                                                      | 5   | 220.16 | 0.11         | 0.10  |
| $\Psi(\text{forest}) p(\text{mangr, palms, forest})$                                          | 6   | 220.27 | 0.22         | 0.10  |
| $\Psi(\text{forest, anthro}) p(\text{PC1, mangr, palms, forest})$                             | 8   | 220.96 | 0.92         | 0.07  |
| $\Psi(\text{village}) p(\text{mangr, palms, forest})$                                         | 6   | 221.22 | 1.18         | 0.06  |
| $\Psi(\text{village, forest, anthro}) p(\text{PC1, mangr, palms, forest})$                    | 9   | 221.32 | 1.28         | 0.06  |
| $\Psi(\text{palms}) p(\text{mangr, palms, forest})$                                           | 6   | 221.34 | 1.29         | 0.06  |
| $\Psi(\text{mangr}) p(\text{mangr, palms, forest})$                                           | 6   | 221.38 | 1.34         | 0.06  |
| $\Psi(\text{forest, anthro}) p(\text{mangr, palms, forest})$                                  | 7   | 221.44 | 1.39         | 0.05  |
| $\Psi(\text{PC1}) p(\text{mangr, palms, forest})$                                             | 6   | 221.45 | 1.41         | 0.05  |
| $\Psi(\text{village, forest, anthro}) p(\text{mangr, palms, forest})$                         | 8   | 221.61 | 1.57         | 0.05  |
| $\Psi(\text{forest, village}) p(\text{mangr, palms, forest})$                                 | 7   | 221.68 | 1.64         | 0.05  |
| $\Psi(\text{anthro}) p(\text{mangr, palms, forest})$                                          | 6   | 222.07 | 2.03         | 0.04  |
| $\Psi(\text{PC2}) p(\text{mangr, palms, forest})$                                             | 6   | 222.16 | 2.11         | 0.04  |
| $\Psi(\text{PC1, village, forest, anthro}) p(\text{PC1, mangr, palms, forest})$               | 10  | 222.55 | 2.51         | 0.03  |
| $\Psi(\text{PC1, village, forest, anthro}) p(\text{mangr, palms, forest})$                    | 9   | 223.33 | 3.29         | 0.02  |
| $\Psi(\text{PC1, village, palms, forest, anthro}) p(\text{PC1, mangr, palms, forest})$        | 11  | 223.41 | 3.36         | 0.02  |
| $\Psi(\text{forest, village, palms}) p(\text{mangr, palms, forest})$                          | 8   | 223.65 | 3.61         | 0.02  |
| $\Psi(\text{PC1, village, palms, forest, anthro}) p(\text{mangr, palms, forest})$             | 10  | 224.95 | 4.9          | 0.01  |
| $\Psi(\text{PC1, village, mangr, palms, forest, anthro}) p(\text{PC1, mangr, palms, forest})$ | 12  | 225.03 | 4.99         | 0.01  |
| $\Psi(\text{PC1, village, mangr, palms, forest, anthro}) p(\text{mangr, palms, forest})$      | 11  | 226.74 | 6.7          | 0.00  |

| Model                                                                                                   | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|---------------------------------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(PC1, PC2, \text{village, mangr, palms, forest, anthro})$<br>$p(PC1, \text{mangr, palms, forest})$ | 13  | 227.03 | 6.98         | 0.00  |
| $\Psi(PC1, PC2, \text{village, mangr, palms, forest, anthro})$<br>$p(\text{mangr, palms, forest})$      | 12  | 228.74 | 8.7          | 0.00  |

#### Green monkeys – rainy season detection probability models

| Model                                                                         | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|-------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(.) p(PC2, PC1, \text{mangr, palms})$                                    | 6   | 292.24 | 0            | 0.46  |
| $\Psi(.) p(PC2, PC1, \text{mangr, palms, forest})$                            | 7   | 293.17 | 0.93         | 0.29  |
| $\Psi(.) p(PC2, PC1, \text{mangr, palms, forest, rainfall})$                  | 8   | 294.62 | 2.38         | 0.14  |
| $\Psi(.) p(PC2, PC1, \text{mangr, palms, forest, anthro, rainfall})$          | 9   | 296.54 | 4.3          | 0.05  |
| $\Psi(.) p(PC2, PC1, \text{palms})$                                           | 5   | 297.35 | 5.11         | 0.04  |
| $\Psi(.) p(PC2, PC1, \text{village, mangr, palms, forest, anthro, rainfall})$ | 10  | 298.41 | 6.17         | 0.02  |
| $\Psi(.) p(\text{forest, palms, PC2})$                                        | 5   | 301.45 | 9.21         | 0.00  |
| $\Psi(.) p(\text{forest, palms, PC2, mangr})$                                 | 6   | 301.45 | 9.22         | 0.00  |
| $\Psi(.) p(PC2, \text{palms})$                                                | 4   | 304.74 | 12.5         | 0.00  |
| $\Psi(.) p(\text{forest, palms})$                                             | 4   | 327.63 | 35.39        | 0.00  |
| $\Psi(.) p(\text{forest})$                                                    | 3   | 329.33 | 37.09        | 0.00  |
| $\Psi(.) p(\text{palms})$                                                     | 3   | 334.3  | 42.06        | 0.00  |
| $\Psi(.) p(PC2)$                                                              | 3   | 337.01 | 44.77        | 0.00  |
| $\Psi(.) p(\text{mangr})$                                                     | 3   | 338.36 | 46.12        | 0.00  |
| $\Psi(.) p(\text{anthro})$                                                    | 3   | 340.75 | 48.51        | 0.00  |
| $\Psi(.) p(PC1)$                                                              | 3   | 341.91 | 49.67        | 0.00  |
| $\Psi(.) p(.)$                                                                | 2   | 342.3  | 50.06        | 0.00  |
| $\Psi(.) p(\text{village})$                                                   | 3   | 344.14 | 51.9         | 0.00  |

#### Green monkeys – rainy season occupancy models

| Model                                                                            | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|----------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(PC1, \text{palms}) p(PC2, PC1, \text{mangr, palms})$                       | 8   | 288.67 | 0            | 0.15  |
| $\Psi(PC1) p(PC2, PC1, \text{mangr, palms})$                                     | 7   | 288.88 | 0.2          | 0.13  |
| $\Psi(PC1, \text{palms}) p(PC2, PC1, \text{mangr, palms, forest})$               | 9   | 289.18 | 0.5          | 0.11  |
| $\Psi(PC1) p(PC2, PC1, \text{mangr, palms, forest})$                             | 8   | 289.48 | 0.81         | 0.10  |
| $\Psi(PC1, \text{village, palms, forest}) p(PC2, PC1, \text{mangr, palms})$      | 10  | 289.59 | 0.92         | 0.09  |
| $\Psi(PC1, \text{village, palms}) p(PC2, PC1, \text{mangr, palms})$              | 9   | 290.18 | 1.51         | 0.07  |
| $\Psi(PC1, \text{mangr}) p(PC2, PC1, \text{mangr, palms})$                       | 8   | 290.51 | 1.84         | 0.06  |
| $\Psi(PC1, \text{palms}) p(PC2, PC1, \text{mangr, palms, forest, rainfall})$     | 10  | 290.62 | 1.95         | 0.06  |
| $\Psi(PC1) p(PC2, PC1, \text{mangr, palms, forest, rainfall})$                   | 9   | 290.94 | 2.27         | 0.05  |
| $\Psi(PC1, PC2, \text{village, palms, forest}) p(PC2, PC1, \text{mangr, palms})$ | 11  | 291.07 | 2.4          | 0.04  |
| $\Psi(\text{mangr}) p(PC2, PC1, \text{mangr, palms})$                            | 7   | 292.17 | 3.5          | 0.03  |
| $\Psi(.) p(PC2, PC1, \text{mangr, palms})$                                       | 6   | 292.24 | 3.57         | 0.02  |

