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par

Thomas PRIN

Compréhension des mécanismes responsables de la faible densité de la population de buffles (*Syncerus caffer caffer*) de la Réserve Nationale de Niassa Mozambique

Jury

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AVANT-PROPOS

Cette thèse a été réalisée dans le cadre du "Projet Buffle" de la Réserve Nationale de Niassa (Mozambique) qui visait à identifier les facteurs responsables de la faible densité de buffles observée dans la Réserve.

Ce projet a été initié en octobre 2009 sur la base d'un financement de la Société d'écotourisme de Metapiri (Mozambique) attribué à la Fondation Internationale pour la Gestion de la Faune (Fondation IGF, Paris, France). Le Projet Buffle a été rédigé par la Fondation IGF en collaboration avec le CNRS (Laboratoire de Biométrie et Biologie Evolutive UMR 5558, Université Claude Bernard, Lyon I, France) et a fait l'objet d'un protocole d'accords signé entre la Fondation IGF et la Société de Gestion et Développement de la Réserve Nationale de Niassa (Sociedade para a Gestão e Desenvolvimento da Reserva Nacional do Niassa, SGDRN, Maputo, Moçambique) pour une durée de trois ans.

Cette thèse a été encadrée par le CNRS (UMR 5558), en collaboration avec le CIRAD (UR Animal et Gestion Intégrée des Risques, AGIRs, Montpellier, France).

RESUME

La Réserve Nationale de Niassa (RNN, Mozambique) est une des plus grandes aires protégées en Afrique (42,140 km^2) et inclut une population humaine d'environ 39,000 résidents au sein de ses limites. La RNN a subit 10 ans de guerre d'indépendance (1964-1974) puis 15 ans de guerre civile (1977-1992), périodes pendant lesquelles les populations animales ont fortement diminué. Malgré d'importants efforts de conservation, les densités de la communauté d'herbivores y sont très faibles comparées à d'autres systèmes de savanes similaires, notamment la densité de la population de buffles qui est considérée comme une espèce clé dans l'industrie locale des trophées de chasse et est donc logiquement devenue une priorité de gestion pour la RNN.

Nous avons répondu à cette problématique à travers trois protocoles. Premièrement, nous avons analysé les données de 5 comptages aériens (2002-2011), réalisés en fin de saison sèche, afin d'explorer les relations entre la distribution de la population de buffles et plusieurs variables environnementales, reflétant les équilibres à long terme et à large échelle avec les ressources clés. Deuxièmement, nous avons étudié les stratégies d'utilisation de l'espace et de sélection de l'habitat de 9 troupeaux de buffles dans des zones contrastées et sur une période de 3 ans. Enfin, nous avons analysé les potentiels impacts directs et indirects des moyens de subsistance des foyers locaux sur le buffle et les ressources naturelles à partir de questionnaires réalisés dans des villages contrastés.

Les résultats montrent que l'arrangement spatial des rivières permanentes et de l'eau résiduelle dans le réseau hydrographique secondaire est principalement responsable de la distribution de la population de buffles dans la RNN en saison sèche. La taille des domaines vitaux fait partie des plus grandes jamais observée pour cette espèce avec de larges mouvements saisonniers en réponse à une ségrégation des ressources. Les feux de brousse contraignent fortement la sélection de l'habitat et leur ampleur limite énormément la disponibilité en fourrage pour le buffle. Aucun évitement évident de la présence humaine (proximité aux villages / routes) n'a été observé par les deux premiers protocoles, mais les réponses aux questionnaires suggèrent un potentiel impact du braconnage sur la dynamique de la population de buffles.

Ces résultats fournissent de précieuses informations aux gestionnaires d'aires protégées. A une si grande échelle, en raison de l'hétérogénéité des covariables environnementales, les actions de gestion doivent être adaptées aux zones contrastées de la RNN.

ABSTRACT

The Niassa National Reserve (NNR, Mozambique) is one of the vastest protected areas in Africa (42,140 km^2) and includes around 39,000 local residents within the limits of the Reserve. NNR suffered from 10 years of independence war (1964-1974) and 15 years of civil war (1977-1992), during which wildlife population decreased substantially. Despite important conservation efforts, the density of ungulate community remains strikingly low compared to other similar savanna systems, especially buffalo which is considered as a key asset for the local trophy hunting industry and has logically become a management priority for the NNR.

We addressed this issue through three main protocols. First, we investigated data from 5 aerial surveys (2002-2011) at the end of the dry season to explore relationships between buffalo distribution and environmental covariates, reflecting large scale and long-term equilibriums with key resources. Second, we investigated space use and habitat selection strategies at annual and seasonal scales by GPS tracking the movements of 9 buffalo herds in contrasted areas over 3 years. Third, we assessed the potential direct and indirect impacts of household's livelihood on buffalo and natural resources using questionnaires in contrasted villages.

Results show that the spatial arrangement of permanent rivers and residual water in seasonal tributaries strongly drives buffalo distribution within NNR in the dry season. Home range sizes were among the largest on record for the species with large seasonal movements in response to segregated resources. Bushfires appeared to strongly constraint habitat selection and the magnitude of their extension to greatly limit the availability of forage for buffalo. No obvious avoidance of human activities (villages/road proximity) was observed by the first two protocols, but responses to the questionnaires suggest a potentially severe impact of poaching on buffalo population dynamics.

Results provide valuable information for wildlife managers. At such a large scale, due to the heterogeneity of environmental covariates, management actions must be adapted to the contrasting zones within NNR.

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Je remercie les personnes et organisations suivantes pour m'avoir apporté leurs appuis et soutiens et m'avoir permis de mener à bien cette étude :

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Pierre Poilecot et Nicolas Ganzin

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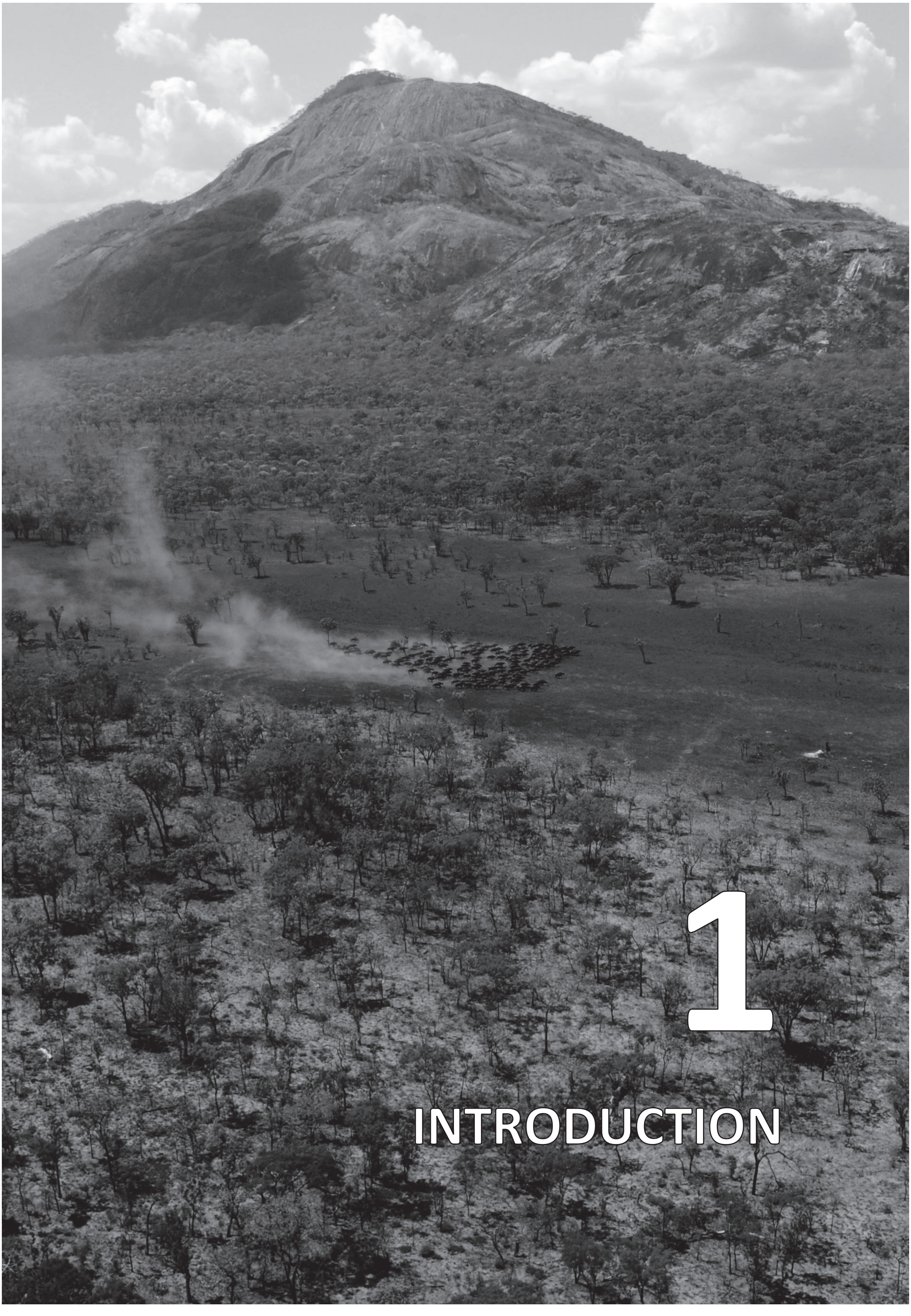
PREAMBULE

Cette thèse est constituée de sept chapitres dont trois (Chapitres 4, 5 et 6) sont au format d'articles en préparation ou soumis dans des revues internationales. Les tables et les figures sont insérées dans le texte et la bibliographie est compilée par chapitre et insérée à la fin de chacun d'entre eux. Trois chapitres étant au format d'articles, certains tableaux et/ou figures sont présentés plusieurs fois dans cette thèse. Afin de faciliter la lecture de cette thèse pour nos collègues et partenaires étrangers, les tables et les figures sont en anglais. Les chapitres 1, 2, 3 et 7 sont rédigés en français. Les annexes, qui incluent un chapitre d'un livre co-écrit et imprimé en novembre 2014, des fiches de terrain et un nombre important de cartes, sont disponibles à la fin du document. Certaines cartes, déjà insérées dans le corps du texte, sont présentées à nouveau dans les annexes au format A4 afin de faciliter leur lecture.

TABLE DES MATIERES



1

INTRODUCTION

INTRODUCTION

L'Etre humain accorde une grande importance à la nature et aux espèces sauvages dans de nombreux contextes et situations mais il les considère, dans son ensemble, comme des ressources. L'impact des humains sur la planète continue son incessante modification des écosystèmes naturels ainsi que la destruction de la biodiversité. Dans un monde où la population humaine ne cesse de croître, les espaces naturels se fragmentent, la biodiversité ne cesse de décliner à des taux alarmants, et la pression sur les ressources reste en constante augmentation (Butchart et al. 2010). Ce triste constat pose une question: quelles sont nos chances de conserver ce monde naturel et les services éco-systémiques qui lui sont associés ? Fort heureusement, la notion de protection de l'héritage naturel est presque universelle, allant de la réserve de chasse traditionnelle aux espaces protégées du patrimoine mondial de l'humanité (Chape et al. 2005; Jones 2006), et approximativement 12% de la surface du globe est aujourd'hui recouverte d'aires protégées (Chape et al. 2008). Bien que l'établissement des ces aires protégées soit un remarquable accomplissement, la faune sauvage s'y trouve souvent confinée par une insularisation progressive (Newmark 2008). Les conflits entre l'homme et la faune n'ont pas disparu, voire dans de nombreux cas ont été amplifiés par la mise en place de nouveaux espaces protégés, associés à une spoliation de l'accès aux terres (Brockington and Igoe 2006). L'efficacité de ces aires protégées est même par endroit remise en cause (Western et al. 2009; Craigie et al. 2010). Assurer une coexistence durable entre l'homme et la faune sauvage reste un enjeu d'actualité majeur dans le monde. Les nouveaux mandats des aires protégées, incluant le développement local et l'amélioration du bien-être (Naughton-Treves et al. 2005; Hutton et al. 2005), en font théoriquement des instruments privilégiés pour relever ce défi planétaire.

Les fortes diversités et densités de la faune sauvage sur le continent africain ont toujours fasciné le monde occidental (Leuthold 1977). L'Afrique abrite des peuplements de grands mammifères (masse corporelle > 5 kg) uniques par leur diversité (Keast 1969) et leur importance dans le fonctionnement des écosystèmes (McNaughton and Georgiadis 1986). Ce continent est caractérisé par une hétérogénéité géologique substantielle, une multitude de reliefs, de climats, et donc de forts gradients de pluviométrie et de végétation. C'est cette diversité d'habitats qui confère à l'Afrique l'incroyable richesse de ses peuplements de grands mammifères. Cependant, l'établissement des aires protégées y a historiquement été associé à l'expulsion des populations locales de leur territoire ancestral (Brockington and Igoe 2006), ce qui a logiquement impacté négativement leurs moyens de subsistance en limitant l'accès aux ressources naturelles (Ghimire et al. 1997). Cette histoire complexe a perpétué l'association négative qu'ont eue les populations locales avec les aires protégées et le défi est désormais de redresser la balance et d'impliquer les populations locales dans un large éventail d'actions et de développement au niveau de la conservation et de la gestion des aires protégées (Twyman 2001; West et al. 2006; Phillipson et al. 2009). Entre 1970 et 2005, il est estimé que l'effectif global des grands mammifères africains au sein des aires protégées a chuté d'environ 60% à l'échelle du continent (Craigie et al. 2010). Ce déclin a des origines complexes aux échelles locales et régionales mais les causes principales semblent être la sur-chasse et la transformation des habitats, toutes deux stimulées par la rapide croissance de la population humaine et la consommation de ressources naturelles (Baillie et al. 2004).

La Réserve Nationale de Niassa (RNN) au Mozambique est une des plus grandes aires protégées du continent (42,140 km^2) dont l'originalité est d'abriter une population humaine d'environ 39,000 habitants dispersés au sein d'une cinquantaine de villages. Le pays a été ravagé par deux guerres successives, la guerre d'indépendance (1964 - 1974) puis la guerre civile (1977 - 1992) pendant lesquelles les populations animales ont fortement diminuées, notamment en raison d'une chasse intensive qui permettait de nourrir les groupes armés. La RNN abrite néanmoins des communautés animales encore bien représentée avec l'ensemble des espèces herbivores (à l'exception du rhinocéros noir, *Diceros bicornis*, et potentiellement de l'antilope rouanne, *Hippotragus equinus*) et carnivores attendues dans la région. De part l'immense superficie de la RNN, ces populations disposent d'une liberté de déplacement à grande échelle. Depuis 1992, le gouvernement a pris des mesures importantes et innovantes pour la gestion de cette zone à travers une collaboration public/privé. La valorisation économique de cet écosystème se fait quasiment essentiellement par le développement du tourisme cynégétique et de nombreux investissements privés ont été consentis depuis la promotion de ce secteur d'activité. Le maintien de l'intégrité de la RNN reste un défi de taille pour les gestionnaires de la zone.

Les données de comptages aériens disponibles depuis 1998 suggèrent que les densités animales de la RNN restent très faibles (Craig 2012) comparées à celles observées dans d'autres aires protégées proches écologiquement (e.g. Parc Kruger en Afrique du Sud, Parc de Hwange au Zimbabwe, Figure 1.1). Ce constat est particulièrement vrai pour la population de buffles (*Syncerus caffer caffer*) de la Réserve, espèce emblématique à forte valeur patrimoniale du continent (le buffle appartient aux '*Big Five*' qui rassemblent cinq mammifères mis en relief par les autorités touristiques en Afrique dans le cadre des safaris photographiques ou de chasse) et qui est considérée comme un élément de valorisation fort notamment dans l'industrie des trophées de chasse. La population de buffles est logiquement devenue une priorité de gestion pour les gestionnaires de la Réserve (SGDRN 2007). Dans ce contexte où les pressions sur la faune sauvage s'intensifient chaque jour, comprendre les processus écologiques qui régissent les besoins des populations d'ongulés africains est un enjeu majeur. Il est indispensable à la mise en place de politiques de conservation de la biodiversité efficaces tout en limitant les conflits entre l'homme et la faune sauvage. La situation de la RNN, une zone en complète reconstruction après des années de conflits armés, sa très large superficie et la présence de villages au sein de la zone, confèrent à la RNN des atouts de choix pour étudier l'écologie des grands herbivores africains, parmi lesquels le buffle.

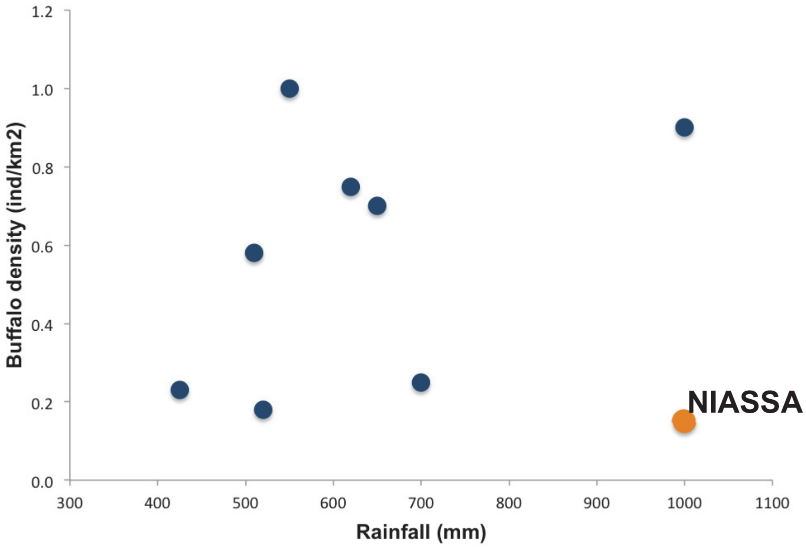


Figure 1.1 - Buffalo population density in NNR and other protected areas situated on old nutrient poor soils in function of mean annual rainfall

La question centrale de cette thèse porte sur la compréhension des mécanismes responsables de la faible abondance de la population de buffles de la RNN. Elle s'inscrit dans la problématique centrale du projet Buffle de Niassa (*Niassa Buffalo Project*) piloté par la Fondation International pour la Conservation de la Faune (IGF). Il existe de nombreux facteurs pouvant limiter les populations de grands mammifères. Hormis des anomalies génétiques générées par des "goulots d'étranglement" démographiques des populations, observées dans l'histoire récente (O'Ryan et al. 1998; van Hooft et al. 2000), ces facteurs peuvent être classés selon deux approches : (i) l'approche *"bottom*-up*"* *(li*t. de bas en haut) lorsque la ressource contrôle la structure et la dynamique de la population et (ii) l'approche *"top-do*wn*"* *(li*t. de haut en bas) lorsque les prédateurs et les agents pathogènes contrôlent la structure et la dynamique de la population (Figure 1.2). Ces deux approches restent aujourd'hui encore largement débattues (Hopcraft et al. 2010). Plusieurs monographies sur le buffle ont montré que la ressource pouvait fortement limiter la population (e.g. Grimsdell 1969; Sinclair 1977; Prins 1996). Les maladies sont également connues pour avoir des impacts importants sur le buffle (Ebedes 1996; Meltzer 1996; Caron et al. 2003), en particulier lorsque les contacts avec le bétail sont fréquents (Foggin 1996; Michel 2002). La récente littérature suggère que les herbivores de masse corporelle importante sont moins sujets à être limités par la prédation (e.g. Sinclair et al. 2003), bien que cela reste à être exploré plus en détail. Cependant, la prédation peut avoir de nombreux effets indirects sur l'utilisation des ressources et de l'habitat (e.g. Creel et al. 2005; Creel et al. 2007 sur le wapiti). Dans le contexte d'un climat tropical, le rôle des feux peut également être crucial car ils ne génèrent pas uniquement des zones de repousses à forte valeur nutritive mais ils peuvent également rentrer en compétition avec les buffles en saison sèche pour l'importante biomasse végétale de faible qualité encore disponible. Les activités humaines sont une source de dérangement additionnelle, qu'il s'agisse de la modification de l'utilisation des ressources et de l'habitat par le buffle ou de la prédation (i.e. braconnage). Dans ce contexte, une liste non-exhaustive d'au moins cinq facteurs peut être envisagée pour tenter de comprendre les mécanismes responsables de la faible densité de buffles observée dans la RNN, ce sont les différents axes du *Niassa Buffalo Project*: (i) la qualité et la quantité du fourrage produit par l'écosystème de la RNN, (ii) la disponibilité de la ressource au cours du temps, potentiellement modifiée par la compétition, le feu ou le risque de prédation (L'écologie de la peur Brown et al. 1999), (iii) la prédation naturelle directe, (iv) la prédation humaine directe et (v) les maladies et la génétique (Figure 1.2).

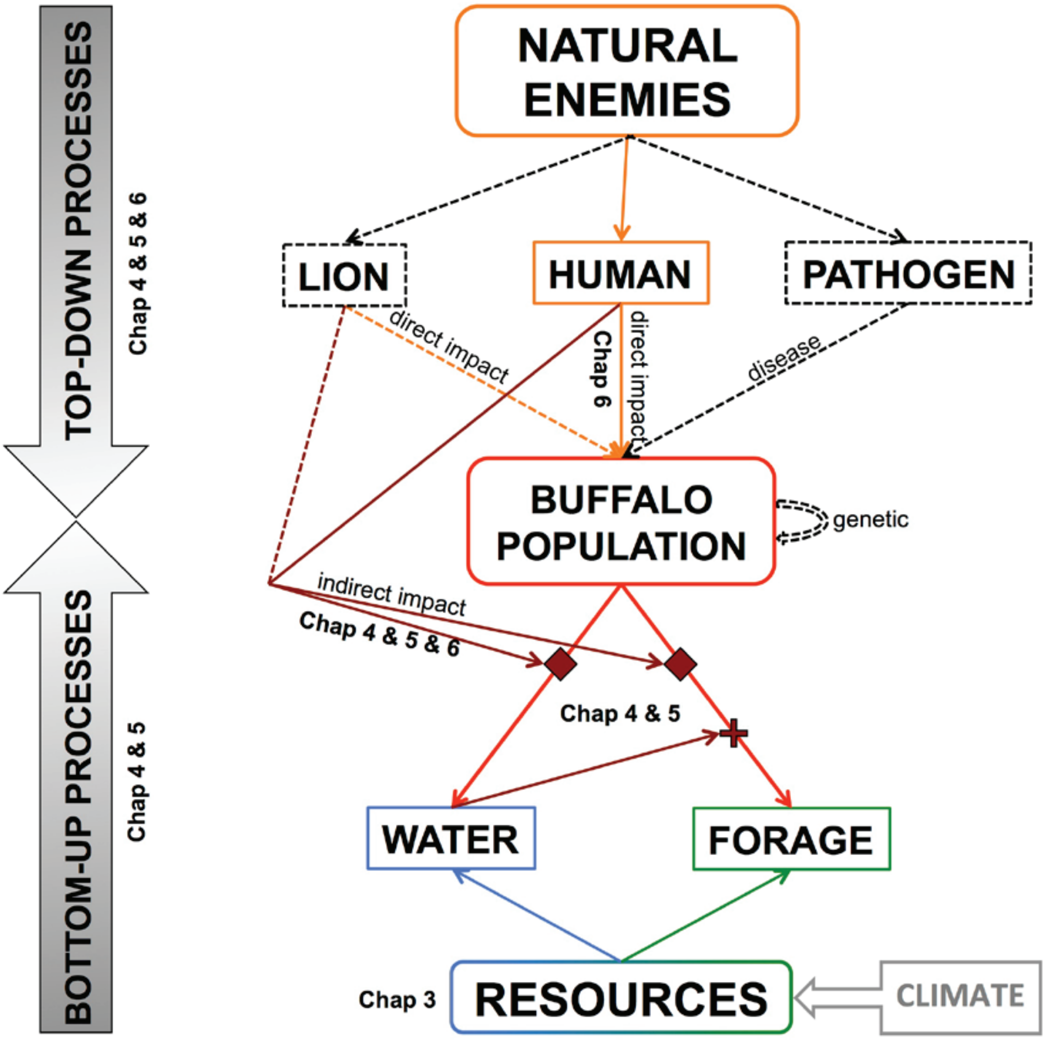


Figure 1.2 - Schematic representation of our approach to understand the mechanisms responsible for the low buffalo population density in Niassa National Reserve

Cette thèse s'inscrivait donc dans un projet de grande ampleur. Chacun des facteurs énumérés ci-avant pourrait faire l'objet d'une thèse à part entière. Il a donc été nécessaire de hiérarchiser les mécanismes potentiellement responsables de la faible densité de buffles observée. Le cœur de mon travail de thèse s'est donc intéressé aux contraintes dans l'approvisionnement en ressources et aux stratégies d'utilisation de l'espace de la population de buffles ainsi qu'à la prédation humaine pour les raisons que je développerai dans la suite de cette introduction. Ancré au sein du *Niassa Buffalo Project*, j'ai également collaboré dans mon travail à apporter des éléments de réponses pour les autres axes du projet, ce qui me permettra de mettre en perspective mon travail sur les ressources et la prédation humaine par rapport aux autres facteurs dans le cadre de la discussion de cette thèse.

Il a longtemps été considéré que les populations d'herbivores étaient contrôlées de manière ascendante (i.e. processus "bottom-up") par les ressources (e.g. Coe et al. 1976; Fritz and Duncan 1994). Dans les écosystèmes de savanes africaines, la distribution spatiale et les stratégies d'utilisation de l'espace des populations animales sont fortement dépendantes de l'hétérogénéité spatiale et temporelle des ressources biotiques et abiotiques (Bailey et al. 1996; Fryxell et al. 2004). Les ressources en eau et en fourrage sont sujettes à une forte variabilité saisonnière et peuvent être ségrégées spatialement à certaines périodes de l'année. Les populations d'herbivores dépendent de zones de ressources clés qui constituent des refuges en saison sèche (Illius and O'Connor 2000). Les grands ongulés sont généralement contraints à faire des compromis entre la nécessité de s'alimenter et de s'abreuver et la disponibilité en eau est elle aussi déterminante et intimement liée à ces zones de ressources clés (Redfern et al. 2003; Chamaillé-Jammes et al. 2008). La dépendance à l'eau varie en fonction des espèces d'ongulés (Owen-Smith 1996). Certains, comme le buffle, ont besoin de boire toutes les 24-48h (Prins 1996), alors que d'autres, généralement les brouteurs (Valeix 2011), sont capables d'extraire de leur alimentation leurs besoins en eau (Western 1975; Owen-Smith et al. 2010).

Néanmoins, le rôle des prédateurs et d'une régulation descendante (i.e. processus "top-down") sont de plus en plus mis en évidence (Sinclair et al. 2003). La prédation fut longtemps considérée uniquement au niveau de la prédation directe mais les risques issus de la prédation, qu'elle soit naturelle et/ou humaine, se sont avérés être une force sélective importante conditionnant potentiellement les stratégies d'utilisation de l'espace des grands ongulés (Ripple and Beschta 2004; Creel et al. 2005; Creel and Christianson 2008). Le paysage du risque, induit par la présence de prédateurs sur une zone, entraine une réponse de la part des proies qui peut se manifester sous de nombreuses formes. L'écologie de la peur (Brown et al. 1999), qui résulte du paysage du risque, peut se manifester au niveau comportemental (Lima 1998), à travers une modification des stratégies d'utilisation de l'espace (Creel et al. 2005), une augmentation de la vigilance (Childress and Lung 2003), des changements dans les tailles des groupes (Fernandez-Juricic 2004; Thaker et al. 2010), ou encore dans les tactiques de déplacements (Sih and McCarthy 2002; Fortin et al. 2005). Dans ces relations prédateurs/proies, le paysage de la peur permet de mesurer à quelle échelle les herbivores favorisent l'occupation d'habitats qui leurs permettent de maximiser leur gain énergétique tout en optimisant leurs chances de survie et de reproduction (Searle et al. 2008).

La distribution de la population d'herbivores de la RNN est fortement polarisée (Craig 2012) et deux zones, la zone Centrale et la zone Est, présentent les plus fortes densités animales ce qui suggèrent que la distribution spatiale des contraintes est cruciale dans l'explication des stratégies d'utilisation de l'espace. Cela s'observe chez les buffles tout comme sur la population d'éléphants, un autre herbivore de masse corporelle importante qui dépend d'importante quantité de fourrage. Cela suggère que la distribution des ressources et/ou les contraintes spatiales à l'utilisation de la ressource doivent être étudiées en détail et que la prédation naturelle est moins à même de jouer un rôle essentiel (les éléphants sont encore moins susceptibles à la prédation naturelle mais suivent le même gradient de distribution que les buffles sur la RNN). La RNN est caractérisée par des savanes boisées peu productives appartenant aux communautés végétales de type *Miombo*. Ces savanes alternent avec des prairies édaphiques inondables dans les zones de dépression où le sol a tendance à être acide (Chidumayo 1997). La strate herbacée est généralement de faible qualité, souvent meilleure dans les prairies mais la croissance y est rapide. De ce fait, la qualité du fourrage diminue rapidement à moins que la strate herbacée soit pâturée ou brûlée. Le buffle est un herbivore ruminant, paisseur, connu pour être capable de se contenter de fourrage de faible qualité (Prins 1996). C'est une espèce grégaire très mobile capable de maintenir un pâturage de bonne qualité à travers l'utilisation de zones de façon cyclique (Bar-David et al. 2009). Si la prédation naturelle est moins susceptible de jouer une régulation descendante sur les buffles de la RNN, la prédation humaine peut fortement impacter cette population, de façon directe comme indirecte. Le buffle est une espèce attractive pour les chasseurs ruraux en raison de sa masse corporelle importante (Marks 1976; Ndibalema and Songorwa 2008). Une chasse intensive de l'espèce peut entrainer son déclin comme cela a été montré en Tanzanie récemment (Metzger et al. 2010). La chasse, au même titre que la prédation naturelle, peut entrainer des réponses comportementales similaires sur la distribution de la population. De plus, les activités des populations locales peuvent bouleverser l'écosystème (e.g. les feux de brousse) et modifier la distribution des ressources et accentuer les contraintes spatiales à l'utilisation de ces dernières. A ma connaissance la RNN est la seule aire protégée d'Afrique australe qui inclut des populations locales au sein même de ses limites. Cette originalité est une source additionnelle forte de dérangement pour les populations animales qu'il m'est apparu essentiel d'étudier en priorité dans la recherche des facteurs responsables de la faible densité de buffles observée dans la RNN. En raison des faibles contacts entre la population de buffles et le bétail, le facteur santé semblait secondaire dès l'initiation du projet.

Très peu de données historiques, qu'il s'agisse de la faune et de la flore, étaient disponibles sur la RNN. Dans ce contexte, afin d'étudier les facteurs potentiellement responsables de la faible densité de buffles sur la RNN, j'ai décidé de focaliser mon travail de thèse sur l'approvisionnement en ressources et les stratégies d'utilisation de l'espace de la population de buffles ainsi que sur la prédation humaine. Afin de répondre aux questions associées au projet, j'ai mobilisé des cadres théoriques variés, qu'il s'agisse de l'écologie des grands herbivores (et en particulier des grands herbivores africains), de l'écologie spatiale, de la sélection de l'habitat, des interactions entre l'homme et la faune sauvage ou encore du rôle de la faune sauvage comme source de protéine dans le régime alimentaire des populations rurales. La structure de ma thèse s'organise en six chapitres qui feront suite à ce premier chapitre introductif.

Le chapitre 2 porte sur les méthodes et les approches mises en œuvre pour répondre aux questions associées à cette thèse. Il n'existait quasiment pas d'archives sur la RNN et il a fallu, dans un premier temps, faire une synthèse des données disponibles et des données qu'il fallait générer pour répondre à notre problématique. Sur une telle superficie, les données satellitaires se sont avérées être un outil de choix. Très peu de données étaient disponibles sur la végétation de la RNN et afin d'étudier l'approvisionnement en ressources et les stratégies d'utilisation de l'espace il était obligatoire d'apporter un premier niveau de connaissances sur cet écosystème. Cette thèse a donc apporté une contribution importante à la connaissance d'un milieu encore mal connu et qui sera présentée dans le chapitre 3. Bien qu'il ne s'agisse pas d'un travail de thèse à part entière, ce chapitre est un premier résultat de ce projet, une présentation générale de la RNN, de son histoire, des ses populations humaines et une description détaillée de l'écosystème à partir des différents protocoles de terrain et des données collectées, traitées et analysées, notamment satellitaires.

En raison de données de comptages aériens disponibles depuis plus de 10 ans sur la zone (et réalisés en fin de saison sèche), et des données sur le milieu physique nouvellement générées, nous nous sommes intéressés aux grandes contraintes qui pesaient sur la distribution spatiale de la communauté d'herbivores dans le chapitre 4. Nous ne nous sommes pas intéressés uniquement à la population de buffles mais à l'ensemble des herbivores de la RNN. La communauté d'herbivores est susceptible de répondre différemment aux grandes contraintes. Ces espèces présentent des écologies différentes, une mobilité plus ou moins importante, des régimes alimentaires plus ou moins spécifiques, une masse corporelle variable et par conséquent une susceptibilité plus ou moins forte à la prédation naturelle et/ou humaine. Ce chapitre nous permet d'identifier les grandes contraintes structurantes qui gouvernent la distribution de la communauté d'herbivores de la RNN à une période clé de l'année, la fin de la saison sèche.

Le chapitre 5 porte spécifiquement sur l'écologie du buffle de la RNN, notamment sur la description des caractéristiques des domaines vitaux et sur la sélection de l'habitat. Le domaine vital est un concept central en écologie car il matérialise un lien entre le déplacement d'un animal et les ressources à sa survie et sa reproduction. C'est un concept clé dans la compréhension des processus écologiques et des mécanismes comportementaux qui structurent les populations animales (Fieberg and Börger 2012). Nous présenterons dans ce chapitre les caractéristiques des domaines vitaux de plusieurs troupeaux de buffles de la RNN, à l'échelle annuelle comme saisonnière. Nous examinerons les interactions spatiales entre les troupeaux ainsi que les caractéristiques des stratégies d'utilisation de l'espace en fonction de deux zones contrastées de la RNN au niveau des covariables environnementales. Nous nous intéresserons ensuite à l'étude de la sélection de l'habitat au sein de ces domaines vitaux. La sélection de l'habitat est un processus hiérarchique qui implique différents niveaux d'organisation (de l'espèce à l'individu), et intervient à différentes échelles spatiales et temporelles (Morrison et al. 2012). Nous identifierons les réponses spatiales des troupeaux aux variations saisonnières de la disponibilité des ressources et décrirons les mécanismes de réponse du buffle dans la RNN à des contraintes qui lui sont propres.

Le chapitre 6 s'intéresse à l'estimation de l'impact potentiel de la présence humaine dans la RNN sur l'abondance et la distribution de la population de buffles. Nous évaluerons la contribution de la viande de brousse dans le régime alimentaire des populations locales à travers une étude socio-économique des foyers de la RNN. Nous identifierons le niveau de dépendance aux ressources naturelles et les impacts directs et indirects de la présence humaine sur la faune sauvage à travers la caractérisation des moyens de subsistance de foyers se trouvant dans des villages contrastés dans leur localisation géographique.

Le chapitre 7 discute de nos résultats et de leurs implications en terme de gestion de la RNN en identifiant les limites de cette étude ainsi que des propositions de recherches futures.

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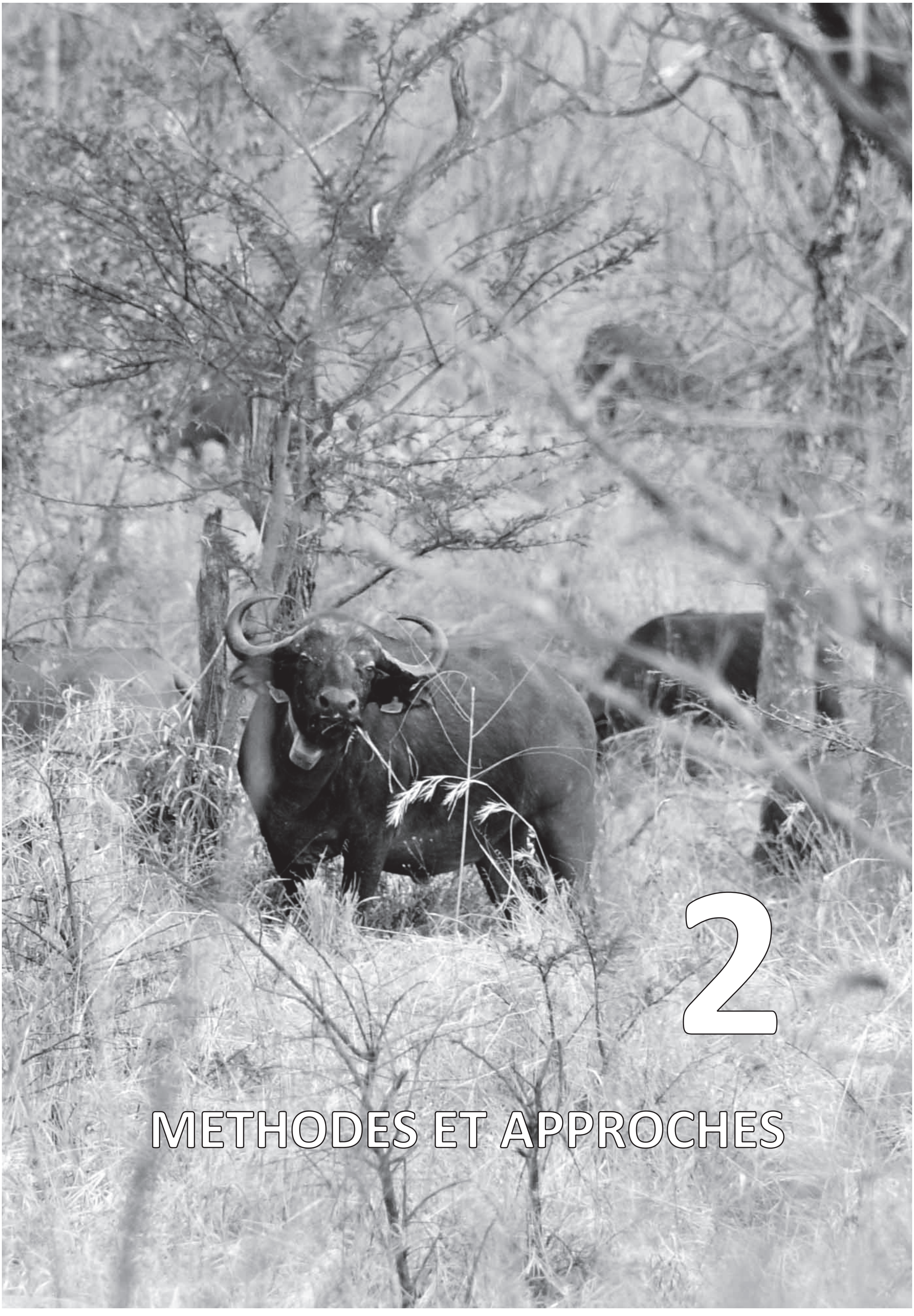

2

METHODES ET APPROCHES

AVANT-PROPOS

CONTEXTE DE L'ETUDE

En 2006, la société gestionnaire de la Réserve Nationale de Niassa (RNN), la SGDRN (cf. Chapitre 3) a lancé un appel d'offre pour l'ouverture à la location de 4 concessions au sein de la RNN. Cet appel d'offre était destiné à des opérateurs privés dans l'objectif de développer des activités de tourisme (tourisme de vision et/ou de chasse sportive) au sein de ces concessions. Pour y répondre, les opérateurs avaient pour impératif de constituer un dossier dans lequel les activités qu'ils souhaiteraient développer au sein de la zone devaient être décrites en détail. Un opérateur, la Société d'écotourisme de Metapiri, avait proposé, sous réserve de l'obtention d'une concession, le financement d'un projet scientifique qui restait à déterminer. En 2007, une concession (i.e. unité de gestion L3, cf. Figure 3.2) leur a été attribuée et la Société d'écotourisme de Metapiri a alors demandé à la Fondation Internationale pour la Gestion de la Faune (IGF, Paris, France) de rédiger un projet scientifique qui se déroulerait sur 3 ans. C'est dans ce contexte qu'est né le "Projet Buffle" de la RNN. Dans le cadre de ce projet de grande envergure, la Fondation IGF identifia rapidement le potentiel de réaliser une thèse de doctorat en son sein et c'est ainsi que cette dernière s'est associée au Centre National de la Recherche Scientifique (CNRS). Le Projet Buffle disposait donc d'une double gérance : le CNRS supervisait la thèse et les protocoles scientifiques mis en place pour y parvenir et la Fondation IGF supervisait quant à elle le projet dans sa globalité tout en rendant compte régulièrement à la société gestionnaire de la RNN des avancements de l'étude qui débuta en 2009.

ORGANISATION - LOGISTIQUE

Une thèse n'est bien entendu pas un journal de bord. Néanmoins, il me paraissait nécessaire et important de décrire brièvement la mise en place logistique d'une étude de grande envergure dans une zone réputée comme la plus reculée du pays et les conditions de vie associées. Il ne s'agit pas de "sciences" à proprement dit mais ces informations permettront aux lecteurs de mieux appréhender le cadre de cette étude ainsi que les objectifs associés.

La RNN, une immensité sauvage dont la superficie dépasse celle de la Suisse, est restée très préservée et peu connue du grand public, qu'il s'agisse du tourisme ou du monde scientifique. Les conflits qui ont ravagé le pays depuis les années 70 et jusqu'au début des années 90 en sont certainement responsables en partie, tout comme les difficultés d'accès, aujourd'hui encore, de cette zone. Excepté quelques données sur la faune (7 comptages aériens totaux depuis 1998) et la flore (3 missions spécifiques sur la végétation depuis 2004), le peu de données scientifiques disponibles sur la RNN impliquait un important travail de terrain afin de répondre aux objectifs fixés par le Projet.

Trois années de terrain ont été nécessaires à la mise en place des protocoles scientifiques et la récolte des données (2010, 2011 et 2012). Entre 7 et 8 mois par an étaient passés sur le site. Un retour en France d'environ 4 mois par an permettait la mise en propre des données collectées, l'évaluation des protocoles et de rendre compte aux différents organismes de l'état d'avancement du Projet (en France et au Mozambique). L'équipe était constituée de trois travailleurs locaux (deux pisteurs et un aide camp) et moi même. Nous vivions en pleine autonomie et avons passé les 8 premiers mois de terrain (2010) en campements volants dans les différents sites de la RNN où se trouvaient les troupeaux de buffles suivis (cf. A1.2). La ville la plus proche dans laquelle il était possible de se ravitailler, d'effectuer des réparations sur notre véhicule et qui disposait d'un aéroport international était la ville de Pemba, en bordure de l'océan indien. Il fallait compter, depuis le Centre de la RNN, 14 heures de voiture pour s'y rendre (500 km), trajet que nous réalisions une fois tous les deux mois environ. Suite à la première année de terrain et aux difficultés associées à la vie en campements volants pendant 8 mois, la SGDRN nous a autorisés à établir un campement de base en bordure de rivière (aucune construction en dur). Deux nouveaux travailleurs locaux sont venus agrandir l'équipe afin d'aider aux travaux du camp et à le garder. Nous pouvions donc y stocker tout notre matériel ainsi que la nourriture et le travail s'organisait désormais en missions de deux semaines pendant lesquelles nous nous rendions sur une zone de la RNN pour travailler sur un ou plusieurs troupeaux puis nous retournions sur le camp afin de mettre au propre les données collectées, remettre en état le matériel potentiellement endommagé et faire un plein de nourriture avant de repartir pour deux nouvelles semaines. Ce camp de base, bien qu'il ne disposait pas de l'électricité, a beaucoup changé nos conditions de travail et nous a permis une meilleure efficacité dans la réalisation de nos protocoles au cours des deux dernières années de terrain.

A - LES DONNEES BUFFLES

A1 - Ecologie du mouvement

Le contexte propre à la Réserve Nationale de Niassa (RNN), à savoir une vaste superficie (42,140 km^2), un faible réseau de pistes, une densité du couvert et une inaccessibilité de la zone pendant plusieurs mois (i.e. saison des pluies) s'est avéré peu propice à la mise en œuvre de protocoles d'observations directs. Le dispositif expérimental déployé pour les besoins de cette étude repose donc majoritairement sur des protocoles d'observations indirects, notamment le tracking GPS.

A1.1 - Matériel

Le système télémétrique déployé a été produit par la firme sud-africaine African Wildlife Tracking (n=33 colliers GPS). Deux types de colliers GPS ont été utilisés (UHF et satellite), la différence provenant de la manière dont les localisations GPS sont transférées. Ces colliers disposent d'une durée de vie comprise entre 1 et 2 ans. Les données des colliers UHF sont téléchargées sur le terrain à partir d'un modem de radiocommunication bidirectionnelle intégré au collier. La liaison se fait par le biais d'un ordinateur portable relié à un modem de radiocommunication de même type. Dans un milieu boisé, le téléchargement des données se fait à une distance d'environ 300 m, cette distance variant en fonction de la configuration du terrain. Ce système nécessite donc l'approche des individus équipés à pied. A l'inverse, les données des colliers satellites sont automatiquement envoyées à un serveur à distance en utilisant la technologie téléphonique satellitaire (Inmarsat). Ces données sont accessibles quasiment en temps réel (i.e. les données sont transmises au serveur toutes les 2 heures) depuis tout ordinateur connecté à Internet. Tous les colliers sont également équipés d'un émetteur VHF destiné à faciliter l'approche au sol des animaux. Les colliers UHF étaient également équipés d'un capteur de température extérieure.

A1.2 - Dispositif d'échantillonnage

Localisation des troupeaux

Sur la base des résultats de cinq comptages aérien totaux antérieurs (Craig, 1998, 2000, 2002, 2004 and 2006) menés sur toute la superficie de la RNN, deux zones (i.e. zone Centrale et zone Est) ont été identifiées comme celles présentant les plus fortes densités animales (toutes espèces confondues) de la RNN. De plus, à travers des discussions avec les différents opérateurs de chasse sportive présents sur la RNN depuis plusieurs années il s'est avéré que les plus grands troupeaux de buffles connus se trouvaient dans ces deux zones. La zone Ouest, plus montagneuse, ne présentait que de faibles densités animales. L'objectif étant le suivi d'une majeure partie de la population de buffles et compte tenu des conditions logistiques complexes à la mise en place d'un suivi dans chacune des zones de la RNN (300 km entre la frontière Est et Ouest de la RNN) il a été décidé d'équiper des animaux dans la zone Centrale et la zone Est.

Déploiement des colliers

Trois sessions d'immobilisation de buffles et de pose de colliers ont été organisées durant cette étude. Nous avons délibérément ciblé des femelles adultes évoluant au sein de troupeaux reproducteurs en partant du principe que les mouvements de ces individus sont supposés être représentatifs de ceux des troupeaux pris dans leur ensemble. Ces sessions d'immobilisation ont toutes été réalisées au moyen d'un hélicoptère en suivant les techniques standard (la Grange 2006). L'anesthésie se faisait au moyen d'une combinaison d'étorphine hydrocloride et de xylazine et était inversée par une injection de diprenorphine hydrochloride. Tous les animaux ont été relâchés sur le site en bonne santé.

Une première session d'immobilisation a été menée du 08 au 11 octobre 2009. Au total, 18 buffles ont été équipés de colliers GPS (10 colliers satellites, 8 colliers UHF). Les colliers ont été répartis sur 8 troupeaux, 4 troupeaux dans la zone Centrale et 4 troupeaux dans la zone Est, chaque troupeau équipé d'un à deux collier(s) satellite(s) et d'un collier UHF. Excepté un troupeau de 25 individus dans la zone Centrale, tous les troupeaux présentaient des effectifs compris entre 100 et 250 individus (en moyenne, 161 ± 65 individus par troupeau; cf. Table 5.2).

Très rapidement après cette première session, il s'est avéré que deux troupeaux initialement immobilisés séparément à plus de 25 km l'un de l'autre semblaient n'être qu'un seul et même troupeau. Il s'agissait du troupeau de 25 individus équipés dans la zone Centrale (initialement troupeau n°7) dont les localisations se sont trouvées rapidement identiques à celles d'un troupeau de plus de 150 buffles plus au Sud (initialement troupeau n°8). Ces individus équipés initialement dans deux troupeaux distincts passaient la majorité de leur temps ensemble au sein d'un troupeau plus large (identifié dans la suite de l'étude comme troupeau n°9). L'ensemble des colliers présentait des taux corrects d'acquisition des localisations excepté un collier UHF qui n'a jamais fonctionné. Néanmoins, quatre mois après la première immobilisation, 4 colliers cessèrent de fonctionner et 3 présentaient des taux d'acquisition inférieurs à 30%.

Table 2.1 - Summary statistics of the deployment of 33 GPS collars in 9 herds in Niassa National Reserve from 2009 to 2011

Herd ID	Collar ID / Type	Zone	Date ON	Date OFF	Months of activity	Collar schedule	Success rate %
1	Sat01 / Sat	Eastern	08/10/2009	29/10/2010	13	6 locs / day	97
	AU345 / UHF		08/10/2009	17/11/2011	26	24 locs /day	64
	Sat15 / Sat		02/11/2010	30/11/2011	13	6 locs / day	38
2	Sat02 / Sat	Eastern	09/10/2009	29/10/2010	14	6 locs / day	52
	AU344 / UHF		09/10/2009	30/08/2010	11	24 locs /day	100
	Sat16 / Sat		02/11/2010	11/08/2011	10	6 locs / day	48
3	Sat04 / Sat	Eastern	09/10/2009	06/11/2010	13	6 locs / day	37
	AU347 / UHF		09/10/2009	17/11/2011	35	24 locs /day	99
	Sat17 / Sat		02/11/2010	01/09/2011	10	6 locs / day	12
	Sat221 / Sat		26/11/2011	28/04/2013	12	24 locs /day	90
4	Sat03 / Sat	Eastern	10/10/2009	03/04/2011	18	6 locs / day	66
	AU346 / UHF		10/10/2009	17/11/2011	35	24 locs /day	100
	Sat18 / Sat		02/11/2010	08/11/2011	12	6 locs / day	64
	Sat220 / Sat		26/11/2011	08/07/2013	12	24 locs /day	92
5	Sat06 / Sat	Central	10/10/2009	22/03/2011	18	6 locs / day	67
	AU348 / UHF		10/10/2009	10/10/2009	0	24 locs /day	0
	Sat14 / Sat		01/11/2010	30/01/2012	15	6 locs / day	78
	AU509 / UHF		01/11/2010	21/11/2011	22	24 locs /day	13
6	Sat05 / Sat	Central	10/10/2009	31/01/2010	4	6 locs / day	53
	Sat07 / Sat		10/10/2009	12/12/2010	14	6 locs / day	78
	AU349 / UHF		10/10/2009	27/12/2009	3	24 locs /day	19
	Sat11 / Sat		01/11/2010	30/03/2011	5	6 locs / day	79
	Sat12 / Sat		01/11/2010	03/12/2011	13	6 locs / day	68
	Sat186 / Sat		25/11/2011	26/04/2013	12	24 locs /day	91
9	Sat08 / Sat	Central	11/10/2009	22/02/2011	17	6 locs / day	4
	Sat09 / Sat		11/10/2009	22/11/2009	2	6 locs / day	21
	Sat10 / Sat		11/10/2009	30/09/2010	12	6 locs / day	6
	AU350 / UHF		11/10/2009	10/11/2010	13	24 locs /day	97
	AU351 / UHF		11/10/2009	22/09/2010	12	24 locs /day	99
10	Sat19 / Sat	Eastern	02/11/2010	05/08/2011	9	6 locs / day	30
	Sat21 / Sat		02/11/2010	05/07/2011	9	6 locs / day	30
11	Sat13 / Sat	Central	01/11/2010	26/12/2011	14	6 locs / day	69
	Sat187 / Sat		25/11/2011	18/03/2013	12	24 locs /day	89

Afin de sécuriser le suivi des troupeaux équipés une deuxième session d'immobilisation a été menée le 01 et 02 novembre 2010 dans le but de poser 10 colliers satellites et de changer le collier UHF défectueux. Un nouveau collier satellite a été placé dans chacun des quatre troupeaux de la zone Est. Afin d'augmenter le suivi de la population de buffles dans une unité de gestion d'intérêt (i.e. unité L5, cf. A3.1) 2 collier satellites ont été placés dans un nouveau troupeau de 50 individus dans la zone Est (troupeau n°10). Un nouveau collier satellite a également été placé dans trois des troupeaux de la zone Centrale (plus le remplacement du collier UHF défectueux) et deux colliers ont été placés dans un troupeau d'intérêt (troupeau n°9). Cependant, à cette période, les troupeaux de la zone Centrale étaient sujets à plusieurs événements de fusion/scission. Il s'en est résulté que parmi les 2 colliers placés dans le troupeau n°9, quelques semaines après la session d'immobilisation, un collier se trouvait dans un autre troupeau déjà équipé (troupeau n°6) et un collier se trouvait seul dans un nouveau troupeau (connu auparavant mais non équipé) de 150 buffles (troupeau n°11). Au final, à l'issu de cette session en 2010, le suivi de 7 troupeaux (parmi les 8 troupeaux initialement équipés en 2009) a été sécurisé et 2 nouveaux ont été équipés de colliers satellites (1 ou 2 collier(s) par troupeau).

De même qu'en 2010, afin de sécuriser le suivi de troupeaux d'intérêt pour la dernière année de protocoles de terrain de l'étude, 4 nouveaux colliers satellites ont été placés lors d'une troisième et dernière session d'immobilisation dans 4 troupeaux (2 troupeaux dans la zone Centrale, 2 troupeaux dans la zone Est).

Programmes d'acquisition des données télémétriques

Afin de caractériser les patrons aux larges échelles (annuelle, intra et inter-saisonnière) les colliers GPS ont été programmés de façon à acquérir des localisations selon deux critères : (i) un nombre suffisant de localisations (i.e. fréquence d'acquisition) en corrélation avec (ii) une durée de fonctionnement.

Les colliers satellites posés en 2009 et 2010 ont été programmés pour acquérir des localisations à intervalles de 4 heures durant toute la session du tracking. Les colliers UHF n'avaient pas à communiquer quotidiennement avec un serveur pour transmettre leurs données. De ce fait, la durée de vie de leur batterie était meilleure et ils ont été programmés pour acquérir des localisations à intervalles de une heure. Les quatre derniers colliers satellites posés en 2011 disposaient d'une nouvelle technologie de transmission de leurs données au serveur qui consommait moins de batterie. De ce fait, ils ont été programmés comme les colliers UHF pour acquérir des localisations à intervalles de une heure.

A1.3 - Bilan du tracking

Au total, 32 buffles ont été équipés de colliers GPS (24 colliers satellites et 9 colliers UHF (un collier UHF remplacé sur un buffle)) répartis sur 9 troupeaux (5 troupeaux dans la zone Est, 4 troupeaux dans la zone Centrale). Le fonctionnement des colliers a permis un suivi de 9 à 35 mois pour tous les troupeaux équipés (Table 2.1).

Un seul collier n'a pas fonctionné immédiatement après la pose (collier UHF). Mis à part ce collier, la durée de fonctionnement moyenne sur l'intégralité des colliers était de 14 ± 7 mois. Les colliers UHF ont fonctionné plus longtemps que les colliers satellites avec en moyenne 21 ± 10 et 12 ± 4 mois d'activités, respectivement. Cinquante deux pourcents des colliers ont fonctionné plus d'un an et seulement 3 colliers ont fonctionné plus de 2 ans (3 colliers UHF) avec un temps maximum d'activité de 35 mois pour deux de ces colliers. Le succès des taux d'acquisition (i.e. nombre de localisations enregistrées par le collier en fonction de la fréquence d'acquisition initialement programmée) était de 61 ± 31% sur l'ensemble des colliers. Là encore les colliers UHF ont présenté de meilleurs résultats que les colliers satellites avec un succès des taux d'acquisition de 74 ± 35 et 57 ± 28%, respectivement.

Le détail du bilan du tracking est présenté Table 2.1 ainsi qu'en Annexe IV pour chacun des colliers.

A2 - Taille et composition des troupeaux

Dans un milieu forestier comme celui de type *miombo* qui couvre 72% de la RNN (Ribeiro et al. 2008) il nous a été difficile, voir impossible, d'estimer le nombre d'individus présents dans un troupeau depuis le sol. L'expérience montre que même depuis les airs, un observateur n'est pas capable de compter avec précision les individus d'un troupeau si ce dernier excède 20 têtes (Norton-Griffiths 1978). La réalisation de photos aériennes permet d'obtenir des données précises quant au nombre d'individus présents dans un troupeau. De plus, les appareils photos actuels permettent d'obtenir des clichés à haute résolution et en zoomant dans les images il devient possible d'évaluer la structure et la composition des groupes.

Grâce à un opérateur de la RNN qui a mis à notre disposition un avion ULM (ultra-léger-motorisé) nous avons pu réaliser des photos aériennes des troupeaux. Deux à trois sessions de vol ont été réalisées chaque année. Idéalement nous souhaitions réaliser trois séries de photos de chaque troupeau suivi, en début, milieu et fin de saison sèche afin d'estimer si l'effectif, la structure et la composition des troupeaux variaient au cours de la saison. Trois à quatre jours étaient nécessaires pour réaliser les clichés de tous les troupeaux. Cependant, en raison des disponibilités de l'ULM qui dépendaient des activités de son propriétaire il ne nous a pas été possible d'établir un protocole fixe de survol à des dates similaires chaque année. Il a donc été décidé de réaliser ces survols de façon aléatoire, "à chaque fois que cela était possible".

Un post-traitement des ces clichés permettaient de compter avec précision le nombre d'individus d'un troupeau. Les photos prises en milieu ouvert (i.e. prairie) donnaient de meilleurs résultats, certains individus se trouvant sous la canopée lorsque les photos étaient prises en milieu forestier. Les mâles adultes étaient facilement identifiables en raison de leur casque proéminent (i.e. bosse formée au niveau du crâne à la jonction des deux cornes). Néanmoins, malgré la haute définition des clichés, il était difficile d'identifier les différentes classes d'âges, notamment d'effectuer une distinction entre les sub-adultes et les adultes. Les veaux (i.e. moins d'un an) étaient bien identifiables.

Ces données ne faisaient pas partie des objectifs principaux de notre étude mais elles constituaient une source d'information non négligeable pour la compréhension du système. Elles ont permis la constitution d'une banque d'images, jusqu'alors inexistante, sur la structure et la composition des troupeaux de buffles de la RNN. Ces données nous ont également apporté de précieuses informations quant aux événements de fusion/scission des troupeaux.

A3 - La Prédation

A3.1 - Prédation naturelle

Depuis 2003 la population de lions de la RNN (estimée entre 800 et 1,000 individus, Begg and Begg 2011) est étudiée par le Niassa Lion Project (http://www.niassalion.org/). Ce projet disposait d'une base de données intéressante pour notre étude, notamment quant à la contribution du buffle dans le régime alimentaire des lions. La zone intensive d'étude de la population de lions se trouvait dans une unité de gestion de la RNN (i.e. unité L5S, cf. Figure 3.2) dans laquelle 28 lions (18 mâles et 10 femelles) ont été équipés de colliers GPS entre 2005 et 2011.

Afin d'étudier les relations prédateurs/proies entre les populations de buffles et de lions de la RNN, deux troupeaux de buffles ont été équipés de colliers GPS dans cette unité de gestion d'intérêt (un troupeau en 2009 et un troupeau en 2010). Les fréquences d'acquisition des localisations des colliers GPS "buffle" (cf. A1.2) ont été programmées pour se faire à des heures précises correspondant à celles auxquelles les localisations des colliers GPS "lion" étaient relevées.

A3.2 - Impact humain

Un des objectifs de l'étude était d'estimer l'impact potentiel de la présence humaine dans de la RNN, notamment par le prélèvement, sur l'abondance et la distribution de la population de buffles. Une des manières d'approcher cette estimation était dans un premier temps d'évaluer la contribution de la viande de brousse (et plus particulièrement du buffle) dans le régime alimentaire des populations locales.

Une étude socio-économique a été réalisée en 2012 auprès de 123 foyers dispersés dans 8 villages de la RNN (cf. Chapitre 6), mais compte-tenu que les activités de chasse des populations locales sont illégales, cette étude a été menée à partir d'un questionnaire axé sur la sécurité alimentaire des populations humaines résidant dans la RNN. Nous avons en effet considéré qu'une étude trop orientée vers la consommation de viande de brousse n'aurait pas permis d'obtenir des réponses honnêtes de la part des interviewés. L'intérêt d'une approche des modes de vie et de production à travers la sécurité alimentaire est également de fournir des éléments pour comprendre le rôle des ressources naturelles et de la RNN dans le quotidien des villageois ainsi que leurs perceptions de la faune, de la conservation et de leurs conditions de vie. Les interviews ont été conduits par un étudiant mozambicain pendant 4 mois. L'étudiant (accompagné d'un traducteur local lorsqu'il n'était pas possible de réaliser ces interviews en portugais) a passé 2 semaines dans chacun des villages.

A4 - Maladies et génétique

Afin de pratiquer des analyses sanguines et génétiques différents prélèvements ont été réalisés au cours du Projet (i.e. sang et peau).

Tout d'abord, lors de la première session d'immobilisation en 2009, l'important déploiement logistique a permis d'établir un laboratoire de terrain équipé d'une centrifugeuse et d'un incubateur. Sur chaque femelle adulte capturée plusieurs prélèvements de sang et de peau étaient réalisés. Les prélèvements de sang étaient immédiatement centrifugés et conservés afin de pratiquer des analyses sérologiques a *posteriori*. Les prélèvements de peau étaient conservés dans l'alcool.

Par la suite, les conditions logistiques ne permettaient pas de disposer d'un laboratoire de terrain. Nous avons donc réalisé des "bio-kits". Ces bio-kits se présentaient sous la forme de pochette cartonnée dans laquelle se trouvait le matériel nécessaire pour réaliser 2 prélèvements sanguins et 2 prélèvements de peau. Les prélèvements sanguins étaient réalisés à l'aide de papier Wathman (i.e. papier buvard) et les prélèvements de peau étaient placés dans des tubes contenant de l'alcool. L'avantage de ces bio-kits est que leur stockage ne nécessitait pas un réfrigérateur. Nous avons distribué des dizaines de bio-kits à tous les opérateurs de chasse sportive de la Réserve afin qu'ils réalisent des prélèvements sur chacun des buffles tués. Tous les bio-kits De même, nous avons utilisé ces bio-kits lors des deux dernières sessions d'immobilisation réalisées en 2010 et 2011.

L'utilisation de papier Whatman ne permet pas de réaliser des analyses sérologiques (i.e. recherche des anticorps) mais des analyses génétiques (recherche des pathogènes eux-mêmes) par des techniques type PCR. Théoriquement, toutes les maladies infectieuses potentielles peuvent être recherchées.

B - LES DONNEES ENVIRONNEMENTALES

B1 - La carte de la végétation

Dès l'initiation du Projet "Buffle" en 2009, grâce à des études récentes (Timberlake et al. 2004; Ribeiro 2005), des informations utiles sur la végétation de la zone étaient disponibles, notamment une description de l'environnement de type *miombo* qui prédomine dans la RNN ainsi qu'un premier inventaire des espèces végétales de la zone. Néanmoins, ces informations n'étaient pas disponibles dans un format "carte" et n'étaient donc pas utilisables dans le cadre d'analyses spatiales. Cependant, deux cartes de la végétation furent retrouvées dans les archives de la SGDRN mais pour lesquelles peu de références étaient disponibles quant aux méthodes utilisées pour les réaliser. Ces cartes se sont avérées très utiles pour apporter une connaissance de base quant à la description de la végétation de la zone, mais elles devaient être complétées par une acquisition d'image satellite et par des missions spécifiques de terrain afin d'obtenir une information assez précise et fiable pour réaliser une carte de la végétation de la zone et faire des analyses de sélection de l'habitat.

Trois missions spécifiques de quinze jours chacune ont été réalisées entre 2010 et 2012 avec l'aide d'un géographe et d'un botaniste. Ces missions ont toutes étaient réalisées au mois de juin, en début de saison sèche. Il était nécessaire de réaliser ces missions le plus tôt possible dans la saison afin de (i) éviter les importants feux de brousse (cf. Chapitre 3 - B4) qui sévissent dans la RNN en saison sèche et (ii) de se trouver dans une période propice à l'identification des espèces herbacées qui sont déjà en fin de cycle à cette période de l'année (i.e. inflorescence non identifiable plus tard dans la saison).

B1.1 - Protocole de terrain

Le protocole de terrain utilisé pour la collecte des données a été élaboré afin de caractériser la végétation à la fois selon des types d'habitats mais aussi selon les ressources fourragères. Les observations réalisées n'avaient pas pour unique objectif de déterminer le type de végétation en fonction de sa structure et des principales espèces ligneuses mais aussi d'évaluer la qualité et l'accessibilité de la biomasse disponible aux populations d'herbivores.

Afin de caractériser la végétation, les mesures étaient réalisées sur les strates ligneuses et herbacées. Seules les données de la strate ligneuse ont été utilisées dans l'exercice de cartographie. Les types de végétation étaient définis selon (i) la structure de la végétation (i.e. proportions d'arbres et arbustes et recouvrement de la canopé) et (ii) les espèces ligneuses et/ou arbustives dominantes.

La méthode d'échantillonnage était basée sur des transects linéaires de 100 m le long desquels les paramètres de la végétation étaient estimés tous les mètres (i.e. 100 points par transect). A chaque point (i.e. mètre) une tige était plantée dans le sol et les paramètres suivants étaient relevés dans une feuille de donnée spécifique :

- présence d'un couvert arboré ou arbustif au dessus ou en dessous de la tige,
- espèce de l'arbre et/ou de l'arbuste,
- espèce(s) herbacée(s) présente(s) ou non à la base de la tige (donnée non utilisée pour l'exercice de cartographie).

Une feuille de donnée vierge est présentée en Annexe VI-A.

Les placettes mesurées ont été sélectionnées afin d'obtenir un ensemble d'échantillons représentatif de l'intégralité de la RNN. Ces placettes devaient se trouver à plus de 100 m d'une route, d'une rivière, ou de tout autre élément qui aurait pu modifier la végétation et rendre la placette non représentative de la zone.

Au cours des trois missions spécifiques une centaine de placettes ont été mesurées. De plus, au cours des différents déplacements (à pied et en voiture) plus de 1500 "points de contrôle" ont été réalisés. Ces points consistaient en une estimation visuelle de la structure et du type de la végétation. Chacun de ces points étaient géoréférencés et utilisés par la suite dans l'exercice de validation de la carte de la végétation. De même, tout au long de la saison, lors des différents déplacements réalisés par l'équipe, des points de contrôle étaient relevés.

B1.2 - Cartographie de la végétation

Un important travail de recherche d'images satellites disponibles pour ce type d'analyse a été réalisé en amont. Notre choix s'est porté sur des images de type Spot, Aster et Landsat qui présentent une résolution suffisante (i.e. 5 à 30 m). Parmi ces trois capteurs, aucun ne fournissait une image couvrant l'intégralité de la zone. Il était donc nécessaire de réaliser une mosaïque à l'aide de plusieurs images satellites. L'objectif était de trouver des images satellites (i) prises à des dates proches (i.e. radiométrie identique), (ii) prises à des dates où la végétation n'était pas dégradée par les feux (i.e. saison des pluies ou début de saison sèche) et (iii) où la couverture nuageuse de chaque image n'était pas trop importante (i.e. inférieure à 20%).

Au final, l'exercice de cartographie de la végétation de la RNN a été réalisé à partir de 4 images satellite Landsat ETM5 d'une résolution de 30m de mai et juin 2008 (cf. Annexe I.K). Le traitement de ces images a été réalisé par classification supervisée (logiciel ENVI®) à partir de 71 relevés de la végétation (i.e. placettes) répartis sur l'ensemble de la zone. La classification supervisée a utilisé l'estimateur du maximum de vraisemblance en intégrant les 7 bandes des images satellites ainsi qu'un modèle numérique de terrain (Shuttle Radar Topography Mission; résolution spatiale 90m). La classification a été appliquée avec un seuil de permittivité statistique de 80% en dessous duquel un pixel n'était pas classifié.

Pour la cartographie de la végétation de la RNN une liste simplifiée des différents types de végétation (cf. Chapitre 3 - B3) a été utilisée. En effet, le nombre de relevés réalisés lors des trois missions spécifiques ne permettait pas une discrimination suffisante des types de végétation dans l'exercice de classification. De ce fait, seulement 6 types de végétation ont été conservés : (i) *miombo* dense, (ii) *miombo*, (iii) *miombo* ouvert, (iv) prairie, (v) *jesse bush* et (vi) forêt riveraine. Trois types "non-végétaux" ont été ajoutés pour la classification : (i) inselberg, (ii) sable et (iii) l'eau. De plus, en raison de la présence de nuages sur les images satellites utilisées et du passage de feux (qui masque le type de végétation au sol ou dégrade la qualité radiométrique du signal), trois autres types ont été ajoutés à la classification : (i) nuage, (ii) ombre de nuage et (iii) zone brûlée. La carte de la végétation est présentée Chapitre 3 et a été réalisée à partir du logiciel ESRI ArcGIS^{TM} (Redlands, CA, USA) version 9.3.

B2 - Les données satellitaires

Dans la RNN, des données de terrain sur la production de la végétation, la pluviométrie et les feux de brousse, étaient inexistantes. Sur des périodes courtes et sur une zone aussi vaste que la RNN (42 140 km^2) il était peu probable de collecter ces données sur le terrain. Cependant, la télédétection est aujourd'hui un outil efficace pour pallier à de telles limitations. De plus, de nombreuses données télémétriques sont désormais proposées gratuitement au public, notamment toutes les images satellites prises par la NASA (National Aeronautics and Space Administration) et éditées par la NASA Earth Observatory.

B2.1 - Production primaire

Le rôle de la production primaire peut être utilisé comme un indicateur fiable quant à l'utilisation de l'espace par la faune sauvage (Ryan et al. 2012). Il a été étudié sur la RNN à partir de deux indices de la végétation, (i) le NDVI (Normalized Difference Vegetation Index) et le EVI (Enhanced Vegetation Index). Nous avons utilisé l'instrument MODIS (Moderate Resolution Imaging Spectroradiometer) de la NASA pour télécharger les produits Mod13Q1 à 250 m de résolution spatiale et 16 jours de résolution temporelle. Différentes plateformes sont disponibles sur le web pour la visualisation et l'obtention de ces produits. A partir d'un script réalisé sous le logiciel R nous avons pu automatiser le téléchargement de ces données et procéder à différents prétraitements à savoir :

- Téléchargement des données brutes à partir d'un serveur FTP (au format HDF (Hierarchical Data Format) qui est un conteneur de fichiers et permet le stockage des différentes bandes d'une image satellite dans un seul et même fichier,
- Clip spatial des images satellites sur la zone d'étude,
- Compilation des produits (initialement sous forme de seizaines / 23 images satellites par an) en un fichier unique annuel,
- Géoréférencement des produits en UTM,
- Génération d'un fichier raster par an pour faciliter les analyses sous R et pour l'utilisation via un logiciel de cartographie (e.g. ESRI ArcGIS^{TM}).

Les données NDVI et EVI ont été téléchargées sur une période de 14 ans (i.e. de 2000 à 2013).

B2.2 - Les feux de brousse

Le rôle des feux de brousse a été évalué à partir de l'instrument MODIS et des produits MCD45 à 500 m de résolution spatiale et à une résolution temporelle journalière. Ces données étaient disponibles à partir d'un serveur FTP sous forme de compilations mensuelles (dans lesquelles l'information temporelle journalière était conservée) et au format TIF.

De même que précédemment (cf. B2.1) à partir d'un script réalisé sous le logiciel R nous avons pu automatiser le téléchargement de ces données et procéder aux prétraitements suivants :

- Téléchargement des données brutes à partir du serveur FTP,
- Clip spatial des images satellites sur la zone d'étude,
- Compilation des produits en un fichier unique annuel,
- Géoréférencement des produits en UTM,
- Génération d'un fichier vecteur par an.

Les données MCD45 ont été téléchargées sur une période de 13 ans (i.e. de 2000 à 2012).

B2.3 - La pluviométrie

Les seules stations météorologiques relevant des données précises quant à la pluviométrie du Nord Mozambique se trouvaient dans les villes de Lichinga (à l'Ouest de la RNN en altitude) et de Pemba (à l'Est de la RNN au bord de l'océan indien). Ces données n'étaient pas utilisables pour notre étude car ces stations se trouvaient à des distances trop importantes de la RNN.

La pluviométrie de la RNN a été évaluée à partir du satellite TRMM (Tropical Rainfall Measuring Mission) de la NASA. Les données ont été téléchargées à partir d'un outil sur le web spécialement conçu par la NASA pour les produits TRMM. Ces produits, à 25 km de résolution spatiale et à une résolution temporelle journalière, étaient disponibles au format HDF. L'outil web permettait le téléchargement des cartes des précipitations pour le monde entier en une seule fois pour une période choisie. Ces cartes ont été téléchargées sur une période de 13 ans (i.e. de 2000 à 2012). A partir du logiciel ENVI® nous avons procédé aux prétraitements suivants :

- Clip spatial des images satellites sur la zone d'étude,
- Compilation des produits en un fichier unique annuel,
- Rectification d'un problème interne aux données disponibles sur le web (i.e. les données étaient inversées, le Nord se trouvait au Sud),
- Géoréférencement des produits en UTM,
- Génération d'un fichier raster par an au format TIFF.

C - AUTRES DONNEES

C1 - Comptages aériens

Depuis 1998, sept comptages aériens de fin de saison sèche ont été réalisés sur l'intégralité de la RNN (e.g. Craig 2012) afin d'estimer les effectifs des populations d'herbivores de la zone et de suivre leurs évolutions au cours du temps. Le protocole utilisé est présenté en détail Chapitre 4.

Ces données ont été mises à notre disposition par la SGDRN (excepté les données des comptages de 1998 et 2000). Nous disposions donc, dès l'initiation du Projet Buffle, d'une base de données considérable quant aux populations d'herbivores de la RNN. Néanmoins, ces données n'avaient jamais été analysées en fonction de différentes variables environnementales et n'avaient permis que l'estimation des effectifs des populations.

De plus, lors des différentes sessions de survols, d'autres observations ont été réalisées et géoréférencées notamment sur la disponibilité en eau, les feux de brousse et les activités illégales (i.e. braconnage, coupe de bois et extraction des ressources minérales). Ces données se sont avérées extrêmement précieuses pour notre étude, notamment afin de connaître les disponibilités en eau pour la population de buffles en fin de saison sèche ainsi que pour valider les données satellitaires MODIS MCD45 sur les feux de brousse (i.e. il était possible de confronter les données satellitaires à des observations de terrain pour déterminer l'exactitude des images satellites).

C2 - Base SIG disponible

Dès l'initiation du Projet Buffle la SGDRN disposait d'une base de données SIG importante de la RNN. Ces données ont été vérifiées sur le terrain et se sont avérées exactes et précises. Toutes les informations suivantes étaient géoréférencées et disponibles sous format vecteur :

- Villages,
- Camps de chasse,
- Réseau routier,
- Réseau hydrographique (subdivisé en 4 catégories, (i) rivières principales, (ii) rivières secondaires, (iii) rivières tertiaires et (iv) rivières mineures),
- Limites des unités de gestion.

A partir des localisations relevées par les colliers GPS ces données nous ont permis différents calculs, notamment au niveau des distances, qu'il s'agisse d'évaluer le dérangement humain (i.e. distances aux route/villages) ou de l'accessibilité à l'eau (i.e. distances aux rivières).

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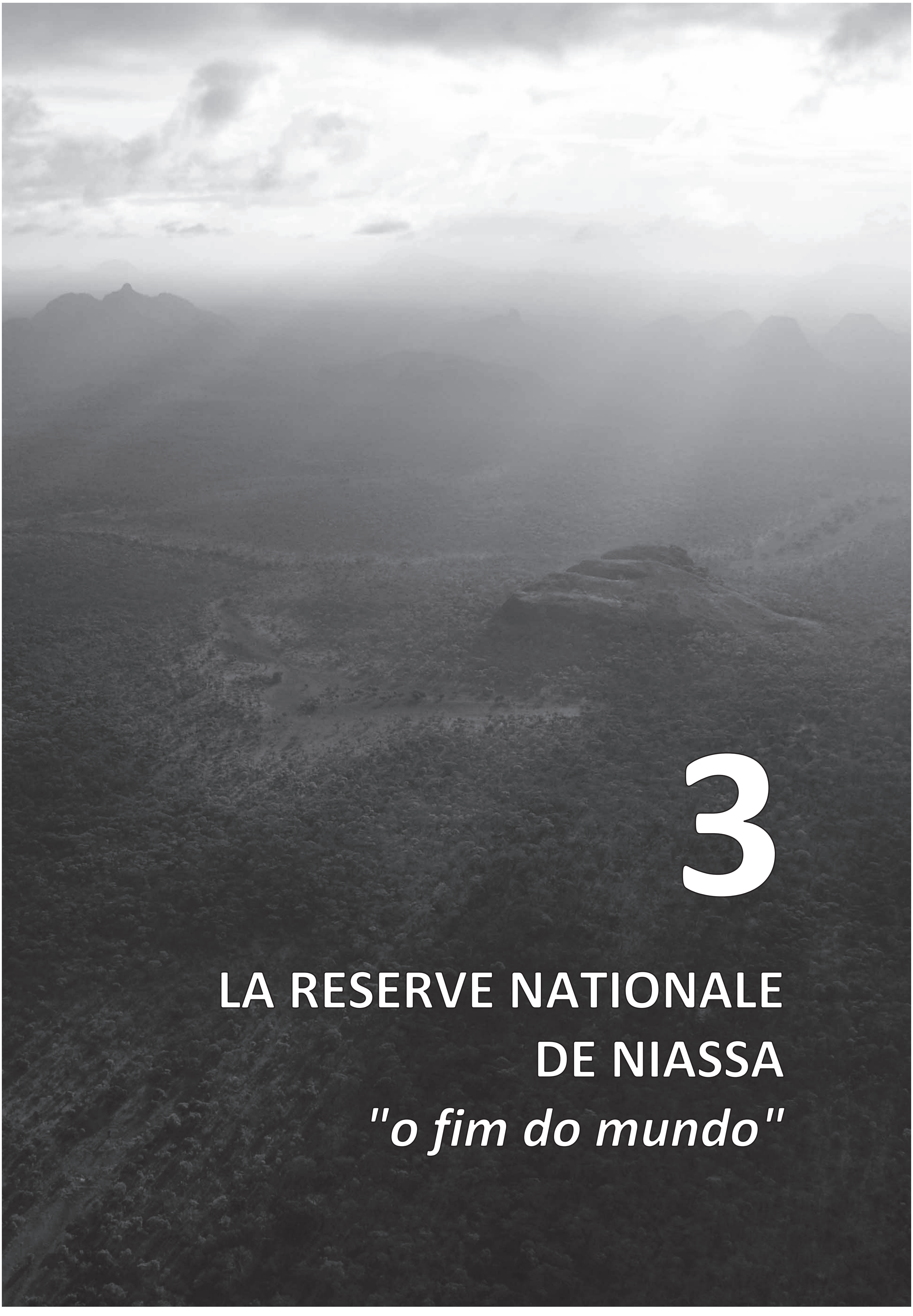


3

LA RESERVE NATIONALE DE NIASSA

"o fim do mundo"

A - HISTOIRE & POPULATION

D'une superficie de 42,140 km^2, la Réserve Nationale de Niassa (RNN) au Mozambique est une des plus vastes aires protégées d'Afrique et représente 5.3% du territoire national et 44.9% des aires protégées du pays (Parcs Nationaux et Réserves Nationales). Elle a également la particularité d'être habitée par plusieurs milliers de personnes regroupées en plusieurs villages. La RNN se trouve à cheval sur la Province de Niassa et la Province de Cabo Delgado au Nord du pays. Sa frontière nord, matérialisée par la rivière Rovuma, suit la frontière internationale du Mozambique avec la Tanzanie (Figure 3.1).

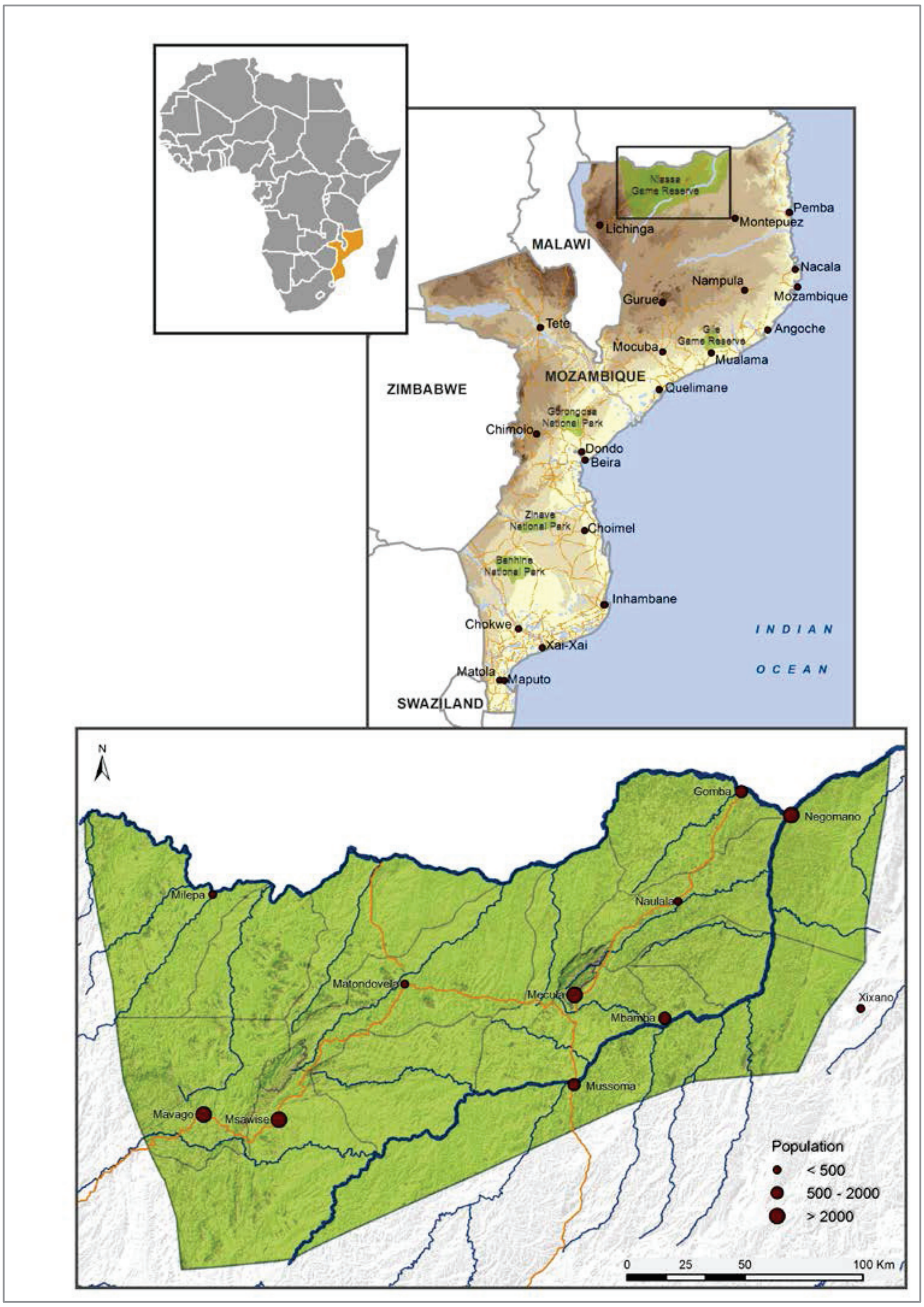


Figure 3.1 - Location of the Niassa National Reserve in Mozambique

A1 - Histoire de la RNN

Quelques documents suggèrent que dans les années 1930, le gouvernement colonial portugais créa une zone de chasse qui avait des limites relativement similaires à celles de la Réserve actuellement. A cette époque, les portugais s'y référaient par "*o fim do mundo*", la fin du monde, en raison de sa situation géographique si reculée. Néanmoins, ce n'est qu'en 1954 que la RNN fut officiellement établie pour la première fois (SGDRN 2007). A partir de cette date la Réserve a subi un nombre important de modifications au niveau de ses frontières et de sa taille jusqu'à un ajustement définitif de ses limites actuelles, identifiées en 1999. Durant la guerre d'indépendance (1964-1974) puis la guerre civile (1977-1992) qui ravagea le pays, la RNN fut abandonnée. Après la signature de l'accord de paix en 1992, le nouveau gouvernement prit des mesures importantes et innovantes et lança un plan de gestion de la RNN à travers une collaboration public/privé. C'est en 1995 que le gouvernement signa un contrat pour la gestion de la RNN avec une société privée, Grupo Madal. Cette décision fut consolidée en 1999 par un décret ministériel qui définit et légalisa les limites d'une aire de conservation centrale (22,920 km^2) et d'une zone périphérique divisée en blocks de chasse (19,220 km^2).

En 1998, le Conseil des Ministres approuva la création d'une entreprise liant le gouvernement au secteur privé, la Société pour la Gestion et le Développement de la Réserve Nationale de Niassa (*Sociedade para a Gestão e Desenvolvimento da Reserva do Niassa*, SGDRN). La SGDRN obtint un bail de gestion de la Réserve signée en 2002 et pour une durée de 10 ans. L'aire de conservation centrale était gérée directement par la SGDRN et les zones de chasse en périphérie étaient gérées par les opérateurs de chasse, ces derniers devant néanmoins répondre à l'autorité de la SGDRN.

Dans une première phase, de 1998 à 2002, les objectifs furent le développement de cette structure, la nomination d'un directeur de la conservation mozambicain, la nomination d'un directeur mozambicain de la SGDRN, le développement des activités de chasse sportive dans la zone périphérique, le renforcements des gardes forestiers et la rédaction d'un plan de gestion de la RNN (Cunliffe et al. 2009).

La deuxième phase, de 2002 à 2006, fut l'élaboration d'une stratégie de développement de la RNN, notamment la levée de fonds à des fins de gestion pour rendre possible une série d'études préliminaires. Le but était de fournir une base solide pour la préparation et le développement d'un nouveau plan de gestion. Ces études comprenaient divers suivis et recherches sur la biodiversité, l'évaluation du potentiel de la RNN pour le développement du tourisme photographique, l'état des lieux du réseau routiers et des infrastructures présentes sur le site, des études socio-économiques des villages et communautés au sein de la RNN ainsi que l'élaboration d'un "business plan".

A la suite de ces différents résultats, une zonation de la Réserve fut établie et aboutit à la subdivision de la RNN en 18 unités de gestion, ou blocks (Figure 3.2), appartenant à trois catégories, zones de conservation "Spéciales", zones de conservation "Etendue Sauvage" et zones de conservation "Ressources" (Table 3.1). Chaque catégorie correspond à un certain niveau de permission quant à l'utilisation des ressources, les zones "Spéciales" étant les plus restrictives et les zones "Ressources" le moins.

La dernière phase, de 2007 à 2012, fut la mise en œuvre du plan de gestion approuvé en 2006 par le Conseil des Ministres.

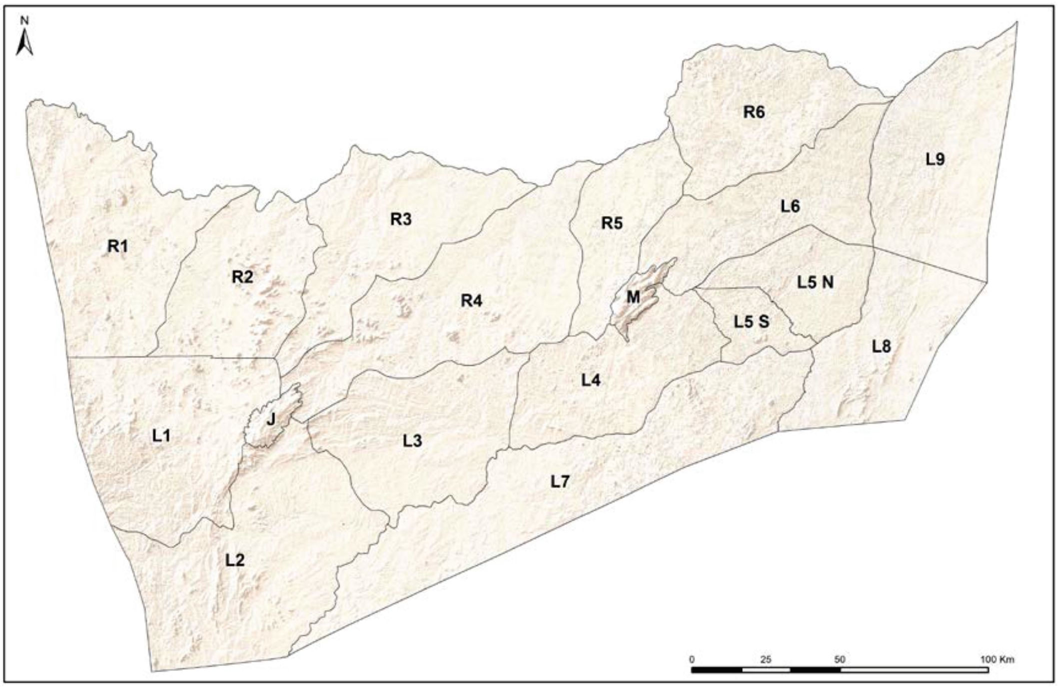


Figure 3.2 - Niassa National Reserve management blocks

Parmi les 18 blocks, les 8 zones de conservation "Ressources" sont gérées par des opérateurs privés de chasse sportive. Ces opérateurs gèrent leur zone tout en répondant aux prérogatives fixées par la SGDRN. Ils explorent les différentes zones de leur concession, construisent des camps pour accueillir les clients, ouvrent des pistes, créent des pistes d'atterrissage et disposent d'équipes de lutte anti-braconnage en complément de celles de la SGDRN. Ils louent chaque année leur zone et 20% de ce montant est reversé aux communautés tout comme les taxes abattage des animaux chassés. Ces sociétés privées emploient plusieurs centaines de travailleurs locaux. Les quotas de chasse sont attribués de manière brute par le Ministère du Tourisme. La SGDRN réévalue ces quotas et les redistribue aux opérateurs en fonction de différents critères (e.g. estimation des effectifs des populations animales sur les unités de gestion, respect des règles de prélèvement sur l'année précédente). Ces quotas restent faibles et représentent moins d'1% des effectifs des populations estimés dans la RNN (e.g. 76 buffles attribués en 2013).