| Model                                                                                           | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|-------------------------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(PC1, PC2, \text{village, palms, forest, anthro}) p(PC2, PC1, \text{mangr, palms})$        | 12  | 292.75 | 4.07         | 0.02  |
| $\Psi(\text{anthro}) p(PC2, PC1, \text{mangr, palms})$                                          | 7   | 292.81 | 4.14         | 0.02  |
| $\Psi(\text{village}) p(PC2, PC1, \text{mangr, palms})$                                         | 7   | 293.12 | 4.44         | 0.02  |
| $\Psi(PC2) p(PC2, PC1, \text{mangr, palms})$                                                    | 7   | 293.44 | 4.77         | 0.01  |
| $\Psi(\text{palms}) p(PC2, PC1, \text{mangr, palms})$                                           | 7   | 294.17 | 5.5          | 0.01  |
| $\Psi(\text{forest}) p(PC2, PC1, \text{mangr, palms})$                                          | 7   | 294.21 | 5.53         | 0.01  |
| $\Psi(PC1, PC2, \text{village, mangr, palms, forest, anthro}) p(PC2, PC1, \text{mangr, palms})$ | 13  | 294.75 | 6.07         | 0.01  |

#### Campbell's monkeys – dry season detection probability models

| Model                                                               | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|---------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(.) p(PC1, \text{village, mangr, forest})$                     | 6   | 432.59 | 0            | 0.31  |
| $\Psi(.) p(PC1, PC2, \text{village, mangr, forest})$                | 7   | 432.94 | 0.35         | 0.26  |
| $\Psi(.) p(PC1, PC2, \text{village, mangr, palms, forest})$         | 8   | 433.7  | 1.11         | 0.18  |
| $\Psi(.) p(PC1, \text{village, mangr})$                             | 5   | 433.73 | 1.14         | 0.17  |
| $\Psi(.) p(PC1, PC2, \text{village, mangr, palms, forest, anthro})$ | 9   | 435.59 | 3            | 0.07  |
| $\Psi(.) p(PC1, \text{mangr})$                                      | 4   | 438.54 | 5.95         | 0.02  |
| $\Psi(.) p(PC1)$                                                    | 3   | 443.74 | 11.15        | 0.00  |
| $\Psi(.) p(\text{mangr})$                                           | 3   | 444.07 | 11.48        | 0.00  |
| $\Psi(.) p(.)$                                                      | 2   | 449.03 | 16.44        | 0.00  |
| $\Psi(.) p(\text{anthro})$                                          | 3   | 449.09 | 16.5         | 0.00  |
| $\Psi(.) p(\text{village})$                                         | 3   | 449.59 | 17           | 0.00  |
| $\Psi(.) p(\text{forest})$                                          | 3   | 450.31 | 17.72        | 0.00  |
| $\Psi(.) p(PC2)$                                                    | 3   | 450.43 | 17.84        | 0.00  |
| $\Psi(.) p(\text{palms})$                                           | 3   | 450.54 | 17.95        | 0.00  |

#### Campbell's monkeys – dry season occupancy models

| Model                                                                                   | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|-----------------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(PC1, \text{village, forest}) p(PC1, \text{village, mangr, forest})$               | 9   | 427.23 | 0            | 0.13  |
| $\Psi(PC1, \text{village, palms, forest}) p(PC1, \text{village, mangr, forest})$        | 10  | 427.62 | 0.39         | 0.10  |
| $\Psi(PC1, \text{village, forest}) p(PC1, PC2, \text{village, mangr, forest})$          | 10  | 427.78 | 0.55         | 0.10  |
| $\Psi(\text{village, forest}) p(PC1, \text{village, mangr, forest})$                    | 8   | 427.96 | 0.73         | 0.09  |
| $\Psi(PC1, \text{village, palms, forest}) p(PC1, PC2, \text{village, mangr, forest})$   | 11  | 427.99 | 0.76         | 0.09  |
| $\Psi(\text{village, forest, palms}) p(PC1, \text{village, mangr, forest})$             | 9   | 428.33 | 1.1          | 0.07  |
| $\Psi(\text{forest}) p(PC1, \text{village, mangr, forest})$                             | 7   | 428.53 | 1.3          | 0.07  |
| $\Psi(\text{village, forest}) p(PC1, PC2, \text{village, mangr, forest})$               | 9   | 428.63 | 1.4          | 0.06  |
| $\Psi(PC1, \text{village, mangr, palms, forest}) p(PC1, \text{village, mangr, forest})$ | 11  | 428.63 | 1.4          | 0.06  |
| $\Psi(\text{palms}) p(PC1, \text{village, mangr, forest})$                              | 7   | 428.85 | 1.62         | 0.06  |

| Model                                                                                                | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|------------------------------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(\text{forest, palms}) p(\text{PC1, village, mangr, forest})$                                   | 8   | 429.31 | 2.09         | 0.04  |
| $\Psi(\text{PC1, village, mangr, palms, forest, anthro}) p(\text{PC1, village, mangr, forest})$      | 12  | 429.89 | 2.66         | 0.03  |
| $\Psi(\text{village, forest, palms, anthro}) p(\text{PC1, village, mangr, forest})$                  | 10  | 430.02 | 2.79         | 0.03  |
| $\Psi(\text{village}) p(\text{PC1, village, mangr, forest})$                                         | 7   | 431.22 | 3.99         | 0.02  |
| $\Psi(\text{anthro}) p(\text{PC1, village, mangr, forest})$                                          | 7   | 431.29 | 4.06         | 0.02  |
| $\Psi(\text{PC1, PC2, village, mangr, palms, forest, anthro}) p(\text{PC1, village, mangr, forest})$ | 13  | 431.65 | 4.42         | 0.01  |
| $\Psi(.) p(\text{PC1, village, mangr, forest})$                                                      | 6   | 432.59 | 5.36         | 0.01  |
| $\Psi(\text{mangr}) p(\text{PC1, village, mangr, forest})$                                           | 7   | 433.61 | 6.38         | 0.01  |
| $\Psi(\text{PC2}) p(\text{PC1, village, mangr, forest})$                                             | 7   | 434.23 | 7            | 0.00  |
| $\Psi(\text{PC1}) p(\text{PC1, village, mangr, forest})$                                             | 7   | 434.5  | 7.28         | 0.00  |