Parmi les 8 zones de conservation "Etendue Sauvage", seules 3 sont à l'heure actuelle exploitées par des opérateurs privés de tourisme de vision. Ces opérateurs réalisent les mêmes activités de gestion sur leur zone que les opérateurs de chasse et répondent également à la SGDRN pour toutes les actions qu'ils souhaitent y mener. Les retombées économiques pour la Réserve et les communautés restent moindres puisque qu'aucune taxe d'abattage n'est perçue.

Un opérateur gère une zone de conservation "Etendue Sauvage" (unité de gestion L5 S) pour la recherche scientifique à travers l'étude des populations de lions de la zone (cf. Chapitre 2). Les autres unités de gestion restent aujourd'hui inexploitées.

Certains opérateurs sont présents dans la RNN depuis plus de 10 ans et d'autres ont récemment lancé leurs activités suite à l'ouverture de nouvelles unités de gestion par la SGDRN pour des opérateurs privés (e.g. unité de gestion L3 attribuée en 2007). L'augmentation du nombre d'opérateurs dans la RNN et/ou du temps depuis lequel ces derniers opèrent sur leur unité entraine une augmentation de la présence de gestion sur la zone ce qui peut supposer entrainer un impact positif sur les efforts de conservation et donc sur les populations animales.

En octobre 2012, une nouvelle phase voit le jour avec un changement de société de gestion. La SGDRN est remplacée par la Wildlife Conservation Society (WCS), une ONG internationale dont l'objectif est la préservation de la nature. WCS a signé un protocole d'accord avec le Ministère du Tourisme pour la cogestion de la RNN.

Table 3.1 - Management unit characteristic

Management unit category	Code *	Name	Size (in km^2)
Resource Conservation Area	L1	Nkalapa	3300
Resource Conservation Area	L2	Luatize	4195
Resource Conservation Area	L3	Metapiri	2653
Wilderness Conservation Area	L4	Incalaue	2236
Wilderness Conservation Area	L5 N	Miuro North	1236
Wilderness Conservation Area	L5 S	Miuro South	574
Wilderness Conservation Area	L6	Jurege	2285
Resource Conservation Area	L7	Mussoma	4353
Resource Conservation Area	L8	Nicondezi	2125
Resource Conservation Area	L9	Ninga	2888
Special Conservation Area	J	Jao Mountain	208
Special Conservation Area	M	Mecula Mountain	230
Resource Conservation Area	R1	Lucheringo	3442
Wilderness Conservation Area	R2	Lucabanga	2243
Resource Conservation Area	R3	Mazeze	2690
Wilderness Conservation Area	R4	Chuilexi	3695
Wilderness Conservation Area	R5	Licombe	1460
Wilderness Conservation Area	R6	Misangese	2327

* L=Lugenda River / R=Rovuma River

A2 - Infrastructures, villages, réseau routier

La RNN s'étend sur 8 districts des Provinces de Niassa et Cabo Delgado. Elle inclut l'intégralité du district de Mecula et la quasi intégralité de celui de Mavago (98%) et leurs centres respectifs, les villes de Mecula et Mavago. Les principales institutions administratives gouvernementales sont présentes dans les villes de Mecula et Mavago. Au niveau de WCS, le camp de base, Mbatamila, fut construit en 1998 à une trentaine de kilomètres de la ville de Mecula (Figure 3.3 - Annexe I.A). Ce camp de base regroupe les bureaux de la Réserve ainsi que le camp des gardes forestiers (*fiscais* en portugais). Quinze postes de contrôle sont dispersés dans la Réserve dans lesquels des équipes de gardes résident en permanence. La majorité de ces postes disposent d'une piste d'atterrissage à proximité afin de faciliter leur approvisionnement.

Le réseau routier est peu développé dans la RNN et est uniquement constitué de pistes de terre. Il existe 3 types de pistes, les pistes principales, secondaires et tertiaires (Figure 3.3 - Annexe I.A). Les pistes principales (routes nationales) et secondaires relient le réseau de villages et les différents postes de contrôle pour une longueur totale de 1,610 km. Il existe de nombreuses pistes tertiaires dans les unités de gestion exploitées par des opérateurs privés (chasse sportive ou tourisme de vision). En fonction des unités de gestion ces pistes sont plus ou moins nombreuses mais la circulation y reste très faible. Seules les pistes principales et secondaires sont accessibles tout au long de l'année. Les pistes tertiaires sont uniquement utilisées en saison sèche. Seul un pont permet de traverser la rivière Lugenda au niveau du village de Mussoma. De même, un pont transfrontalier permet de traverser la rivière Rovuma au niveau du village de Negomano pour se rendre en Tanzanie. Depuis la côte Est du Mozambique il s'agit du seul pont transfrontalier. Plus proche de la côte le seul moyen de passer en Tanzanie en véhicule reste la traversée en bac de la rivière.

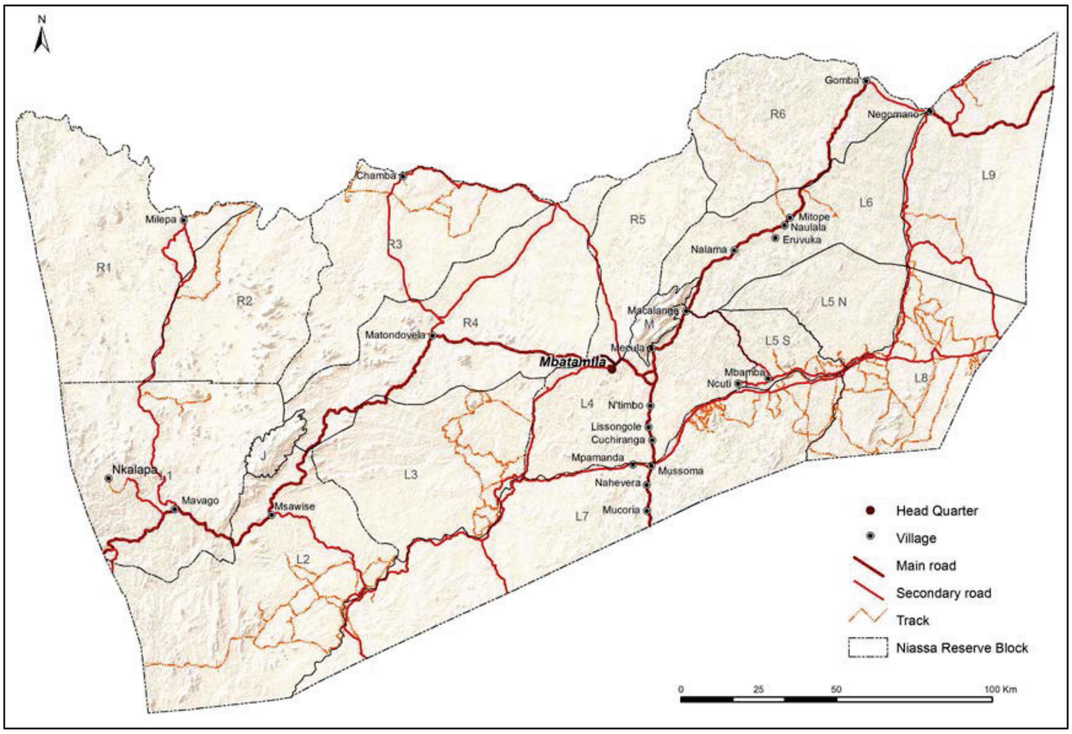


Figure 3.3 - Main villages and road network in the Niassa National Reserve

A3 - Population

La population appartient majoritairement aux groupes ethniques Yao et Macua, ce dernier étant plus représenté dans l'Est de la Réserve. Parmi les interviews réalisées auprès de plus de 100 foyers lors d'une enquête sur la sécurité alimentaire et les conditions de vie (cf. Chapitre 6 également), 71% étaient Yao et 24% Macua. Ces 2 groupes ethniques ont un long passé historique avec la région qui date de plusieurs siècles. Lorsque la Réserve fut proclamée officiellement en 1954 de nombreuses familles et leurs ancêtres vivaient déjà dans la zone. Néanmoins, avant cette date et par la suite il y a eu de nombreux mouvements de population notamment entre 1930 et 1950 en raison de l'importante production de coton par le gouvernement colonial qui força de nombreux travailleurs à se déplacer sur les lieux d'exploitation mais aussi entre 1965 et 1992 suite à la guerre d'indépendance et à la guerre civile qui ravagea le pays.

Au total, près de 39,000 personnes vivent au sein de la RNN dispersés sur une cinquantaine de villages (Figure 3.3) qui comprennent entre 50 et 6,000 habitants. Il y a peu de communication entre les différentes communautés (notamment entre les villes de Mavago et Mecula) en raison du réseau routier peu développé. Le taux d'accroissement de la population est fort et est compris entre 2.8 et 4.9% dans la ville de Mecula (Cunliffe 2009). Les données de recensements de la région montre une forte augmentation de la population depuis les 10 dernières années accompagnée d'une augmentation du nombre de villages.

La taille moyenne (± standard deviation (SD)) des foyers est de 6 ± 2.4 personnes. L'activité principale est l'agriculture de subsistance caractérisée par une rotation des cultures, avec des surfaces par foyers réduites (1 seul champs de 2.5 ± 2.2 hectares par foyer en moyenne). Par conséquent, les communautés sont fortement dépendantes de l'utilisation des ressources naturelles pour satisfaire des besoins de base (notamment sous forme de bois pour la construction des habitations ou le feu pour cuisiner). Les communautés sont caractérisées par un fort degré de pauvreté, une faible sécurité alimentaire (environ 6 mois d'autonomie en moyenne), un faible accès aux infrastructures (e.g. école) aux services (e.g. santé) et un taux élevé de conflit avec la faune sauvage, notamment les éléphants et les lions. Plus de 98% des foyers interviewés considéraient que les hommes et la faune sauvage ne pouvaient pas vivre ensemble. Depuis les années 2000, 34 attaques de lions ont été répertoriées dans la RNN (2.9 attaques par an) causant 21 blessés et 13 morts.

Les foyers cultivent principalement le maïs (100% des foyers interrogés), le manioc (50%), le riz et les haricots (30%) et les cacahuètes (20%). Ils possèdent quelques animaux domestiques, notamment des poules (6 ± 10) et des chèvres (1 ± 3). Depuis une dizaine d'années, des populations de chiens domestiques font leur apparition dans la RNN. Estimés à 144 individus en 2006, leur population a atteint 583 individus en 2011 (Begg and Begg 2011). Ces chiens ne sont pas vaccinés et leur apparition représente un risque non négligeable pour les populations animales sauvages. En raison de la faible sécurité alimentaire, les foyers sont contraints d'acheter différents produits pour répondre à leurs besoins nutritionnels quotidiens. Cependant, dans les foyers interviewés, parmi les hommes et femmes de plus de 18 ans, seulement 10.2% possédaient un travail officiel (e.g. administratif, hôpital). Les sources de revenus des foyers sont principalement la vente (i.e. vente de produits de base et/ou de services), la pêche, la collecte et la vente de miel ou encore l'offre de services pour le voisinage (appelé *ganyo* dans la RNN) en échange d'une rémunération (cf. Chapitre 6 pour une description détaillée des différentes sources de revenus). Le commerce d'échange est également un facteur important dans les foyers (53.5% le pratique).

Le mode agricole caractérisé par une rotation des cultures entraine un fort degré de mobilité de la population. Lorsque les nutriments dans le sol sont épuisés il est nécessaire de défricher de nouvelles zones pour y installer un nouveau champ. En moyenne, les foyers de la RNN changent leur champ tous les 6.5 ans (Cunliffe 2009). Avec l'augmentation de la population, l'espace vient à manquer. Généralement, lorsqu'il est nécessaire de marcher plus de 3 heures par jour pour rejoindre son champ les foyers changent d'habitation. Les deux principaux facteurs qui maintiennent les foyers dans un village sont les liens familiaux et la qualité du sol. Lorsqu'il est nécessaire de se déplacer pour trouver un nouveau lieu de culture, les facteurs qui rentrent en compte dans l'établissement d'une nouvelle habitation sont la qualité du sol et la proximité d'une route. Il n'existe aucune règle de la société de gestion de la RNN quant à l'établissement de nouveaux champs sur la zone. Ce fort degré de mobilité au sein de la RNN peut avoir un impact potentiellement fort sur la faune sauvage (i.e. distribution, effectif) ainsi que sur le maintien d'habitats favorables.

A4 - Activités humaines

En marge de l'agriculture de subsistance, la principale activité au sein de la RNN est la pêche qui se pratique principalement pendant la saison sèche (d'avril à novembre). La pêche est autorisée dans la RNN mais uniquement à des fins de consommation propre. Néanmoins, des licences sont attribuées par l'administration locale moyennant une taxe. Le faible contrôle quant à l'attribution des licences rend difficile l'estimation du nombre de pêcheurs et de leurs impacts dans la RNN. Une étude menée par Begg en 2004 a identifié 36 camps de pêcheurs (en moyenne 8 pêcheurs par camp) sur une portion de rivière de 25 km. La majorité des pêcheurs étaient locaux (76%) ou provenant d'un district voisin (23%) et 1% venaient de Tanzanie.

La chasse est aussi pratiquée dans la RNN mais est, quant à elle, totalement illégale (excepté la chasse sportive, cf. A1). Outre le braconnage des éléphants pour l'ivoire dont nous ne parlerons pas ici, elle se pratique elle aussi à des fins de subsistance et/ou commerciales. La chasse se pratique peu avec des armes à feu (4 armes confisquées en 2012, 6 en 2013) mais surtout à partir de pièges, notamment des collets. Elle se pratique principalement pendant la saison sèche lorsque les animaux sont contraints par la disponibilité en eau et qu'il est plus facile de les pister (notamment après le passage des feux). Les braconniers érigent de longues barrières à l'aide de bois coupé pouvant atteindre jusqu'à plusieurs kilomètres. Un espace libre est laissé tous les 50 mètres environ dans lequel est placé un collet. Ces collets sont principalement métalliques et peuvent capturer toutes les espèces d'herbivores, y compris des buffles. En 2012, 499 collets ont été collectés par les équipes de lutte anti-braconnage contre 442 collets en 2013 (les chiffres quant à l'effort de patrouille (i.e. nombre de sorties, nombre de kilomètres parcourus, etc.) n'ont pas été compilés ces deux années). Suite à sept comptages aériens réalisés depuis 1998 sur l'intégralité de la RNN (Craig 2012) le nombre de lignes de collets observées depuis les airs a été compilé. Depuis 1998, ce nombre est en constante augmentation passant de 50 lignes de collets en moyenne en 1998 à près de 200 en 2011. Selon les estimations de Craig (2012), le nombre de lignes de collets sur l'intégralité de la RNN pourrait atteindre 2061 ± 426 ce qui laisse présager l'impact non négligeable de ces pratiques sur la faune sauvage.

Des activités illégales de coupes de bois précieux sont également présentes dans la RNN, notamment dans le Nord-Est de la Réserve en raison de la proche frontière avec la Tanzanie et du pont transfrontalier du village de Negomano par lequel le bois peut quitter le pays. En 2009, dans l'unité de gestion L9 (Figure 3.3), plus de 150 sites de coupes illégales ont été repérés depuis les airs. Les espèces principalement prélevées sont l'*Afzelia quanzensis* et le *Pterocarpus angolensis*.

De même, l'extraction illégale des ressources minérales, notamment le rubis et l'or, se pratique dans la RNN. Une mine de rubis se trouve à la frontière des unités de gestion L2 et L3. Malgré les efforts de la société de gestion pour boucher la mine, cette dernière est ré-ouverte chaque année et une cinquantaine de mineurs y travaillent quotidiennement. L'orpaillage se pratique essentiellement sur la Rivière Rovuma, à la frontière entre le Mozambique et la Tanzanie. Néanmoins, plusieurs sites d'orpaillage ont été récemment démantelés au cœur de la RNN, sur la Rivière Lugenda. Cette activité très polluante contamine durablement l'environnement notamment en raison de l'utilisation de mercure lors de la phase d'agglomération des poussières et particules d'or.

Ces deux dernières activités (i.e. bois précieux et ressources minérales) représentent des alternatives d'utilisations des sols et d'importants conflits potentiels entre la RNN et le développement économique de la province (voir du pays), sans parler du désastre écologique qu'elles peuvent engendrer. Bien que décrétée "Réserve Nationale" dans les années 50, la RNN devra faire face à de nombreuses tensions à l'avenir quant à ces activités illégales qui sous-entendent de fortes pressions financières associées.

B - L'ECOSYSTEME

B1 - Faune

La RNN abrite les plus grandes concentrations de faune sauvage au Mozambique avec l'ensemble des espèces herbivores (à l'exception du rhinocéros noir, *Diceros bicornis*, et potentiellement de l'antilope rouanne, *Hippotragus equinus*) et carnivores attendues dans la région (SGDRN 2007). Les résultats disponibles de sept comptages aériens réalisés depuis 1998 sur l'intégralité de la RNN (Craig 1998, 2000, 2002, 2004, 2006, 2009 et 2012) ont permis d'estimer les effectifs des populations d'herbivores de la zone (Table 3.2). Parmi les espèces de carnivores charismatiques, la RNN abrite une population d'environ 800-1,000 lions (*Panthera leo*) adultes (Begg and Begg 2011) ainsi qu'au moins 450 lycaons (*Lycaon pictus*) (Begg and Begg 2007).

Table 3.2 - Population estimates and densities of the main herbivore species in NNR in 2011

Colloquial name	Population estimates *	Density/km^2
African elephant	12 029 ± 2 531	0.28
Bushbuck	242 ± 114	0.01
Bushpig	251 ± 171	0.01
Cape buffalo	6 214 ± 2 752	0.15
Common eland	3 136 ± 1 480	0.07
Common reedbuck	765 ± 259	0.02
Common waterbuck	1 662 ± 558	0.04
Crawshay's zebra	3 844 ± 829	0.10
Greater kudu	1 397 ± 420	0.03
Grey duiker	10 683 ± 819	0.25
Johnston’s impala	1 019 ± 489	0.02
Johnston’s wildebeest	877 ± 583	0.10
Lichtenstein’s hartebeest	3 799 ± 1 035	0.09
Sable antelope	9 662 ± 1 857	0.20
Warthog	4 629 ± 892	0.10
Bushpig	251 ± 171	0.01

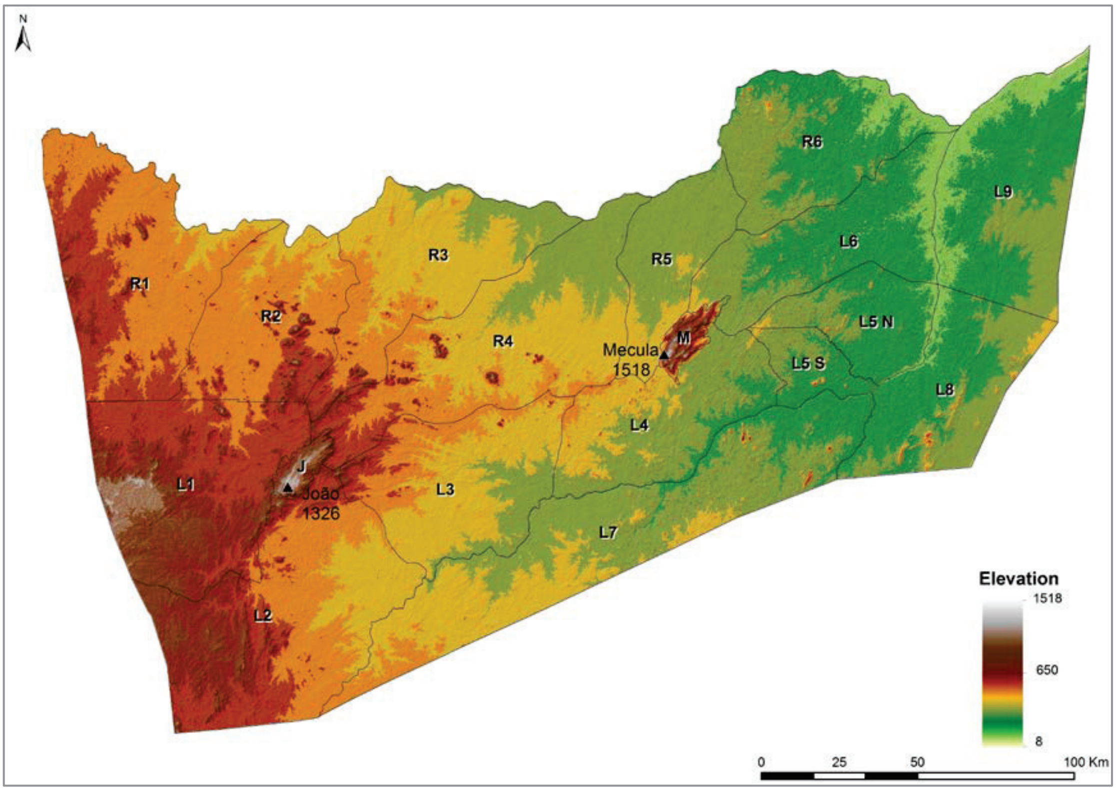
* from Craig 2012

Malgré les années de conflit (1975-1992), la RNN a conservé une remarquable diversité et richesse de ses populations animales. Il existe trois sous-espèces remarquables présentes dans la RNN, le gnou de Johnston, le zèbre de Crawshay's et l'impala de Johnston. Bien que ces dernières années le braconnage des éléphants a augmenté de façon dramatique, la RNN abrite encore une population estimée à plus de 12,000 individus. Elle abrite également une population de plus de 9,000 sables et plus de 6,000 buffles.

Comparées aux densités observées dans des aires protégées situées sur des sols de même type, les densités de mammifères de la RNN restent faibles (SGDRN 2007). Il est cependant difficile de savoir si ces faibles densités sont naturelles ou le résultat d'une chasse intensive dans la zone pendant les années de conflit, notamment pour nourrir les troupes. Ceci est particulièrement vrai pour le buffle (cf. Annexe II) qui présente des densités de 0.15 individus au kilomètre carré. Les densités de buffles dépendent de nombreux facteurs, notamment de la distribution spatiotemporelle des ressources (eau; qualité et quantité du fourrage) et du contexte épidémiologique (Cornélis 2012). La densité de buffles de la RNN est cinq à vingt fois plus faible que celle observée dans d'autres aires protégées écologiquement proches (cf. Chapitre 1 - Figure 1.1). Dans la Réserve du Sélous (Sud de la Tanzanie), le Parc National du Kruger (Afrique du Sud) ou le Parc National de Hwange (Zimbabwe), les densités moyennes de buffle sont comprises entre 1 et 3 individus au kilomètre carré. Ceci est particulièrement vrai lorsque des pluies importantes (800-1,200 mm/an dans la RNN) devraient favoriser une relative abondance des espèces de grands herbivores (Bell 1982; Fritz et al. 2002). Bien que les écosystèmes de type *miombo* sont connus pour présenter des faibles biomasses animales en ce qui concerne les populations de grands herbivores (Campbell 1996), ces faibles densités de buffles sont logiquement devenues une priorité pour la société de gestion de la RNN.

B2 - Le milieu physique

La RNN est située dans l'écorégion des forêts de type *Miombo* de l'Est (WWF 2001). Cette écorégion est majoritairement confinée aux faibles altitudes des plateaux de l'Est-Africain. Sa géologie est caractérisée par des schistes et gneiss métamorphosés du Précambrien supérieur (Bridges 1990). Les sols sont fortement drainés et filtrés, pauvres en nutriments et acides avec une faible matière organique.



D'un point de vue topographique le paysage de la RNN se compose d'un plateau légèrement vallonné aux alentours de 300-600m d'altitude. Ce plateau s'élève dans l'ouest de la zone pour retomber graduellement à 150m d'altitude à la frontière Nord-Est de la RNN, à la confluence des rivières Rovuma et Lugenda (Figure 3.4 - Annexe I.C). Il existe d'importants affleurements monolithiques granitiques, appelés *inselbergs*, qui émergent du panorama et viennent briser ce paysage relativement plat. Il s'agit de reliefs résiduels isolés créés par l'érosion (George 1970). La plus importante formation dans la RNN est l'inselberg de Mecula qui culmine à une altitude de 1,518m. Le paysage est entrecoupé de vastes vallées où circulent des rivières peu profondes résultant d'un système de drainage complexe.

La RNN présente un réseau hydrographique dominé par deux cours d'eau principaux, les Rivières Lugenda et Rovuma, qui sont de larges rivières (allant jusqu'à 1,000 m de large) à fort débit pérenne et qui présentent une succession de chenaux pierreux (à dominance dans l'ouest) et de larges parties sableuses (à dominance dans l'est). Entre ces deux cours d'eau, le système de drainage est alimenté par de très nombreuses rivières saisonnières ainsi qu'un extensif réseau de zones inondées saisonnièrement. Ce vaste réseau hydrographique est subdivisé en quatre classes: (i) les rivières principales (Lugenda et Rovuma), (ii) les rivières secondaires qui s'assèchent partiellement en fonction des saisons mais maintiennent des chaines irrégulières de mares, (iii) les rivières tertiaires et (iv) les rivières mineures (Figure 3.5 - Annexe I.D). Ces deux dernières classes s'assèchent complètement en saison sèche. Le réseau hydrographique présente peu de trous d'eau, ces derniers résultant plus de l'eau maintenue dans certains lits de rivières en saison sèche (Annexe I.E).

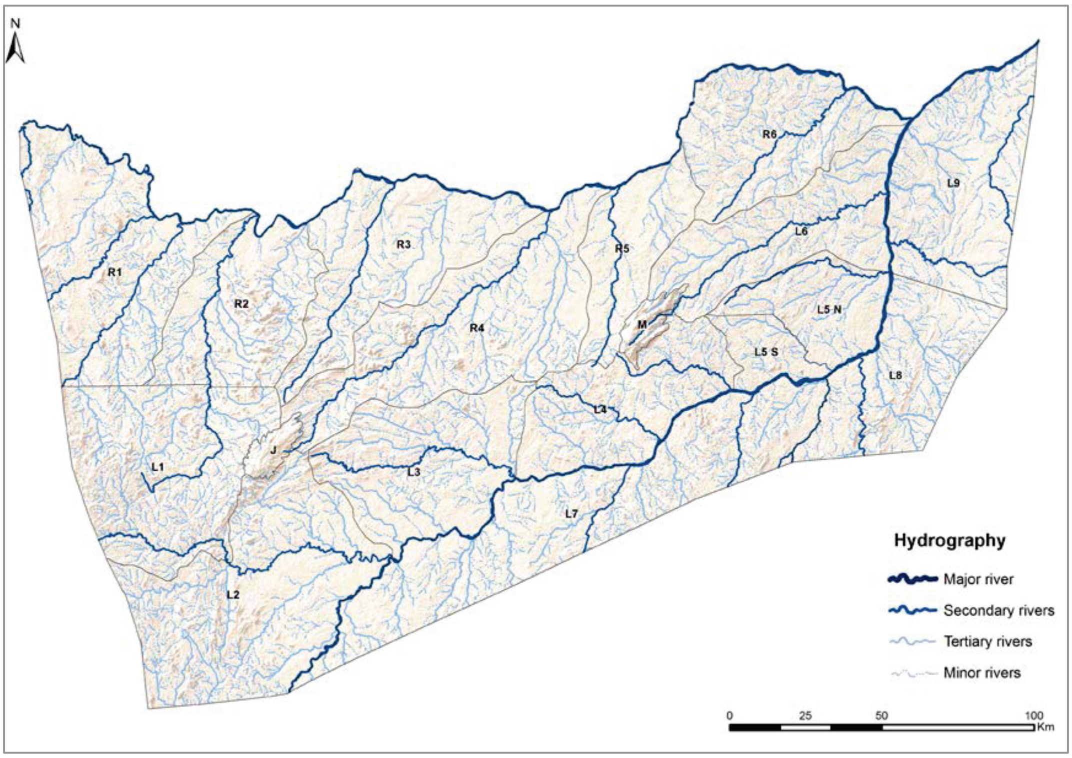


Figure 3.5 - River system in Niassa National Reserve subdivided in 4 classes

La RNN est soumise à un climat tropical saisonnier caractérisé par 2 saisons principales, une saison humide chaude de la mi-novembre à la fin avril et une longue saison sèche de 6 à 7 mois (mai à novembre). Durant la saison des pluies la moyenne des précipitations se situe entre 250 et 350 mm de pluies par mois (800 à 1,200 mm par an). Cette moyenne varie le long d'un gradient Est/Ouest avec une pluviométrie plus forte dans l'Ouest que dans l'Est (Figure 3.6 - Annexe I.F-G). Des pics allant jusqu'à 1,400 mm de pluies par an peuvent être observés certaines années dans l'Ouest de la zone. Ce climat tropical comprend des températures, variables selon l'altitude, allant de 15 à 30°C pendant la saison des pluies et de 10 à 20°C pendant la saison sèche. La fin de la saison sèche (octobre-novembre) est néanmoins soumises à des températures plus chaudes se rapprochant de celles de saison des pluies.

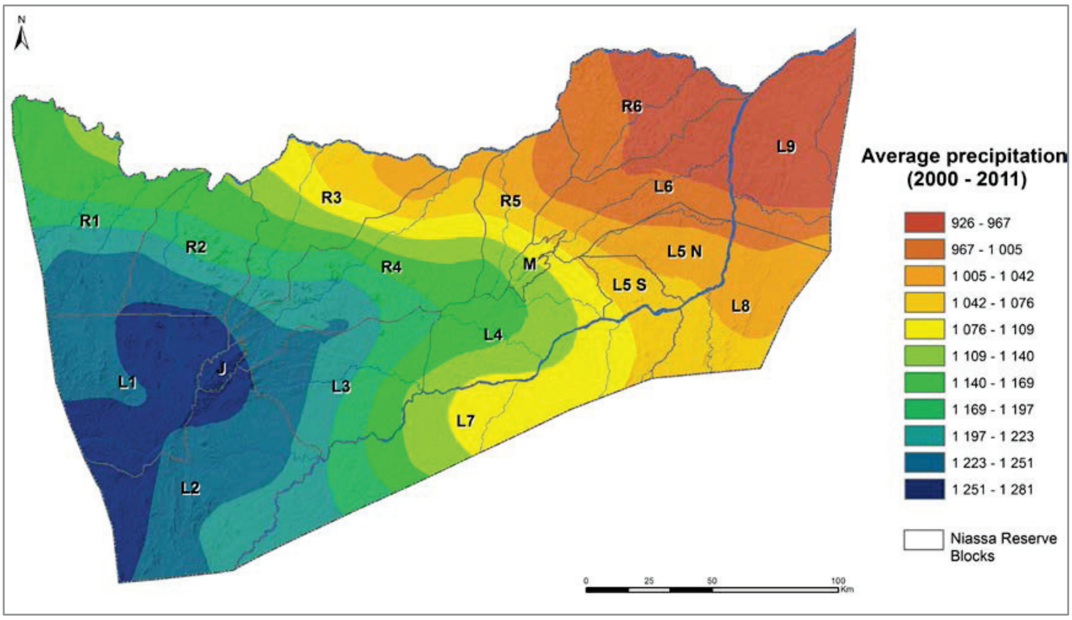


Figure 3.6 - Mean annual rainfall in Niassa National Reserve between 2000 and 2011

B3 - Végétation

La RNN est située dans l'écorégion des forêts de type *Miombo* de l'Est (WWF 2001) et appartient à la région floristique du centre régional d'endémisme zambézien (White et al. 1983). Elle présente une unité cartographique de végétation de type 26 : "Forêt claire zambézienne sèche de type *miombo*".

Le *miombo* est le type de végétation le plus important du centre régional d'endémisme zambézien. Soixante-douze pourcents de la RNN en est recouvert (Ribeiro et al. 2008). Le *miombo* supporte une grande richesse florale et est dominé par des arbres à feuilles caduques de la famille des Légumineuses, notamment les genres *Brachystegia*, *Julbernardia* et/ou *Isoberlinia* (Campbell 1996, Chidumayo 1997, Poilecot and Timberlake 2007). La canopée y dépasse rarement 15 mètres de hauteur.

Suite aux trois missions spécifiques réalisées entre 2010 et 2012 (cf. Chapitre 2 pour les méthodes et l'échantillonnage), 9 types de végétation ont été identifiés au sein de la RNN : (i) *miombo* dense, (ii) *miombo*, (iii) *miombo* ouvert, (iv) prairie boisée, (v) prairie, (vi) *jesse bush,* (vii) prairie de bordure de rivière, (viii) forêt riveraine et (ix) forêt de montagne.

Le type ***miombo* dense** est caractérisé par des arbres de 10 à 20 mètres de hauteur aux larges houppiers, dominés par des espèces communes du *miombo* telles que *Brachystegia spiciformis*, *B. boehmii* et *Julbernardia globiflora*. D'autres espèces comme *Diplorhyncus condylocarpon* et *Pseudolachnostylis maprouneifolia* sont également abondantes dans les sous-étages du couvert ligneux. Le recouvrement de la canopée atteint souvent 80%. La strate arbustive est limitée et hétérogène. Le couvert herbacé est raisonnablement abondant et en général composé d'espèces de qualité nutritive bonne à moyenne telles que *Digitaria eriantha*, *Themeda triandra*, *Andropogon chinensis* et *Diheteropogon amplectens*.

Le type ***miombo*** est relativement similaire au type *miombo* dense mais avec une recouvrement de la canopée plus faible atteignant généralement 60%. La strate arbustive y est également limitée et le couvert herbacé est raisonnablement abondant et en général composé d'espèces de qualité nutritive bonne à moyenne.

Le type ***miombo* ouvert** est lui aussi typique des forêts de *miombo* mais avec un recouvrement de la canopée plus faible atteignant 30-40%. La strate arbustive y est plus développée. Ce type est ouvert avec un couvert herbacé abondant et composé d'espèces de qualité nutritive bonne à moyenne.

Le type **prairie boisée** est généralement situé sur des sols pauvres et pierreux et est caractérisé par une strate arborée et arbustive limitée dont le recouvrement de la canopée n'excède pas 20%. Les espèces typiques du *miombo* y sont observées mais peuvent y être remplacées par des espèces des genres *Acacia* et *Combretum*. La strate arbustive est limitée mais offre un fourrage de saison sèche intéressant. Le couvert herbacé est abondant et majoritairement composé d'*Andropogon chinensis, Loudetia flavida, L. simplex, Diheteropogon amplectaens* et d'autres espèces secondaires comme *Stereochlaena cameronii*, *Andropogon pseudapricus* and *Heteropogon contortus.* En fonction des espèces herbacées dominantes la qualité nutritive varie de bonne (e.g. *Loudetia simplex*) à mauvaise (e.g. *Andropogon chinensis*).

Le type **prairie** sont des zones ouvertes avec une quasi absence de recouvrement ligneux (10% ou moins). Elles se trouvent généralement en bas des vallées dans des zones plus humides et probablement plus fertiles et apparaissent souvent à la suite d'un gradient de moins en moins dense de types de *miombo*. Elles sont composées d'un couvert herbacé abondant et de bonne qualité avec des espèces telles que *Hyparrhenia rufa, H. glabriuscula, H. filipendula, H. nyassae* et *Loudetia simplex.*

Le type ***jesse bush*** est caractérisé par une forêt dense sèche et une strate arbustive épaisse. Ce type se trouve généralement proche des larges rivières (e.g. Lugenda). De grands arbres tels que *Adansonia digitata, Acacia nigrescens, Berchemia discolor, Hyphaene petersiana, Millettia stuhlmanni* et *Afzelia quanzensis* dominent la strate arbustive composée de *Dalbergia nitidula, Euphorbia cooperi, Cleistochlamys kirkii*, *Combretum mossambicense, Croton pseudopulchellus, Dichrostachys cinerea, Pteleopsis myrtifolia,* et *Schrebera trichoclada.* Le couvert herbacé est généralement peu développé.

Le type **prairie de bordure de rivière** est une prairie hautement productive qui se trouve le long des larges rivières pérennes comme la Lugenda. Ces zones sont généralement de petites surfaces mais présentent un couvert herbacé très riche avec des espèces telles que *Panicum* maximum, *Urochloa mossambicensis, Hyparrhenia rufa, Sorghum arundinaceum, Eriochloa rovumensis* et *Cynodon dactylon.*

Le type **forêt riveraine** se trouve le long des rivières et est majoritairement composé d'arbres et arbustes aux feuilles persistantes. Le recouvrement de la canopée y est proche de 100%. Les espèces principales de la strate supérieure sont *Faidherbia albida, Lonchocarpus capassa, Millettia stuhlmannii, Ficus sycomorus, Xanthocercis zambesiaca* et *Kigelia Africana.* La strate inférieure se compose de *Xylopia parviflora, Voacanga thouarsii, Tricalysia lanceolata, Trichilia emetica, Friesoldielsia obovata, Cleistochlamys kirkii, Bridelia micrantha, Bauhinia tomentosa* et *Antidesma venosu.* En bordure des rivières, en contact direct avec l'eau, des espèces telles que *Ficus capreifolia, Phyllanthus reticulates, Combretum obovatum* et *Mimosa pigra* peuvent être rencontrées. Le couvert herbacé est généralement peu développé.

A partir de 4 images satellites Landsat ETM5 à 30 m de résolution et d'une liste simplifiée des différents types de végétation (cf. Chapitre 2 pour détail) une classification supervisée a permis la cartographie de 93% de la RNN (le reste étant constitué de zones non classifiées ou de zones brûlées, de nuages et d'ombres de nuages). Les 1,500 points de contrôle collectés lors des missions spécifiques ont été utilisés pour valider la cartographie de la végétation. Les mesures de précision de la cartographie de la végétation ont montré une bonne correspondance entre les résultats de la classification et les points de contrôle avec une exactitude globale de 80%. Les erreurs provenaient surtout de la zone Ouest de la RNN où un échantillonnage insuffisant a entraîné des confusions, notamment au niveau des types *miombo* dense et *miombo*. Etant donné qu'aucun troupeau de buffles n'était suivi dans la zone Ouest nous avons considéré que ces erreurs avaient peu d'effet sur les résultats des analyses de sélection de l'habitat (cf. Chapitre 5). La carte de la végétation de la RNN est présentée en Figure 3.7 et en Annexe I.B.

L'indice de végétation de la différence normalisée (Normalized Difference Vegetation Index, NDVI) est une mesure de la verdure qui donne une valeur grossière de l'activité photosynthétique de la végétation (NASA, Earth Observatory) et représente la distribution spatiale de la production primaire. A partir des données MODIS (produit Mod13Q1 : résolutions 250m et 16 jours) compilées de 2000 à 2012, il est possible de montrer que le NDVI moyen de la RNN varie de façon importante dans le temps et dans l'espace. Avec une phénologie saisonnière marquée par un départ de croissance végétale (*flush*) au mois de novembre, un pic de production au mois d'avril, et une décroissance progressive jusqu'au mois d'octobre. De plus, à l'instar de la pluviométrie, la décroissance progressive au cours de la saison sèche se fait le long d'un gradient Est/Ouest (i.e. le front de décroissance progresse d'Est en Ouest) (Figure 3.8). La qualité de la végétation (i.e. valeur nutritive) disponible pour les populations herbivores est donc hétérogène en fonction des zones, particulièrement au cours de la saison sèche. De même, la biomasse herbacée sèche nécessaire aux départs de feux de brousse est elle aussi hétérogène dans le temps et dans l'espace.

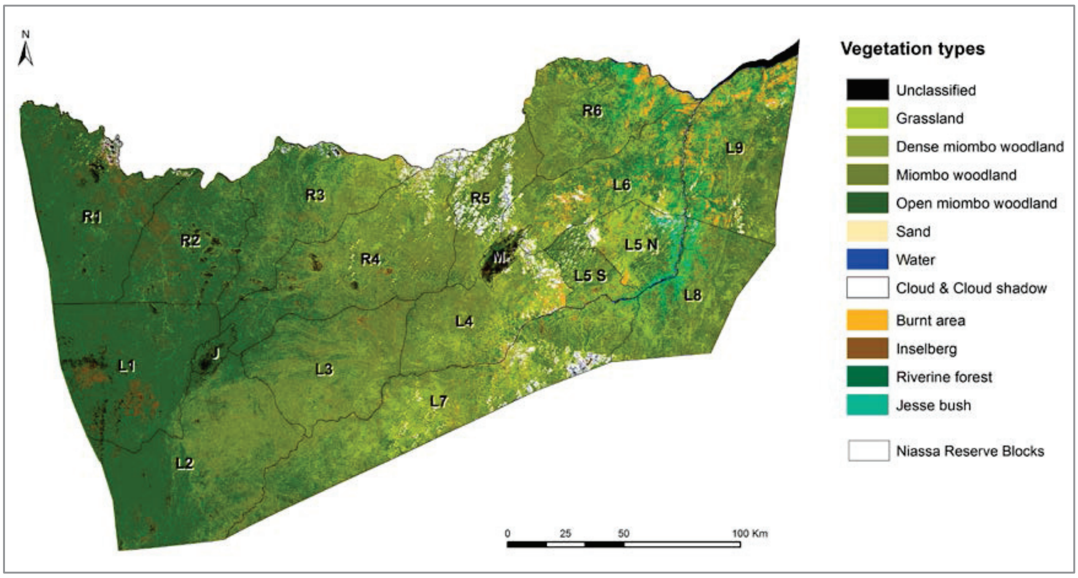
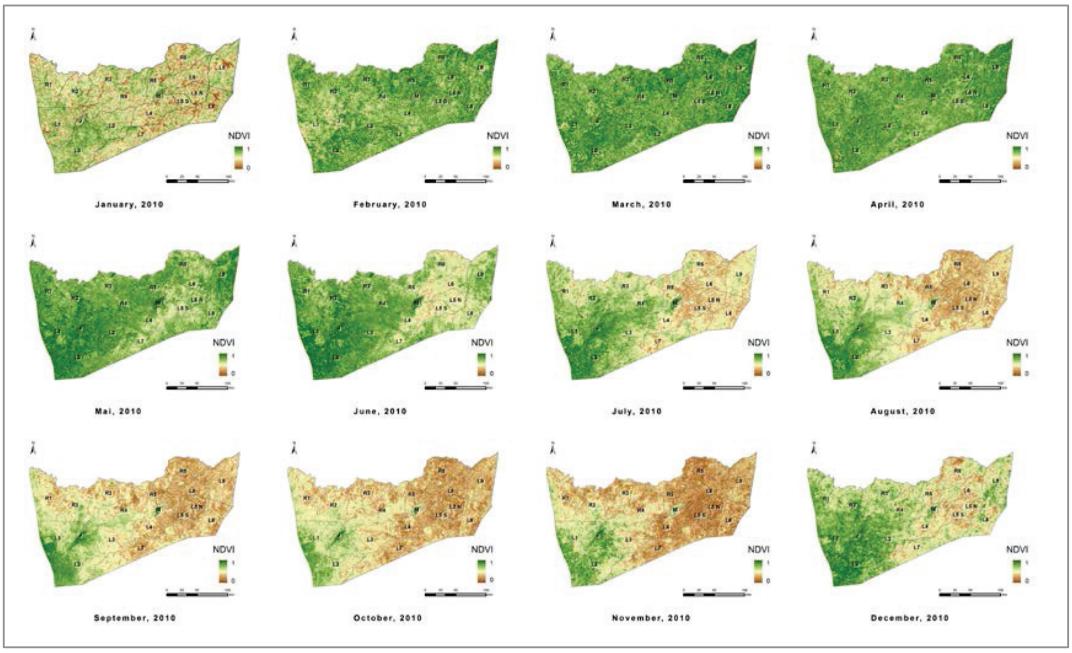


Figure 3.7 - Vegetation map of the Niassa National Reserve obtained from supervised classification of Landsat 5 ETM imagery of May-June 2008

Cf. Annexe I pour la visualisation des cartes au format A4

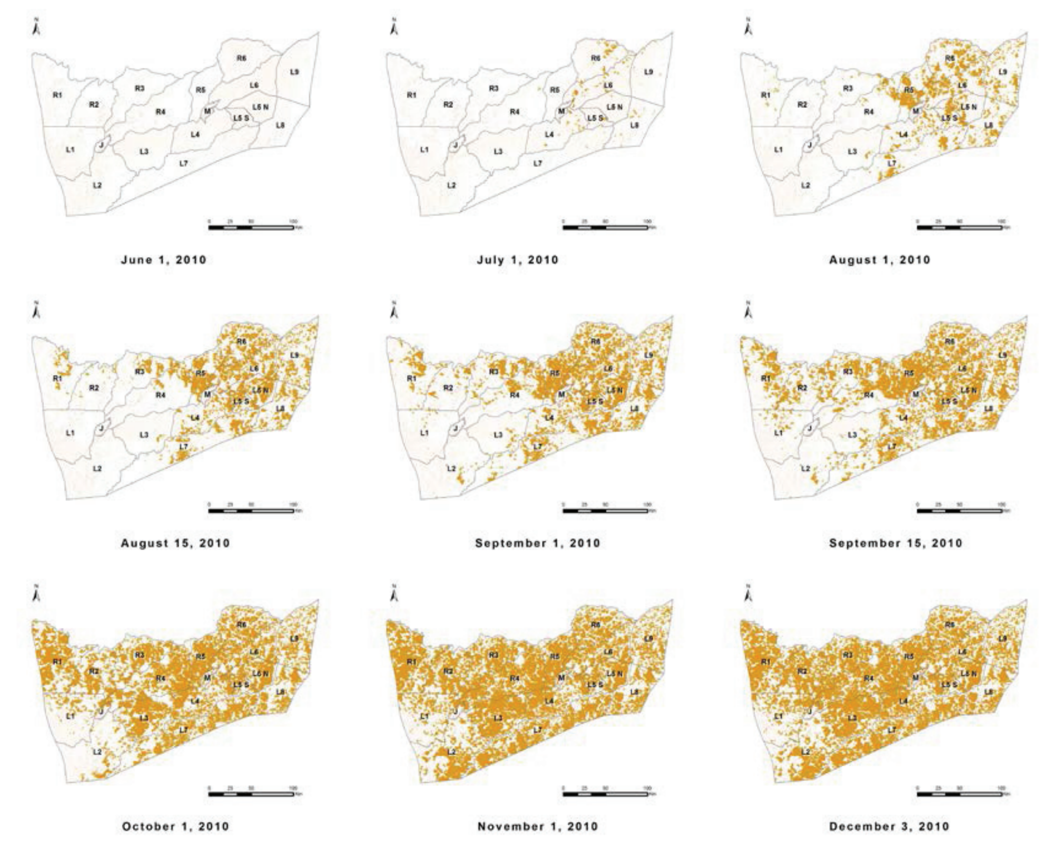


January, 2010
February, 2010
March, 2010
April, 2010
Mai, 2010
June, 2010
July, 2010
August, 2010
September, 2010
October, 2010
November, 2010
December, 2010

Figure 3.8 - Mean NDVI in Niassa National Reserve in 2010. Vegetal growth increases in November to reach a peak in April and gradually decreases from the East to the West until October

B4 - Les feux de brousse

Le feu est l'un des facteurs écologiques les plus importants affectant les forêts de type *miombo* (Chidumayo 1997). Les feux en saison sèche y sont réguliers et fréquents.