#### Campbell's monkeys – rainy season detection probability models

| Model                                                                         | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|-------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(.) p(\text{PC1, village, palms, forest})$                               | 6   | 596.98 | 0            | 0.22  |
| $\Psi(.) p(\text{PC1, palms, forest})$                                        | 5   | 597.31 | 0.33         | 0.19  |
| $\Psi(.) p(\text{PC1, village, palms, forest, anthro})$                       | 7   | 597.65 | 0.66         | 0.16  |
| $\Psi(.) p(\text{PC1, village})$                                              | 4   | 598.42 | 1.44         | 0.11  |
| $\Psi(.) p(\text{PC1, PC2, village, palms, forest, anthro})$                  | 8   | 598.71 | 1.73         | 0.09  |
| $\Psi(.) p(\text{village})$                                                   | 3   | 599.56 | 2.58         | 0.06  |
| $\Psi(.) p(\text{PC1, forest})$                                               | 4   | 600.08 | 3.1          | 0.05  |
| $\Psi(.) p(\text{PC1, PC2, village, palms, forest, anthro, rainfall})$        | 9   | 600.59 | 3.61         | 0.04  |
| $\Psi(.) p(\text{PC1})$                                                       | 3   | 601.57 | 4.59         | 0.02  |
| $\Psi(.) p(.)$                                                                | 2   | 602.3  | 5.31         | 0.02  |
| $\Psi(.) p(\text{PC1, PC2, village, mangr, palms, forest, anthro, rainfall})$ | 10  | 602.52 | 5.54         | 0.01  |
| $\Psi(.) p(\text{forest})$                                                    | 3   | 602.6  | 5.62         | 0.01  |
| $\Psi(.) p(\text{PC2})$                                                       | 3   | 603.11 | 6.13         | 0.01  |
| $\Psi(.) p(\text{palms})$                                                     | 3   | 603.81 | 6.83         | 0.01  |
| $\Psi(.) p(\text{anthro})$                                                    | 3   | 603.95 | 6.96         | 0.01  |
| $\Psi(.) p(\text{mangr})$                                                     | 3   | 604.27 | 7.28         | 0.01  |

#### Campbell's monkeys – rainy season occupancy models

| Model                                                                           | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|---------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(\text{PC1, forest}) p(\text{PC1, village, palms, forest})$                | 8   | 591.63 | 0            | 0.16  |
| $\Psi(\text{PC1, forest}) p(\text{PC1, palms, forest})$                         | 7   | 592.01 | 0.38         | 0.13  |
| $\Psi(\text{PC1, forest}) p(\text{PC1, palms, forest, village, anthro})$        | 9   | 592.29 | 0.65         | 0.11  |
| $\Psi(\text{PC1, mangr, forest}) p(\text{PC1, village, palms, forest})$         | 9   | 592.35 | 0.71         | 0.11  |
| $\Psi(\text{PC1, mangr, forest, anthro}) p(\text{PC1, village, palms, forest})$ | 10  | 592.4  | 0.77         | 0.11  |
| $\Psi(\text{pc1}) p(\text{PC1, village, palms, forest})$                        | 7   | 592.67 | 1.04         | 0.09  |
| $\Psi(\text{forest}) p(\text{PC1, village, palms, forest})$                     | 7   | 592.7  | 1.06         | 0.09  |
| $\Psi(\text{PC1, forest}) p(\text{PC1, village})$                               | 6   | 593.4  | 1.76         | 0.06  |

| Model                                                                                  | $K$ | AIC    | $\Delta AIC$ | $w_i$ |
|----------------------------------------------------------------------------------------|-----|--------|--------------|-------|
| $\Psi(PC1, PC2, mangr, forest, anthro) p(PC1, village, palms, forest)$                 | 11  | 593.48 | 1.85         | 0.06  |
| $\Psi(PC1, PC2, village, mangr, forest, anthro) p(PC1, village, palms, forest)$        | 12  | 595.47 | 3.84         | 0.02  |
| $\Psi(.) p(PC1, village, palms, forest)$                                               | 6   | 596.98 | 5.35         | 0.01  |
| $\Psi(anthro) p(PC1, village, palms, forest)$                                          | 7   | 597.04 | 5.41         | 0.01  |
| $\Psi(PC1, PC2, village, mangr, palms, forest, anthro) p(PC1, village, palms, forest)$ | 13  | 597.47 | 5.84         | 0.01  |
| $\Psi(mangr) p(PC1, village, palms, forest)$                                           | 7   | 597.89 | 6.25         | 0.01  |
| $\Psi(PC2) p(PC1, village, palms, forest)$                                             | 7   | 598.04 | 6.4          | 0.01  |
| $\Psi(village) p(PC1, village, palms, forest)$                                         | 7   | 598.54 | 6.91         | 0.00  |
| $\Psi(palms) p(PC1, village, palms, forest)$                                           | 7   | 598.85 | 7.22         | 0.00  |