June 1, 2010

July 1, 2010

August 1, 2010

August 15, 2010

September 1, 2010

September 15, 2010

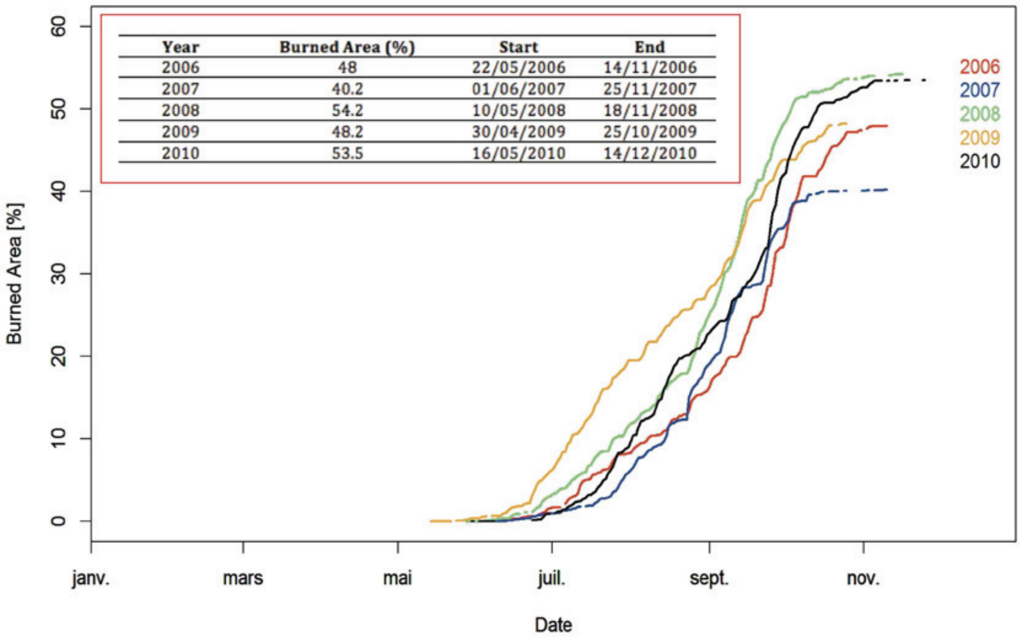
October 1, 2010

November 1, 2010

December 3, 2010

Figure 3.9 - Time series of bushfires in Niassa National Reserve in 2010

L'origine des feux est souvent accidentelle, notamment lorsque les locaux préparent leurs champs pour les cultiver, lorsqu'ils collectent du miel ou préparent du charbon. Les feux sont également amorcés par les braconniers, soit pour faire fuir les animaux et les conduire dans une zone précise, soit pour les attirer plus tard sur des repousses herbacées après le passage d'un feu, soit pour les pister facilement ou encore pour effacer leurs traces lorsque ces derniers sont poursuivis par des patrouilles de lutte anti-braconnage. De plus, les locaux mettent également le feu volontairement pour nettoyer une zone, qu'il s'agisse de nettoyer une zone le long d'un village pour éviter le passage d'un feu incontrôlable ultérieurement ou bien le long d'une route ou d'un sentier pour une meilleure sécurité (i.e. meilleure visibilité) ou encore pour faciliter les déplacements à pied ou en vélo (e.g. pêcheurs pour transporter à vélo le produit séché de leur pêche). Enfin, les opérateurs de chasse sportive mettent également le feu dans leur unité de gestion afin de pouvoir pister plus facilement les animaux.



Year	Burned Area (%)	Start	End
2006	48	22/05/2006	14/11/2006
2007	40.2	01/06/2007	25/11/2007
2008	54.2	10/05/2008	18/11/2008
2009	48.2	30/04/2009	25/10/2009
2010	53.5	16/05/2010	14/12/2010

Figure 3.10 - Cumulative frequency distribution of bushfires in NNR from 2006 to 2010

A partir des données MODIS (produit MCD45 : résolutions 500m et 1 jour) compilées de 2000 à 2012, il est possible de montrer qu'au sein de la RNN les feux se produisent uniquement en saison sèche entre les mois de mai et décembre avec un pic de fréquence au mois d'août pendant la saison sèche chaude (Figure 3.9 - Annexe I.J). Ils sont uniquement alimentés par la biomasse herbacée (Campbell 1996), le matériel ligneux participant peu au front principal du feu mais pouvant maintenir une combustion plusieurs jours après le passage d'un feu. Le feu est donc corrélé à la production herbacée. Comme nous l'avons vu précédemment (cf. B3 - Figure 3.8), la production primaire décroit progressivement d'Est en Ouest entre les mois d'avril et d'octobre. Logiquement, les premiers feux apparaissent dans l'Est de la RNN, au mois de juin, et progresse vers l'Ouest au cours de la saison sèche (Figure 3.9). Chaque année, près de 50% de la RNN brûle (Figure 3.10) ce qui représente une surface de plus de 20,000 km^2. Si les feux de début de saison sèche peuvent conduire à une repousse herbacée de qualité (van de Vijver et al. 1999) et à des dégâts moindres sur les populations végétales (i.e. la végétation est encore verte et humide), les feux de fin de saison sèche ont un impact bien plus néfaste en raison de leur intensité, notamment sur les espèces ligneuses (Chidumayo 1997). La quantité de fourrage disponible pour les populations d'herbivores au cours de la saison sèche se voit donc fortement impactée par les nombreux feux présents sur la zone, notamment en fin de saison sèche lorsque les feux, intensifiés par une biomasse herbacée sèche abondante, ne génèrent quasiment aucune repousse jusqu'aux premières pluies (novembre).

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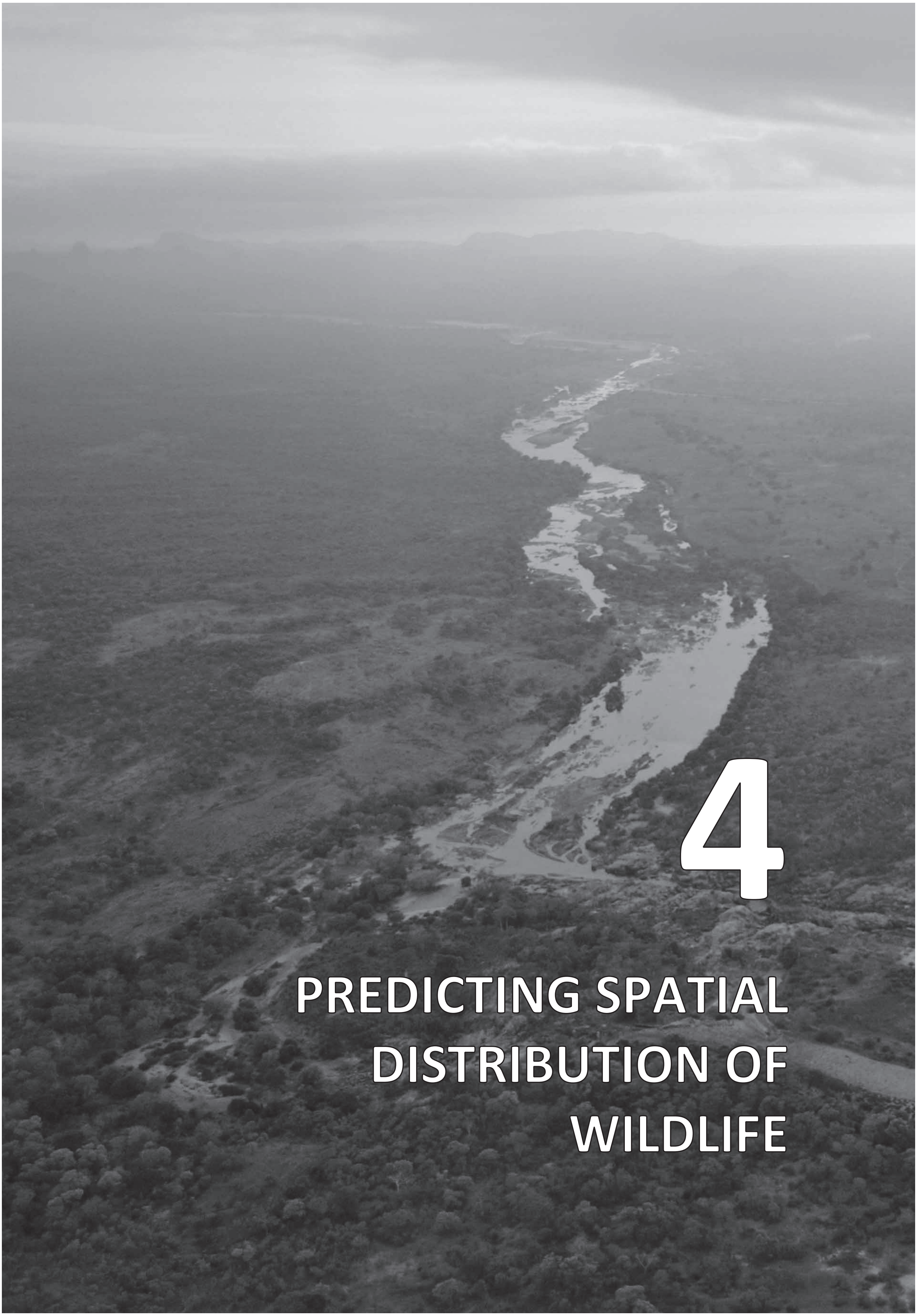

4

PREDICTING SPATIAL DISTRIBUTION OF WILDLIFE

Predicting spatial distribution of wildlife in relation to environmental covariates: an application to aerial surveys in Niassa National Reserve, Mozambique

Thomas Prin - Vladimir Grosbois - Colin Craig - Annelise Tran - Hervé Fritz - Anabela Rodrigues - Philippe Chardonnet - Marie Gely - Daniel Cornelis

Abstract Reliable analyses of space-use patterns of free-ranging animals are fundamental for understanding ecological processes, and beyond for conservation or management purposes. In semi-arid areas such as African savannah, the distribution patterns of large herbivores in dry season reflect large scale and long-term equilibriums with key resources, and provide valuable information for decision making. In this paper, we explored census data from 5 dry season aerial surveys (2002-2011; Niassa National Reserve) using generalized linear models (GLM) to address relationships between large ungulates distribution and environmental covariates. Results show that distribution patterns in NNR are mainly driven by distance to water, longitudinal zoning, land cover and primary production. As expected, rivers impact the distribution of grazers (buffalo, hartebeest, reedbuck, waterbuck and wildebeest) and one mixed feeder (impala). In contrast, results do not support the hypothesis of a relative water independence of browsers compared to grazers. No obvious avoidance of human activities (villages proximity) was observed, but non perturbations such as poaching may not be reflected in our analysis. In NNR, the distribution of herbivores may not necessarily be driven by the same covariates depending on the area due to large scale heterogeneity of environmental covariates. The benefits and limitations of our analytical approach, aimed at valorising aerial census data are discussed.

Keywords Herbivore distribution; African ungulates; Resource trade-offs; Generalized linear model; GLM; Landscape scale; Niassa National Reserve

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A - INTRODUCTION

Understanding the drivers of large herbivore spatial distribution is recognised as a significant tool for decision making by wildlife managers, as distribution can provide helpful clues to the nature of mechanisms having effect on a specific population or a community (Franklin 1995; Austin 1998; Guisan and Zimmermann 2000; Austin 2002; Scott et al. 2002; Elith and Burgman 2003; Redfern et al. 2003). This is especially true in large remote protected areas with limited resources for which choices have to be made as to where to invest. The challenge is even greater when little knowledge exists on the biomes or species to be managed, or when the site's history has led to massive disruptions in the system.

This is the case of Niassa National Reserve (NNR), one of the vastest protected areas of the African continent (42,140 km^2) that suffered from 15 years of civil war (1977-1992). The area still supports the full complement of herbivores, including endemic subspecies (e.g. Niassa wildebeest, *Connochaetes taurinus johnstoni*), and is mostly covered by *miombo* savannas, for which few references exist as far as large herbivore community functioning is concerned (Caro 1999). One of the original features of NNR is the fact that villages are included within the limits of the protected area (SGDRN 2007), a feature that calls for investigating the effect this human settlement could have on the functioning of the ungulate community. Indeed, impacts of humans on the density and distribution of large mammals in Africa is well known (Noss 1995; Barnes et al. 1997; Noss 1998; Lahm et al. 1998; Blom 2001). However, the effect of human disturbance varies greatly, depending on its nature and intensity, and understanding this interaction is essential for managing protected areas (Prins and Reitsma 1989; White 1994; Fitzgibbon et al. 1995; Oates 1996; Hall et al. 1998; Blom et al. 2005). However, large mammal densities and distribution are also influenced by a range of ecological factors, including vegetation and altitude, distance to water or fire, as these condition the quantity and quality of food resources available throughout the year, and ultimately population and community dynamics (e.g. Murray and Illius 2000; Redfern et al. 2003; Archibald and Bond 2004; Redfern et al. 2005; Klop et al. 2007). As NNR starts to rebuild its wildlife population in such a context, the distribution patterns of herbivores have logically become a management priority and a challenging issue.

Light aircrafts have been widely used as an important tool in wildlife management since the mid-1950s on the African continent with the overall objective to provide insight into wildlife population trends (Jachmann 2002). During the last decades, the growing availability of remote sensing data has made information available on a large range of biophysical parameters. Although both aerial survey and remote sensing data are potentially affected by many sources of bias and using them for testing hypotheses requires caution, they provide a useful source of information for investigating the determinants of wild ungulate species distribution (e.g. Redfern et al. 2003; Smit et al. 2007a; Chirima et al. 2012; Bhola et al. 2012; Kiffner et al. 2012).

Between 2002 and 2011, 5 dry season aerial wildlife censuses were conducted over the entire NNR (Craig 2012), thus covering a wide area and potentially allowing an empirical investigation of the factors driving the distribution of wildlife at landscape-scale.

Figure 4.1 - A map of Africa and Mozambique showing the study site, the Niassa National Reserve

As aerial surveys were carried out in the second half of the dry season, we hypothesized that the distribution may reflect the long-term equilibrium of the large herbivores with their dry-season resources and the trade-off associated with distance to water (Illius and O'Connor 2000). This relationship could also be mediated by the occurrence of bush fires, which may create favourable patches in places with early burns or in contrast destroy dry-season resource in places with late burns (Sensenig et al. 2010; Burkepile et al. 2013). We finally aimed at testing the possible overriding effect of human disturbance which is also likely to generate variation in herbivore distribution. For this purpose, we fitted generalized linear models to presence/absence survey data (see Franklin 1995; Guisan and Zimmermann 2000; Austin 2002; Scott et al. 2002 for similar approaches).

B - METHODS

B1 - Study area

The Niassa National Reserve (NNR) is located in northern Mozambique along the border with Tanzania. The NNR is one of the largest African protected areas, covering an area of 42,140 km^2 (Figure 4.1). This protected area supports the largest concentrations of wildlife in Mozambique with the full complement of herbivores (excluding black rhino and possibly roan antelope) and carnivores expected in the region (SGDRN 2007). Rock art in the area shows that NNR has always supported a human population and more than 39,000 local residents live today inside the protected area, spread across 50 villages. Shifting subsistence agriculture is the primary land use and main economic activity (Cunliffe et al. 2005). Cattle are absent due to tsetse fly (*Glossina spp*.), the vector for the disease *trypanosomiasis*, but smaller livestock, primarily goats and chickens, and domestic dogs are present in the larger villages.

The NNR is located within the Eastern *Miombo* Woodland eco-region (WWF 2001). The landscape comprises a mostly gently undulating plateau at around 300-600 m altitude, rising to a higher plateau and hills in the west at around 1,370 m, and gradually falling to 150 m at the north-eastern boundary at the confluence of the Rovuma and Lugenda Rivers. Seventy-two percent of the NNR is covered by dry Zambezian Miombo woodland (Ribeiro et al. 2008). Five broad land cover types were recognized within the NNR: forest, riverine, deciduous woodland, *dambos* or wetlands and granite *inselbergs* (Timberlake et al. 2004). This vegetation supports a great floral richness and dominant tree species include *Brachystegia spiciformis*, *B. boehmii*, *B. allenii*, and *Julbernardia globiflora*. The dry *miombo* canopy is generally less than 15 m in height and leafless for 1 month or more during the dry season. The *miombo* woodlands of the NNR are subject to annual anthropogenic fires (Ribeiro et al. 2008).

The drainage is dominated by the Rovuma and Lugenda Rivers, which are large (up to 1,000 meters width) sand bed rivers with a strong perennial flow. The central watershed between these two rivers feeds numerous seasonal rivers as well as an extensive seasonally inundated wetland network (SGDRN 2007).

The NNR experiences a seasonal tropical climate with most rainfall concentrated in the hot summer months from mid-November through April. This season is followed by a long winter drought, lasting up to 7 months (Werger and Coetzee 1978). Mean annual rainfall ranges between 800 and 1,200 mm per annum, and varies along a west-east gradient with higher rainfall in the west. Mean maximum temperatures range between 15-30°C during the hot season (hot-dry and hot-wet) and 10-20°C in the cold-dry season.

B2 - Aerial censuses

Five aerial wildlife censuses were undertaken in the NNR since 2002 (end dry season; Table 4.1), using a stratified systematic transect sampling method (Norton-Griffiths 1978).

The NNR was divided in 16 blocks, which were surveyed along parallel transects spaced 4 km apart using a Cessna 185 (4-seater aircraft). A sampling intensity of 10% was used in all surveys. Transects were selected at the required sampling intensity at even intervals from a randomly chosen starting position within each block. Transects were orientated so as to lie more or less at right angles to the major rivers.

Table 4.1 - Aerial censuses

Year	Period
2002	04/10 to 18/10
2004	05/10 to 23/10
2006	04/10 to 25/10
2009	29/09 to 19/10
2011	01/10 to 19/10

A pair of rods attached to the lift struts defined the boundaries of strips on each side of the aircraft. The width of the strips was measured empirically by flying at various heights and at right angles across an airstrip on which numbers had been painted at 10 m intervals. Observers seated in the back of the aircraft called out the outermost and innermost numbers seen within the strip, and the difference between the numbers was used to calculate the “calibrated strip width” for 300 ft. above ground. The rods were adjusted to provide a strip width of 200 m per side.

This aircraft was equipped with a radar altimeter and a Global Positioning System (GPS). Transects were flown at a speed of 100 knots or less, and at a height of 300 ft above ground level (a.g.l.). The track of the aircraft was recorded at 20 second intervals. A pair of observers seated in the back called out sightings of animals observed (Table 4.2) within the sampling strip (see Calibration, below). A recorder seated in the front noted down these sightings (species, herd size and GPS location). Finally, a record of the height a.g.l. was made every 30 seconds by the pilot using radar altimeter to allow the calculation of the mean height for each transect.

Based on the above mentioned sampling design, the area surveyed was divided in sampling units. For this purpose, the polygons formed by the area surveyed along each transect were divided in suits of adjacent polygons (more or less 400 m side, depending on the strip width of each transect and on the straightness of the movement trace of the aircraft).

Table 4.2 - Species considered in this study

Colloquial name	Scientific name	Feeding strategy
Bushbuck	*Tragelaphus scriptus*	Browser
Greater kudu	*Tragelaphus strepsiceros*	Browser
Grey duiker	*Sylvicapra grimmia*	Browser
Cape buffalo	*Syncerus caffer caffer*	Grazer
Common reedbuck	*Redunca arundinum*	Grazer
Common waterbuck	*Kobus ellipsiprymnus*	Grazer
Crawshay's zebra	*Equus quagga crawshayi*	Grazer
Johnston’s wildebeest	*Connochaetes taurinus johnstoni*	Grazer
Lichtenstein’s hartebeest	*Alcelaphus lichtensteinii*	Grazer
Sable antelope	*Hippotragus niger*	Grazer
Warthog	*Phacochoerus aethopicus*	Grazer
African elephant	*Loxodonta Africana Africana*	Mixed feeder
Common eland	*Taurotragus oryx*	Mixed feeder
Johnston’s impala	*Aepyceros melampus johnstoni*	Mixed feeder
Bushpig	*Potamochoerus larvatus*	Omnivorus

A total of 36,596 polygons (i.e. statistical units) were generated for the 5 aerial censuses. A spatial joint was then performed between these polygons and wildlife observations in order to assign every observation to one sampling unit. Similar spatial joints were applied between these polygons and the environmental covariates presented below. All species recorded during the surveys (Table 4.2) were considered in this analysis. Only the elephant population was considered into two groups because resource use may differ between bull groups and mixed herds.

B3 - Model covariates

B3.1 - Temporal and spatial segments

As the data came from 5 successive aerial censuses, the "*year*" covariate was considered to examine possible demographic changes over the 10 years study period (2002 to 2011).

Similarly, the exploratory analysis of the environmental covariates considered in our analysis (see details below) showed the existence of large-scale longitudinal gradients. For example, our study area was characterized by gradients of primary production and rainfall decreasing from west to east. Bush fires also occurred earlier in the eastern section and covered larger areas than in the western section. We thus segmented our study area in 3 zones (hereafter referred to as "*western*", "*central*" and "*eastern*" zones) to account for such a longitudinal zoning. We thus considered that the effects of environmental covariates on probabilities of wildlife observation could differ according to this "*zone*" covariate.

B3.2 - Vegetation map

The main land cover types of the NNR were mapped using Landsat ETM5 satellite scenes. The study area was covered using 4 adjacent and cloud-free scenes (1 of May 2008 and 3 of June 2008). This type of sensor provides a spatial resolution (30 m) adapted for the extraction of the habitats. Once downloaded, the scenes were pre-processed (geometric and radiometric corrections; mosaic) using ENVI® software. The scenes were processed by a supervised classification (ENVI®) based on 71 vegetation sampling plots spread across the study area (June 2010, 2011 and 2012 field campaigns). The supervised classification was processed using the Maximum Likelihood classifier acting on all seven bands of the scenes and on a digital elevation model (Shuttle Radar Topography Mission; 90m spatial resolution). The classification was applied with a permissive statistical threshold of 80% below which a pixel was unclassified. The sampling plots consisted in 100 meters linear transects along which the floristic composition was characterised. Six land cover types were derived and considered for the classification process of the scenes: (i) Grassland, (ii) Open *Miombo* Woodland, (iii) *Miombo* Woodland, (iv) Dense *Miombo* Woodland, (v) Riverine Forest, (vi) *Jesse* Bush (Table 4.3). For mapping purposes, 2 other land cover classes were added: (vii) Bare Rocks (*inselbergs*), and (viii) Riverbeds. The land cover classes adequately covered 93% of the study area (the rest consisting in unclassified or burnt areas, clouds, and cloud shadows).

Around 1,500 ground control points (GCP) were used to validate the results obtained through satellite image classification. These GCP collected during the 3 above-mentioned filed campaigns consisted in a quick visual estimation of the structure and type of land cover. Accuracy measures of the land cover map showed a good agreement between the classification results and the ground-truth data (GCP), with an overall accuracy of 80%. Errors come mostly from the western zone where a weak sampling led to confusions, especially between 2 close land cover types: *Miombo* Woodland and Dense *Miombo* Woodland. As a consequence, the western zone (16,302 km^2) was not considered in the generalized linear modelling of observation probabilities.

A spatial joint then was performed between the sampling units (polygons) and the vegetation map in order to assign vegetation characteristics to each sampling unit. Two covariates were derived from the vegetation map: (i) the dominant (most represented) land cover type within the sampling unit and (ii) the opening up of the vegetation. The land cover types Dense *Miombo* Woodland, *Miombo* Woodland, Riverine Forest and *Jesse* Bush were considered as "closed", and the others as "open".

B3.3 - Primary production, bush fires and human disturbance

The role of primary production on wildlife distribution in NNR was investigated using two vegetation indexes (Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI)) provided by the Moderate-Resolution Image Spectroradiometer (MODIS) instrument (Mod13Q1 product: 250 m & 16 days resolutions). Ten scenes covering the 5 aerial surveys periods were used (5 NDVI scenes and 5 EVI scenes).

Table 4.3 - Land cover types' characteristics

VEGETATION CLASS	CANOPY COVER	SHRUB LAYER	HERBACEOUS LAYER	DOMINANT TREE SPECIES	DOMINANT HERBACEOUS SPECIES	PROPORTION EAST/CENTER %
Grassland	10% or less	10% or less	Good quality perennial grass	Typical *miombo* species or *Acacia* or *Combretum*	*Hyparrhenia sp., Andropogon sp., Loudetia sp.*	52 / 48
Open *Miombo* Woodland	30 - 40 %	30 - 40 %	Generally abundant of medium to good quality	Typical *miombo* species	*Digitaria sp., Themeda sp., Andropogon sp.*	62 / 38
***Miombo* Woodland**	60%	limited	Fairly abundant of medium to good quality	*Brachystegia spiciformis*, *B. boehmii*, *Julbernardia globifora, Diplorhynchus condylocarpon, Pseudolachnostylis maprouneifolia*	*Digitaria sp., Themeda sp., Andropogon sp.*	16 / 83
Dense *Miombo* Woodland	80%	limited	Fairly abundant of medium to good quality	Typical *miombo* species	*Digitaria sp., Themeda sp., Andropogon sp.*	26 / 74
Riverine Forest	100%	100%	Highly productive and palatable	*Faidherbia albida, Lonchocarpus capassa, Millettia stuhlmannii, Ficus sycomorus, Xanthocercis zambesiaca, Kigelia Africana*	*Panicum sp., Urochloa sp., Hyparrhenia sp., Sorghum sp., Eriochloa sp., Cynodon sp.*	100 / 0
Jesse Bush	80%	80%	Poorly developed	*Adansonia digitata, Acacia nigrescens, Berchemia discolor, Hyphaene petersiana, Dalbergia nitidula*	-	100 / 0

Similarly, the role of bush fires was assessed by the MODIS burned area product (MCD45 product: 500 m & 1 day resolutions). Two covariates were derived from the MODIS burned area product: (i) a burnt/non burnt covariate (hereafter referred to as "*burnt status*") and (ii) the delay since the last fire in the polygons (hereafter referred to as "*fire delay*"). A given sampling unit was considered as burnt if more than 50% of its area was burnt.

Human disturbance was assessed by computing maps (30 m spatial resolution) of the nearest distance to the local villages and to the road network (hereafter referred to as "*distance to villages*" *and* "*distance to roads*").

B3.4 - Rainfall and surface water

The influence of rainfall on wildlife distribution in NNR was tested using data provided by the Tropical Rainfall Measuring Mission product (TRMM: 25,000m & 1 day resolutions). Two series of covariates were derived from the TRMM: (i) the spatial distribution of the rainfall during the whole rainy season preceding every aerial census and (ii) the spatial distribution of cumulative rainfall during the two months preceding the aerial census.

The role of surface water on the distribution of wildlife was assessed by computing two maps (30 m spatial resolution). The first (hereafter referred to as "*distance to main rivers*") displayed the distribution of the nearest distances to the 2 main Rivers of the NNR (Lugenda and Rovuma). Both are from 200 m to 900 m wide and are characterized by a perennial flow. The second map (hereafter referred to as "*distance to secondary rivers*") displayed the distribution of the nearest distances to the 15 large seasonal tributaries. These tributaries dry out only partially in the dry season, turning into an irregular chain of ponds limited to the minor bed.

B3.5 - Covariates collinearity

Collinearity among quantitative explanatory covariates was assessed following Graham (2003). Levels of collinearity expected to bias analyses ($r \geq 0.28$) were detected between several pairs of covariates: distance to roads and to villages; distance to villages and to secondary rivers; distance to main rivers and primary production (both NDVI and EVI); distance to main rivers and mean annual rainfall; mean annual rainfall and primary production (both NDVI and EVI); NDVI and EVI. As a consequence, 4 covariates were removed from the initial set: distance to roads, EVI, mean annual rainfall and cumulative rainfall over the 2 months preceding the survey. The later two covariates were also discarded because their spatial resolution (25,000 m²) was much lower than (i) the resolution of the other covariates and (ii) the resolution of wildlife sampling units (i.e. numerous sampling units had the same value for the rainfall covariate).

B3.6 - Spatial autocorrelation

Spatial autocorrelation was assessed using Moran's I test for binary responses. Spatial autocorrelation was tested for 1,000 meter wide distance classes ranging from 1,000 to 10,000. Results revealed significant spatial autocorrelation for 6 out of 8 species. The spatial scale up to which significant spatial autocorrelation was detected varied from 1 to 3 km depending on the species considered (Table 4.4).

B4 - Statistical model

Generalized linear models (GLM) with binomial distribution were used to address the relationships between binary wildlife observation events and environmental explanatory covariates. For a given wildlife species, each statistical unit (characterized by a polygon and a year) was attributed either the value "observed" or the value "not observed". A complementary *loglog* link function was used to account for variation in size of the statistical units, the log of which was included as an offset in the model.

A maximal model was first defined which included all potential explanatory covariates. As exposed above, we considered the possibility that the central and the eastern zone could be characterized by differing ecosystems. It was thus important to account for potential difference between ecosystems in the pattern of association between wildlife presence and environmental covariates. All interactions between potential explanatory covariates and the Zone covariate were thus included in the maximal model. We also considered that the effect of NDVI and fire on wildlife presence could vary among land cover types. Indeed we considered that NDVI variation can reflect differently variation in primary productivity depending on the land cover category (Ito et al. 2006; Holdo et al. 2009). We also considered that the consequences of fire on the attractiveness of a land patch can differ depending on the type of vegetation on this land patch (Archibald et al. 2009; Devineau et al. 2010). We thus included in the maximal model interactions between the covariates land cover type and NDVI, burnt status and fire delay. A backward model selection procedure based on Akaike's information criteria (AIC) comparisons among models was used to identify a model nested in the maximal model and which included only terms which removal increased model AIC by more than 2 points. This procedure was implemented using the stepAIC function in MASS R library. Because of its ecological importance and in order to compare the observation probability of different species, the land cover type covariate was always included in the selected model.

The selected models were then fitted again to the observation data in the presence of an auto-regressive term (*ar* parameter). The autoregressive term was built as a weighted average of the value of the binary observation response variable of the other polygons on the same year. For each species a neighbourhood was defined which radius corresponded to the maximum distance at which spatial autocorrelation had been detected (see above). The weights used were an inverse function of the distance inside the neighbourhood (0 outside). The statistical significance of each term included in the selected model was tested in the presence of the auto-regressive term using a Likelihood Ratio Test.

The predictive power of each model was evaluated using the area under the curve (AUC) based on the receiver operating characteristic (ROC) curve (Wintle and Bardos 2006). We considered a model as valid for AUC value larger or equal to 0.7.

Finally, estimations of observation probabilities derived from the final models (including autoregressive terms when necessary) were mapped for each species using ArcGis (version 10.1; ESRI, Inc., Redlands, California) (e.g. Figures 4.4 & 4.6).

C - RESULTS

C1 - Covariates and interactions significant - Model validation

A final GLM was selected for each species (Table 4.5). As cross-validation revealed that the selected model had an AUC value larger or equal to 0.7 for only 8 of the 15 species initially considered (Table 4.4), the model results were interpreted further for these 8 species only. For the 7 other species, we considered that the explanatory power of the selected model was too low to have any biological relevance. Thus, the explanatory covariates considered were unsuitable to explain and/or predict the distribution of these species.

Table 4.4 - Model selected using AUC cross-validation - Spatial autocorrelation characteristics

Model	No. of parameters	AUC	Spatial autocorrelation (*ar*) in km	*P* value of the *ar* parameter
Buffalo	14	0.71	2	0.019
Bushbuck	20	0.75	0	-
Hartebeest	12	0.71	1	0.013
Impala	12	0.88	2	< 0.001
Kudu	16	0.70	0	-
Reedbuck	12	0.73	3	< 0.001
Waterbuck	13	0.82	3	< 0.001
Wildebeest	10	0.70	1	< 0.001

Distances to main and to secondary rivers had significant effects for 7 and 6 out of 8 species, respectively. In most instances the probability of observation decreased as the distance to the rivers increased (for distance to secondary rivers see Appendix V - Figure V.9).

The land cover type covariate was selected for 5 out of 8 species, with patterns widely varying among species. NDVI had a significant effect on observation probability for 3 out of 8 species. The relationship between NDVI and observation probability was positive for 2 out of these 3 species (Appendix V - Figure V.10). The covariates burnt status and fire delay had significant effects on observation probability of 2 and 1 species out of 8, respectively.

At least one interaction between the zone covariate and an environmental covariate was included in the selected model for 5 out of 8 species. The three environmental covariates most involved in such interactions were the distance to main rivers, NDVI and land cover type, suggesting that the influence of these environmental covariates on species distributions varied between the central and the eastern zone.

Year had significant effects on observation probability for 5 out of 8 species. However, except that observation probability was high in 2009 for most species, the temporal variation pattern differed among species.

C2 - Specific responses

BUFFALO The significant covariates for this large grazer were distance to rivers (both main and secondary), NDVI, land cover type and year. Observation probability decreased as distance to rivers increased (Figure 4.2.a) and as NDVI value decreased. Observation probability was higher in riverine forest and *jesse* bush than in the other land cover types (but estimations had large standard errors; Figure 4.5.a). Map of the spatial distribution of the predicted buffalo observation was derived from our analysis (Figure 4.4).

HARTEBEEST The significant covariates for this large grazer were distance to rivers (both main and secondary), land cover type and zone. The observation probability and the distance to rivers covariates (both main and secondary) were positively correlated in the eastern zone but negatively correlated in the central zone (Figure 4.3.a). In the central zone, observation probabilities were highest for open land cover types such as open *miombo* woodland, *miombo* woodland and grassland (Figure 4.5.b).

REEDBUCK The analysis for this species was restricted to the central zone due to very few observations (n=6) in the eastern zone. The covariates presenting significant effects on the observation probability for this species were distance to main rivers, burnt status, fire delay and year. Observation probability increased with distance to main rivers, suggesting an avoidance of the main river system (Figure 4.2.c). Observation probabilities were highest for open land cover types such as *miombo* woodland, grassland and open *miombo* woodland (Figure 4.5.d). Observation probability was slightly higher in burnt areas, more specifically in recently burnt areas.

KUDU Distances to main and secondary rivers, NDVI, zone and year have significant effects on the probability of observation of this fairly generalist browser.
Observation probability decreases as distance to main rivers increases in the central zone and it increases in the East (Figure 4.3.b). In both zones, observation probability decreases as distance to secondary rivers increases. Same pattern as the distance to main rivers is observed for NDVI, the observation probability decreases as NDVI increases in the Central zone and it increases in the East. In the eastern zone, the slope of the curve is shallow: observation probability increases by 0.10 between a NDVI value of 0.4 and a NDVI value of 0.8. Observation probability is higher in riverine forest and *jesse* bush than in the other land cover types but standard errors are wide for these two classes (Figure 4.5.e).

Table 4.5 - Covariates and interactions between covariates significant for generalized linear model analysis of 16 species

	Species	Buffalo	Bushbuck	Hartebeest	Impala	Kudu	Reedbuck	Waterbuck	Wildebeest	Bushpig	Duiker	Eland	Elephant Bull	Elephant Family	Sable	Warthog	Zebra
	n Total	152	87	270	101	264	72	93	65	51	4039	184	263	606	887	764	422
	Eastern/Central	67/85	41/46	48/222	63/38	172/92	6/66	42/51	26/39	24/27	1839/2200	81/103	143/120	298/308	269/618	197/225	197/225
		AUC ≥ 7 (cross validation)								AUC < 7 (cross-validation)							
COVARIATES IN MODEL	D_Villages																
	D_Main_Rivers	*		*	*	*	*	*	*		*	*		*	*		*
	D_Sec_Rivers	*	*	*	*	*		*			*				*	*	*
	NDVI	*	*			*					*		*	*	*	*	
	Land Cover Type	*	*	*	*			*			*	*	*	*	*	*	*
	Veget. Op/Cl.																
	Burnt status				*		*			*	*	*		*	*	*	*
	Fire delay						*								*	*	*
	Zone		*	*	*	*			*		*	*	*	*	*	*	*
	Year	*	*			*	*	*		*	*	*	*	*	*	*	*
INTERACTION WITH ZONE	D_Villages																
	D_Main_Rivers Eastern/Central			+/-		=/+			+/-		-/-	+/-			+/-		=/-
	D_Sec_Rivers Eastern/Central			+/-							-/-				+/-		
	NDVI Eastern/Central		+/=			+/-							+/-	+/=			
	Land Cover Type		*								*		*	*			*
	Burnt status				*						*						
	Fire delay														*		
	Year										*	*	*		*	*	
INTERACTION WITH LAND COVER TYPE	NDVI																
	Burnt status										*	*		*			
	Fire delay																

For each species, the * symbol indicates significant covariates and interactions in the model. When an interaction with the zone covariate is significant, the +/- symbols indicate the sign of the correlation between the covariate in the eastern/central zones (or = when no correlation is observed). Hypothetically, observation probabilities are lower as distance to rivers (main and secondary) increase and observation probability is higher as NDVI value increase. If this is the case, the covariate is positively correlated in the zone considered.

D_Villages, distance to villages; D_Main_Rivers, distance to main rivers; D_Sec_Rivers, distance to secondary rivers; Veget. Op/Cl., opening up of the vegetation

IMPALA The model presents the highest AUC (0.88). Distances to main and secondary rivers, land cover type, burnt status and zone have significant effects on observation probability of this mixed feeder. Observation probability decreases strongly as distance to main rivers increases (Figure 4.2.b). Twenty kilometres away from the main rivers the observation probability is nil. Same pattern is observed for distance to secondary rivers but the relationship has a shallower slope. In the central zone observation probability in burnt areas is twice as high as in non-burnt areas. The opposite pattern is observed in the eastern zone but with a weaker difference. Estimations of observation probabilities are highest for riparian land cover types such as riverine forest, *jesse* bush and riverbed (Figure 4.5.f). Map of the spatial distribution of the predicted impala observation was derived from our analysis (Figure 4.6).

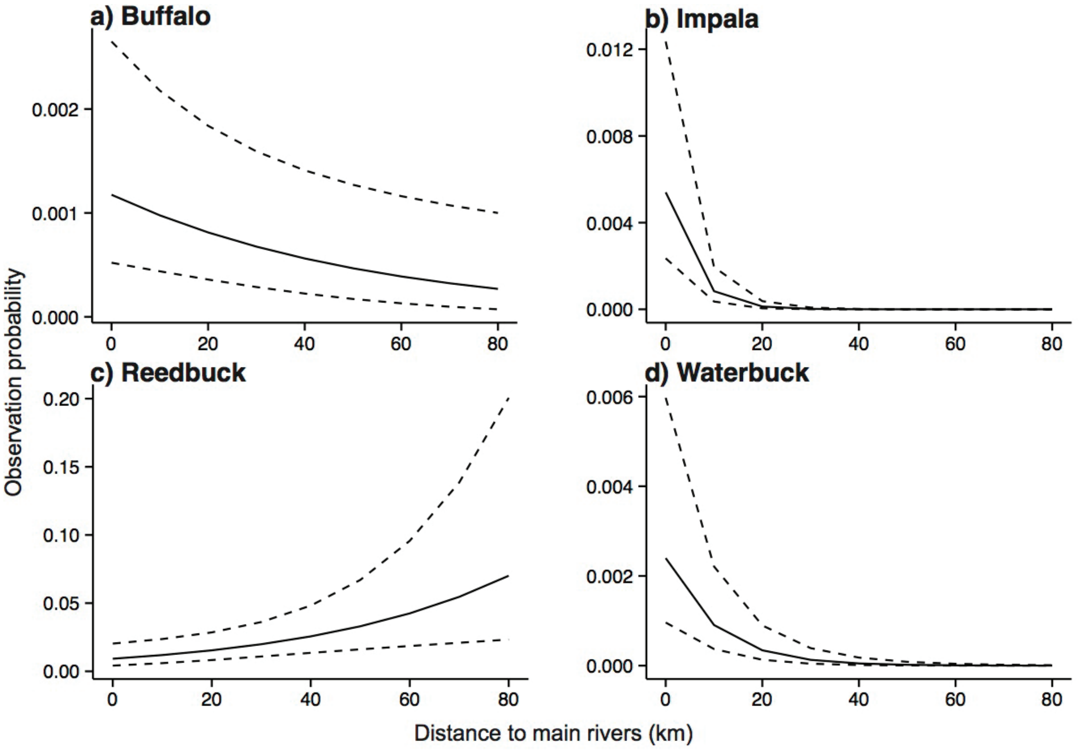

Figure 4.2 - Observation probability of 4 species in relation to the distance to main rivers

BUSHBUCK Distances to secondary rivers, NDVI, land cover type, zone and year have significant effects on observation probability of this browser. Observation probability decreases as distance to secondary rivers increases. NDVI has no effect in the central zone but a strong effect in the East where the observation probability reaches one for a NDVI value of 0.8. Moreover, in the eastern zone, the observation probability estimation is highest in dense *miombo* woodland and riverine forest, two classes characterized by a relatively dense tree layer. No effect of land cover types is detected in the central zone except that the estimation of observation probability is relatively high for riverbed but with a wide confidence interval (Figure 4.5.c).

WATERBUCK Distances to main and secondary rivers, land cover type and year have significant effects on observation probability of this selective grazer. The observation probability of this strongly water-dependent antelope decreases as distances to main and secondary rivers increase. Forty kilometres away from the main rivers the estimation of observation probability is nil (Figure 4.2.d). Same pattern is observed for distance to secondary rivers but the effect is weaker. Observation probability estimation is higher in riverine forest and riverbed than in the other land cover types (Figure 4.5.h).

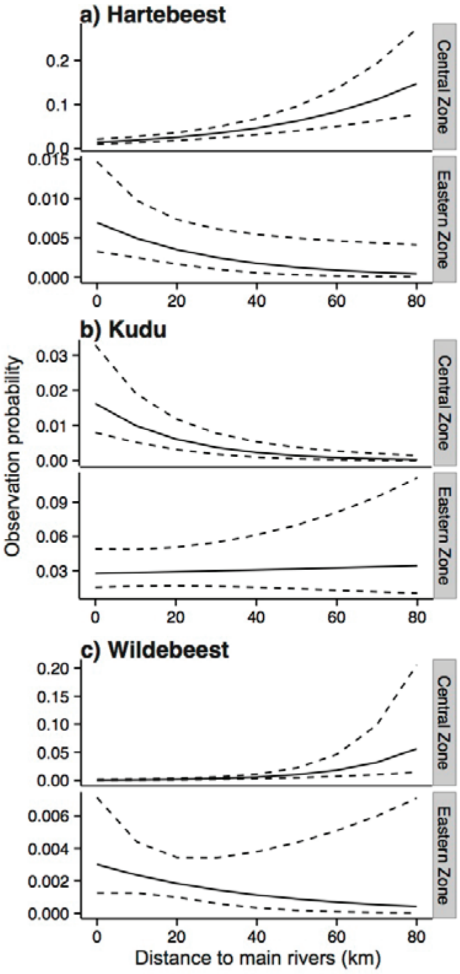

Figure 4.3 - Observation probability of 3 species in relation to the distance to main rivers with significant interaction with the zone covariate

WILDEBEEST Distances to main rivers and zone have significant effects on observation probability of this medium grazer. As for hartebeest, the observation probability estimation decreases as distance to main rivers increase in the eastern zone and it increases in the Centre (Figure 4.2.g). The observation probability estimation in the central zone is twenty five times higher than in the East. Estimations of observation probabilities are highest for open land cover types such as grassland, *miombo* woodland, and open *miombo* woodland. A high probability estimation is observed in *jesse* bush but with a wide confidence interval (Figure 4.5.g).