## Appendix 6.1

R script of spatiotemporal models ran using R-INLA.

```
# install R-INLA
> install.packages("INLA", repos=c(getOption("repos"),
INLA="https://inla.r-inla-download.org/R/stable"), dep=TRUE)
> library(INLA)

# import datasets
> LF_dataset <- read.table("LF_dataset_2.csv", header = TRUE, sep = ",")
> LF_coordinates <- read.table("LF_coordinates_UTM.csv", header = TRUE,
sep = ",")
> borders <- read.table("borders_UTM.csv", header = TRUE, sep = ",")

# define dataset
> n_stations <- length(LF_coordinates$Station.ID)
> n_data <- length(LF_dataset$Site)
> n_occasions <- as.integer(n_data/n_stations)

# transform covariates
> mean_covariates <- apply(LF_dataset[,6:27], 2, mean)
> sd_covariates <- apply(LF_dataset[,6:27], 2, sd)
> LF_dataset[,6:27] = scale(LF_dataset[,6:27], mean_covariates,
sd_covariates)
> LF_dataset$logCHIMP_det = log(LF_dataset$CHIMP_det + 1)

> LF_loc = cbind(LF_coordinates$UTMX, LF_coordinates$UTMY)
> borders_UTM = cbind(borders$UTMX, borders$UTMY)

# build triangulation mesh
> mesh = inla.mesh.create.helper(points=LF_loc,points.domain=borders_UTM,
offset=c(100, 3000), max.edge=c(800, 6000), min.angle = c(26,21))

# plot mesh
> plot(mesh)
> lines(borders_UTM, lwd=6)
> points(LF_loc, pch=20,cex=6, col=2)

# SPDE
> spde = inla.spde2.matern(mesh=mesh, alpha=2)

> LF_Dataset_cord_UTM = read.csv("LF_Dataset_cord_UTM.csv", header =
TRUE)
> LF_dataset$UTMX <- LF_Dataset_cord_UTM$UTMX
> LF_dataset$UTMY <- LF_Dataset_cord_UTM$UTMY

> A.est =
inla.spde.make.A(mesh,loc=as.matrix(LF_coordinates[LF_dataset$Site,c("UTM
X","UTMY")]),group=LF_dataset$time,n.group=n_occasions)
```

```

> if (!exists("i_day")) { i_day = 10 }
> which_date = unique(LF_dataset$Occasion)[i_day]
> A.pred = inla.spde.make.A(mesh, group=i_day, n.group=n_occasions)
> field.indices =
inla.spde.make.index("field",n.spde=spde$n.spde,n.group=n_occasions)

# Stack
> stack.est = inla.stack(data=list(logCHIMP_det=LF_dataset$logCHIMP_det),
A=list(A.est, 1), effects=list(c(field.indices, list(Intercept=1)),
list(LF_dataset[,6:27])),tag="est")
> scaled.mesh.loc = list(UTMX=(rep(scale(mesh$loc[,1],
mean_covariates["UTMX"], sd_covariates["UTMX"]), n_occasions)),
UTMY=(rep(scale(mesh$loc[,2], mean_covariates["UTMY"],
sd_covariates["UTMY"]), n_occasions)))

> stack.pred = inla.stack(data=list(logCHIMP_det=NA), A=list(A.pred),
effects=list(c(field.indices, scaled.mesh.loc, list(Intercept=1))),
tag="pred")
> stack = inla.stack(stack.est, stack.pred)

# Run models
# Intercept only
> formula_1 <- (logCHIMP_det ~ -1 + Intercept + f(field, model = spde,
group = field.group, control.group = list(model="ar1")))
> result_1 = inla(formula_1, data = inla.stack.data(stack, spde=spde),
family = "gaussian", control.predictor = list(A=inla.stack.A(stack),
compute=TRUE), control.compute = list(dic = TRUE))

# Best model
> formula_26 <- (logCHIMP_det ~ -1 + Intercept + mango_baobab +
orange_lime_papaya + other_wild + palm_fruit + dist_road +
dist_agriculture + dist_village + hum_det + f(field, model = spde, group
= field.group, control.group = list(model="ar1")))
> result_26 = inla(formula_26, data = inla.stack.data(stack, spde=spde),
family = "gaussian", control.predictor = list(A=inla.stack.A(stack),
compute=TRUE), control.compute = list(dic = TRUE))

```

## Appendix 6.2

Details of the human spatiotemporal model ran to extract the human detection covariate for chimpanzee models.

Posterior mean, standard deviation, credible interval quantiles and mode of the intercept for the human spatiotemporal model.

|           | Mean  | $\pm$ SD | 2.5%  | 50%   | 97.5% | Mode  |
|-----------|-------|----------|-------|-------|-------|-------|
| Intercept | 0.193 | 0.031    | 0.131 | 0.193 | 0.256 | 0.193 |

Posterior estimates (mean, standard deviation, and credible interval quantiles) of hyperparameters of human model.

| Parameter           | Mean    | $\pm$ SD     | 2.5%   | 50%    | 97.5%  |
|---------------------|---------|--------------|--------|--------|--------|
| $\sigma_\epsilon^2$ | 0.0076  | $\pm 0.0019$ | 0.0045 | 0.0074 | 0.0119 |
| $\sigma_\omega^2$   | 0.4098  | $\pm 0.4861$ | 0.066  | 0.2532 | 1.708  |
| $a$                 | 0.8587  | $\pm 0.0321$ | 0.7863 | 0.8621 | 0.9114 |
| $\rho$              | 215.209 | $\pm 97.064$ | 66.74  | 202.90 | 435.83 |

$\sigma_\epsilon^2$  = measurement error of variance referred to as nugget effect (Cressie and Wikle 2015);  $\sigma_\omega^2$  = marginal variance of the Gaussian Markov Random Field (Lindgren et al. 2011);  $a$  = temporal autocorrelation coefficient AR(1);  $\rho$  = empirically derived spatial autocorrelation.



### Appendix 6.3

List of chimpanzee spatiotemporal models considered for this study. Models are listed in ascending order based on their Deviance Information Criterion (DIC). *Italic* indicates experimental covariates.

| #  | Model formula <sup>1</sup>                                                                                                                                                 | DIC       |
|----|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|
| 1  | logCHIMP_det ~ -1 + Intercept + mango_baobab + orange_lime_papaya + other_wild + palm_fruit + dist_road + dist_agriculture + dist_village + hum_det                        | -876.183  |
| 2  | logCHIMP_det ~ -1 + Intercept + mango_baobab + orange_lime_papaya + other_wild + <i>palm_fruit_flower</i> + dist_road + dist_agriculture + dist_village + hum_det          | -873.4836 |
| 3  | logCHIMP_det ~ -1 + Intercept + cashew + mango_baobab + orange_lime_papaya + other_wild + <i>palm_fruit_flower</i> + dist_road + dist_agriculture + dist_village + hum_det | -873.1251 |
| 4  | logCHIMP_det ~ -1 + Intercept + other_wild + <i>mango</i> + palm_fruit + dist_village + dist_road + dist_agriculture                                                       | -871.8642 |
| 5  | logCHIMP_det ~ -1 + Intercept + mango_baobab + orange_lime_papaya + other_wild + <i>palm_fruit_flower</i> + dist_road + dist_agriculture + dist_village                    | -865.6124 |
| 6  | logCHIMP_det ~ -1 + Intercept + cashew + mango_baobab + orange_lime_papaya + other_wild + <i>palm_fruit_flower</i> + dist_road + dist_agriculture + dist_village           | -863.8927 |
| 7  | logCHIMP_det ~ -1 + Intercept + other_wild + <i>mango</i> + <i>orange</i> + palm_fruit + dist_village + dist_road + dist_agriculture                                       | -863.6144 |
| 8  | logCHIMP_det ~ -1 + Intercept + <i>mango</i> + palm_fruit + dist_village + dist_road + dist_agriculture                                                                    | -863.2789 |
| 9  | logCHIMP_det ~ -1 + Intercept + mango_baobab + orange_lime_papaya + other_wild + palm_fruit + dist_road + dist_agriculture + dist_village                                  | -863.2046 |
| 10 | (logCHIMP_det ~ -1 + Intercept + other_wild + <i>mango</i> + <i>lime</i> + palm_fruit + dist_village + dist_road + dist_agriculture                                        | -862.7232 |
| 11 | logCHIMP_det ~ -1 + Intercept + other_wild + <i>mango</i> + <i>orange</i> + <i>lime</i> + palm_fruit + dist_village + dist_road + dist_agriculture                         | -860.8915 |
| 12 | logCHIMP_det ~ -1 + Intercept + <i>mango</i> + <i>lime</i> + palm_fruit + dist_village + dist_road + dist_agriculture                                                      | -854.6223 |
| 13 | logCHIMP_det ~ -1 + Intercept + mango_baobab + orange_lime_papaya + <i>palm_fruit_flower</i> + dist_road + dist_agriculture + dist_village                                 | -853.9072 |
| 14 | logCHIMP_det ~ -1 + Intercept + mango_baobab + palm_fruit + dist_road + dist_agriculture + dist_village                                                                    | -853.1466 |
| 15 | logCHIMP_det ~ -1 + Intercept + mango_baobab + orange_lime_papaya + palm_fruit + dist_road + dist_agriculture + dist_village                                               | -852.5249 |
| 16 | logCHIMP_det ~ -1 + Intercept + <i>mango</i> + <i>orange</i> + <i>lime</i> + palm_fruit + dist_village + dist_road + dist_agriculture                                      | -849.7772 |
| 17 | logCHIMP_det ~ -1 + Intercept + other_wild + <i>mango</i> + <i>orange</i> + <i>lime</i> + <i>baobab</i> + palm_fruit + dist_village + dist_road + dist_agriculture         | -837.9667 |
| 18 | logCHIMP_det ~ -1 + Intercept + mango_baobab + other_wild + palm_fruit + dist_road + dist_agriculture + dist_village + hum_det                                             | -836.8573 |

| #  | Model formula <sup>1</sup>                                                                                                                                                                                          | DIC       |
|----|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|
| 19 | logCHIMP_det ~ -1 + Intercept + other_wild + palm_fruit + dist_village + hum_det + dist_road + dist_agriculture                                                                                                     | -836.8367 |
| 20 | logCHIMP_det ~ -1 + Intercept + <i>all_cultivated</i> + <i>all_wild_fruit</i> + dist_road + dist_agriculture + dist_village + hum_det                                                                               | -833.7548 |
| 21 | logCHIMP_det ~ -1 + Intercept + mango_baobab + orange_lime_papaya + other_wild + palm_fruit + dist_road + dist_agriculture + dist_village + dist_forest + hum_det                                                   | -833.0964 |
| 22 | logCHIMP_det ~ -1 + Intercept + cashew + mango_baobab + orange_lime_papaya + <i>all_wild_fruit</i> + dist_road + dist_agriculture + dist_village + hum_det                                                          | -829.1476 |
| 23 | logCHIMP_det ~ -1 + Intercept + other_wild + palm_fruit + dist_village + dist_road + dist_agriculture                                                                                                               | -825.9653 |
| 24 | logCHIMP_det ~ -1 + Intercept + cashew + mango_baobab + orange_lime_papaya + palm_fruit + other_wild + dist_village + dist_road + dist_agriculture + dist_forest + hum_det                                          | -824.8204 |
| 25 | logCHIMP_det ~ -1 + Intercept + <i>mango</i> + <i>orange</i> + <i>lime</i> + <i>papaya</i> + <i>baobab</i> + palm_fruit + other_wild + dist_village + dist_road + dist_agriculture + dist_forest + hum_det          | -824.8046 |
| 26 | logCHIMP_det ~ -1 + Intercept + cashew + <i>mango</i> + <i>orange</i> + <i>lime</i> + <i>papaya</i> + <i>baobab</i> + palm_fruit + other_wild + dist_village + dist_road + dist_agriculture + dist_forest + hum_det | -824.0081 |
| 27 | logCHIMP_det ~ -1 + Intercept + palm_fruit + dist_road + dist_agriculture + dist_village                                                                                                                            | -823.9704 |
| 28 | logCHIMP_det ~ -1 + Intercept + other_wild + <i>mango</i> + <i>orange</i> + <i>lime</i> + palm_fruit + dist_village + dist_road + dist_agriculture + hum_det                                                        | -823.1168 |
| 29 | logCHIMP_det ~ -1 + Intercept + cashew + <i>mango</i> + <i>orange</i> + <i>lime</i> + <i>papaya</i> + <i>baobab</i> + palm_fruit + other_wild + dist_village + dist_road + dist_agriculture + hum_det               | -823.0156 |
| 30 | logCHIMP_det ~ -1 + Intercept + <i>mango</i> + <i>orange</i> + <i>lime</i> + <i>papaya</i> + palm_fruit + other_wild + dist_village + dist_road + dist_agriculture + dist_forest + hum_det                          | -820.7377 |
| 31 | logCHIMP_det ~ -1 + Intercept + other_wild + <i>mango</i> + <i>orange</i> + <i>lime</i> + palm_fruit + dist_village + dist_road + dist_agriculture + dist_forest                                                    | -819.2387 |
| 32 | logCHIMP_det ~ -1 + Intercept + cashew + <i>mango</i> + <i>orange</i> + <i>lime</i> + <i>papaya</i> + <i>baobab</i> + palm_fruit + other_wild + dist_village + dist_road + dist_agriculture + dist_forest           | -819.1689 |
| 33 | logCHIMP_det ~ -1 + Intercept + <i>mango</i> + <i>orange</i> + <i>lime</i> + <i>baobab</i> + palm_fruit + other_wild + dist_village + dist_road + dist_agriculture + dist_forest + hum_det                          | -818.652  |
| 34 | logCHIMP_det ~ -1 + Intercept + other_wild + <i>mango</i> + <i>orange</i> + <i>lime</i> + <i>papaya</i> + palm_fruit + dist_village + dist_road + dist_agriculture                                                  | -818.1593 |
| 35 | logCHIMP_det ~ -1 + Intercept + <i>mango</i> + <i>orange</i> + <i>lime</i> + <i>papaya</i> + <i>baobab</i> + palm_fruit + dist_village + dist_road + dist_agriculture + dist_forest + hum_det                       | -812.0253 |
| 36 | logCHIMP_det ~ -1 + Intercept                                                                                                                                                                                       | -779.4442 |

<sup>1</sup> Formulae reported in table omit “+ f(field, model = spde, group = field.group, control.group = list(model="ar1"))” which was included in all models.