SPECIES WITHOUT VALID MODEL Among the sixteen species considered, eight present a model with a low explanatory power. Many covariates are significant for these species (Table 4.5) but we cannot predict accurately their spatial distribution. However, we still have some patterns for the main covariates that we would like to present, especially for two emblematic and abundant species in NNR, elephant (Appendix V - Figure V.7) and sable antelope (Appendix V - Figure V.8).

For elephant, the observation probability estimation increases as distance to main rivers increases. NDVI has almost no effect in the central zone but a strong effect in the East where the observation probability is nil until NDVI value reaches 0.4 and increases by 0.50 between a NDVI value of 0.4 and a NDVI value of 0.8. Estimations of observation probabilities are highest for forest land cover types such as *jesse* bush, dense *miombo* woodland and riverine forest in the eastern zone. No effect of land cover types is detected in the central zone.

For sable, same pattern is observed for the main and the secondary rivers, the observation probability decreases as distance to rivers increase in the eastern zone and it increases in the Centre. The observation probability decreases as NDVI increases. Estimations of observation probabilities are lowest for land cover types such as riverine forest and *jesse* bush.

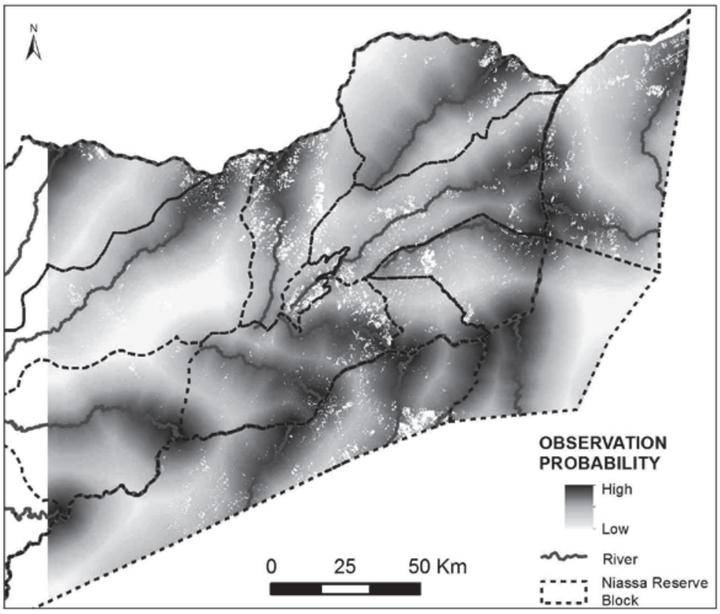

Figure 4.4 - Map of the spatial distribution of the predicted buffalo observation probability over the 10 years study period

D - DISCUSSION

When considering the processes that may generate the distribution data analysed, one crucial point (as already underlined out in the introduction) is the very large area covered with a high spatial resolution. Thus the processes involved are likely to include demographic mechanisms processes influencing spatial variation in abundance at large spatial scales as well as movements and habitat use mechanisms generating spatial variation in abundance at small spatial scales. As a consequence the results of our correlation approach are difficult to interpret.

Another important point to discuss is the potential effect of detection issues (for instance observation probability being high in recently burnt area could be due to a better detection (i.e. greater visibility)). Visibility could also affect our ability to correctly estimate the influence of vegetation type on the probability of presence.

Observer bias represents the most important source of bias in aerial techniques (Norton-Griffiths 1978), and bias is generally related to the quality of the observers in terms of eyesight, experience and ability to concentrate during long flights (Jachmann 1995, 2012). The "year" covariate accounted for these observer differences in our analyses. It is worth noticing that biases were minimized because the same pool of observers was used over the seven aerial censuses. However, most species presented a high observation probability in 2009, and this effect is probably partly due to the pairing of the two best observers (Craig 2012).

Our analyses of dry-season herbivore distribution in the NRR indicate some significant relationships between landscape-scale factors and the herbivore distributions, with distance to water, longitudinal zoning, land cover and ecosystem primary productivity (NDVI) being most determinant. The results can be considered as quite robust because of the very large sample size (*n* = 36,596). Surveys were conducted in well-defined blocks using identical techniques and methods over the 10 years study period which improves the reliability of the data.

Among the sixteen species considered (here elephant bulls and families are separated species), only height presented a model with significant explanatory power. We identified two possible reasons for the lack of adequate model for seven recorded species with enough data (i.e. excluding bushpig): (i) the very high number of sighting and even distribution of sedentary species such as duiker and warthog prevented to identify any robust model and (ii) high mobility and being habitat generalist may explain why models were not discriminatory for sable, elephant, eland and zebra. The large number of observations for duikers, elephant families, zebra and sable allowed for identifying a large number of significant covariates (Table 4.5) but with no overall explanatory power.

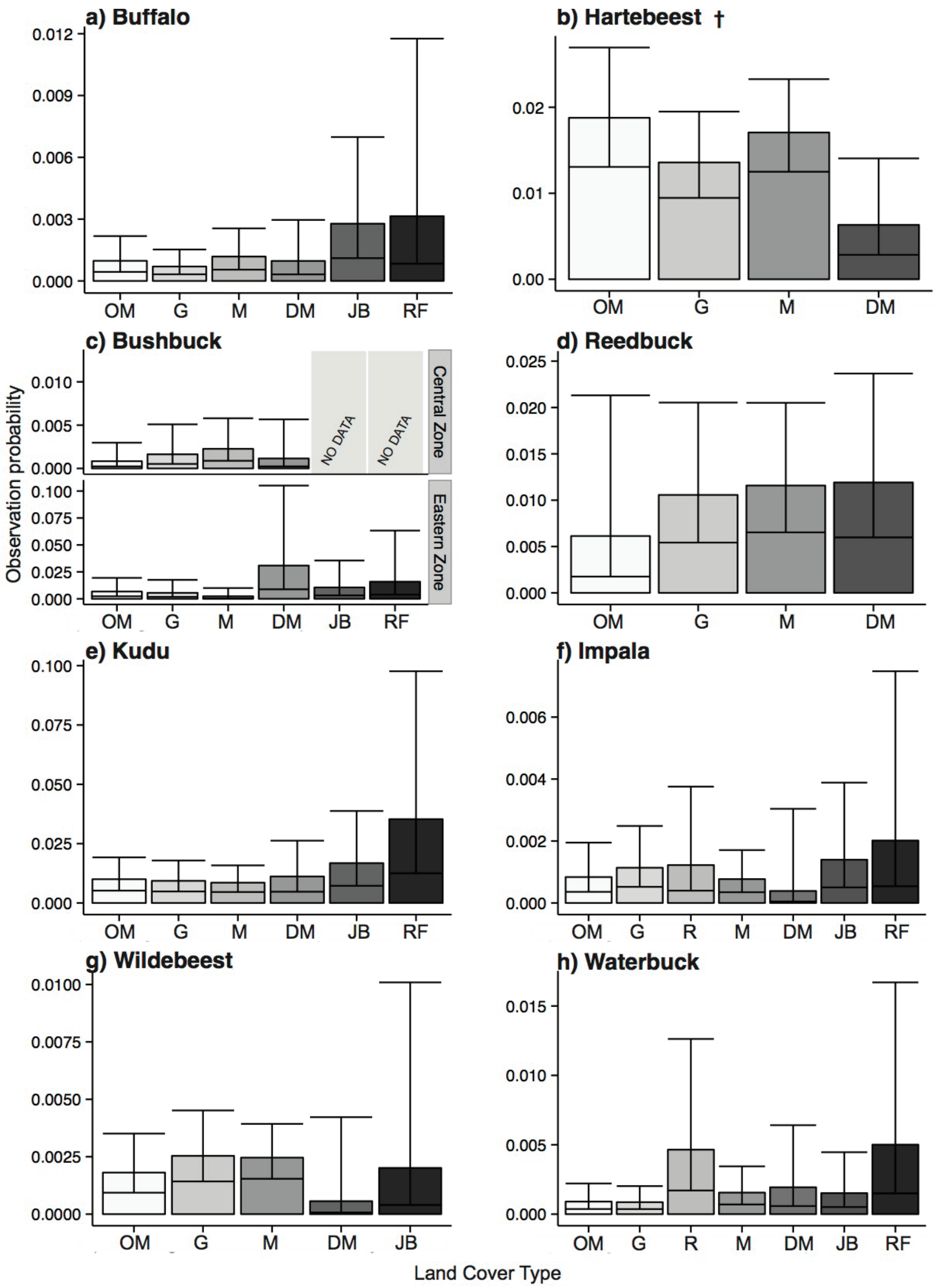

Figure 4.5 - Observation probability of 8 species in relation to the land cover type. OM, Open Miombo Woodland; G, Grassland; M, Miombo Woodland; DM, Dense Miombo Woodland; JB, Jesse Bush; RF, Riverine Forest; R, Riverbed.
† for hartebeest observation probability are 20 times lower in the eastern than in the central zone and are not displayed here.

In species for which a model with a reasonable explanatory power could be identified (Table 4.4), as expected distance to water has a key role in the system indicating some significant relationships between dry-season herbivore distribution and water available. Previous studies have well documented that location of water sources influences herbivore distributions, particularly during the dry season (Western 1975; Fryxell et al. 1988; Bergstrom and Skarpe 1999; Redfern et al. 2003). Rivers are influencing the landscape distribution of our grazers and the mixed feeder, considered as water-dependent. Our results do not support the hypothesis of a relative water independence of browsers compared to grazers (Western 1975) as kudu and bushbuck observation probability is higher along the river system, but this is probably due to the greater proportion of thickets and palatable browse in riverine vegetation. Hartebeest and wildebeest, two medium-size grazers, present an inverted curve in the central zone (Figure 4.3.a,c). This zone has numerous waterholes that were not considered in the analysis (non exhaustive data) while the river system is the only available water in the eastern zone. More spatially homogeneous distribution of surface water reduces the trade-off between access to grazing and travelling to water sources, which seems to favour these two species in the central zone as observation probability was twenty times higher than the East. Reedbuck, only analysed in the central zone, presents the same pattern. As riverine areas typically have higher predation risk (Bhola et al. 2012) and dominated by thickets, reedbuck probably avoids them in NNR and select primarily for its specialised habitat requirements , i.e. tall grass, reed beds (found in the *dambos*) or herbaceous cover (Skinner and Chimimba 2005) and is satisfied with small waterholes.

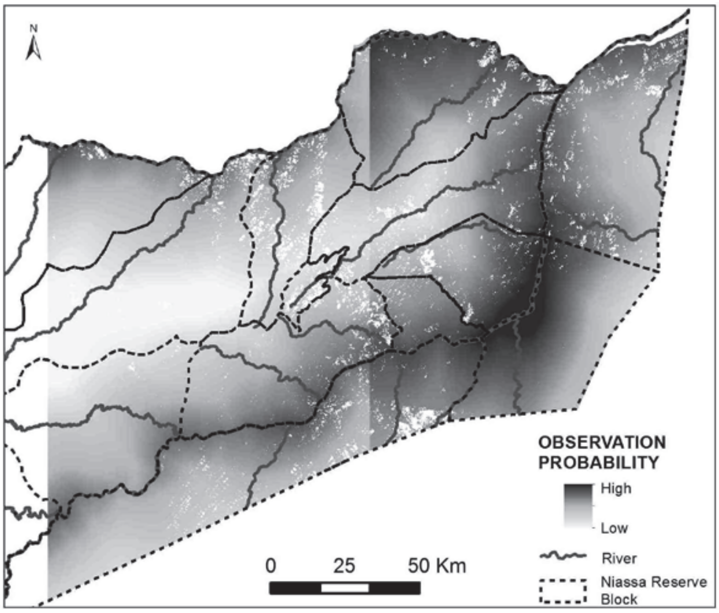

Figure 4.6 - Map of the spatial distribution of the predicted impala observation probability over the 10 years study period

Working on such a large scale (25,837 km^2 for our analysis) implies constraints to the spatial distribution of herbivores and these constraints may differ between the zones considered. Our analyses suggest a marked spatial heterogeneity in the selected environmental covariates of the NNR ecosystem, with a significant longitudinal zoning in interaction with other covariates. The environmental gradients (topography, rainfall, primary production and fires) define contrasting zones where the spatial distributions of herbivore species may not necessarily depend on the same environmental covariates.

Distribution of herbivores was responsive to land-cover but responses were variable among species. Dense *miombo* woodland, which has a fairly abundant herbaceous cover and a limited shrub layer (Table 4.3), always showed a lower observation probability (except for browsers). Among grazers, browsers and mixed feeders *jesse* bush and riverine forest often showed a high observation probability but with a wide confidence interval. However, these two land cover types are only found in the East and close to the river system and because distance to water has a key role in the system at the end of the dry season these covariates logically presented levels of collinearity which could bias analyses. Moreover, within the constraints set by water availability, grazers showed higher observation probabilities in open vegetation types such as grassland, open *miombo* woodland and *miombo* woodland. For grazers, browsers and mixed feeders considered in our analysis there is no marked difference in their patterns of land cover utilisation, which suggests that these herbivore face a similar trade-off between nutritional requirements and water availability, although this trade-off varies according to the species' water dependence, size and gut morphology (Gordon 2003; Clauss and Hummel 2005; Gaillard et al. 2008).

The two covariates considered as reflecting fire disturbance seemed to influence spatial distribution for only two species out of eight for which adequate models were obtained. Reedbuck and impala, showed mostly a preference for recently burnt areas. Fire is known to be an important component of ungulate behaviour (Allred et al. 2011) and it is widely recognized that grazing herbivores prefer to feed on grass regrowth following savanna fires rather than on unburnt grass swards (Klop et al. 2007). Around 50% of the NNR burn each year from the end of June to the beginning of November (48.6% of our 36,596 sampling units were burnt). In our analysis the spatial distribution of herbivores does not seem influenced significantly by fire disturbance. If fires can produce a good quality grass regrowth at the beginning of the dry season, in contrast they only produce burnt patches without grass regrowth and hence reducing forage quantity at the end of the dry season in NNR. The selection for burnt spot may also be biased by the fact visibility profile changes, with herbivores being easier to spot in burnt areas.

Human disturbance considered as the distance to villages in our analysis was not an influential explanatory covariate. There is no obvious avoidance of villages in the spatial distribution of herbivores. However, perturbations such as poaching activities may not be reflected in our analysis, especially because poaching techniques in NNR are mostly through snaring, which is not disturbing. The spatial influence of villages is also limited in regard of the gigantic size of the NNR, which may thus be difficult to detect in such a coarse approach of animal distribution. Fine-scale movement analyses and habitat selection may be more appropriate to identify such disturbance influences.

Identifying the drivers of large herbivore spatial distribution can benefit wildlife managers, as it allows the identification of major environmental constraints faced by animal populations and/or communities in a particular area. For instance, our analyses suggest an important spatial heterogeneity of the environmental covariates in the ecosystem and therefore different behavioural adjustments made by herbivores in contrasting zones within the NNR. At such a large scale, management actions must be adapted to the zones considered. The data used in this study were primarily collected for assessing large herbivore population statuses in NNR, but were not collected to perform our analyses even though they generated informative preliminary assessment of the large-scale environmental constraints, and in the future may help identifying trends in space and time with associated plausible hypotheses (e.g. Redfern et al. 2003; Funston and Mills 2006; Redfern et al. 2006; Smit et al. 2007b). Developing specific data collection methods to evaluate the landscape-scale determinants of herbivore distributions in the different zones of NNR would benefit wildlife manager further, helping to unravel the likely contrasted ecology of herbivore sub-populations facing very different constraints over such a large area.

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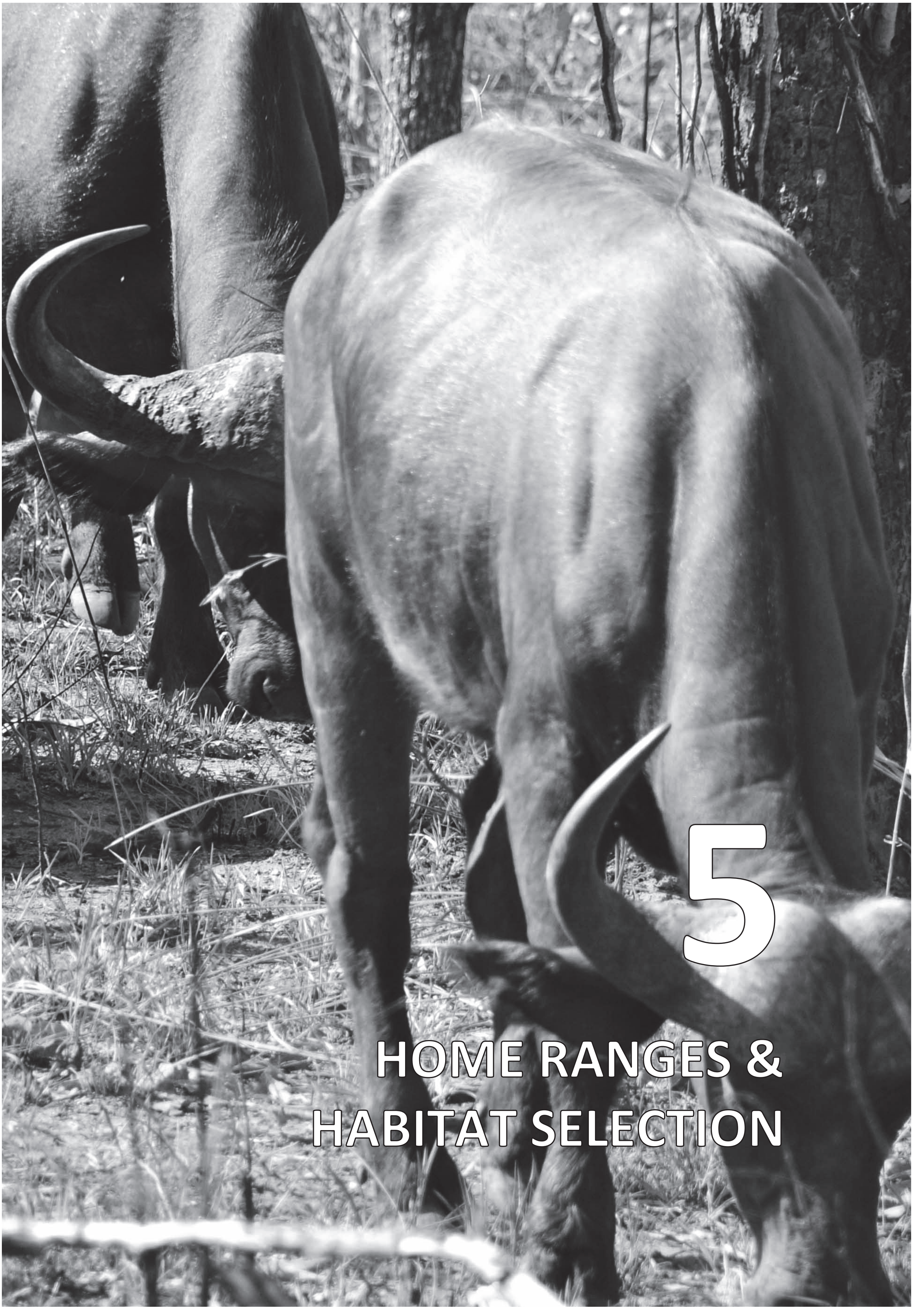


5

HOME RANGES & HABITAT SELECTION

Home ranges and habitat selection of African buffalo in Niassa National Reserve, Mozambique

Thomas Prin - Simon Chamaille - Annelise Tran - Marie Gely - Hervé Fritz - Daniel Cornelis

In preparation for *Wildlife Monographs*

A - INTRODUCTION

African savannahs are ecosystems characterised by a high degree of heterogeneity of resources. Both biotic and abiotic resources are often spatially segregated and their availability and quality vary seasonally (Bell 1982; Walker 1993; Mueller et al. 2009). In such a context, wild ungulate are expected to adapt patterns of space-use dynamics and habitat selection accordingly, in order to maximize forage intake and fitness (McNaughton 1990; Winnie et al. 2008; Chamaillé-Jammes et al. 2013), (Bailey et al. 1996; Fryxell et al. 2004). In addition, risk (e.g. natural or human predation) also matters in natural ecosystems and mitigating risks in the so-called "landscapes of fear" also directly impacts animal behaviour (Valeix et al. 2009). Space use thus results from permanent trade-offs between several constraints (e.g. predation risk, bushfires, water availability, human disturbance) simultaneously operating at different spatiotemporal scales.

The African buffalo is a large gregarious grazer ranging in a wide variety of vegetation types, from open grasslands to evergreen forests, and including all intermediate habitats (in fact, wherever permanent water is found) (Sinclair 1977). The species is classified as a "bulk grazer" than can cope with fairly poor-quality forage. Herd size varies across the continental distribution range, from as few as 20 in dense tropical forest to as many as 2000 individuals in the floodplains of eastern and southern Africa (Prins and Reitsma 1989; Prins 1996). The availability of surface water and cover are commonly cited as the main constraints on habitat use of buffaloes. Buffalo must drink at least every two days (Sinclair 1977). In a seasonal tropical climate, water availability varies widely over the year and is often restricted to a few perennial rivers and/or waterholes in the dry season. In these conditions, buffaloes face a trade-off between nutritional and water requirements (Redfern et al. 2003) and some populations are known to undertake seasonal movements (Funston et al. 1994; Halley et al. 2002; Cornélis et al. 2011; Naidoo et al. 2012a). Several previous studies reported that buffalo has a tendency to use exclusive HRs (Prins 1996; Halley et al. 2002; Ryan et al. 2006; Cornélis et al. 2011) whereas other reported overlaps between neighboring home ranges (HR) (Grimsdell 1969; Conybeare 1980; Mloszewski 1983; Cornélis et al. 2011). Although predated by lion, this large body-size herbivore is more likely to be ultimately limited by resources than by natural (Sinclair et al. 2003) and human predation (Prins 1996) or competition for resources (Hibert 2010). The Cape buffalo, a subspecies ranging in eastern and southern Africa, is characterized by the largest body mass (from 400 to 800 kg). In this study, we examined patterns of space-use dynamics and habitat selection of buffalo in the Niassa National Reserve, a protected area that suffered from 15 years of civil war (1977-1992) during which wildlife population decreased substantially (SGDRN 2007).

Although NNR benefits from substantial conservation efforts, the ungulate community remains strikingly low, especially the buffalo population (Craig 2012). The landscape of NNR is characterised by a dystrophic woodland savanna dominated by poorly productive *miombo* communities (Campbell 1996), interspersed with wetter grassland patches in the lower catena. Villages are included within the NNR (around 39,000 residents) and their potential impacts on wildlife populations are well known in Africa (Craigie et al. 2010). NNR is also subject to important dry season bushfires (either driven for management purposes or by poachers). Although appropriate fires are known to stimulate a high nutritional – but short-term – regrowth, their distribution and extent also is likely to impact substantially the availability of dry grass cover, an important resource for “bulk grazers” such as buffalo.

In NNR, the buffalo herds thus were expected to face particularly severe conditions due to a spatiotemporal segregation in the availability of water and forage coupled with several constraints (e.g. human disturbance, bushfires). In this study, we investigated at annual and seasonal scales how buffalo herds use space in relation to surface water, habitat types, primary production, bushfires, human disturbance and share space with neighbouring herds. For this purpose, we monitored the movements of 33 females in 9 herds for several years in contrasted areas of the NNR in order to compare their space use strategies. We expected space-use patterns to be constrained by access to water and bushfires in the dry season, human disturbance and spatial avoidance between herds all year. We expected habitat selection to reflect these constraints and that buffaloes would select greener areas as well as anticipated seasonal movements between wet and dry season in response changes in the resource phenology, here the disappearance of ephemeral surface water or greening of grasses in less depleted areas.

B - MATERIAL AND METHODS

B1 - Study area

The Niassa National Reserve (NNR) is located in northern Mozambique along the border with Tanzania. The NNR is one of the largest African protected areas, covering an area of 42,140 km^2 (Figure 5.1). This protected area supports the largest concentrations of wildlife in Mozambique with the full complement of herbivores (excluding black rhino and possibly roan antelope) and carnivores expected in the region (SGDRN 2007). Rock art in the area shows that NNR has always supported a human population and around 39,000 local residents live today inside the protected area, spread across 50 villages. Shifting subsistence agriculture is the primary land use and main economic activity (Cunliffe et al. 2005). Cattle are absent due to tsetse fly (*Glossina spp*.), the vector for the disease *trypanosomiasis*, but smaller livestock, primarily goats and chickens, and domestic dogs are present in the larger villages.

Figure 5.1 - Maps of Africa and Mozambique showing the study site, the Niassa National Reserve

The NNR is located within the Eastern *Miombo* Woodland eco-region (WWF 2001). The landscape comprises a mostly gently undulating plateau at around 300-600 m altitude, rising to a higher plateau and hills in the west at around 1,370 m, and gradually falling to 150 m at the north-eastern boundary at the confluence of the Rovuma and Lugenda Rivers. Seventy-two percent of the NNR is covered by dry Zambezian Miombo woodland (Ribeiro et al. 2008). Five broad land cover types were recognized within the NNR: forest, riverine, deciduous woodland, *dambos* or wetlands and granite *inselbergs* (Timberlake et al. 2004). This vegetation supports a great floral richness and dominant tree species include *Brachystegia spiciformis*, *B. boehmii*, *B. allenii*, and *Julbernardia globiflora*. The dry *miombo* canopy is generally less than 15 m in height and deciduous for 1 month or more during the dry season. The *miombo* woodlands of the NNR are subject to annual anthropogenic fires every year (Ribeiro et al. 2008).

The drainage is dominated by the Rovuma and Lugenda Rivers, which are large (up to 1,000 meters width) sand bed rivers with a strong perennial flow. The central watershed between these two rivers feeds numerous seasonal rivers as well as an extensive seasonally inundated wetland network (SGDRN 2007).

The NNR experiences a seasonal tropical climate with most rainfall concentrated in the hot summer months from mid-November through April. This season is followed by a long winter drought, lasting up to 7 months (Werger and Coetzee 1978). Mean annual rainfall ranges between 800 and 1,200 mm per annum, and varies along a west-east gradient with higher rainfall in the west. Mean maximum temperatures range between 15-30°C during the hot season (hot-dry and hot-wet) and 10-20°C in the cold-dry season.

B2 - Herds movements

The movements of 33 adult buffalo cows were monitored from October 2009 to July 2013. Movements were monitored using GPS collars (African Wildlife Tracking ©, South Africa). The sampling targeted herds encompassing a minimum of 100 individuals, located in the Central and Eastern sections of NNR. From 2 to 5 collars were deployed in 9 distinct herds (Table 5.1). We used 2 types of collars (UHF and satellite), differing in the way they transfer GPS locations. Data from UHF collars were downloadable from the ground using a handheld receiver connected to a laptop computer. This system required locating collared individuals (using VHF) and approaching them within 300 meters. In contrast, data from satellite collars were automatically sent to a remote server using satellite phone (Inmarsat) communications, and were thus accessible in near-real time using Internet. Satellite and UHF collars were scheduled to acquire 6 and 24 GPS readings per day, respectively (as a result of a trade-off between energy consumption, batteries lifespan and an expected tracking duration of 2 years). In total, 9 UHF and 24 satellite collars were deployed over 3 collaring sessions (Table 5.1). Animals were tele-anaesthetized from helicopter using standard techniques (la Grange 2006). Anaesthesia was induced by a combination of etorphine hydrochloride and xylazine, and reversed by injection of diprenorphine hydrochloride. The field operations conformed to the legal requirements of the countries in which they were carried out. All animals were released on site in good shape.

Table 5.1 - Summary statistics of the deployment of 33 GPS collars in 9 herds in Niassa National Reserve from 2009 to 2013

Herd ID	Collar ID / Type	Zone	Date ON	Date OFF	Months of activity	Collar schedule	Success rate %
1	Sat01 / Sat	Eastern	08/10/2009	29/10/2010	13	6 locs / day	97
	AU345 / UHF		08/10/2009	17/11/2011	26	24 locs /day	64
	Sat15 / Sat		02/11/2010	30/11/2011	13	6 locs / day	38
2	Sat02 / Sat	Eastern	09/10/2009	29/10/2010	14	6 locs / day	52
	AU344 / UHF		09/10/2009	30/08/2010	11	24 locs /day	100
	Sat16 / Sat		02/11/2010	11/08/2011	10	6 locs / day	48
3	Sat04 / Sat	Eastern	09/10/2009	06/11/2010	13	6 locs / day	37
	AU347 / UHF		09/10/2009	17/11/2011	35	24 locs /day	99
	Sat17 / Sat		02/11/2010	01/09/2011	10	6 locs / day	12
	Sat221 / Sat		26/11/2011	28/04/2013	12	24 locs /day	90
4	Sat03 / Sat	Eastern	10/10/2009	03/04/2011	18	6 locs / day	66
	AU346 / UHF		10/10/2009	17/11/2011	35	24 locs /day	100
	Sat18 / Sat		02/11/2010	08/11/2011	12	6 locs / day	64
	Sat220 / Sat		26/11/2011	08/07/2013	12	24 locs /day	92
5	Sat06 / Sat	Central	10/10/2009	22/03/2011	18	6 locs / day	67
	AU348 / UHF		10/10/2009	10/10/2009	0	24 locs /day	0
	Sat14 / Sat		01/11/2010	30/01/2012	15	6 locs / day	78
	AU509 / UHF		01/11/2010	21/11/2011	22	24 locs /day	13
6	Sat05 / Sat	Central	10/10/2009	31/01/2010	4	6 locs / day	53
	Sat07 / Sat		10/10/2009	12/12/2010	14	6 locs / day	78
	AU349 / UHF		10/10/2009	27/12/2009	3	24 locs /day	19
	Sat11 / Sat		01/11/2010	30/03/2011	5	6 locs / day	79
	Sat12 / Sat		01/11/2010	03/12/2011	13	6 locs / day	68
	Sat186 / Sat		25/11/2011	26/04/2013	12	24 locs /day	91
9	Sat08 / Sat	Central	11/10/2009	22/02/2011	17	6 locs / day	4
	Sat09 / Sat		11/10/2009	22/11/2009	2	6 locs / day	21
	Sat10 / Sat		11/10/2009	30/09/2010	12	6 locs / day	6
	AU350 / UHF		11/10/2009	10/11/2010	13	24 locs /day	97
	AU351 / UHF		11/10/2009	22/09/2010	12	24 locs /day	99
10	Sat19 / Sat	Eastern	02/11/2010	05/08/2011	9	6 locs / day	30
	Sat21 / Sat		02/11/2010	05/07/2011	9	6 locs / day	30
11	Sat13 / Sat	Central	01/11/2010	26/12/2011	14	6 locs / day	69
	Sat187 / Sat		25/11/2011	18/03/2013	12	24 locs /day	89

Among the 33 collars, 4 stopped working within the 6 first months of activity. Five collars stopped before 1 year of activity and 7 collars worked for 1 full year. Fourteen collars worked for more than 1 year and 3 lasted more than 2 years with a maximum of 35 months of activity for 2 collars. The success rates of the collars (i.e. the ratio acquired/scheduled locations) ranged from 6 to 100% (except 1 UHF collar which never worked). Collars activity and success rates are summarized in Table 5.1.

B3 - Home range and space sharing computation

Global and seasonal (dry/wet; see definition below) home ranges (HR) were computed using the location-based kernel density (LKDE) estimator on data (n=27). Utilization distributions (UD) were computed up to the 0.95 isopleth (Worton 1989, Powell 2000) using a smoothing factor (h) set to 1,000 meters for intra and inter-study comparison purposes (Laver and Kelly 2008). In addition, as the Lugenda River constituted a natural border for all tracked individuals, HR boundary biases were corrected as proposed by Benhamou and Cornelis (2010). For comparative purpose, global and seasonal HRs were also computed using minimum convex polygon (MCP) estimator. Although MCP tends to heavily overestimate HR areas and ignores the distribution of space use within HR contours, this method (involving location samplings at low intensity) has been widely used in previous studies (see Getz and Wilmers 2004).

The series of GPS locations of each individual were segmented into "dry" and "wet" sub-series using break points based on environmental covariates rather than based on an arbitrary (i.e. calendar) basis, as our large study was characterized by strong environmental gradients in the timing of rainfall and fire. For example, 2 months may separate the first events of rain or fire between herds located in the central and eastern zones, respectively. For each collared individual, the breakpoint between the dry and the wet season was defined as the date at which cumulative rainfall within HR contours (LKDE, 95%) reached 10 mm. Similarly, we defined the breakpoint between the wet and the dry season as the date at which 10% of the HR area was burnt (see below for details on fire and rainfall covariates data). For each season we kept only individual data that did cover the season entirely, and overall data from 6 consecutive seasons (3 wet and 3 dry seasons) were used. The global HRs were computed using the entire data acquired by a GPS collar but only when data covered at least a year.

We quantified the extent to which the collared individuals shared space by computing the volume of the intersection between all pairs of individual global HRs (with 95% isopleth) (Germain et al. 2008). This measure ranges between 0 (no area shared) and 100% (identical UDs). Then, a hierarchical cluster analysis was performed to display inter-individual association within our 27 data sets (Figure 5.4).

Analyses were performed using the standard implementations offered by the adehabitatHR package (Calenge 2006) for the R software (R Core Team).

B4 - Environmental covariates

B4.1 - Vegetation map

The main land cover types of the NNR were mapped using Landsat ETM5 satellite scenes (Figure 5.2). The study area was covered using 4 adjacent and cloud-free scenes (1 of May 2008 and 3 of June 2008. This type of sensor provides a spatial resolution (30 m) adapted for the extraction of the habitats. Once downloaded, the scenes were pre-processed (geometric and radiometric corrections; mosaic) using the ENVI® software. The scenes were processed by a supervised classification (ENVI®) based on 71 vegetation sampling plots spread across the study area (June 2010, 2011 and 2012 field campaigns). The supervised classification was conducted using the Maximum Likelihood classifier acting on all seven bands of the scenes and on a digital elevation model (Shuttle Radar Topography Mission; 90 m spatial resolution). The classification was applied with a permissive statistical threshold of 80% below which a pixel was unclassified. The sampling plots consisted in 100 meters linear transects along which the floristic composition was characterised. Six land cover types were derived and considered for the classification process of the scenes: (i) Grassland, (ii) Open *Miombo* Woodland, (iii) *Miombo* Woodland (iv) Dense

Miombo Woodland, (v) Riverine Forest, (vi) Jesse Bush (Table 5.2). For mapping purposes, 2 other land cover classes were added: (vii) Bare Rocks (*inselbergs*), and (viii) Riverbeds. A land cover class was assigned to 93% of the study area (the rest consisting in unclassified).

Table 5.2 - Land cover types' characteristics

VEGETATION CLASS	CANOPY COVER	SHRUB LAYER	HERBACEOUS LAYER	DOMINANT TREE SPECIES	DOMINANT HERBACEOUS SPECIES	PROPORTION EAST/CENTER %
Grassland	10% or less	10% or less	Good quality perennial grass	Typical *miombo* species or *Acacia* or *Combretum*	*Hyparrhenia sp., Andropogon sp., Loudetia sp.*	52 / 48
Open *Miombo* Woodland	30 - 40 %	30 - 40 %	Generally abundant of medium to good quality	Typical *miombo* species	*Digitaria sp., Themeda sp., Andropogon sp.*	62 / 38
***Miombo* Woodland**	60%	limited	Fairly abundant of medium to good quality	*Brachystegia spiciformis*, *B. boehmii*, *Julbernardia globifora*, *Diplorhynchus condylocarpon*, *Pseudolachnostylis maprouneifolia*	*Digitaria sp., Themeda sp., Andropogon sp.*	16 / 83
Dense *Miombo* Woodland	80%	limited	Fairly abundant of medium to good quality	Typical *miombo* species	*Digitaria sp., Themeda sp., Andropogon sp.*	26 / 74
Riverine Forest	100%	100%	Highly productive and palatable	*Faidherbia albida, Lonchocarpus capassa, Millettia stuhlmannii, Ficus sycomorus, Xanthocercis zambesiaca, Kigelia Africana*	*Panicum sp., Urochloa sp., Hyparrhenia sp., Sorghum sp., Eriochloa sp., Cynodon sp.*	100 / 0
Jesse Bush	80%	80%	Poorly developed	*Adansonia digitata, Acacia nigrescens, Berchemia discolor, Hyphaene petersiana, Dalbergia nitidula*	-	100 / 0

Around 1,500 ground control points (GCP) were used to validate the results obtained through satellite image classification. These GCP collected during the 3 above-mentioned field campaigns consisted in a quick visual estimation of the structure and type of land cover. Accuracy measures of the land cover map showed a good agreement between the classification results and the ground-truth data (GCP), with an overall accuracy of 80%. Errors came mostly from the Western area where a weak sampling led to confusions, especially between 2 close land cover types: *Miombo* Woodland and Dense *Miombo* Woodland. In this study, classification errors observed in the Western Section of NNR had little effect in our analyses since buffalo tracking was implemented in the Central and Eastern sections.

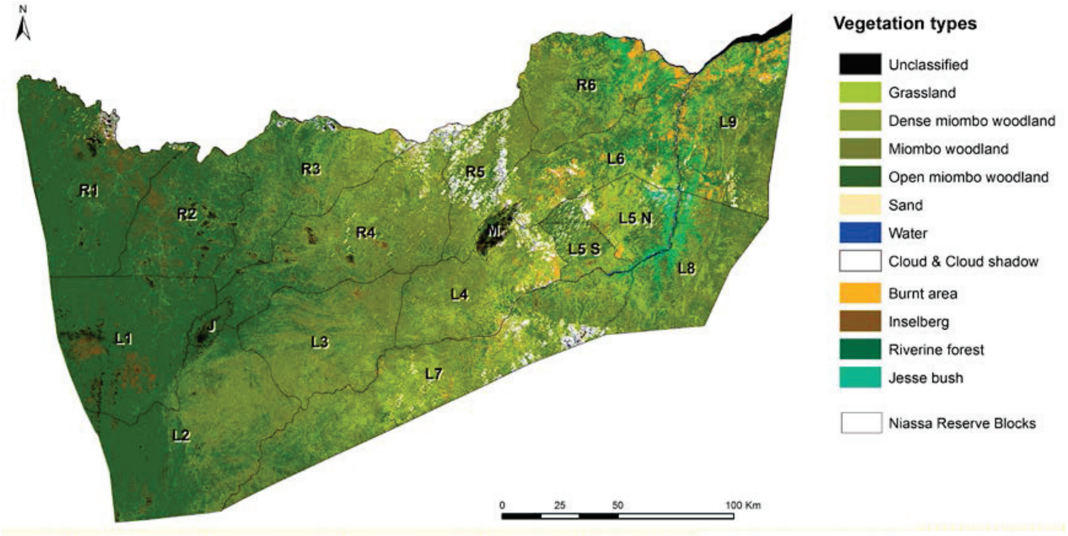


Figure 5.2 - Vegetation map of the Niassa National Reserve

B4.2 - Other covariates

We used the Normalized Difference Vegetation Index (NDVI) provided by the Moderate-Resolution Image Spectroradiometer (MODIS) instrument (Mod13Q1 product: 250 m & 16 days resolutions) as a proxy of primary production.

Similarly, we used the MODIS burned area product (MCD45 product: 500 m & 1 day resolutions) as a proxy of the role of bushfires. Two covariates were derived from the MODIS burned area product: (i) a burnt/non burnt covariate (hereafter referred to as "*burnt status*") and (ii) the time to the last fire at the GPS collar coordinates in a same year (hereafter referred as to "*fire delay*").

The rainfall data available for NNR was the Tropical Rainfall Measuring Mission product (TRMM: 25,000 m & 1 day resolutions). The spatial resolution of TRMM product was too low to test the influence of local rainfall amounts on habitat selection. However, we used these data to identify seasons (see B3).

We created two maps of the distribution of surface water (at a 30 m spatial resolution to match the vegetation data): The first map (hereafter referred to as "*distance to all rivers*") displayed the distribution of the nearest distances to any river of the NNR. The river system is NNR is divided into 4 categories (SGDRN 2007), (i) main rivers, (ii) secondary rivers, (iii) tertiary rivers and (iv) minor rivers. Tertiary and minor rivers dry out entirely in the dry season. The second map (hereafter referred to as "*distance to dry season water*") displayed the distribution of the nearest distances to a source of water available in the dry season. The water available in the dry season corresponds to the 2 main Rivers, the 15 seasonal tributaries and numerous waterholes.

We computed two maps of human disturbance at a 30 m spatial resolution to match the vegetation data: the nearest distance to the local villages (hereafter referred to as "*distance to village*") and the nearest distance to the road network (hereafter referred to as "*distance to road*").

B5 - Statistical model

We modeled habitat selection using resource selection functions (RSF). RSF are statistical models used to measure the likelihood of a location to be used if available, possibly accounting for its environmental characteristics (Manly et al. 2002). NNR experiences substantial seasonal changes in the distribution of water which obviously affects the distribution of the buffalo population. As a consequence, we estimated separate RSF models for dry and wet seasons. Although the hierarchical structure of the data (several buffaloes within a herd, sometimes several wet (or dry) seasons for the same individuals) suggested using mixed-models or generalized estimating equations (GEE) models, these models had convergence problems and we reverted to building a RSF model for each season for each collard buffalo (n=20 wet-season models; n=28 dry-season models). Also, because GPS location data could be sequentially correlated (Koper and Manseau 2012), we subsampled our data at a 3-hours sampling rate.

Habitat selection analyses were performed treating HRs independently for each collared buffalo. Indeed, although spatial analyses showed that several animals ranged within the same home range contours, preliminary investigations of association patterns of individuals showed the individuals spent a low proportion of their time together. Habitat selection was investigated within the seasonal HR contours (95% isopleth) of each collared individual (study design 3, sensu Thomas and Taylor, 2006). For each GPS location, we generated 5 random (“available”) GPS locations within the seasonal HR contours (95% isopleth) of the individual. All environmental covariates were extracted for both used and available locations. Studying habitat selection at a lower level (e.g. study design 2, considering the whole study area as a space available, Thomas and Taylor, 2006), would have been meaningless because the herds we tracked displayed exclusive space use patterns (see Results).

For each season we built a full model with all covariates and interactions which we considered *a priori* as ecologically meaningful, based on previous studies or our field observations. In each season the same full model was fitted to all individuals and we focused on interpreting the model coefficients (effect size, significance).

The habitat types were included in the dry and wet seasons models. We considered that NDVI variation reflects variation in primary productivity differently in different habitat types (Ito et al. 2006; Holdo et al. 2009a) and hence we included the interaction between NDVI and the habitat types in the dry and wet seasons models. Human disturbances (i.e. distance to village and distance to road covariates) were also included in both models. We logically included in the dry season models the distance to water available at this time of the year. In the wet seasons model we included the distance to any rivers. Because the attractiveness of a habitat type and its forage quality can differ depending on the distance to water available we also included in both models the interaction distance to water (dry season) or distance to any river (wet season) and habitat types. We included in the dry season models the effect of fire (i.e. burnt status and time to last fire covariates).

RSF models were estimated using generalized linear models with binomial distribution for errors and a logit link, and their fit assessed using k-fold cross validation (with 10 bins, randomly withholding 20% of the data at each of the 1,000 iterations; Boyce et al. 2002). The k-fold cross validation score obtained for the full model was compared with a k-fold cross validation score obtained from a null model (i.e. model without covariates) to test for the global model fit. For each model, the predictive importance of each covariate was defined as the improvement in fit brought by the covariate: we calculated the difference in fit (k-fold cross validation score) between the full model (i.e. all covariates included) and a reduced model without the covariate of interest.

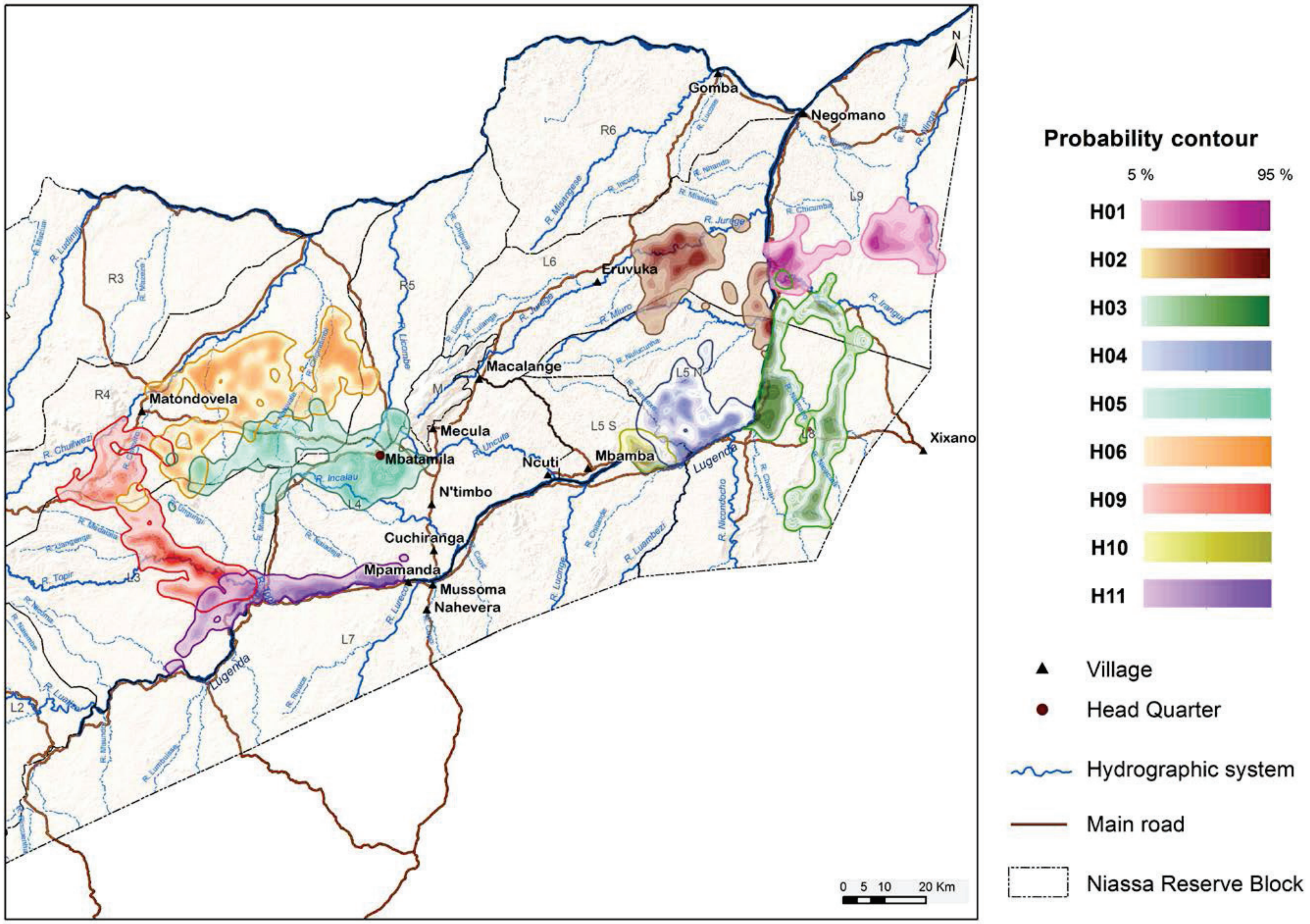


Figure 5.3 - Global home ranges of 9 herds in Niassa National Reserve from 2009 to 2013 using location-based kernel density estimation (LKDE)

C - RESULTS

C1 - Home ranges

C1.1 - Global home ranges

The 9 herds exhibited large global HR sizes across the NNR (Table 3). Mean (±Standard Deviation (*SD*)) HRs size was 524.9 ± 204.6 km^2 for our LKDE with 95% probability contour of location distribution, 121.1 ± 46.3 km^2 for our LKDE with 50% probability contour of location distribution and an MCP of 1181.8 ± 560 km^2.

Table 5.3 - Global home ranges of buffalo in Niassa National Reserve during 2009-2012

Herd ID (Size*)	Collar ID	Home range are (km^2)		
		Kernel 95%	Kernel 50%	MCP
1 (140)	Sat01	372.4	93.9	984
	AU345	412.7	103.9	
	Sat15	396.4	102.2	
2 (250)	Sat02	498.4	117	1139
	AU344	484.2	107.5	
	Sat16	396.3	91.2	
3 (250)	Sat04	550.3	104.8	1374
	AU347	627	112.3	
	Sat17	446.4	82.4	
	Sat221	536.6	115.1	
4 (200)	Sat03	425.5	130.2	657
	AU346	405.8	131.3	
	Sat18	385.2	117.2	
	Sat220	382.4	124.5	
5 (100)	Sat06	791	174	1561
	Sat14	789.8	177.9	
	AU509	591.2	89.6	
6 (110)	Sat05	650.9	122.1	2070
	Sat07	978.8	242.4	
	AU349	729.7	136.8	
	Sat11	457.8	95.8	
	Sat12	903.6	225.3	
	Sat186	806.6	158.1	
9 (200)	Sat08	647.8	176.9	1778
	Sat09	245.2	64.8	
	Sat10	542.2	135.5	
	AU350	693.5	158.6	
	AU351	693	148.8	
10 (50)	Sat19	104.6	23.5	119
	Sat21	102.1	24.1	
11 (150)	Sat13	370.3	84.9	954
	Sat187	378.2	101.3	

* Estimated size from the date of collaring

Mean global HRs size appeared to be higher in the central zone (641.9 ± 195.8 km^2) than in the eastern zone (407.9 ± 134.4 km^2). All herds in the eastern zone had a portion of their home range along the Lugenda River (Figure 5.3). In the central zone, except for one herd which had its annual home range along the Lugenda River (i.e. herd 11), no herd came closer to the Lugenda or Rovuma Rivers. The Lugenda River acted as a natural boarder and no herd crossed it over the 3 years study period (Figure 5.3) (cf. Appendix III for details).

C1.2 - Overlap

Figure 5.4 illustrates the inter-individual association within our 27 data sets obtained from the percentage of HRs overlap (LKDE with 95% isopleth). The height in the figure (i.e. y-axis) represents the distance linkage computed between collars. All collars deployed in the same herd were in this dendrogram found to be closer from each other than from other buffaloes from other herds, indicating that our a priori sampling of herds was successful. Among the combinations of collars placed within the 9 herds, 7 pairs of herds presented HRs overlaps. The percentage of inter-individual association within this 7 pairs of herds ranged from 2 to 18% showing a strong spatial segregation (i.e. territoriality) among the herds in NNR. Spatial segregation was higher between herds in the eastern zone compare to the central zone.

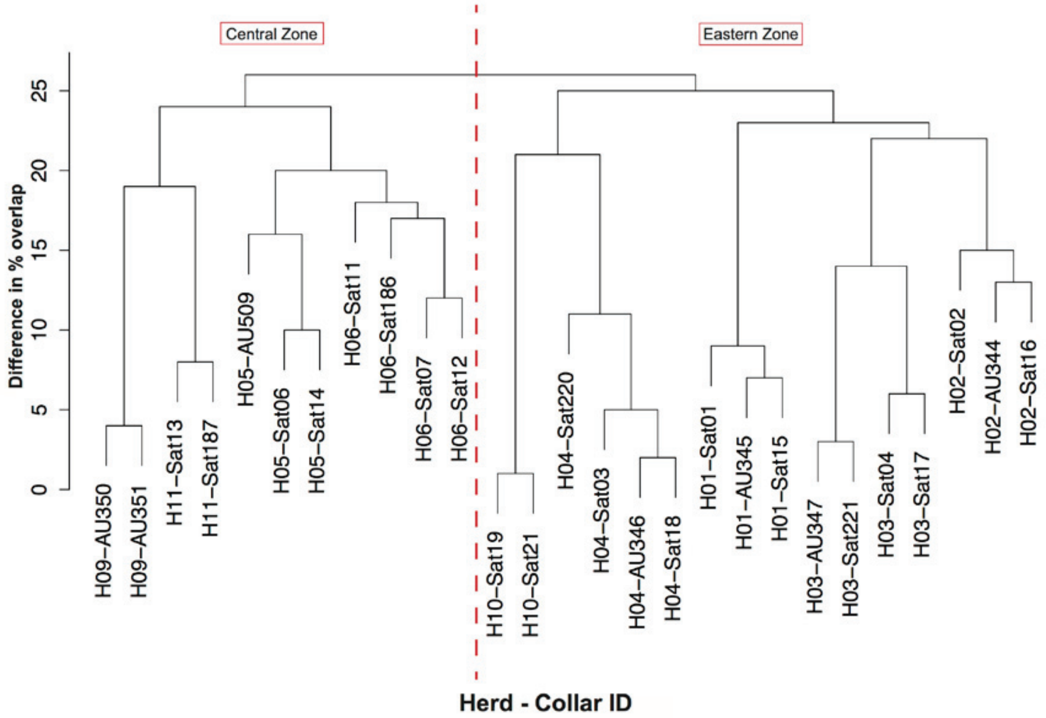


Figure 5.4 - Inter-individual association between 27 GPS collars within 9 herds in Niassa National Reserve obtained from the percentage of HRs overlap (LKDE with 95% isopleth)

C1.3 Seasonal home ranges (cf. Appendix III)

We observed seasonal differences in home range sizes. The mean home ranges size is 304 ± 210.1 km^2 in the dry season and 377.9 ± 155.5 km^2 in the wet season (LKDE with 95% isopleth). But if we consider the two zones (i.e. central and eastern) differences are larger. In the Central zone mean HR size was 502 ± 211 km^2 in the dry season and 508.3 ± 141.8 km^2 in the wet season. In the Eastern zone mean HR size was 182.2 ± 70.1 km^2 in the dry season and 309.3 ± 112.6 km^2 in the wet season. At the beginning of the rainy season, herds located in the eastern zone undertook important movements from Lugenda permanent River to remote forage areas, resulting in seasonal home ranges spatially disjoint (e.g. Figure 5.6). Similar - but less marked - spatial shifts were also observed in the central zone (e.g. Figure 5.7).

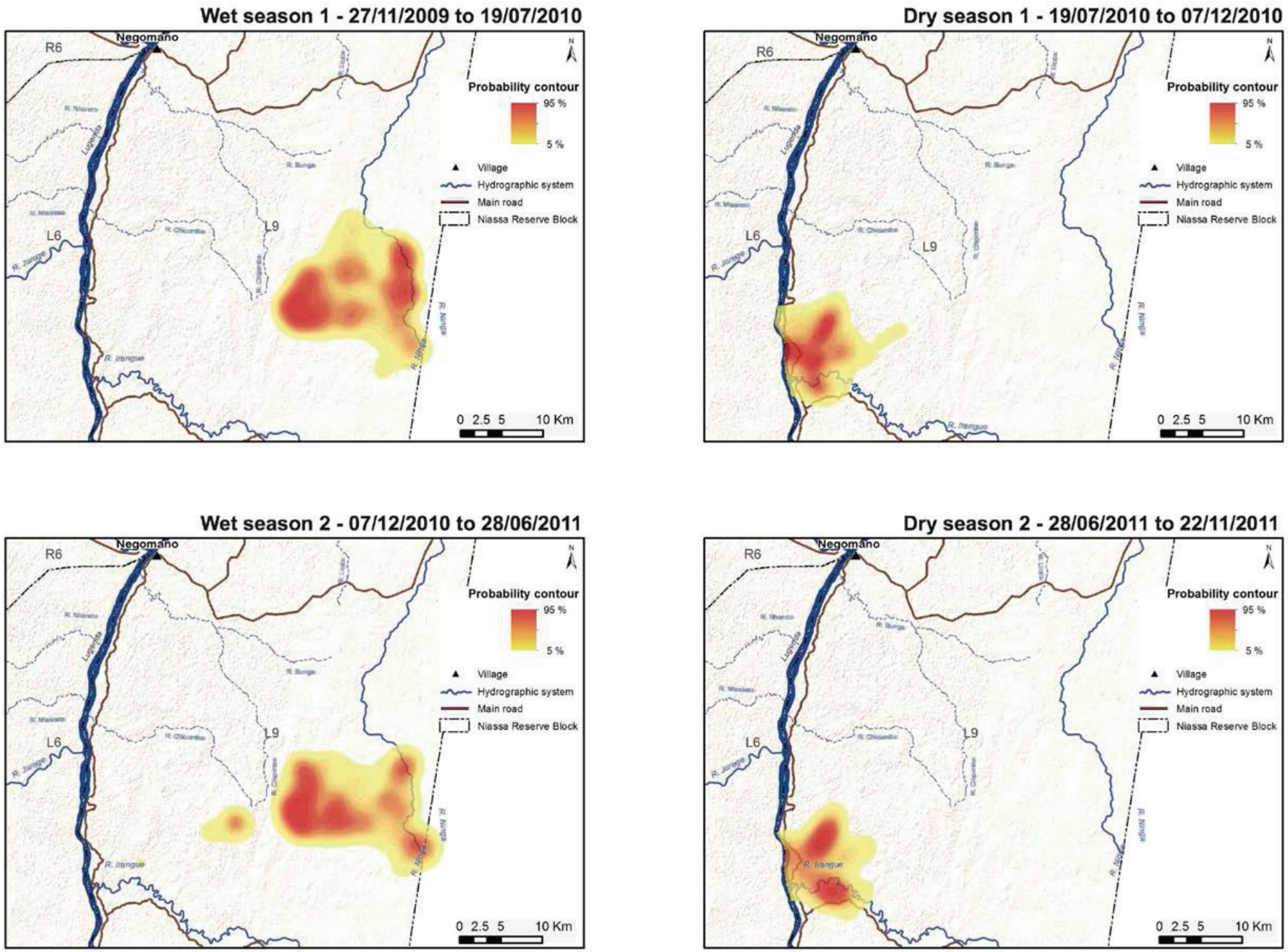


Figure 5.6 - Seasonal home range of buffalo cow AU345 (Herd 1) from December 2009 to December 2012 (2 dry seasons / 2 wet seasons) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit block L9)

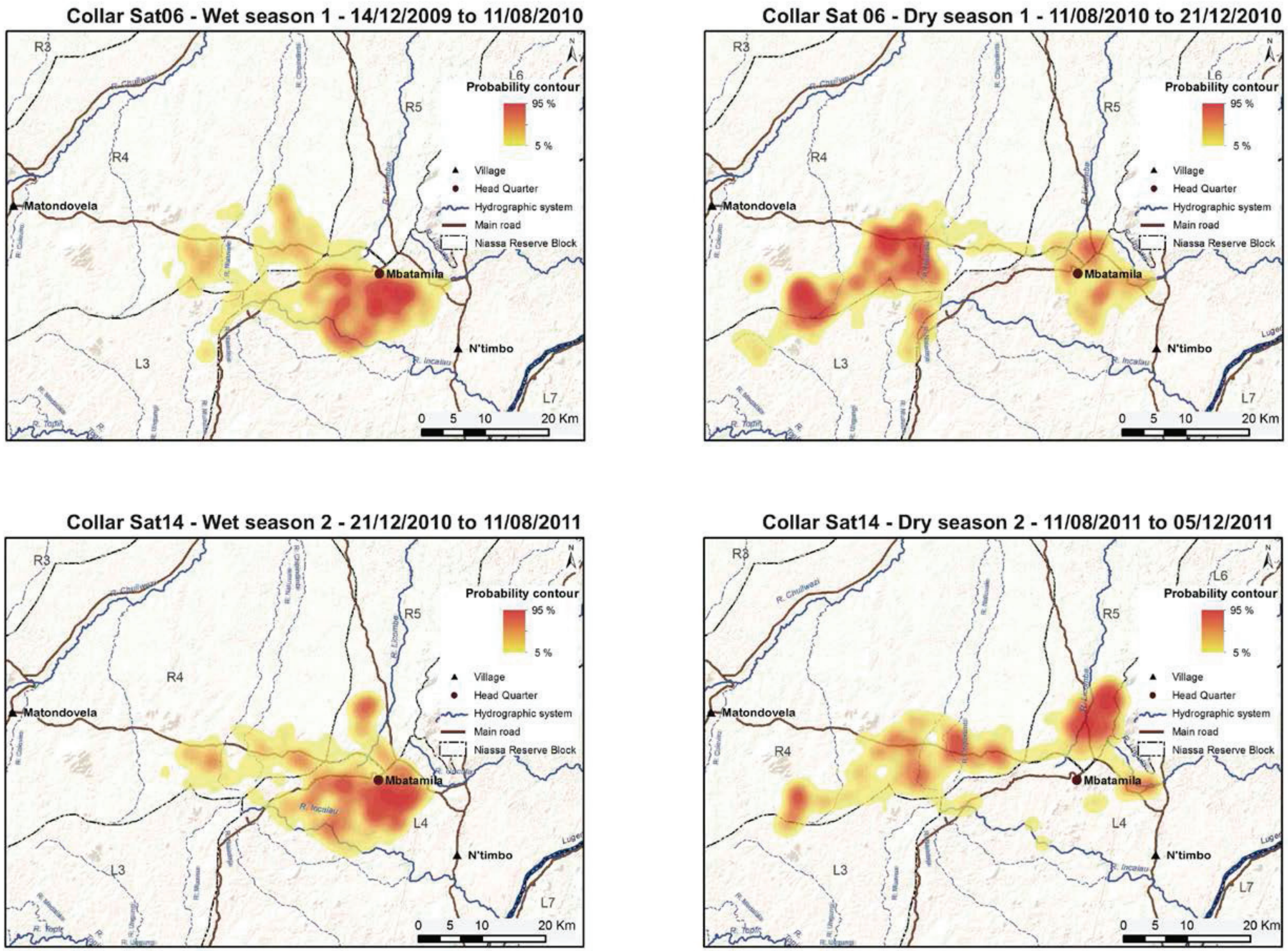


Figure 5.7 - Seasonal home range of buffalo cows Sat06 and Sat14 (Herd 5) from December 2009 to December 2012 (2 dry seasons / 2 wet seasons) using location-based kernel density estimation (LKDE) in Niassa National Reserve (central zone / Management unit blocks L3-L4-R4-R5)

C2 - Habitat selection

C2.1 - Models validation

Results from the cross-validations showed that most models had a good fit, with cross validation score often > 0.8 and much larger than what was obtained with a null model (Figure 5.8.a-c).

In both seasons, habitat type was the environmental variable having the most important effect on the quality of the fit. In most dry season models the burnt/unburnt attribute was also important in predicting space use. The contribution of the environmental variables to the patterns of habitat selection was shown to be moderate, and generally very variable between individuals.

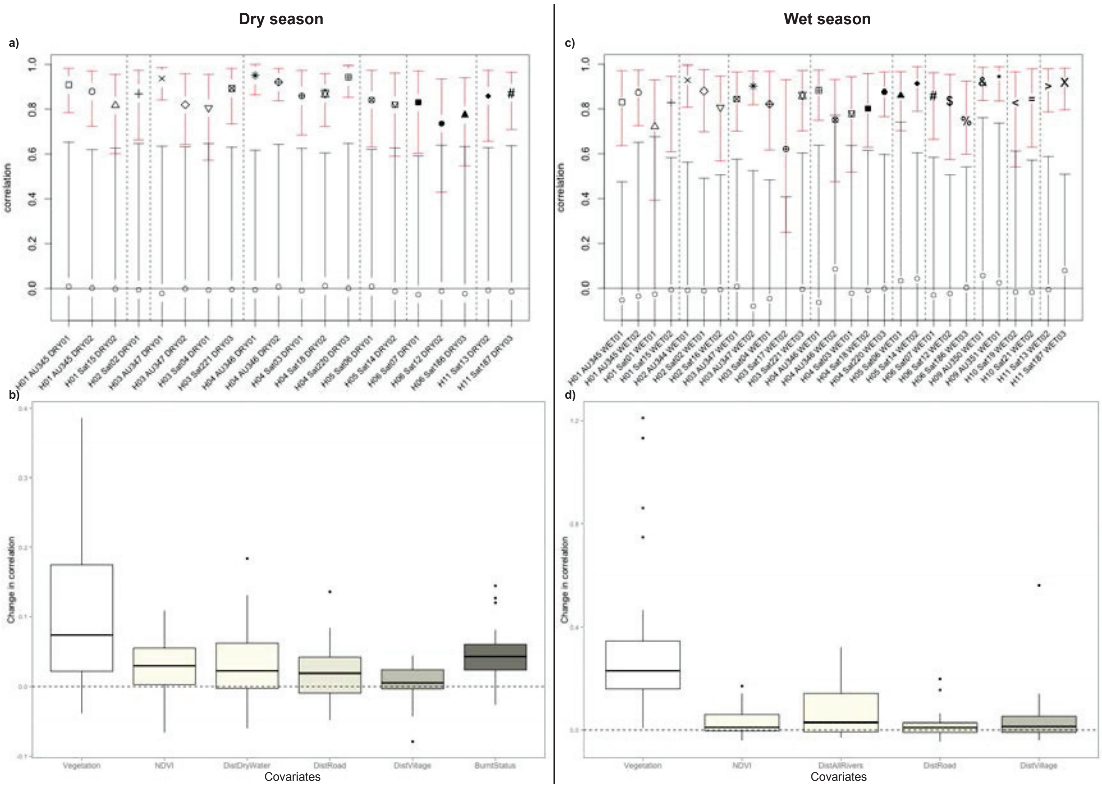


Figure 5.8 - (a,c) k-fold cross validation scores of the RSF models for dry (a) and wet (c) seasons - vertical dotted lines distinguish between herds; (b,d) Variable importance estimated as the increase in cross-validation score provided by the inclusion of the variable in a reduced model having all variables but the one of interest. Variable importance is displayed using boxplots of values obtained for all models.

<u>Comment for sections C2.2 and C2.3:</u> interpretation of our RSF models is illustrated by a **relative probability of use** in function of several covariates. In order to not bias the reading of the figures bellow, the relative probability of use was scaled on a y-axis where 0 value represents the maximal probability of use and -1 the minimum probability of use.

C2.2 - Dry season

Buffaloes selected open habitats, especially grassland and open *miombo* woodland. It was twice less likely to find buffaloes in *miombo* woodland than in grassland (Figure 5.9).

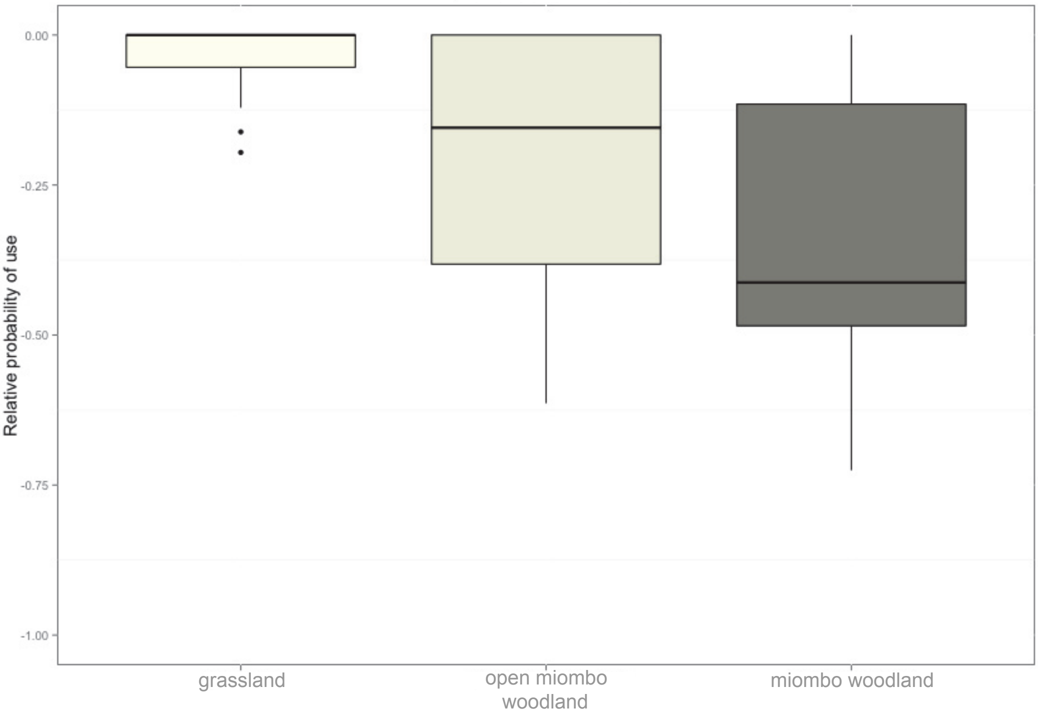


Figure 5.9 - Relative probability of use in relation to the 3 main land cover types in the dry season

Within each habitat types, areas with high NDVI values were often selected. For grassland in the central zone, relative probability of use increased by 0.4 from a NDVI value of 0.2 to 0.45. In the eastern zone, the relative probability of use of a grassland increased by 0.6 from a NDVI value of 0.2 to 0.65 (Figure 5.10.b). The relative probability of use strongly decreased as distance to water increased as illustrated in Figure 5.10.a for grassland. The maximal probability of use of a grassland occurred less than 2 km away from water available. More than 5 km away from water available the relative probability of use was close to its minimum. Only 2 buffaloes from herd 4 in the first dry season analyzed presented an inverted curve. The effects of NDVI and distance to water had the same patterns for open *miombo* woodland and *miombo* woodland. Effects were less marked in the other habitat types.

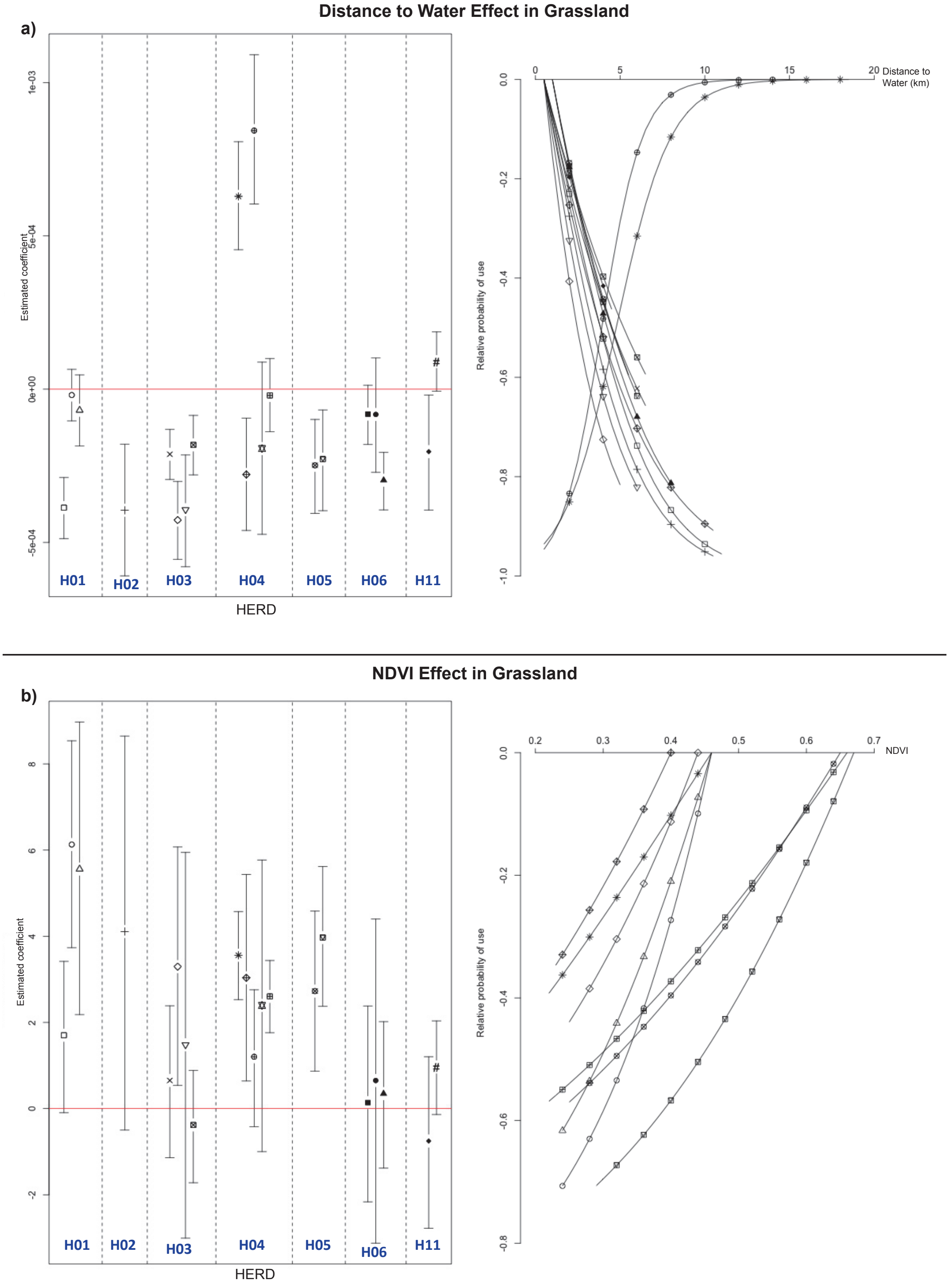


Figure 5.10 - Effects of distance to water (a) and NDVI (b) for the 20 buffalo candidates in the dry season. Estimated coefficients correspond to the generalized linear model (GLM) estimation for each candidate with 95% confidence intervals. Positive coefficients and intervals denote selection for grassland with high NDVI value (b) and negative coefficients and intervals denote selection for grassland close to river (a). Relative probability of use was only represented when the effect was significant in the model.

Buffaloes selected unburnt areas. The relative probability of use of a habitat decreased by more than 0.6 one week after a fire. Three weeks later the probability of use increased by almost 0.2, but it was still twice less likely to find a buffalo in a burnt area compared to an unburnt one. More than 2 months after a fire, the relative probability of use of a habitat decreased by 0.75 compared to an unburnt one (Figure 5.11).

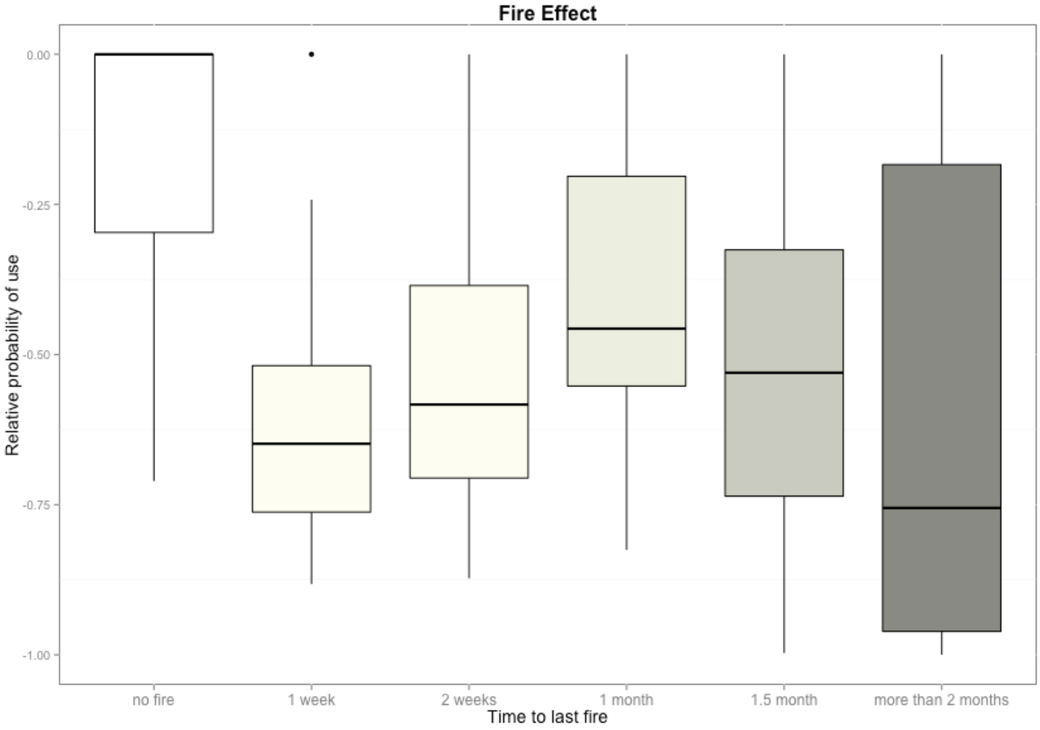


Figure 5.11 - Relative probability of use of a habitat in relation to the time to the last fire in the dry season

Except for three buffaloes (one in herd 1 and two in herd 6), the relative probability of use decreased as distance to road increased (Figure 5.12.a). Distance to village had significant effect for nine buffaloes and except for three buffaloes (one in herd 1, one in herd 5 and one in herd 6) the relative probability of use increased as distance to village increased (Figure 5.12.b).

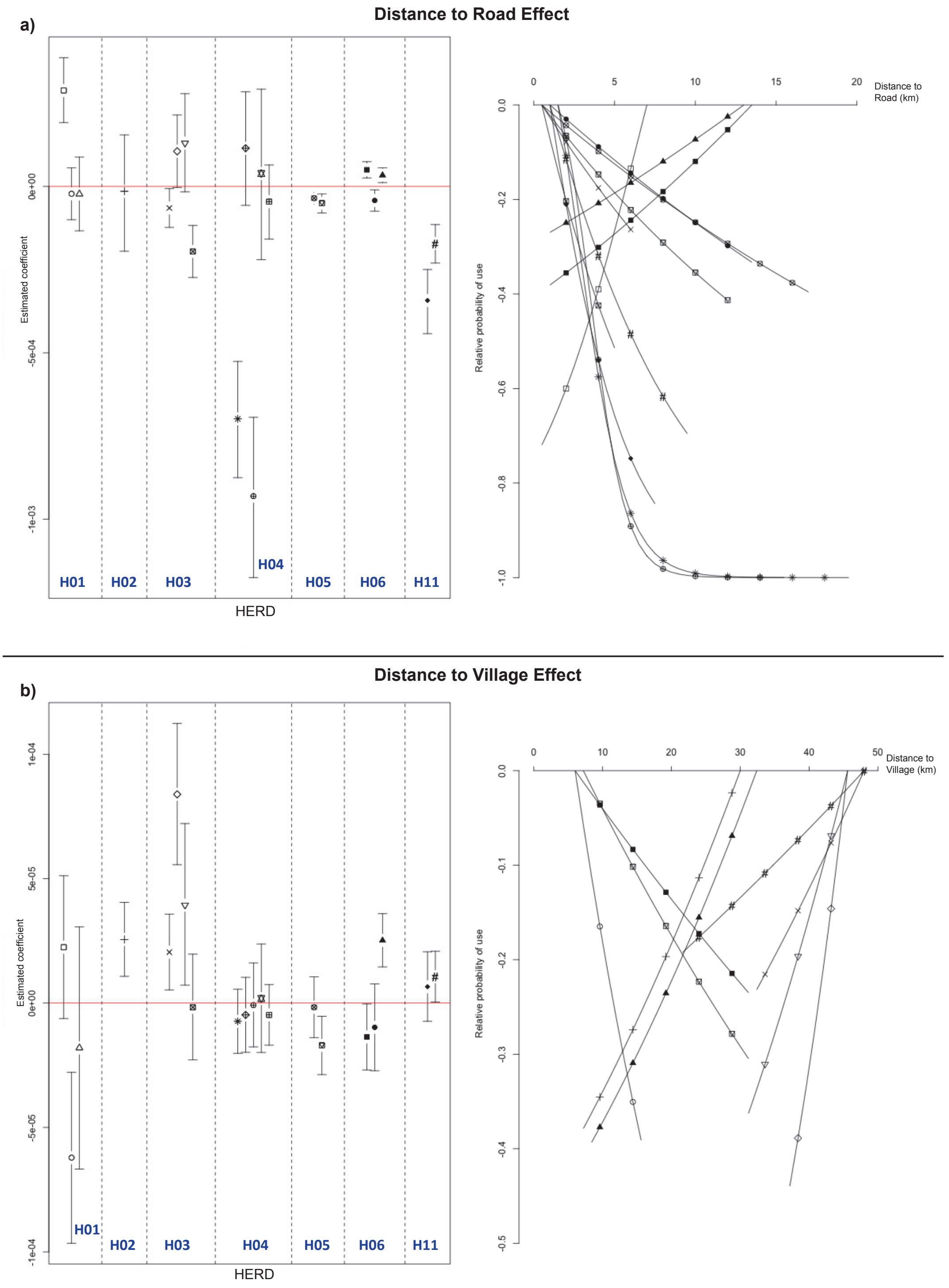


Figure 5.12 - Effects of distance to road (a) and distance to village (b) for the 20 buffalo candidates in the dry season. Estimated coefficients correspond to the generalized linear model (GLM) estimation for each candidate with 95% confidence intervals. Positive coefficients and intervals denote avoidance for vegetation patch close to road (a) and for vegetation patch close to village (b). Relative probability of use was only represented when the effect was significant in the model.

C2.3 - Wet season

Buffaloes also selected open habitat types in the wet season, especially grassland (Figure 5.13).

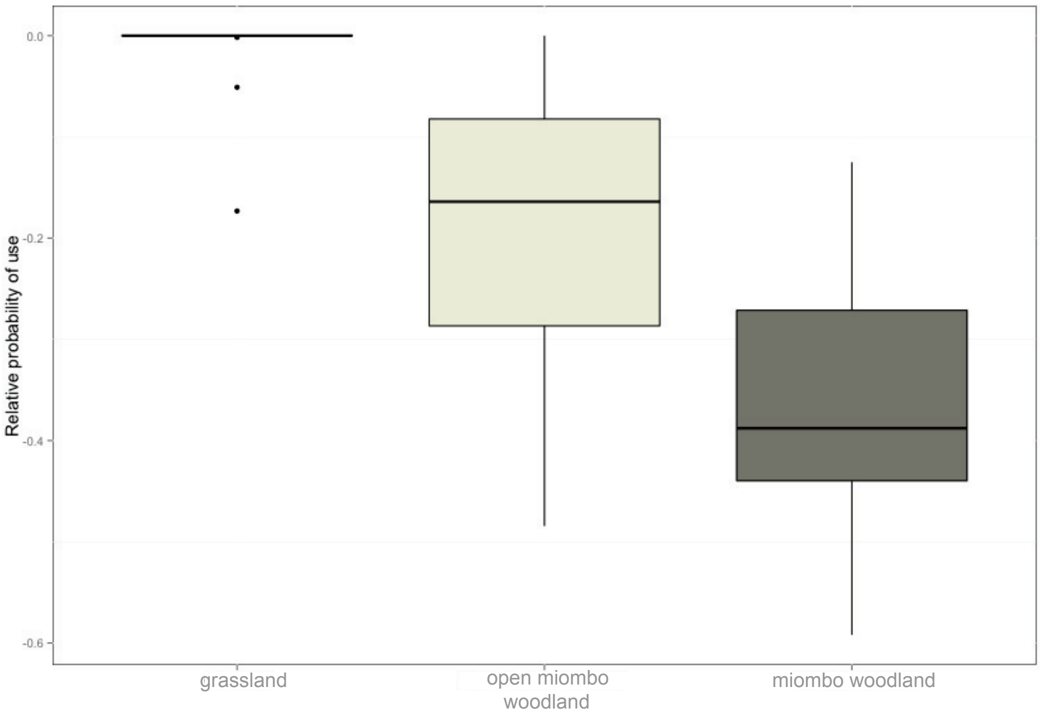


Figure 5.13 - Relative probability of use in relation to the 3 main land cover types in the wet season

Within each habitat type, areas showing high NDVI values were often selected. For grassland the relative probability of use was maximal for NDVI value of 0.7 except for one buffalo in herd 3 (Figure 5.14.b). Similarly, the relative probability of use was maximal for NDVI value of 0.7 in *miombo* woodland. Except for five buffaloes, there was no significant effect of NDVI in open *miombo* woodland. In contrast, in dense *miombo* woodland, the relative probability of use was maximal for NDVI value around 0.4 and decreased as NDVI value increased.

In the wet season, when water is not a limiting factor, buffaloes showed selection for habitats close to rivers. The maximal relative probability of use for a grassland occurred less than 1 km away from a river (Figure 5.14.a). Similar patterns were observed for open *miombo* woodland, *miombo* woodland and dense *miombo* woodland.

In contrast, the effect of human disturbances was unclear in the wet season. There was no clear pattern of avoidance of roads (Figure 5.15.a) and/or villages (Figure 5.15.b).

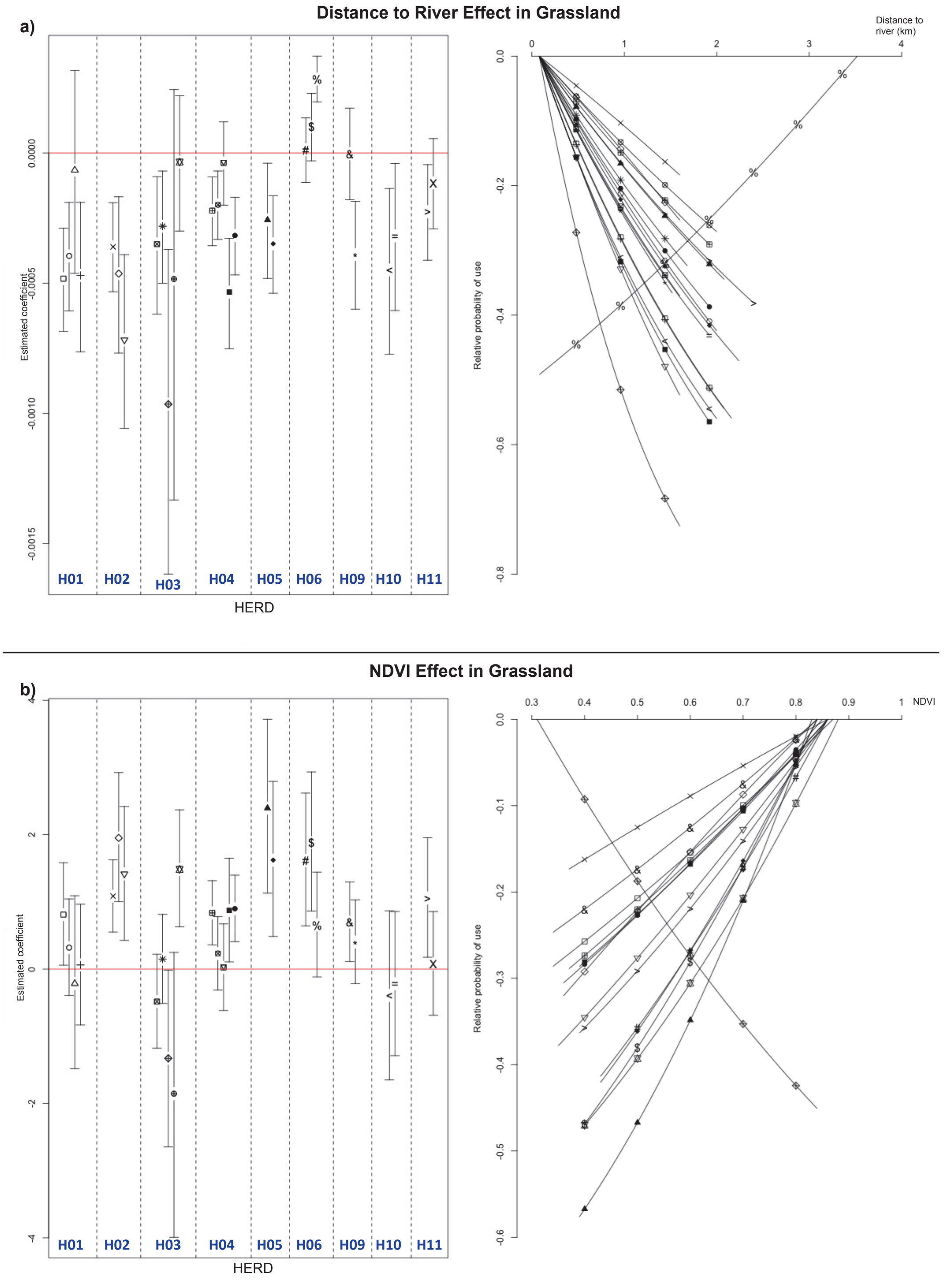
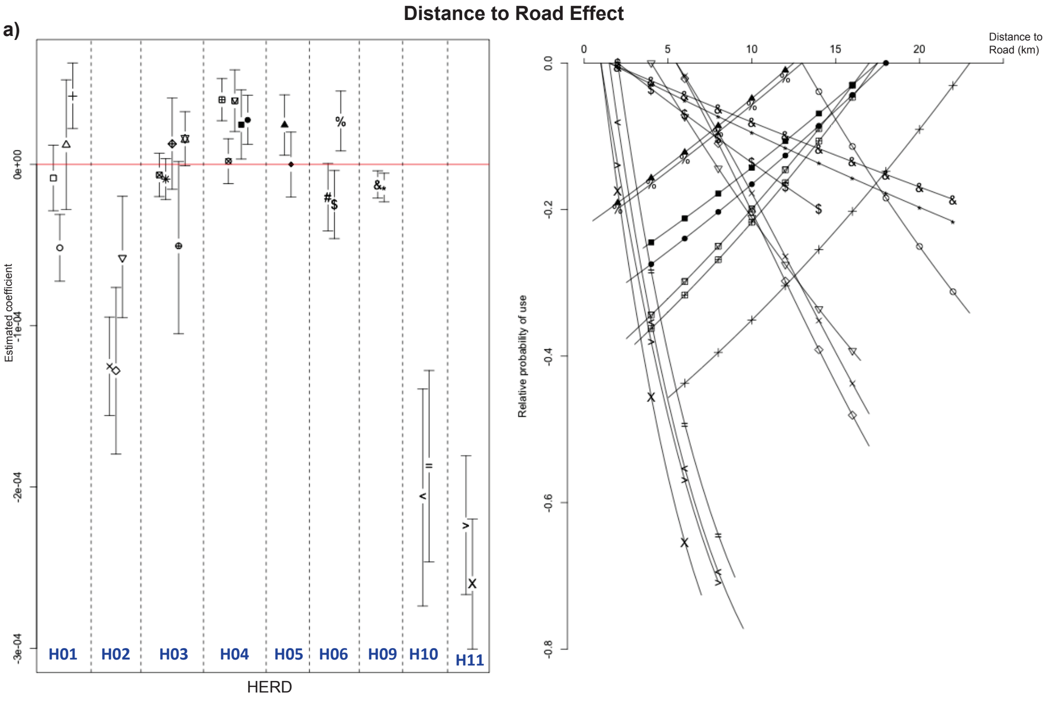


Figure 5.14 - Effects of distance to water (a) and NDVI (b) for the 28 buffalo candidates in the wet season. Estimated coefficients correspond to the generalized linear model (GLM) estimation for each candidate with 95% confidence intervals. Positive coefficients and intervals denote selection for grassland with high NDVI value (b) and negative coefficients and intervals denote selection for grassland close to river (a). Relative probability of use was only represented when the effect was significant in the model.