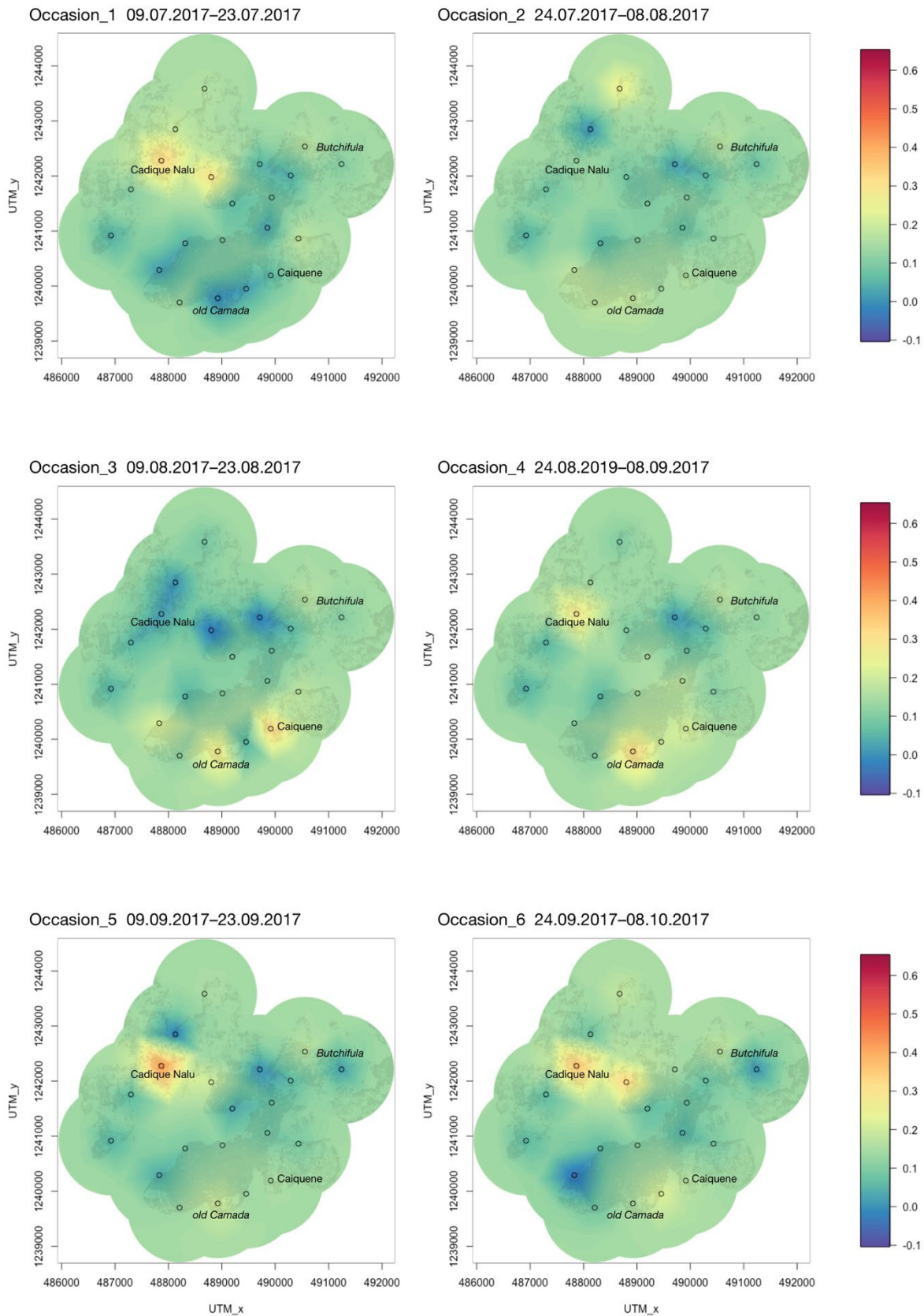
## Appendix 6.4

Posterior mean of the intercept and covariate coefficients  $\beta$  for full model, including standard deviations, credible intervals quantiles and mode.

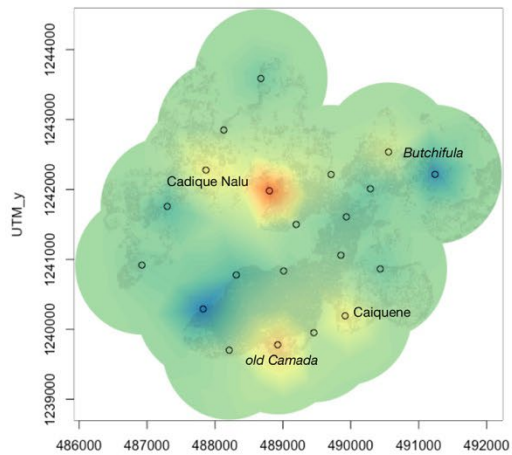
| Covariate          | mean    | $\pm$ SD     | 2.5%    | 50%     | 97.5%   | mode    |
|--------------------|---------|--------------|---------|---------|---------|---------|
| Intercept          | 0.1446  | $\pm 0.0206$ | 0.1035  | 0.1447  | 0.1850  | 0.1449  |
| cashew             | 0.0000  | $\pm 0.0113$ | -0.0223 | 0.0000  | 0.0222  | 0.0000  |
| mango_baobab       | -0.0133 | $\pm 0.0120$ | -0.0369 | -0.0133 | 0.0104  | -0.0133 |
| orange_lime_papaya | 0.0116  | $\pm 0.0120$ | -0.0120 | 0.0116  | 0.0352  | 0.0116  |
| palm_fruit         | 0.0189  | $\pm 0.0099$ | -0.0005 | 0.0189  | 0.0383  | 0.0190  |
| other_wild         | 0.0018  | $\pm 0.0098$ | -0.0175 | 0.0018  | 0.0211  | 0.0018  |
| dist_village       | 0.0797  | $\pm 0.0228$ | 0.0350  | 0.0796  | 0.1252  | 0.0793  |
| dist_road          | -0.0940 | $\pm 0.0228$ | -0.1392 | -0.0939 | -0.0492 | -0.0938 |
| dist_agriculture   | 0.0342  | $\pm 0.0201$ | -0.0054 | 0.0342  | 0.0738  | 0.0342  |
| dist_forest        | 0.0060  | $\pm 0.0203$ | -0.0337 | 0.0059  | 0.0465  | 0.0056  |
| hum_det            | 0.0007  | $\pm 0.0140$ | -0.0267 | 0.0007  | 0.0282  | 0.0007  |

## Appendix 6.5

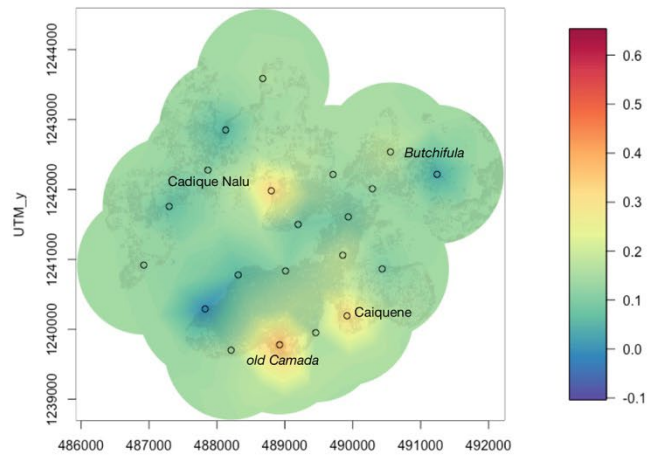
Posterior mean of chimpanzee intensity of space use across 12 months. Each map represents a sampling occasion (N = 24).