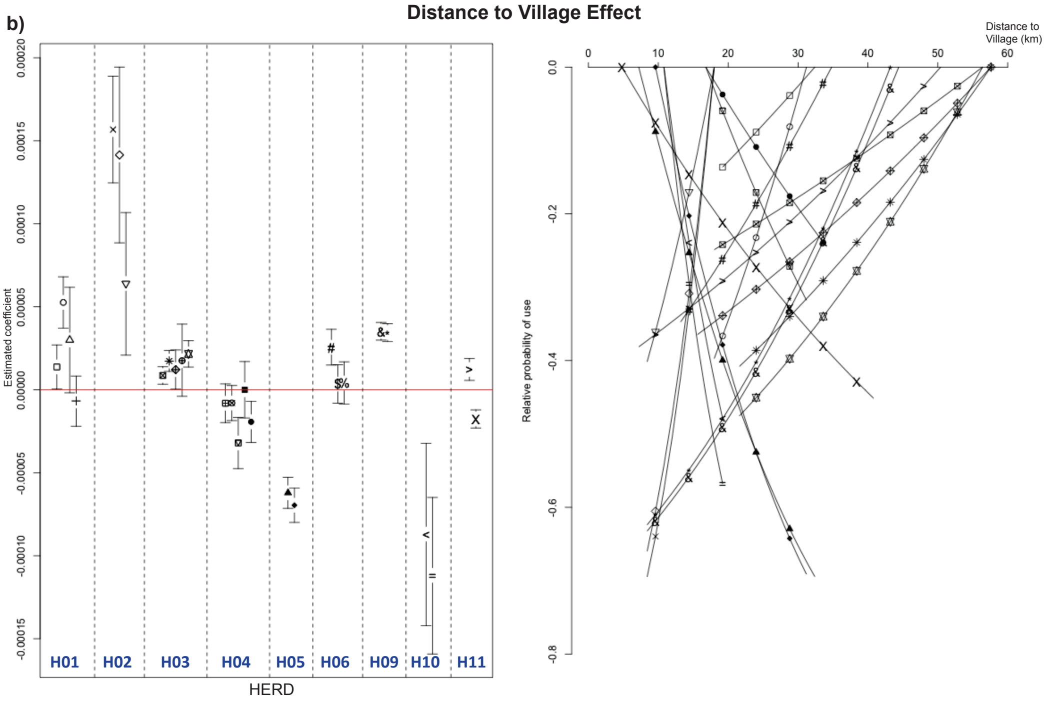


Figure 5.15 - Effects of distance to road (a) and distance to village (b) for the 28 buffalo candidates in the wet season. Estimated coefficients correspond to the generalized linear model (GLM) estimation for each candidate with 95% confidence intervals. Positive coefficients and intervals denote avoidance for vegetation patch close to road (a) and for vegetation patch close to village (b). Relative probability of use was only represented when the effect was significant in the model.

D - DISCUSSION

D1 - Home ranges

The HR sizes in NNR are among the largest recorded for African buffalo. Ryan (2006) suggested that an upward limit of approximately 290 km^2 exists on HR size regardless of buffalo herd size (based on MCP method which tends to produce larger estimates than LKDE). Our LKDE with 95% isopleth and MCP estimates are substantially larger than this value for most of our buffaloes. We did not study the relationship between HR size and herd size but previous studies (e.g. Sinclair 1977) have been reexamined and the analysis reveals that the larger HR size estimates also corresponded to larger herds. However, Ryan (2006) compared in his analysis the annual HR size with average annual herd size and found no correlation. Compared to other studies (Leuthold 1972; Funston et al. 1994) which had similar herd sizes to our average herd size (161 ± 65 buffaloes, collaring time, cf. Table 5.2) our average HR size is still among the largest recorded in Africa. The larger HR sizes are generally observed in open and low-rainfall regions where resources are spatially segregated, forcing buffalo to perform seasonal movements (Cornélis et al. 2011; Naidoo et al. 2012a).

Global HRs size appeared to be larger in the Central zone than in the Eastern zone. The environmental covariates could explain this difference as they vary considerably in time and space in the two zones. Indeed, the seasonal phenology shows the existence of large-scale longitudinal gradients. Our study area is characterized by gradients of primary production and rainfall decreasing from west to east. The Eastern zone gets drier sooner in the dry season and thus, bushfires occur earlier. In addition, the only water available in the Eastern zone in the dry season is the Lugenda River. This contrasts with the Central zone, where numerous natural waterholes are present. The strong constraints observed in the dry season in the Eastern zone may induce smaller home ranges.

Large seasonal movements approaching migrations were reported by several authors (Sinclair 1977; Cornélis 2012; Bennitt 2012). HR sizes appeared to be larger in the wet season for the Eastern zone than in the dry season. This contrast with studies from Kruger National Park (South Africa), which found larger HR sizes in the dry season (Ryan et al. 2006; Winnie et al. 2008) but is similar to studies in Tanzania (Prins 1996), in Botswana (Halley et al. 2002) and in Namibia (Naidoo et al. 2012b), where HR sizes were larger in the wet season. For the Central zone, no seasonal effect was noted on HR sizes. The reduction of size in the dry season seen in prior studies is likely to be closely tied to the availability and spatial arrangement of water sources. As underlined above, the numerous natural waterholes in the Central zone scattered across the landscape, in contrast with the Eastern zone where the only water available in the dry season was the Lugenda River, are likely to be responsible of the similar seasonal HR sizes in the Central zone.

D2 - Spatial arrangements of home ranges

In this study, neighboring herds clearly tended to segregate their space use. Herds ranging along the Lugenda River systematically used one side of the river instead of centering their home range on the River. Moreover, although the Lugenda River does not constitute physical barrier to movement (a few buffalo bulls were observed crossing it), no herd was observed crossing the River in three years of study. In addition, we directly observed several times two herds established on opposite banks of the river, drinking at the same time of the day.

In our study, we found a quasi-absence of direct contacts suggesting that HRs were not actively defended. The studied herds thus appeared to exploit exclusive HRs without spending substantial energy in their defense. Similar space patterns were observed in buffalo herds in Western African (Cornélis et al. 2011) suggesting that social relationships between herds might act as a high-level constraint on habitat selection.

Our results suggest that the spatial arrangement of water resources and potentially their regime (permanent or not) play a key role in the social and foraging behavior of buffalo. Indeed, herds exploiting common segments of permanent rivers (Eastern zone) were shown to display a higher degree of spatial segregation than those drinking on a network of temporary pans (Central zone). In our view, this may result from two non-exclusive possible explanations. First, defending a network of scattered water pans against conspecifics requires much more energy than defending a linear system. Second, water availability in pans is subject to inter-annual variations (depending on waterfall) and temporary pans thus constitute a less predictable environment than permanent water systems. Buffalo would thus make a less exclusive use of space where the availability of resources (here water) is less predictable.

In NNR buffalo population, inter-herd behavioral avoidance may act as a high-level constraint on foraging processes and may also contribute to constraint population dynamics since an exclusive space use is likely to generate density dependence (Gordon 1997; Both and Visser 2003; Cornélis et al. 2011).

D3 - Habitat selection

We showed how space-use dynamics of buffalo herds were related to dynamics of forage and water resources. During the dry seasons, the herds in the Eastern zone were forced to range close to the only water available, the permanent Lugenda River. Patterns were not so clear in the Central zone where buffalo herds used waterholes and remaining water in secondary rivers in the dry seasons (except one herd which had its global HR along the Lugenda River). Habitat selection analysis emphasized the importance of close proximity to water, a preference for open habitats with high NDVI values and an important constraint in the dry seasons related to bushfires. Our results did not support the hypothesis that human disturbance in NNR may act as a space use constraint at the scale of our analysis although the effect certainly is relevant at different selection levels (e.g population distribution range).

We found that buffalo selected for open habitats such as grassland and open *miombo* woodland which are characterized by a high percentage of grass cover, both at both intra- and inter-seasonal scales. Other studies have found preferences for open grassy areas, even among the forest-dwelling buffalo of central Africa (Melletti et al. 2007). Selecting against dense habitat types is consistent with suggestions in prior studies to reduce likelihood of palatable grasses. The habitat types used in our analysis were classified according to vegetation surveys carried out by our team (cf. Chapter 3 - B3). Given the extent of our study area, the mapping was primarily designed to characterize the structure of the vegetation and the main tree and herbaceous species. Further investigation of the botanical composition of the herbaceous layer would certainly improve our comprehension of buffalo's preferences for given habitats in NNR.

In the dry and wet seasons, buffalo showed a preference for close proximity to water (Figure 5.10 and 5.14 in grassland). Buffalo are often described as riverine habitat animals (e.g. Prins 1996), but the level of details of our vegetation map did not allow for testing such selection for riverine vegetation. The selection for grasslands close to water in both wet and dry seasons result from two different processes. In the dry season, the proximity to water is a vital source hence constraining grazing close to perennial river and waterholes. In the wet seasons, buffalo may tend to graze close to rivers because the grass resources are more favourable, with higher biomass, more moisture content and more palatable species.

We found a positive relationship between NDVI values and the selection of open habitats (i.e. *miombo*, open *miombo* and grassland) indicating that buffalo selected greener areas within seasonal HRs. The NDVI is related to the greenness or the amount of vegetative biomass in an area (Pettorelli et al. 2005) and thus, high NDVI values would suggest more productive habitats. Winnie (2009) suggested that buffalo, in poorer quality environments, might be focusing their foraging on high quality forage hotspots. However, NDVI measures the photosynthetic activity of woody and herbaceous vegetation without distinction. Previous studies found that NDVI might be inappropriate to predict space-use patterns of grazers at a small spatial scale (Ito et al. 2006; Holdo et al. 2009b; Cornélis 2012) but it appeared to be a good covariate in our analysis for a predictive model of buffalo habitat selection in NNR.

Avoidance of burnt areas by buffalo has been observed in previous studies (e.g. Sinclair 1977). In contrast, others have speculated that burnt areas are attractive to buffalo after sufficient regrowth occurs (Ryan et al. 2006) because of the increased nutrient concentrations in post-fire regrowth (van de Vijver et al. 1999). Bushfires are part of the miombo woodlands ecology but their effects (direct and indirect) on vegetation can differ widely (Chidumayo 1997). Our results showed that buffalo avoid burnt areas compare to unburnt ones. Almost 50% of the NNR burn every dry season. Most bushfires occur late in the dry season when they are considered to be very damaging to the vegetation (Zolho 2005). We noted in the field that bushfires occurring from the mid-dry season (i.e. August) until the end of it did not produce dry season regrowth in NNR. However, the effect of fire may be favourable for the grassland production in the following growing season, but we did not measure this effect. In other word, bushfires in NNR wipe out substantial areas of low quality grasses suitable for buffalo and this The disappearance of dry season forage through fire, even though tall dry grasses are low quality food resources, may increase the nutrition constraint experienced by large herbivores in the lean period of the year, and may have significant effects on populations of species relying on bulk forage to survive through the dry season, such as buffalo in particular.

Contrary to our hypothesis, buffaloes did not select areas far from villages and/or roads at the scale of our analysis. However, we studied habitat selection within the seasonal HRs and none of them had a village within its borders (cf. Figure 5.3). Villages may act as a strong constraint to habitat selection at levels not investigated in this paper (e.g. home range settlement or population distribution range). NNR holds a very loose road network with little traffic, and distance to road does not appear to constraint habitat selection patterns in buffalo. Finally, poaching activities were not reflected in our analysis and better spatial data on human activities within the NNR may improve our comprehension of the system.

Conclusion

HR sizes in our study area were among the largest recorded for Cape buffalo. Since HR size is directly related to the availability and distribution of grazing, water and shelter, it might reflect adaptations to a poor quality environment in the NNR. In both dry and wet seasons buffaloes showed a preference for open habitat types with high NDVI values and a preference for close proximity to water. Surface water availability is thus a major constraint in the dry seasons, especially in the Eastern zone where buffaloes only used the perennial Lugenda River, hence the reduced dry season HR sizes in this section of NNR. The presence of water is also responsible for the observed large seasonal shifts. Space use strategies appeared different at the scale of zones within NNR, and management implications may consider several zones independently. For both studied zones, bushfires appeared to be a strong constraint and may reduce greatly the quantity of forage available to the buffalo population. The management of bushfires may be key to the conservation strategy of buffaloes in NNR, particularly where their movements are restricted by water availability. Further investigation to assess predation risk from both human and natural predators would be necessary to better understand space use patterns of the buffalo population in NNR.

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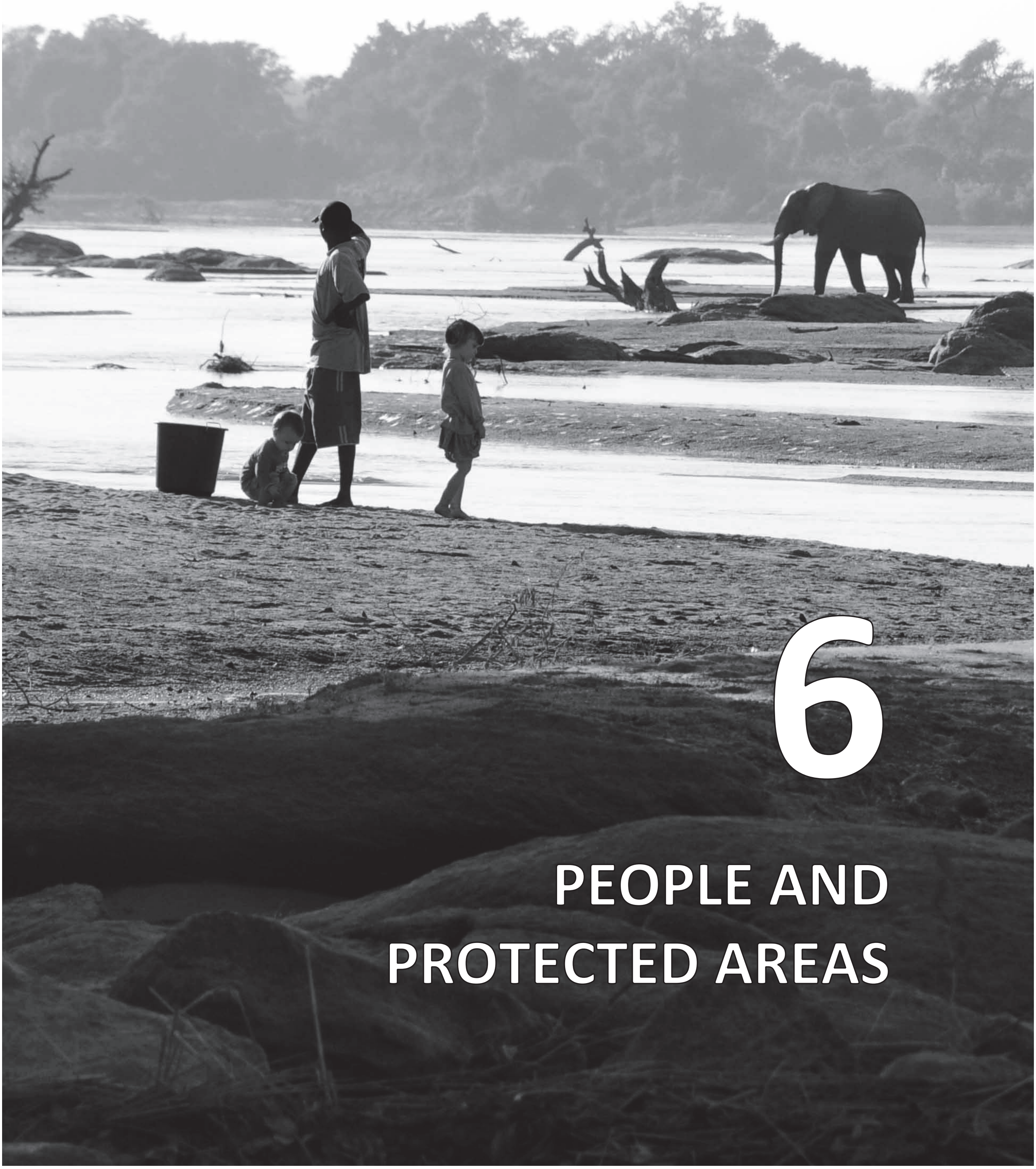

6

PEOPLE AND PROTECTED AREAS

Spatial heterogeneity in environmental constraints conditions: the dependency to natural resources for people living inside Niassa National Reserve (Mozambique) and the associated conservation issues

Thomas Prin - Hervé Fritz - Chloé Guerbois

In preparation for *Conservation and Society*

A - INTRODUCTION

The establishment of protected areas, considered as the core element for biodiversity conservation and large mammals in particular (Chape et al. 2005) , was historically associated with land dispossession and the eviction of local populations (Brockington and Igoe 2006). The exclusionary paradigm has negatively impacted the livelihoods of people living in protected areas, often undermining their access to natural resources (Ghimire et al. 1997). For several years, and especially since the IUCN World Parks Congress in Durban, South Africa, in 2003, protected areas are recognised by conservationist as an indispensable tool to ensure the sustainability of the planet's biological systems and the health and welfare of people (Wilkie et al. 2006). They also recognise the need to increase social sciences to manage human wildlife interactions for better conservation outcomes (West et al. 2006; Phillipson et al. 2009). The challenge faced by protected areas now is to correct the imbalance and to involve local people in a range of activities and developments. However, on the African continent, most information available relate to rural people living on the edge of protected areas (e.g. Naughton-Treves et al. 2005; West et al. 2006), and only few studies exists on local populations living within protected areas boundaries (e.g. Twyman 2001).

This is the original feature of the Niassa National Reserve (NNR, Mozambique), one of the vastest protected areas of the African continent (42,140 km^2), where local communities are included within the Reserve. Households in NNR are characterized by a high degree of poverty and low food security (Cunliffe et al. 2009). Little is known about NNR, whether on wildlife or on household socio-economics, food security and local attitudes toward conservation. In order to improve conservation strategies, a deeper understanding of rural people's relationships with their environment is needed, and a recognition of local knowledge and practices needs to be incorporated in parks management plans to ensure conservation success (Twyman 2001).

Residents of rural areas across the world depend on natural resources for their livelihoods, survival and health (Lockwood et al. 2006; Milgroom et al. 2014), and natural resources harvested play an important role in southern Africa by providing households needs and sources of income (Cavendish 2000; Shackleton and Shackleton 2000; Twine et al. 2003; Hunter et al. 2011). These resources are often classified in terms of wood (e.g. timber for construction and firewood) and non-wood products (e.g. thatching grass, wild fruits, honey, wild meat, including fish and bushmeat) (Guerbois 2012). Natural resources can also play a role as a safety-net for rural household economy (Shackleton and Shackleton 2000). Traditionally, wild meat has provided a secured source of protein for rural people of Africa and has been a supplemental source of income (Ndibalema and Songorwa 2008) but hunting and fishing activities have direct effects on wildlife populations and indirect effects on ecosystems and are often linked (Rowcliffe et al. 2005).

When local populations live within the limits of a protected area it raises complex conflict problems at three levels: (i) the land-use and access to natural resources, (ii) the coexistence of people and wildlife often referred to as human-wildlife conflicts and (iii) the distribution of the protected area economic benefits to rural communities. Rules for governing use and access to natural resources often affect people livelihood and well being (West et al. 2006) and protest is likely to be loud where households are highly dependent on the harvesting of natural products (Wapalila 2008). Though various approaches exist to resolve conflicts that occur between people and wildlife, not all can be applicable or adequate depending on local circumstances, but conflict resolution will be crucial to the success of conservation development plans (Woodroffe et al. 2005). Another challenge faced by most protected areas is the small contribution of the wildlife sector in sustaining local communities’ livelihoods compared to other land use practices. As a result, local people perceive wildlife conservation as a legal responsibility, if not constraint, rather than an economic and social advantage or opportunity (Wilkie et al. 2006).

This paper explores the households' livelihood and food security issue in NNR, and the degree of reliance on natural resources. We also aim at understanding how human activities within NNR may affect wildlife populations by illustrating the complexity and diversity of resource use by people and the associated livelihoods within NNR. At a scale as large as the NNR, we tested the hypothesis that communities' livelihood exhibit spatial heterogeneity according to the geographical situation of villages. We explored the potential direct and indirect impacts of human population on wildlife by testing the level of accessibility and reliance on natural resources depending on the households' geographical situation. Such understanding is an essential first step to assess the direct and indirect effects of local people on natural resources as well as to predict the consequences of biodiversity loss for local economies and livelihoods. It is also necessary to promote better coexistence between people and wildlife and thus ensure the success of integrated conservation plans.

B - METHODS

B1 - Study area

The Niassa National Reserve (NNR) is located in northern Mozambique along the border with Tanzania. NNR straddles two Mozambican Provinces, the Niassa Province and Cabo Delgado Province. The NNR covers an area of 42,140 km^2 (Figure 6.1). This protected area supports the largest concentrations of wildlife in Mozambique with the full complement of herbivores (excluding black rhino and possibly roan antelope) and carnivores expected in the region (SGDRN 2007). The NNR is located within the Eastern *Miombo* Woodland eco-region (WWF 2001) and is characterized by nutrient-poor soils with low organic matter. Seventy-two per cent of the NNR is covered by dry Zambezian *Miombo* woodland (Ribeiro et al. 2008). The NNR experiences a seasonal tropical climate with most rainfall concentrated in the hot summer months from mid-November through April. This season is followed by a long winter drought, lasting up to 7 months (Werger and Coetzee 1978). Mean annual rainfall ranges between 800 and 1,200 mm per annum, and varies along a west-east gradient with higher rainfall in the west.

Figure 6.1 - Maps of Africa and Mozambique showing the study site, the Niassa National Reserve

First declared as protected area in 1954, the area is managed under a form of partnership between the private sector and the Government. The Society for the Management and the Development of the NNR (*Sociedade para a Gestão e Desenvolvimento da Reserva do Niassa*, SGDRN) signed a lease contract with the Government and had exclusive rights for the management of the Reserve for 10 years (2002-2012). SGDRN has recently been replaced by the Wildlife Conservation Society (WCS), which is now managing the NNR under the same regulatory rules. Rock art in the area shows that NNR has always been inhabited. The civil war in Mozambique (1975-1992) has left the area sparsely populated but the human population within NNR is increasing (SGDRN 2011). More than 39,000 local residents live today inside the protected area across 50 villages. Shifting subsistence agriculture is the primary land use and main economic activity (Cunliffe et al. 2005). Cattle are absent due to tsetse fly (*Glossina spp*.), the vector for the disease *trypanosomiasis*, but smaller livestock, primarily goats and chickens, and domestic dogs are present in the larger villages. Economically, the area benefits from the wildlife industry (photographic but mostly trophy hunting safaris) with nine private companies operating in the area in specific management units.

Natural resources use is relatively open everywhere in the NNR. Human settlement and farming are uncontrolled. Firewood collection, thatching grass extraction and wood harvesting are authorised and unregulated. Fishing activities are allowed inside the protected area for personal consumption. Fishing licenses are delivered by local administrations but large discrepancies exist between the number of licenses and the high number of fishermen found on the main fishing rivers (SGDRN 2011). Poaching and mining are strictly forbidden. SGDRN underlined the general lack of rules for governing the use of NR by communities as a major management issue (SGDRN 2007).

B2 - Data collection

Semi-structured interviews were conducted between July and September 2012 following a stratified sampling of 123 households randomly selected in 8 villages on a gradient of distance to rivers and human densities. All interviews were conducted in Portuguese or local languages by a Mozambican student and a local translator. Because bushmeat consumption is illegal within the NNR we developed a questionnaire (cf. Appendix VI - B) focused on food security to obtain honest answers from the interviewees. Questionnaires were divided into four sections: (i) household socio-economics, (ii) local perceptions and attitudes toward food security and diet, (iii) diet and (iv) a conclusion with open questions about the implications of living within a protected area. To avoid *a priori* biases in data collection, responses were recorded in full. For the statistical analyses, we classified the responses *a posteriori* to minimize the number of modalities in each variable, yet to save as much information as possible.

In the first part of the interview focusing on the household socio-economics, we asked people with close-ended questions to describe household composition, farming activities, sources of incomes, and livestock ownership. We investigated the diversification of their selling activities to obtain cash by asking people to tick in a list of potential incomes (e.g. fishing, cutting bamboo, making basket, hunting). We included an income in our list called "*Ganyo*" which corresponded to occasional labour between neighbours in exchange of a salary (i.e. selling services). Information about farming activities included number of fields, farming practices, cultivated crops, crop production and main constraints to farming.

As a second step we started investigating food security issues by asking people if they had enough food for the household for the past three years. We then asked them to list all reasons they could think about for not having enough food over the past years.

As a third step, we asked people to describe their diet with a detailed description of the relish, called "*Caril*" locally, associated with their staple starch food. To assess protein consumption, and the contribution of bushmeat to it, we asked people how many times per week they had a meal with a close-ended list of *Carils.* We then asked people to rank the bushmeat sources from a fixed list of herbivore species according to the frequency of consumption. We also investigated monthly temporal variability in the availability of wild meat (i.e. fish and bushmeat) over the year. Among wild meats we made a distinction between fresh and dry meat. Then, we recorded people preferences within wild meats.

As a final step we asked people in a form of an open discussion to describe their feelings and the implications of living within a protected area and to express their opinion on the management of the NNR and on how and who could solve the food issues.

B3 - Data processing

Because of the sampling design (n=123 households in 8 villages) and to evaluate spatial variation in livelihoods and human-wildlife interactions we aggregated villages in three groups that we thought functionally contrasted. The *Town* group (n=64) regrouped households living in (or close to) the main village (i.e. Mecula, cf. Figure 1) and was characterised by a high human population density and an easy access to a national road and to market. The *River* group (n=36) regrouped households living in villages along the main perennial river (i.e. Lugenda River). The *Remote* group (n=23) regrouped households living in small villages (i.e. less than 500 people) and was characterised by a low access to road network and a high distance to perennial river (i.e. more than 40 km).

We classified the responses on incomes *a posteriori* because some incomes mentioned were not included initially in the list (cf. Appendix VI - B), generating three other modalities. Income *Resources* relates to household selling natural resources transformed or not (e.g. thatching grass, honey, canoe, brick) but not collecting the product (i.e. households were a "middleman" between the collecting person and the buyer). Income *Sell* refers to households relying on selling activities (any products as a middleman) and income *Field* for households selling crop production, in general a surplus but not always. To investigate the diversity of incomes we built a covariate to account for the number of incomes performed in a household.

The factors perceived to influence crop production were classified *a posteriori* into four modalities including *Climate* when responses were related to weather issues, *Fertility* when related to soil issues, *Wildlife* when related to damages from wild species in the fields and *Manpower* when related to human labour force issues.

People's perception of the NNR was categorised as "Good" and "Bad". The objectives of the NNR were categorised in three groups: *Conservation* when responses were conservation-oriented, with a sense of integration of the various issues with a more general view on the conservation of natural resources; *Protection* when related to wildlife protection per se, with an emphasis on prohibition of use or control; and *Keep* when responses were related to "keep the wildlife" with the idea of keeping the wildlife away from people, i.e. contain wildlife within its restricted domain or prevent wildlife to interact with people.

B4 - Data analysis

We performed our analysis using the *Group* level to focus on spatial variations in livelihoods and in human-wildlife interactions. As we had no GPS information at household level, choosing to constitute three groups according to distance to rivers and main road allowed us to investigate the effects of both natural environment and infrastructures on people livelihoods within NNR. For all sections of our questionnaires we first tested for significant differences between groups. We used chi-squared test (χ^2) to examine significant differences in contingency tables and nonparametric Kruskal-Wallis test (KW) when working on proportions. To estimate paired difference between two groups we used nonparametric Wilcoxon test (W). Results are presented as means ± standard deviations unless specified in the text.

We performed logistic regressions (Generalised Linear Model, glm) for binomial data when investigating the determinants of categorical responses (e.g. the probability to answer *Ganyo* as an income). We tested all potentially explanatory variables in our models, but only significant variables were included in the final models. On quantitative response variables we also performed linear regression with a backward procedure to identify significant explanatory variables.

We performed a Multiple-Correspondence-Analysis (MCA) to investigate how incomes influenced the access to wild protein, and describe the characteristics of the three different village groups.

All analyses were performed with the R 3.0.2 software (R Development Core Team 2013).

C - RESULTS

C1 - Production system

People in NNR rely mainly on subsistence farming and 91.87% of the interviewed households (n=123) mentioned having at least one field. Field size ranged from 0.6 to 15 hectares, with a mean of 2.5 ± 2.2 ha. The main cultivated crop was maize (96% of the households). There was no significant effect of *Group* on farming activities characteristics. Only 15% of the households interviewed owned goats whilst 44% owned chicken. We did not find any differences in the proportion of livestock owners in the different groups. Poultry included on average 6 ± 10 chickens and livestock 1 ± 3 goat(s), without differences between groups. Households were able to secure 5.9 ± 2.5 months of crops per year from their own production on average. There was no significant difference between groups (KW=1.55, df=2, *p* =0.46) with 6.3 ± 2.9, 5.6 ± 2.2 and 5.4 ± 1.7 months of crops secured in the Town, River and Remote group, respectively.

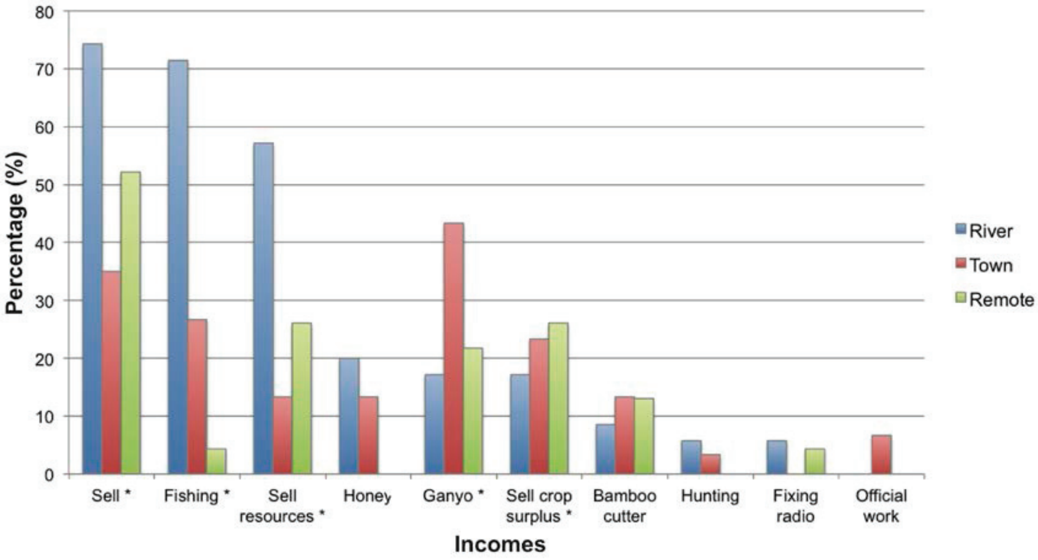

Figure 6.2 - Percentage of households mentioning the difference sources of incomes for the 3 groups.
** indicate when the income had significant effect with the Group covariate (glm, test= χ^2, p<0.05)*

The main incomes included selling industrial products, fishing, selling natural resources transformed or not, producing honey, providing services (i.e. *ganyo*) and selling crop (Figure 6.2). We investigated the differences in diversity of incomes between groups (KW=15.8, df=2, *p* =0.0004), and found that households in the River group had a higher number of incomes (mean=2.2 ± 1) than Town and Remote group (W=1431.5, *p*=0.002 and W=623, *p*=0.0002, respectively). There was no significant difference (W=814.5, *p*=0.18) between Town (mean=1.7 ± 1.5) and Remote group (mean=1.2 ± 0.8). The sources of incomes in the River group were mainly composed by selling (i.e. general and natural resources sales) and fishing activities. Households in the Town group relied more on services activities than in the two other groups. The main income in the Remote group was related to selling.

Further, almost 10% of the adults in the interviewed households benefited from the salary of one employed member, official work in administration or hospital mostly, as a source of income. The main income in the Remote group was related to selling.

Trading is another important component of Niassa economy as practised by 53.51% of the respondents and concerns essentially food (e.g. maize for rice, maize for fish, rice for salt). At household level, the probability of trading was not related to *Group* (glm, test=χ^2, p=0.47), however it increased with the number of secured months with crops (glm χ^2=12.65, p=0.0004; slope=1.69, p=0.005).

C2 - Food strategy

C2.1 - Diet composition

The main staple starch food was maize (92% of responses) and rice (8%). Main *carils* mentioned in the diet composition included fish (27% of the interviewees), beans (26%), green-peas (21%) and manioc leaves (19%). There was no significant difference between groups for the mean number of meals accompanied by a *caril* per week (9.3 ± 3.9, 9.3 ± 3.7 and 7.8 ± 4.4 in Town, River and Remote group, respectively).

However, we found significant differences between groups for the proportion of *carils* from vegetable protein and animal protein (χ^2=19.39, df=2, p<0.001). Only 9% of the *carils* came from animal protein (domestic and game) for *Remote*, against 24% for *Town* and 58% for *River*. Furthermore, there was a significant difference between groups in the frequency distribution of the various *carils* per week (Table 6.1). Bean was more cited in Town and Remote groups compared to River group (Table 6.1, Wilcoxon test). Fresh and dry fish consumption was higher for *River* compared to *Town* and *Remote*. The consumption of fresh bushmeat was higher for *Remote* and *River* compared to *Town* (Table 6.1).

Table 6.1 - Mean number of meals with caril per week in the household's diet (KW=Kruskal-Wallis test between groups)

	Town	Remote	River	Statistical test (df=2)
Bean*	2.63 ^{a}	2.43 ^{a}	1.61 ^{b}	KW=26.91, p<0.001
Fresh fish*	0.89 ^{a}	0.39 ^{b}	2.50 ^{c}	KW=43.06, p<0.001
Dry fish*	2.63 ^{a}	0.43 ^{b}	2.00 ^{c}	KW=35.53, p<0.001
Fresh bushmeat*	0.70 ^{a}	1.39 ^{b}	1.03 ^{b}	KW=8.98, p=0.01
Dry bushmeat	0.97	1.22	0.86	KW=1.39, p=0.50
Chicken	0.59	0.87	0.53	KW=0.92, p=0.63
Goat	0.28	0.22	0.17	KW=0.18, p=0.91
Egg	0.41	0.35	0.39	KW=0.29, p=0.86

* *Carils* showing significant differences between groups

^{a,b,c} groups with different letters are significantly different (Wilcoxon test, p<0.05)

No data available for green-pea and manioc leaves

All groups combined, the most common wild meats were fish, duiker, zebra and buffalo (Figure 6.3). *Town* and *River* households had a higher percentage of fish offer compared to *Remote* where it was easier to find duiker. Water dependent species such as waterbuck and cane rat were more cited in River group. There were significant differences between groups for several species (Figure 6.3). The fish offer was significantly lower in *Remote* than in the other groups, as well as waterbuck zebra, cane rat, bushbuck eland and impala. By contrast, we did not find significant differences for duiker, buffalo and sable.

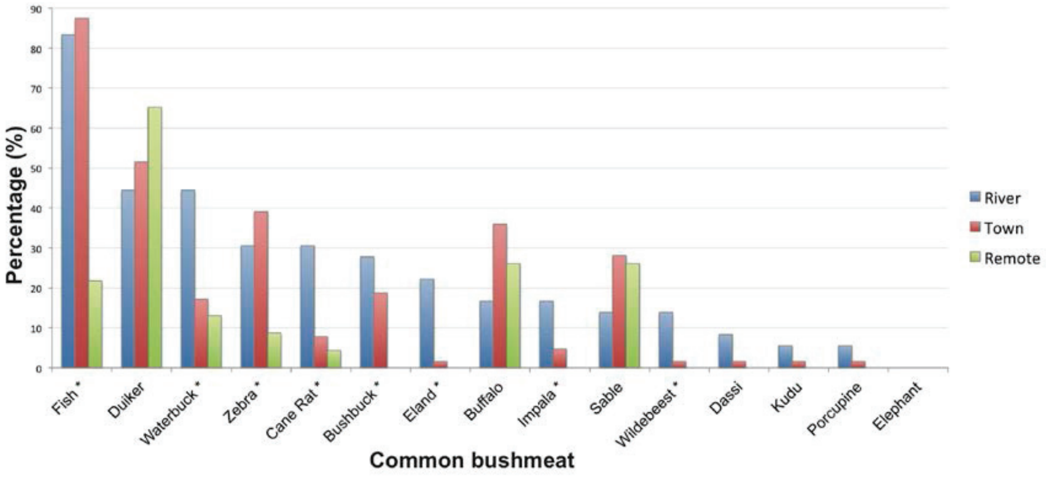

Figure 6.3 - Proportion of the most common bushmeat in the 3 groups
* indicate when the bushmeat had significant effect with the Group covariate (glm, test=χ^2,*p*<0.05)

C2.2 - Temporal constraints

Overall, the availability of fish and bushmeat was greater during the dry season, from May to September (Figure 6.4). When investigating contrasts between fish and bushmeat availability within groups, we found no difference in the distribution except for *River* (χ^2=26.59, df=8, *p*<0.001), where bushmeat availability increased more than fish at the end of the dry season.

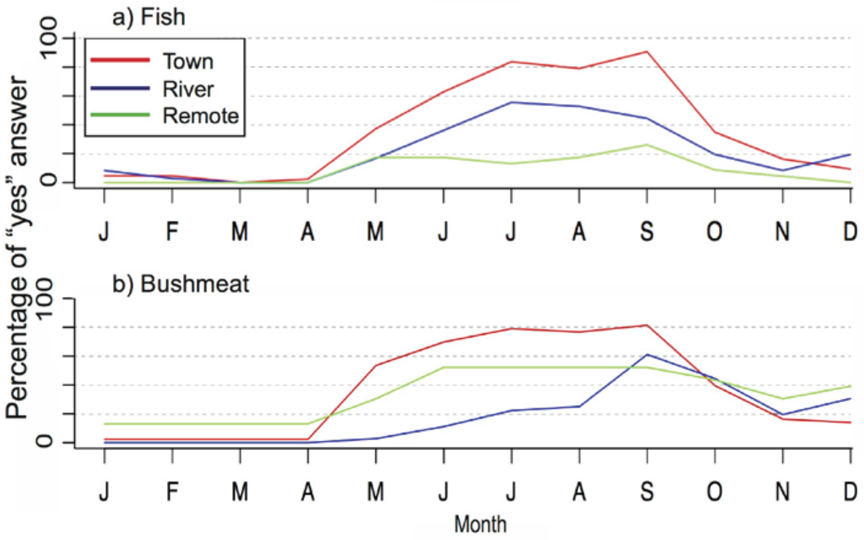

Figure 6.4 - Fish and bushmeat availability over the year

Further, the changes in availability of bushmeat were contrasted between groups (χ^2=62.71, df=16, p<0.001) with a higher availability for Town early in the dry season compared to the two other groups. In the wet season, the Remote group had the highest availability of bushmeat. There was no significant difference between groups in the seasonal changes in fish, with a consistent higher availability for Town compare to River and for River compare to Remote group.

C2.3 - Economic buffer to protein access

We investigated in more details how incomes influenced the access to wild protein (Figure 6.5). PC1 of the MCA accounting for 26% of the total variance opposed households mostly relying on fishing, selling resources and general selling activities to those who did not. PC2 of the MCA accounting for 20% of the total variance opposed households consuming fresh and dry bushmeat each week to those who did not. We represented our 3 groups as an illustration on the first 2 axes of the MCA. Along the PC1, River group was associated with several income activities, especially fishing and selling resources, and was opposed to Town and Remote group. River group also correlated with fresh fish consumption in opposition to the 2 other groups who did not. Remote group was more correlated with fresh and dry bushmeat consumption. The consumption of fish appeared related to income sources. Conversely, bushmeat appeared disconnected from any incomes as it was positioned orthogonally to all income sources in the MCA.

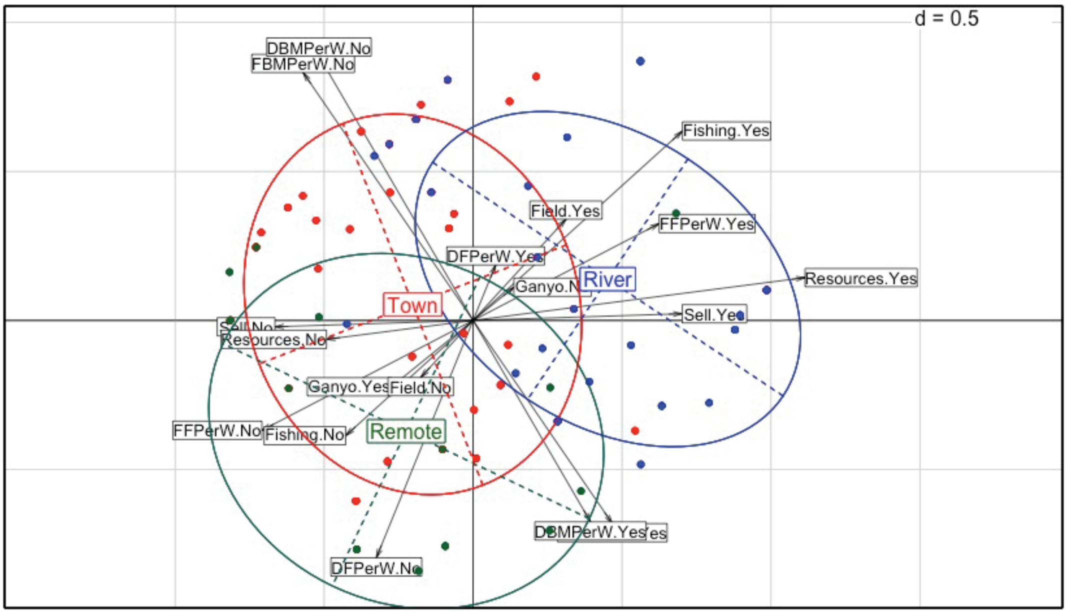

Figure 6.5 - Multiple-Correspondence-Analysis between incomes and wild protein access (n=111)

To refine these results, we tested the probability to reply "yes" to wild meat (fresh and dry) consumption each week according to the various income sources recorded (as in Figure 6.2) on the one hand and trading on the other hand (Table 6.2). The probability to consume fish increased with the income sources such as fishing, honey production, selling natural resources transformed or not, *ganyo* and selling in general. In contrast, the increase in the probability to consume bushmeat was associated with trading and poorly explained by the access to income sources, except weakly by honey production.

Table 6.2 - Activities influencing the probability of answering "yes" to wild meat consumption

Covariate	Significant income (glm, test= χ^2, $p<0.05$)			
Dry bushmeat per week	Honey (Estimate=1.21, SE=0.68, *p*=0.07)		Trade (Estimate=1.06, SE=0.39, *p*=0.007)	
Fresh bushmeat per week	Trade (Estimate=0.83, SE=0.39, *p*=0.031)			
Dry fish per week	Fishing (Estimate=1.60, SE=0.65, *p*=0.014)		*Ganyo* (Estimate=1.38, SE=0.65, *p*=0.035)	
Fresh fish per week	Fishing (Estimate=2.77, SE=0.54, *p*<0.001)	Honey (Estimate=1.07, SE=0.62, *p*=0.08)	Resources (Estimate=1.22, SE=0.44, *p*=0.006)	Sell (Estimate=0.77, SE=0.37, *p*=0.04)

C2.4 - Preferences

Interviewed households preferred meat (87%) to fish (with no *Group* effect), and domestic meat (82%), here goat and chicken, rather than bushmeat. All respondents mentioned higher preferences for fresh (94%) than dry bushmeat. The same applied for fish, with households in Town and River groups preferring fresh (100% and 86%, respectively) to dry fish in contrast to *Remote* (26%; χ^2=47.2, df=2, *p*<0.001). Fresh and dry fish were never mentioned as preferred *caril* (Figure 6.6), whereas goat was the most preferred *caril*, except for *River* households who mentioned fresh bushmeat (χ^2=8.94, df=2, *p*=0.011).