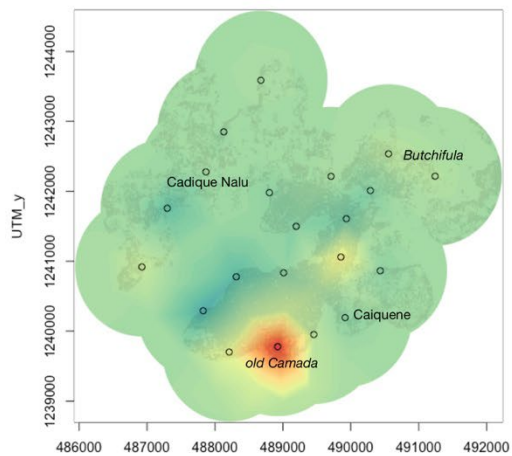
Occasion\_7 09.10.2017–23.10.2017



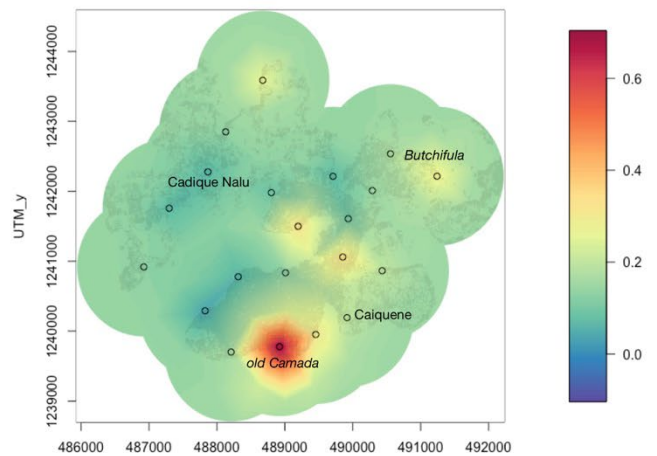
Occasion\_8 24.10.2017–08.11.2017



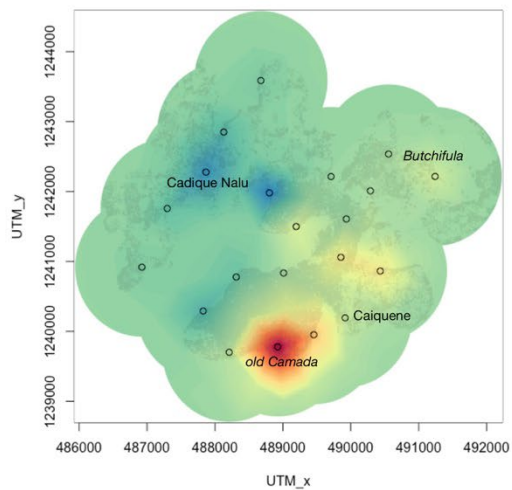
Occasion\_9 09.11.2017–23.11.2017



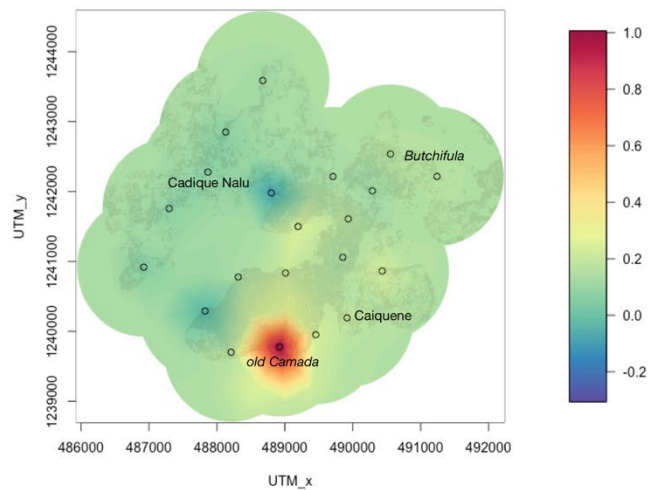
Occasion\_10 24.11.2017–08.12.2017



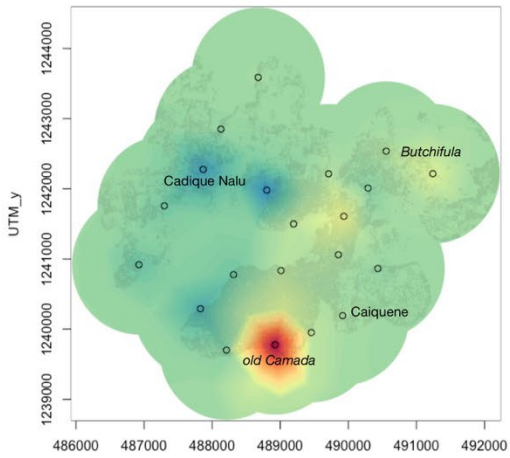
Occasion\_11 09.12.2017–23.12.2017



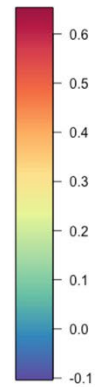
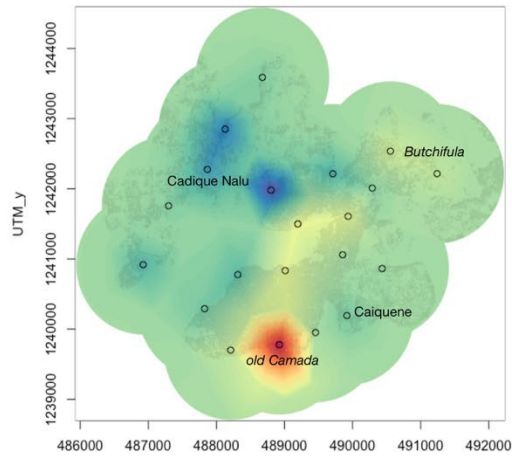
Occasion\_12 24.12.2017–08.01.2018



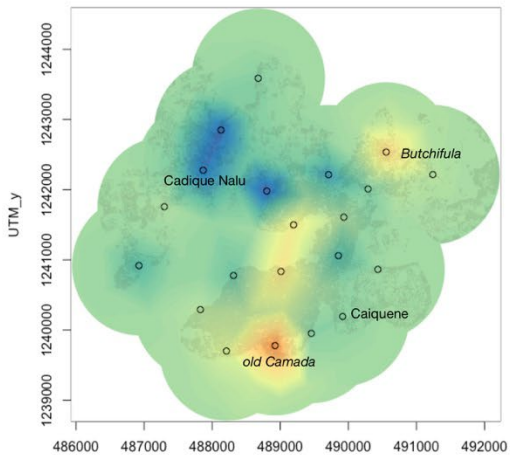
Occasion\_13 09.01.2018–23.01.2018



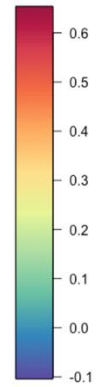
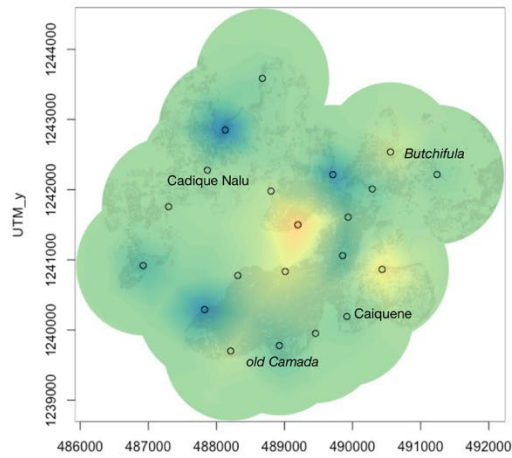
Occasion\_14 24.01.2018–08.02.2018



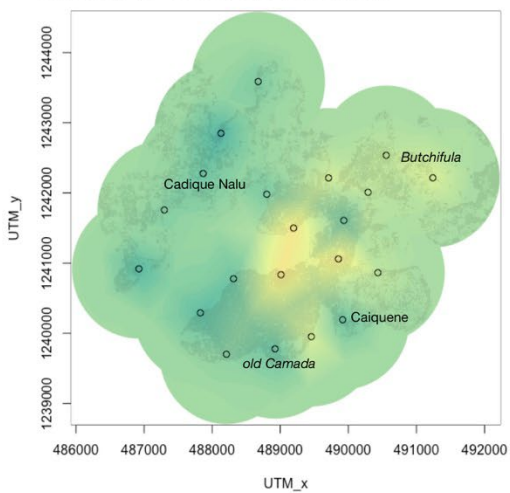
Occasion\_15 09.02.2018–23.02.2018



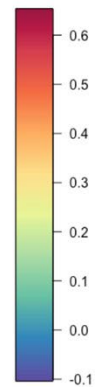
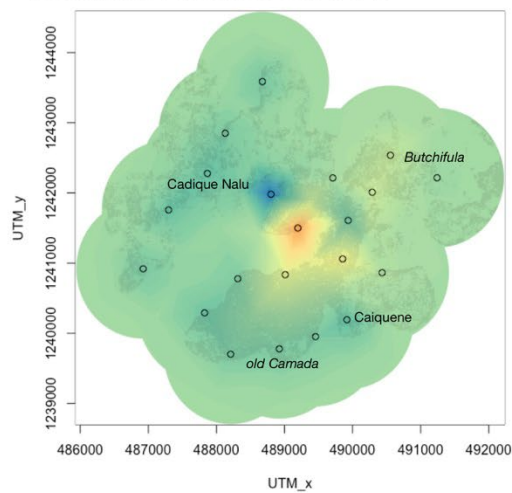
Occasion\_16 24.02.2018–08.03.2018



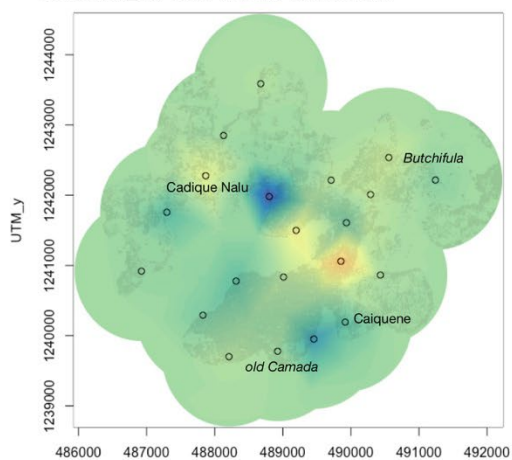
Occasion\_17 09.03.2018–23.03.2018



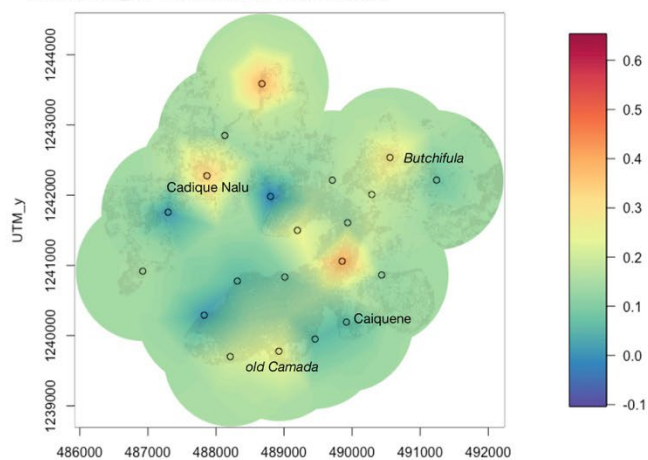
Occasion\_18 24.03.2018–08.04.2018



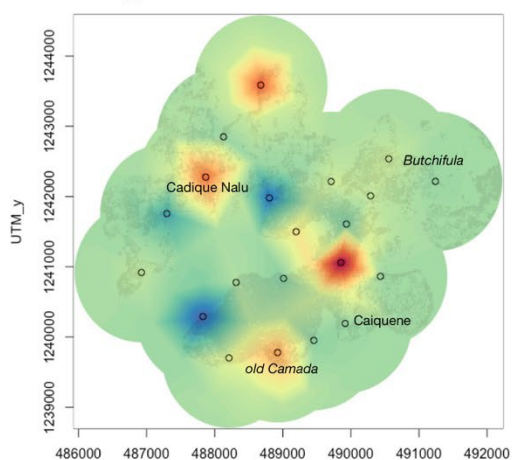
Occasion\_19 09.04.2018–23.04.2018



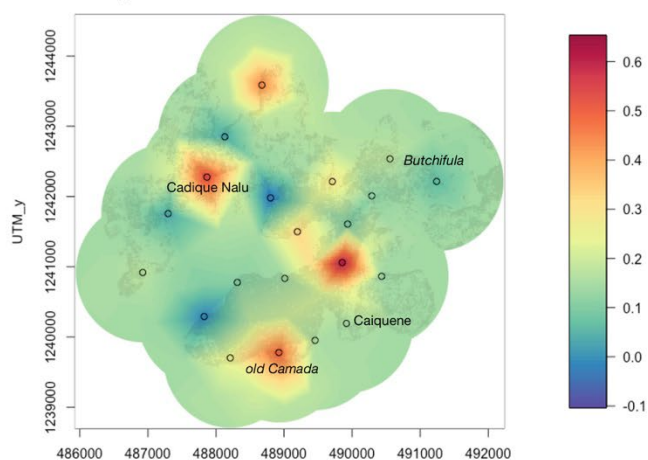
Occasion\_20 24.04.2018–08.05.2018



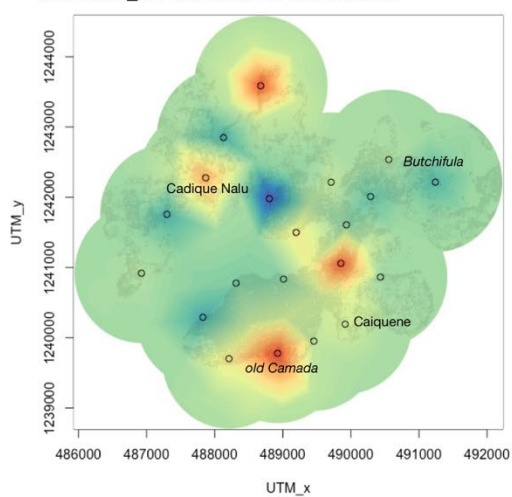
Occasion\_21 09.05.2018–23.05.2018



Occasion\_22 24.05.2018–08.06.2018



Occasion\_23 09.06.2018–23.06.2018



Occasion\_24 24.06.2018–05.07.2018