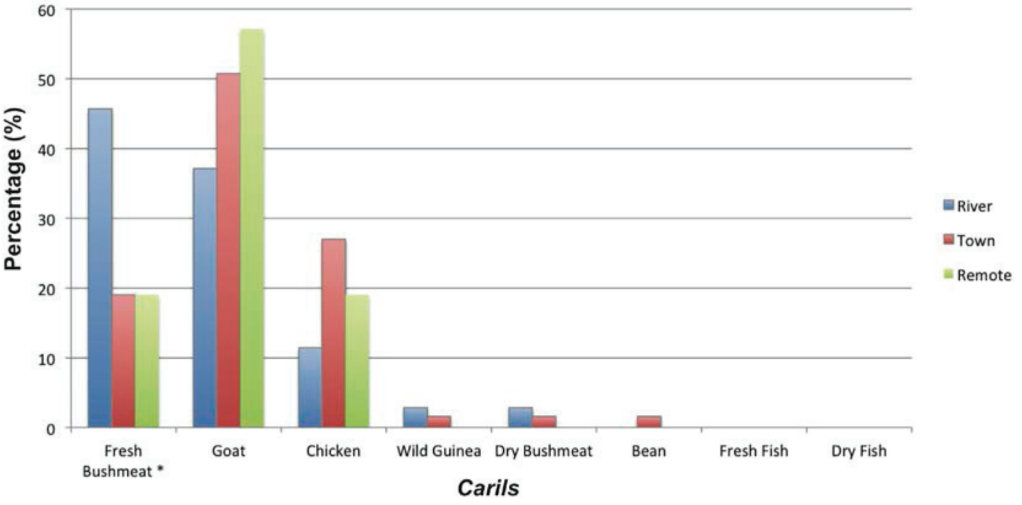

Figure 6.6 - Percentage of households mentioning preferred carils in the 3 groups answering to a closed-ended list

* indicate when the *caril* had significant effect with the Group covariate (glm, test=χ^2, p<0.05)

C3 - Food security

When answering to the question "do you have food supply problem?", 60% of the households replied "yes". The best model to explain the probability of mentioning food security problems included the *Group covariate*, the number of months with secured crops and the *ganyo* income (Table 6.3).

Table 6.3 - Factors affecting the probability to reply "yes" to the question "do you have food supply problem?" (glm, modalities marked "Int" used as references)

Parameters	Resid . df	Deviance	Resid. Dev	*P*-values	Modalities	Estimates	SE	*p*
Intercept	103		137.61			2.899	0.90	***0.001***
Group	101	33.755	103.85	<0.001	Town^{Int}			
					Remote	-0.691	0.59	0.248
					River	3.246	1.11	0.003
Income *Ganyo*	100	5.669	98.18	0.017	No^{Int}			
					Yes	-1.343	0.54	0.013
Months secured	99	15.923	82.26	<0.001		-0.3739	0.12	0.002

Figure 6.7 illustrates the outputs of the model described in Table 6.3 as a function of the number of months with secured crops. For a better reading we fixed the income *Ganyo* variable at "No". River group had the highest probability to mention food supply problem as almost 100% of the interviewees in River group said "yes", and even with 12 secured months of crops the probability remained as high as 60%. The probability to mention food supply problem was higher in the Town than in the Remote group and dropped considerably from around 75% to 10% of "yes" when increasing from 0 to 8 secured months of crops.

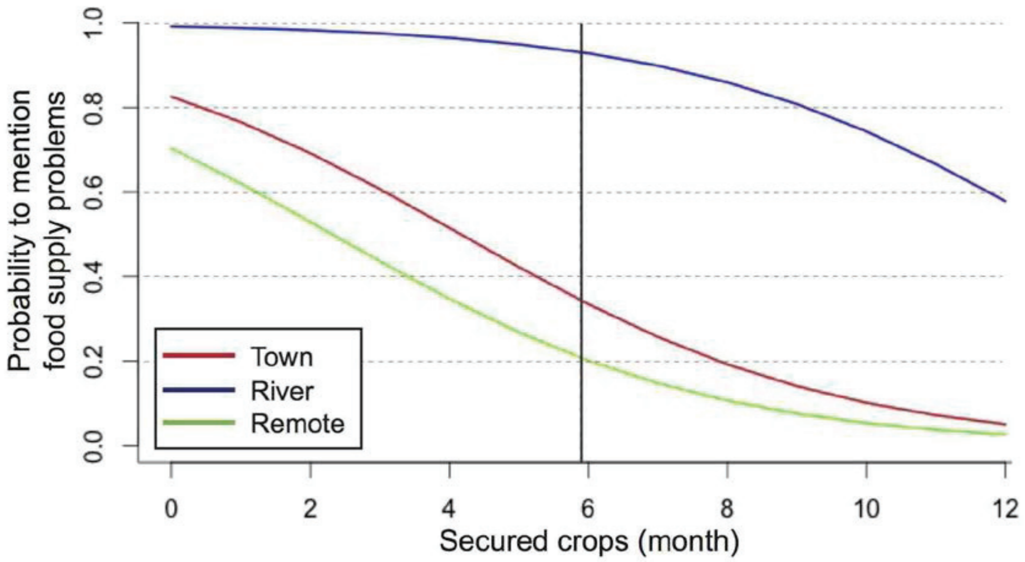

Figure 6.7 - Probability to answer "yes" to the question "do you have food supply problem?" in relation with the number of months with secured crops
Black line represents the mean number of months with secured crops for the 123 households

We investigated the factors influencing the number of secured months with enough crops to ensure adequate food supply (Table 6.4). There was no *Group* effect influencing the number of secured months of crops. The number of secured months increased with field turnover. People perceiving soil fertility and manpower as the main reasons for insufficient harvest were those with the fewest number of secured months of crops. Those mentioning wildlife damage had a number of secured months close to the average value of all interviewees, whereas those mentioning climate had the highest number of secured months.

Table 6.4 - Linear contribution of the parameters modelling the number of months with secured crops (lm performed separately for the two parameters and estimates calculated for each modality used as reference)

Parameters	$F_{df,res}$	r^2	*P*-values	Modalities	Estimates	SE	*p*
Perceived reasons for insufficient harvest	$F_{3,52}$=4.68	0.17	0.006	Climate	7.80	0.78	<0.001
				Wildlife	5.81	0.54	<0.001
				Manpower	4.80	0.78	0.008
				Fertility	4.20	0.63	0.4
Field turnover	$F_{1,101}$=15.58	0.13	<0.001	No	5.29	0.28	<0.001
				Yes	7.29	0.42	<0.001

In the dry season, 5.6% of respondents in the River group mentioned having enough food against 33.9% and 34.8% in the Town and Remote groups, respectively (χ^2=10.79, df=2, *p*=0.005). Proportions were higher for the wet season with 34.3%, 54.2% and 60.9% in River, Town and Remote respectively, with only a tendency for a significant difference (χ^2=4.96, df=2, *p*=0.08).

C4 - Perception toward living in a protected area

Sixty-nine percent of the households found a benefit to live in a protected area (Table 6.5). Households from the River group found more benefits to live in the NNR compare to those from Remote and Town groups. River group mentioned more benefits from natural resources compare to Town and Remote group. Eighty-seven percent of the households had a good feeling about the NNR entity.

Respondents from the River group perceived that it was easier to secure food living in the protected area in opposition to Remote group. We identified three significant different objectives perceived by the groups for the meaning of NNR. River group had a "protection" feeling about the NNR objective. A "conservation" feeling was observed in Remote group and a feeling of "keeping the wildlife" was observed in Town group. When asked if people and wildlife can live together, 98% of the households replied "no" but 94% replied that it was necessary to protect the wildlife.

Answering to "how to solve food problem?", the River group perceived a necessity to increase fishing activity compared to Remote group for which it was necessary to increase farming activity. Town group perceived other alternatives to solve food problem such as economic activities (e.g. Sell, *Ganyo*). When asked "who can solve food problems?" 91.12% of the interviewed households cited tribal authorities to resolve food problem rather than government. The households never cited the NNR entity.

Table 6.5 - Summary of the groups perceptions regarding NNR entity, food security and wildlife

	Perceived factor	Town	River	Remote	Statistical test
NNR Perception	Benefit to live in NNR	55% of "yes"	93% of "yes"	67% of "yes"	$\chi^2=12.25$, df=2, $p=0.002$
	Kind of benefit	Other	Natural resources	Other + Natural resources	$\chi^2=35.61$, df=4, $p<0.001$
	Feeling about NNR entity	8% bad	6% bad	39% bad	$\chi^2=16.74$, df=2, $p<0.001$
	NNR entity objective	"Keep"	"Protect"	"Conservation"	$\chi^2=15.98$, df=2, $p=0.003$
Food security perception	Easier to secure food in NNR	65% of "yes"	86% of "yes"	36% of "yes"	$\chi^2=14.66$, df=2, $p<0.001$
	How solve food issues	Other	Fishing activity	Farming activity	$\chi^2=14.09$, df=4, $p=0.007$
	Who can solve food issues	91% cited tribal authorities			-
Wildlife perception	People and wildlife together	98% of "no"			-
	Important to protect wildlife	94% of "yes"			-

D - DISCUSSION

D1 - Limitation of the study

The stratified random sampling used for household selection covered slightly less than 10% of the households currently in our study area. This low sampling effort mainly results from the logistical constraints associated with the vast area and poor communication network. We chose to aggregate the villages into three groups to cater for the heterogeneity in village samples, but we grouped them in order to better suit one of the aim of our study, which was understanding the heterogeneity in geographical determinants of human impacts on wildlife and natural resources within NNR. As we managed to identify some major geographical differences through the group effects, it seems that this choice proved efficient in investigating the assumed spatial heterogeneity, despite the initial low sampling intensity in some villages. For logistic reasons and to match with the geographic boundaries of the 'Niassa buffalo project' that funded the study, we did not survey the western part of the RNN which hosts around 40% of the human population. The western area is ecologically different from the rest of the NNR (cf. Chapter 3) with the highest rainfall and different land cover types which may induce differences in the farming production. It also harbors the highest human population densities as well as the lowest wildlife population densities (Begg and Begg 2011). Interactions between communities living within the western half of the NNR and the ones in the other half are limited, partly due to the very limited road network (Cunliffe et al. 2009). Thus, our results may be considered as only representative of the communities living in the central and eastern part of the NNR.

Some variables used in our analyses were qualitative and issued from analyzing open answers in semi-structured interviews, which led us to categorize a posteriori some of the responses. Consequently, our results could be partly influenced by the interpretation of these responses. As substantially argued, qualitative analyses are always liable to some subjectivity (Drury et al. 2011; Guerbois et al. 2013). However, we also tried to be systematic by including and testing all covariates in our analyses, hence testing for the robustness of our conclusions through convergent results. Having lived for three years within the NNR we believe our assessment is meaningful regarding the local context. If quantitative analyses have often been used in social sciences surveys, the use of qualitative approaches can significantly complement and enhance such analyses because issues are then actively explored and confronted instead of addressing problems through standardization (Drury et al. 2011).

Finally, the interviews conducted may not be optimal to depict the effect of human activities on mammal populations within NNR. More questions about human practices and bushmeat consumption may be envisaged. However, the objective here was to get a broad overview of the functioning of Niassa socio-ecological system without creating reluctance of the local people toward scientific approaches. This study is thus a first step to the understanding of human-wildlife interactions and household livelihoods within NNR.

D2 - The contrasted contribution of wildlife and natural resources use in Niassa National Reserve

D2.1 - Living in NNR

The main livelihood activity in NNR is subsistence farming and communities are characterized by a high degree of poverty and food insecurity. Households are only able to secure six months of crops per year on average and we observe a small proportion of livestock owners (15% owned goats; 44% owned chicken; no cattle). The long dry season, the low soil fertility and the presence of the tsetse flies (*Glossina spp*.) constitute major constraints to human livelihood within NNR. In rural areas, bushmeat is often an important alternative source of meat from livestock, particularly where tsetse flies are prevalent (Barnett 1998). Further, the low labor forces at household level, the poor education level and the increasing crop raiding events by elephants and meso-herbivores can be considered as environmental presses that may amplify the food security issue. As the decrease in livestock and agricultural production are often associated with increasing reliance on wild resources for food (Brashares et al. 2004), this situation may compromise the Reserve conservation objectives.

Income-generating activities are an important part of the households production system. We observe strong spatial variations in sources of incomes which are mainly determined by the access to rivers and natural resources. Households in the River group have on average more diverse sources of incomes than those in the two other groups and fishing constitutes the main activity. Only few incomes are performed in the Remote group which relies more on selling activities (i.e. sell resources and services). The diversification of incomes is recognized as an important strategy to improve households' standard of living (Niehof 2004). In the Town group, activities related to services (e.g. *ganyo*) constituted most incomes and reflect the development of the tertiary economy within NNR. This tertiary economy seems mostly promoted by the production sector based on the use of natural resources.

D2.2 - The role of natural resources

Livelihoods in NNR are characteristically reliant upon natural resources. In addition to the use of natural resources such as shelter and fuel for cooking (in the form of firewood), they have an important place in the diet (i.e. fish and bushmeat) and the sources of income. Among the incomes mentioned by our interviewees, 60% of them were related to natural resources. Hence, activities such as shifting cultivation and the consumptive use of wildlife resources tend to act in direct opposition to stated conservation goals of the Reserve.

Shackleton (2007) estimated that the direct-use value and income generation from natural resources contribute roughly to 20% of the total household income in savanna regions of southern Africa. Our results suggest that this value is likely to be higher for people living inside NNR. Natural resources also serve as "safety nets" for rural households during times of hardship precipitated by shocks, such as crop failure and natural disasters (Shackleton and Shackleton 2004; Paumgarten 2005; Hunter et al. 2011). Hence, because of their direct and indirect effects on the environment, accounting for people dependences on natural resources in the NNR future management plan may be crucial for ensuring proper conservation of biodiversity.

D2.3 - Contribution of wildlife to food security

Our results show that wild meat (i.e. fish and bushmeat) is an important source of protein in the households diet. The spatial location of households affects the wild meat consumption and the source of animal protein is mainly fish for River and Town groups compared to the Remote group which relies mainly on bushmeat. Another survey in NNR revealed that 86% of the interviewed people (n=1128 individuals in 34 villages) had eaten fish and 47% bushmeat at least once in the past week (Begg and Begg 2011). Among bushmeat, a wide variety of species is available in NNR and differs spatially as riverine species such as waterbuck is common in River group and ubiquitous species such as duiker, buffalo and sable are common in Remote group. This spatial heterogeneity may also have a high impact on conservation objectives. Interestingly, while the consumption of fish was related to incomes (i.e. incomes fishing, honey production, selling natural resources transformed or not, *ganyo* and selling in general), we did not find any evidence of income activities related to bushmeat. However, bushmeat consumption appeared more related to trading activity. Hunting is illegal in the NNR and thus bushmeat is part of an informal economy. Domestic meat protein is scarce and expensive and bushmeat is more readily available and cheaper in NNR (Begg and Begg 2011).

Wildlife in NNR is also responsible of crop destruction which is the second cause perceived for insufficient harvest (Table 6.4). In Town group, because of the high human density, people are farming far from the household and cannot actively protect their fields at night resulting in a higher perceived level wildlife impacts, hence more conflict with wild animals.

D3 - Human impacts on wildlife and natural resources

Human activities in NNR have direct impacts on wildlife populations through hunting and fishing activities and indirect effects on ecosystem due to the modification, fragmentation and transformation of habitats. Further, it appears that poorer households consume more bushmeat in NNR because it provides a cheap and accessible source of food. However, our results illustrate that these impacts can differ spatially and temporarily.

D3.1 - Fish and bushmeat consumptions

Whilst it seems clear that humans have direct impacts on wildlife population dynamics through harvesting fish and hunting (mainly snaring), it is difficult to estimate the amount of fish caught every year and so is the level of off-take of bushmeat in NNR. Given the number of meals accompanied with fish and/or bushmeat, the impacts may not be insignificant for wildlife populations (cf. Box). High densities of fishing camps are found within the NNR along the Lugenda river (Begg et al. 2005) but due to a lack of data on the perennial rivers it is difficult to evaluate the fish stock available in the Reserve. Fish mainly composes the main contribution to animal protein in the diet especially in River and Town groups.

Hunting and fishing are seasonal activities reflecting both seasonal ability to perform the activities and seasonal variations in agriculture labor requirement. The slack period in agriculture is in the dry season (i.e. May to mid-November). During this period, the flow of the perennial rivers allows fishing activities. Furthermore, mostly because animals are constrained by the water available, hunting activities are more efficient during the dry season. Our results illustrate that the availability of bushmeat and fish occur mostly in the dry season, from May to September, with spatial differences in availability between groups. The availability of fish and bushmeat is higher for Town group in the early dry season and may be the result of market accessibility. River group has a high availability of bushmeat in the late dry season. At this time, fishing activities are on going and come to an end and may let more time to hunt. Households in the Remote group are far from a river and with difficult access to transport and market. They clearly rely on bushmeat and present the highest bushmeat availability in the wet season.

Box - Estimation of bushmeat consumption per year in Niassa National Reserve with a focus on buffalo bushmeat

Around 39,000 local residents live today inside the NNR. The average household size is 6 ± 2.4 individuals which gives us an estimate of 7,300 households living within the protected area. One portion of bushmeat weights on average 250g and feeds a household for a meal (Begg 2011). Given that bushmeat is available mostly from May to September (i.e. 20 weeks) and is eaten on average 1.91 ± 1.83 times per week per household then the amount of bushmeat is 69,715 ± 66,795 kg of meat. **This is 70 tons of bushmeat taken out of the bush between May and September.** Among the households interviewed, buffalo meat was the most common bushmeat in 28% of the cases. This represents around 20 tons of buffalo bushmeat. If we consider that an adult buffalo cow with a weight of 450-680 kg gives a deboned meat yield of 170-220kg (Grobler 1996), 20 tons of **buffalo meat represent around 103 adult buffalo cows**.

This is a raw estimation of the bushmeat consumption in NNR but it illustrates the strong potential impact on wildlife. The last buffalo census in NNR estimated the population to 6200 buffaloes (Craig 2012). The buffalo meat consumption represents almost 2% of the population each year. With the hunting techniques used (i.e. mostly snaring), untargeted sex/age individuals are killed which may influence greatly the impacts on the wildlife population.

D3.2 - People livelihoods and fires

Fishing and hunting activities as well as several other income-generating activities may have indirect impacts on wildlife populations. Human activities may for instance change fire regimes, through their seasonal occurrence, frequency, spatial pattern and intensity, and the human and ecological consequences of these changes are likely to vary according to which fire parameters have been affected (Kamau and Medley 2014). More than 50% of the NNR burn every dry season (cf. Chapter 3). Our results illustrate the importance of natural resources and markets (selling variables) in the households' production system and these activities induce people movements within Niassa. Hence for several reasons, villagers in Niassa use bushfires to fulfill their activities. For safety issues, people burn because it is easier to spot a dangerous animal and it is easier to walk in a burnt area. Moreover, fishermen burn because it is easier to travel with their bikes carrying large and heavy baskets of dry fish. Honey hunters use long sticks of dry grass to smoke out bees and then they throw the burning sticks which may generate important bushfires. Poachers burn to track animals and to easily identify their movements and set snare lines. Last, because of their agricultural techniques, farmers burn new fields but fire often propagate. As fertility is perceived as the main constraints to agricultural production and field turnover perceived as increasing crop production, the pressure for lands dedicated to agriculture is likely to increase. In the dry season, a fire can propagate for days and may impact wildlife populations significantly (e.g. through the reduction in dry forage quantity), which are already under strong environmental pressure at this time of the year. Potentially, regarding the various income sources associated groups, River group may have the highest direct and indirect impacts on wildlife populations.

D4 - Implications for NNR management

The NNR system presents a panel of socio-ecological constraints including a long dry season, poor soil fertility, a prevalence of tsetse flies, human encroachment and human wildlife-conflicts, resulting in food security problems. In such systems, natural resources play a significant role in the households' livelihood.

Households in NNR are mostly non-livestock owners and show a preference for domestic meat rather than wild meat (i.e. bushmeat). Domestic animals are often perceived as savings or insurance against illness or disasters (Milner-Gulland and Bennett 2003) but they also are a secure protein source in the diet. But domestic meat protein is scarce and expensive and bushmeat is more readily available and cheaper in NNR (Begg and Begg 2011). However, the rarity of domestic meat needs to be considered in our understanding because it may bias our results as interviewees often have a tendency to mention scarce items (Golden et al. 2013). Moreover, households show a preference for meat compared to fish. Because domestic meat is rare managers need to be aware that the emergence of a commercial bushmeat subsidiary is not negligible. Although the level of pressure on wildlife may not be threatening yet, it is necessary to understand why people eat bushmeat, and the roles its consumption play within a household (e.g. low price, preferences (based on taste or culture), prestige factors). Understanding why these patterns exist is important when developing policies intended to alter bushmeat consumption (Schenck et al. 2006). In Serengeti ecosystem, for example, the combined effects of human population growth, poverty and lack of cheap alternative sources of protein have accelerated illegal off-take of wild meat (Ndibalema and

Songorwa 2008). Fish mainly composes the proportion of animal protein in diet and we advocate the necessity to assess fishing activities in NNR as previous studies have shown that years of poor fish supply coincided with increasing bushmeat demands (Brashares et al. 2004; Wilkie et al. 2005).

Managers need to understand people's relationships with their environment, and incorporate these knowledge, experiences and attitudes into decision-making, planning and implementation processes (Leach et al. 1999). Households in NNR mention that they cannot live with wildlife but they want to protect it and cultural factors strongly influence people's willingness to tolerate wildlife (Woodroffe 2000). The most widespread conflicts involving people and wildlife are crop raiding, livestock depredation and killing of people (Woodroffe et al. 2005). Many 'conflict' species (e.g. elephants, large carnivores) are also keystone species and lethal techniques (i.e. killing the pest) can only be considered as solutions in extreme cases. In NNR, conflicts may differ spatially (e.g. fields in Town group are far from households and cannot be protected at night; important wildlife conflict associated to the riverine ecosystem for the River group) and the problem can be addressed only through an adaptive management approach. It is essential to bring local people into the process of solving conflict by taking responsibility for the human-wildlife conflict problems. However, for managers with a goal of not drawing people to settle inside the NNR, to invest considerable effort to solve human-wildlife conflicts is not necessarily the best option as they also act as regulators.

Niassa National Reserve is to our knowledge the only protected area including native residents and there is no doubt that the human population within NNR has a huge direct and indirect impact on wildlife population. Our analysis illustrated that human activities and attitudes toward wildlife and conservation differ spatially (i.e. with geographical situation of villages). Managers need to consider both the heterogeneity in human impacts but also this heterogeneity in attitudinal profiles. Profit-thinking profile seem to be nearest to rivers, where the environment seems more 'profitable'. Business center referring to the Town group developed alternative sources of incomes however this kind of land-use (urban center surrounded by fields) may also increase crop raiding susceptibility hence conflict with wildlife. Our analysis suggested that the strong spatial heterogeneity of our groups is also linked to their degree of reliance on natural resources and their perception of it. Managers also need to identify differences between use of resource and dependence on it. Close monitoring of reserve-people interactions should be carried out to ensure that local people's actual use of natural resources does not compromise the biological conservation objectives of the reserve and that opportunities for considering local people's interests and needs are not ignored (Stræde and Treue 2006).

Local populations within NNR must also clearly identify their interests for working with the managers toward coexisting with wildlife, their objectives and range of actions. Our results illustrate that when it comes to who can solve (and how) the food problems, the managing company is never mentioned. Complex histories of resource use and land dispossession, combined with preservationist conservation policies, have perpetuated the negative associations local people have with protected areas (Twyman 2001). However, our results illustrate that local people are happy to live within NNR, thus managers should involve local people in a range of activities and developments surrounding conservation and NNR. Furthermore, local populations may need to accept the costs of coexisting with wildlife and managers must recognize the conversion of wildlife areas into other uses to make conservation programmes self-sustainable in NNR.

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7

DISCUSSION GENERALE

A - RESUME DES PRINCIPAUX RESULTATS

Comme évoqué en introduction de cette thèse, les facteurs responsables des faibles densités de buffles observées sur la RNN peuvent être classifiés selon une approche ascendante (approche "bottom-up"), lorsque la population est contrôlée par la ressource, ou une approche descendante (approche "top-down"), lorsque la population est contrôlée par les prédateurs et les agents pathogènes (cf. Chapitre 1 - Figure 1.2). Bien que de nombreux chasseurs locaux nous aient indiqué qu'il y avait "beaucoup plus" de buffles dans la RNN avant les 25 années de guerre pendant lesquelles les populations animales de la RNN diminuèrent fortement, nous ne disposions que de très peu d'informations historiques sur la faune et la flore de la RNN et en trois ans passés sur le terrain, il nous était impossible d'investiguer tous les facteurs potentiellement responsables de la faible densité de buffles. Nous avons donc décidé de focaliser nos protocoles sur les contraintes dans l'approvisionnement en ressources et aux stratégies d'utilisation de l'espace de la population de buffles ainsi qu'aux impacts directs et indirects de la prédation humaine. Nous avons néanmoins collaboré au cours de ce projet à apporter des éléments de réponses aux autres facteurs susceptibles d'impacter la population de buffles de la RNN que nous discuterons ici.

Pour répondre à la question centrale de cette thèse nous avons suivi le déplacement de 9 troupeaux de buffles au moyen de 33 colliers GPS. En raison d'une faible connaissance de l'environnement à l'initiation du projet, un important travail de collecte de données environnementales a été réalisé, qu'il s'agisse d'un travail de terrain afin de réaliser une cartographie de la végétation de la RNN, d'identifier l'eau disponible en saison sèche, ou d'un travail de récupération et de traitement de données satellitaires (production primaire avec l'indice NDVI, pluviométrie, feux de brousse).

Nous avons cherché dans un premier temps, à partir des données de comptages aériens disponibles sur 10 ans et des données environnementales nouvellement générées, à évaluer les grandes contraintes structurantes de la distribution spatiale de la communauté d'herbivores de la RNN, à une période clé, la fin de la saison sèche, période à laquelle la ségrégation spatiale des ressources est maximale. Cette étude nous a notamment permis de mettre en évidence l'existence d'un gradient longitudinal fort au niveau des covariables environnementales entre la zone Centrale et la zone Est de la RNN. Le long de ce gradient les populations d'herbivores sont soumises à des contraintes plus ou moins marquées en saison sèche et sont donc susceptibles d'adopter des stratégies d'utilisation de l'espace différentes en fonction des zones considérées. Il nous est apparu important de ne pas focaliser cette première analyse uniquement à la population de buffles mais de considérer l'ensemble de la communauté d'herbivores afin d'identifier si les espèces étaient susceptibles de répondre différemment aux contraintes environnementales en fonction de leurs caractéristiques écologiques (i.e. masse corporelle et susceptibilité à la prédation, stratégie alimentaire et besoin de s'abreuver, mobilité, organisation sociale). La distribution de la population de buffle était, quant à elle, fortement contrainte à cette large échelle d'analyse par l'eau disponible et répondait également aux types d'habitat ainsi qu'à l'indice de production primaire (i.e. NDVI).

Nous avons ensuite caractérisé les domaines vitaux des 9 troupeaux suivis, à l'échelle annuelle ainsi qu'à l'échelle saisonnière. Tous les troupeaux présentaient des tailles de domaines vitaux parmi les plus grandes jamais enregistrées chez le buffle du Cap. Ces troupeaux présentaient un mouvement migratoire en début de saison sèche, particulièrement les troupeaux de la zone Est, qui ont tous établi leur domaine vital le long de la rivière pérenne Lugenda qui semble, dans cette zone, être la seule source d'eau disponible à cette période. Bien que des mouvements migratoires aient été observés chez les troupeaux de la zone Centrale, ces derniers étaient moins marqués qu'à l'Est. Nous avons pu établir que ces mouvements migratoires étaient réalisés, entre la saison des pluies et la saison sèche, lorsque environ 10% de la surface du domaine vital annuel étaient brûlés et, entre la saison sèche et la saison des pluies, lorsque 10 mm de pluie cumulée étaient tombés dans la surface du domaine vital annuel. Excepté un troupeau dans la zone Centrale qui a établi son domaine vital annuel le long de la Rivière Lugenda (i.e. troupeau n°11), les autres troupeaux de cette zone n'utilisaient jamais la Lugenda et se satisfaisaient de poches d'eau stagnante présentes dans le lit des rivières secondaires ainsi que de trous d'eau naturels en saison sèche. Dès l'arrivée des premières pluies, ce qui correspondait à la levée de la contrainte "eau" pour les buffles, les troupeaux effectuaient une migration inverse pour se rendre dans des zones où la qualité et la quantité de fourrage devaient être plus propices à satisfaire leurs besoins alimentaires journaliers. En raison d'une migration moins marquées par les troupeaux de la zone Centrale en saison sèche, ces derniers présentaient des tailles de domaine vitaux globaux inférieures en moyenne à ceux de la zone Est. Les troupeaux de la zone Est présentaient des tailles de domaines vitaux plus faibles en saison sèche qu'en saison des pluies, probablement en raison de la forte contrainte spatiale dans la zone Est en saison sèche, où la Rivière Lugenda constitue la seule source d'eau disponible. Ce trait n'était pas ou peu observables chez les troupeaux de la zone Centrale, probablement en raison des sources d'eau plus dispersées dans le paysage qui leurs permettaient de couvrir une plus grande surface afin de satisfaire leurs besoins alimentaires. Un résultat intéressant de nos analyses, et qu'il nous est encore difficile d'interpréter, est qu'aucun troupeau n'a traversé la Rivière Lugenda en saison sèche. A partir du milieu de la saison sèche, cette rivière est peu profonde (de 50 cm à 1 m) et donc potentiellement traversable facilement par un troupeau de buffles. Le lit de la rivière est quant à lui supérieur à 500 m de large en moyenne (pouvant atteindre jusqu'à 1 km de large dans la zone Est par endroit). Même en fin de saison sèche, lorsque la ressource était fortement ségrégée, aucun troupeau n'a entrepris de traverser cette rivière qui agissait comme une véritable frontière naturelle. En raison d'un faible recouvrement spatial observé entre les domaines vitaux des troupeaux adjacents, il est possible que l'utilisation des ressources soit fortement contrainte par un comportement d'évitement entre troupeaux (e.g. Prins 1996).

Nous nous sommes ensuite intéressés aux patrons de sélection de l'habitat de nos 9 troupeaux à l'échelle saisonnière sur 6 saisons consécutives (i.e. 3 saison des pluies et 3 saisons sèches). Au travers de cette approche nous avons pu examiner l'incidence de la distance à l'eau, de la production primaire, des types d'habitat, des distances aux villages et aux routes, et des feux de brousse sur les stratégies d'utilisation de l'espace des buffles. En saison sèche comme en saison des pluies, les buffles ont exprimé une sélection pour les types d'habitat ouverts (i.e. prairie, *miombo* ouvert et *miombo*) se trouvant à proximité des rivières (ou des trous d'eau naturels en saison sèche). Les buffles ont également montré une sélection pour les types d'habitat présentant une forte production primaire (i.e. NDVI élevé). En saison sèche, notre analyse a montré que les feux de brousse influençaient fortement les patrons de sélection de l'habitat et une semaine après le passage d'un feu il était quasiment trois fois moins probable de trouver un buffle sur un type d'habitat. Deux mois après le passage d'un feu, la probabilité de trouver un buffle dans un type d'habitat était quatre fois plus faible que sur un habitat non brûlé. Nos résultats ont également montré que près de 50% de la RNN brûle chaque année. En plus d'un évitement important des zones brûlées, les feux réduisent de manière considérable la quantité de fourrage disponible à la population de buffles en saison sèche. Contrairement à notre hypothèse initiale, nos analyses n'ont pas suggéré un fort évitement des villages et routes par les buffles de la RNN en général, mais les résultats sont contrastés en fonction des troupeaux. A cette échelle d'analyse (study design 3 Thomas and Taylor 2006) et compte-tenu du manque de données spatiales détaillées sur les activités humaines, il n'est pas surprenant que les analyses ne nous permettent pas de conclure finement quant au dérangement possible de la population humaine sur la population de buffles, à moins d'effets extrêmement marqués. Par conséquent, le dérangement ne doit pas être considérable, et les effets potentiels sur les buffles doivent être associés à d'autres mécanismes.

L'absence d'effets marqués à l'échelle des domaines vitaux doit être confrontés aux résultats des enquêtes de terrain auprès des villageois. En effet, sur la base de questionnaires réalisés dans des villages contrastés de part leur localisation géographique et le nombre d'habitants, nous avons pu mettre en évidence un impact direct et indirect de la population humaine sur la population de buffles. Ces questionnaires ont également permis de réaliser une description socio-économique des foyers au sein de la RNN ainsi que leur niveau de dépendance aux ressources naturelles. Nos analyses ont montré que la viande de brousse, et notamment celle du buffle, était une part importante de la consommation de protéines des foyers. Nous avons estimé qu'une centaine de buffles étaient prélevés illégalement sur la RNN chaque année, ce qui ne devrait suffire à limiter la population de buffle. Nos résultats ont également illustré des différences significatives dans les moyens de subsistance des foyers en fonction de leur localisation géographique dans la RNN (i.e. business center, villages le long de la rivière et villages excentrés) ainsi que des différences au niveau de leur perception, qu'il s'agisse des conflits avec la faune, de l'entité Réserve Nationale ou encore de la société gestionnaire de la RNN.

Comme nous l'évoquions ci-avant, notre étude a également contribué à apporter des éléments de réponses à plusieurs facteurs susceptibles d'être responsables de la faible densité de buffles observée sur la RNN mais qui n'ont pas fait l'objet du cœur de notre thèse. Tout d'abord, pour ce qui est de l'impact des pathogènes (i.e. maladies), les différents échantillons de sang que nous avons collecté ont été analysés à Maputo (Mozambique) par un vétérinaire mozambicain. Ses travaux se sont focalisés sur la tuberculose bovine, la brucellose bovine, la theilériose bovine et la fièvre aphteuse. Bien que présentant une prévalence élevée pour la fièvre aphteuse, les résultats de ces analyses ont montré que la population de buffles de la RNN était saine et que les pathogènes ne pouvaient être responsables d'une forte mortalité ou d'une réduction de fécondité de la population de buffles (Branco 2014). Enfin, les échantillons de peau prélevés dans la RNN ont été transmis à une étudiante en doctorat dans le cadre de ses travaux sur la génétique du buffle au niveau du continent africain. Ses résultats ont permis d'écarter l'hypothèse d'un goulot d'étranglement démographique dans lequel se trouverait la population de buffles de la RNN. Ses résultats indiquent que les buffles de la RNN sont génétiquement sains. En ce qui concerne la prédation naturelle par le lion, les données suggèrent des effets plus conséquents. En effet, les résultats du "Niassa Carnivore Project" indiquent une densité de lions adultes de 2.2 individus au 100 km^2 sur la RNN (Begg and Begg 2011). Dès que nous avions l'information qu'un buffle avait été prédaté par un lion, nous nous sommes rendus sur place et avons transmis ces données, si elles étaient exactes, à l'équipe afin de participer à la récolte de données quant aux proies préférentielles des lions. Leurs résultats indiquent que le buffle apparait en quatrième position des proies préférentielles des lions sur la RNN et qu'ils contribuent à 12% des proies prélevées par les lions par an. Si l'on considère qu'un lion adulte consomme quotidiennement 8.5 kg de viande par jour (Carbone et al. 2007) et qu'en moyenne le poids d'un individu dans la population de buffle est de 450 kg (Coe et al. 1976), cela nous donne une consommation de 767 individus par an (soit 12% de la population de buffles selon les dernières estimations (Craig 2012)). A l'échelle de la RNN, l'impact numérique direct de la prédation naturelle semble donc bien plus fort que la prédation humaine. L'hypothèse d'un "predator pit" qui maintiendrait la population de buffles de la RNN à une faible densité n'est donc pas à exclure. Si nous considérons que l'effectif de la population de buffles de la RNN a fortement chuté pendant les années de guerre, le taux de prédation naturelle estimé (ainsi que la prédation humaine) permettrait d'expliquer le maintien de la faible densité de buffles observée sur la RNN.

B - LIMITES DE L'ETUDE

B1 - L'effectif de la population de buffles

Estimer l'effectif d'une population d'herbivore n'est jamais chose facile, d'autant plus lorsqu'il s'agit d'une espèce grégaire comme le buffle (Norton-Griffiths 1978). Les comptages aériens sont sujets à de nombreux biais (e.g. effort d'échantillonnage, problème de détection) mais la source de biais la plus importante est le "biais observateurs" qui est lié à la qualité des observateurs en termes de capacité à voir, d'expérience et de capacité à rester concentrés pendant de longues heures de vol (Jachmann 1995; Jachmann 2012). Cependant, malgré les biais qui résultent de ce type de comptage, ces biais ont été reproduits à l'identique lors des 6 derniers protocoles de comptages (entre 2000 et 2012) puisque les mêmes observateurs ont été utilisés, la méthode de comptage était exactement la même et l'effort d'échantillonnage était de 10% à chaque session (le comptage réalisé en 1998 est traité indépendamment car seulement 7% de la RNN a été couvert à cette époque). Vient s'ajouter à cela un problème propre à la population de buffles: le buffle est une espèce pour laquelle il est particulièrement difficile d'obtenir une estimation précise de l'effectif de la population puisqu'ils ont tendance à former de grands troupeaux et lors d'un survol aérien, le calcul de l'estimation finale sera fortement dépendant du nombre d'observations d'individus seuls, de petits groupes (e.g. de 5 à 20 buffles) ou de grands troupeaux (i.e. plus de 100 individus). Ceci se retrouve dans les résultats des comptages réalisés sur la RNN, notamment en 2000 et 2006 ou aucun grand troupeau n'a été observé (Figure 7.1). Ces biais et erreurs dans la méthode utilisée pour estimer l'effectif de la population de buffles de la RNN viennent poser une question quant à la crédibilité des résultats issus de ces comptages. Néanmoins, ils ne remettent pas en cause la question centrale de cette thèse à savoir la faible densité de la population de buffles. En effet, la dernière estimation (Craig 2012) indique une population de buffles de 6214 ± 2753 individus ce qui correspond à une densité de 0.15 ind/km^2. Même si nous doublions l'estimation de l'effectif de la population, la densité serait de 0.29 ind/km^2 et nous resterions bien en dessous des densités observées dans d'autres aires protégées de savanes sur des sols pauvres et aux pluviométries voisines (e.g. Parc de Hwange, Parc de Kafue; cf. Chapitre 1 - Figure 1.1). Afin d'obtenir une estimation plus précise de la population de buffles de la RNN il aurait été nécessaire de réaliser un comptage aérien spécialement conçu pour cette espèce mais les coûts associés n'ont pas rendu ce protocole possible pour notre étude. De plus, si un tel comptage était réalisé, il sera nécessaire de photographier chacun des troupeaux observés afin de réaliser une post-analyse et d'identifier avec précision le nombre d'individus présents dans un groupe. Il est estimé que même avec de l'expérience, au delà de 20 individus, un observateur depuis les airs ne peut pas estimer avec précision la taille d'un troupeau (Norton-Griffiths 1978).

Une autre méthode de comptage largement utilisée est la méthode dite de capture-marquage-recapture (CMR) basées sur le contrôle d'individus identifiés (Schwarz and Seber 1999). Notre étude aurait pu bénéficier de la méthode CMR, notamment pour estimer les paramètres démographiques de la population à travers une description précise des classes d'âges et de leur survie apparente.

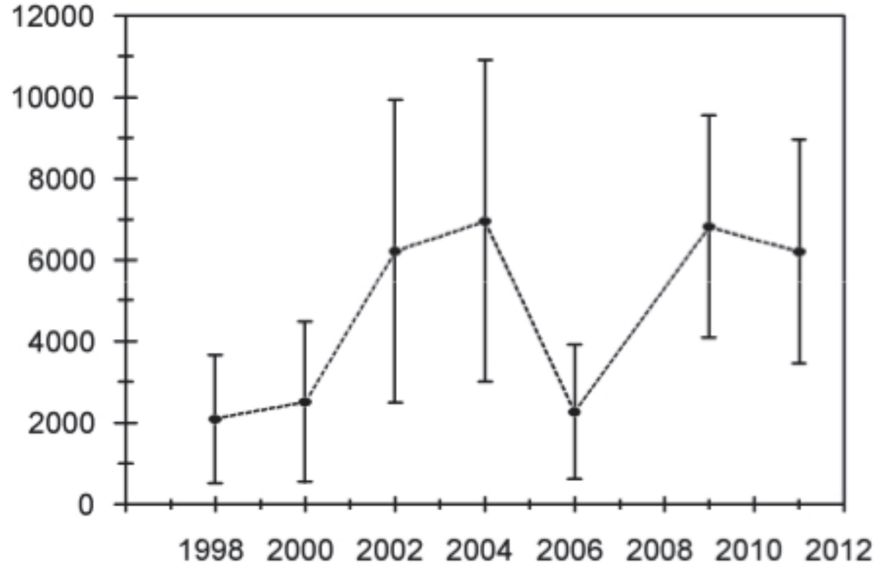

Figure 7.1 - Trend in buffalo estimates from aerial surveys in Niassa National Reserve (from Craig 2012)

Les coûts associés à des captures de masse n'ont pas permis la mise en place de tels protocoles pour notre étude. Néanmoins, à chaque fois que cela était possible, nous avons photographié depuis les airs les troupeaux de buffles suivis. Ces photos, prises en haute-définition, permettent d'identifier le nombre exact d'individus dans un groupe ainsi que de décrire les classes d'âges ainsi que le sex-ratio (i.e. structure et composition des troupeaux). Elles constituent la base d'une banque d'images qu'il sera nécessaire d'alimenter dans le futur afin d'obtenir des informations plus précises quant à la structure et la composition de la population de buffles de la RNN.

B2 - Organisation sociale du buffle

Bien que le buffle présente un comportement grégaire, nous pouvons nous demander si le suivi d'un à trois individus simultanément dans un même troupeau est bien représentatif du déplacement et de la distribution spatiale de l'ensemble du troupeau (en moyenne 161 ± 65 individus par troupeau; cf. Chapitre 5 - Table 5.2). Il a été montré chez le buffle que la cohésion des troupeaux n'est pas constante mais que ces derniers sont sujets à des événements de fusion et scission au cours du temps, selon des mécanismes qui demeurent méconnus. Nous en avions notamment fait l'expérience lors de la première pose de colliers GPS, lorsque deux troupeaux équipés à 25 km l'un de l'autre se sont avérés n'être qu'un seul et même troupeau. Nous avons initié une analyse sur la proximité (i.e. distance) entre les localisations de paires de colliers placés dans un même troupeau, à la même date et heure. Certaines paires de colliers présentaient un niveau de proximité fort (Figure 7.2) alors que d'autres ne se trouvaient ensemble qu'une partie de l'année (Figure 7.3). Cependant, l’analyse du partage de l’espace entre individus d’un même troupeau a mis en évidence des taux moyens de chevauchement de l'ordre de 70% (cf. Chapitre 5 - Figure 5.4). En conséquence, en dépit d'un degré de cohésion parfois faible au sein d'un même troupeau, il est probable que les femelles présentent des patrons de sélection de l'habitat similaires. De plus, nos analyses de sélection de l'habitat ont été réalisé par individu et non par troupeau afin d'améliorer l'interprétation des patrons de sélection de l'habitat de la population de buffles de la RNN.

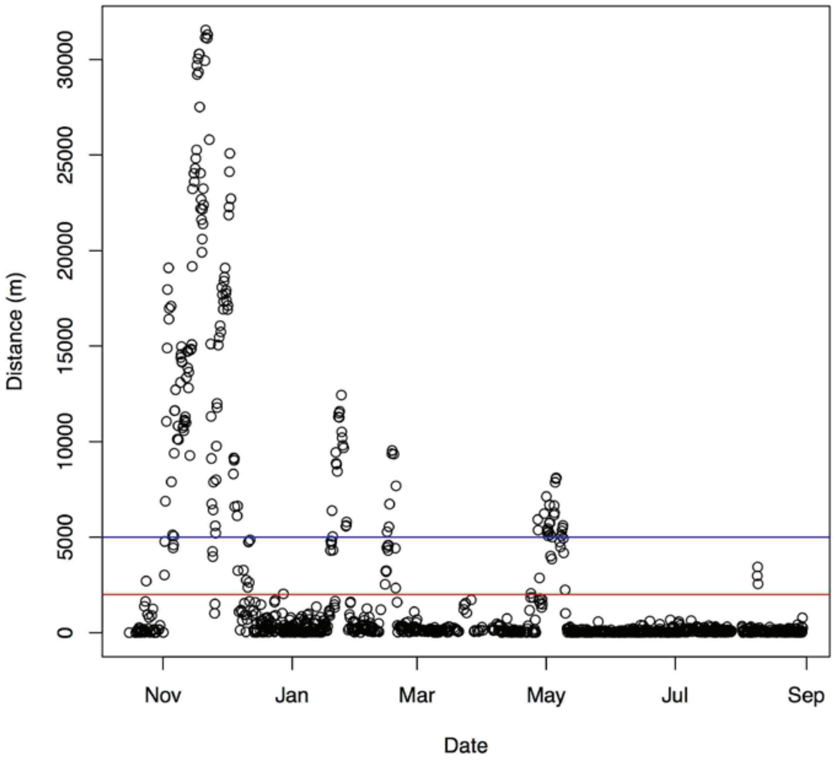

Figure 7.2 - Spatial proximity between 2 GPS collars at the same time of the day within the herd n°2 in 2010

Ces mécanismes de fusion/scission des troupeaux de buffles restent aujourd'hui mal connus et une analyse approfondie de nos données permettrait d'améliorer la connaissance de ces processus.

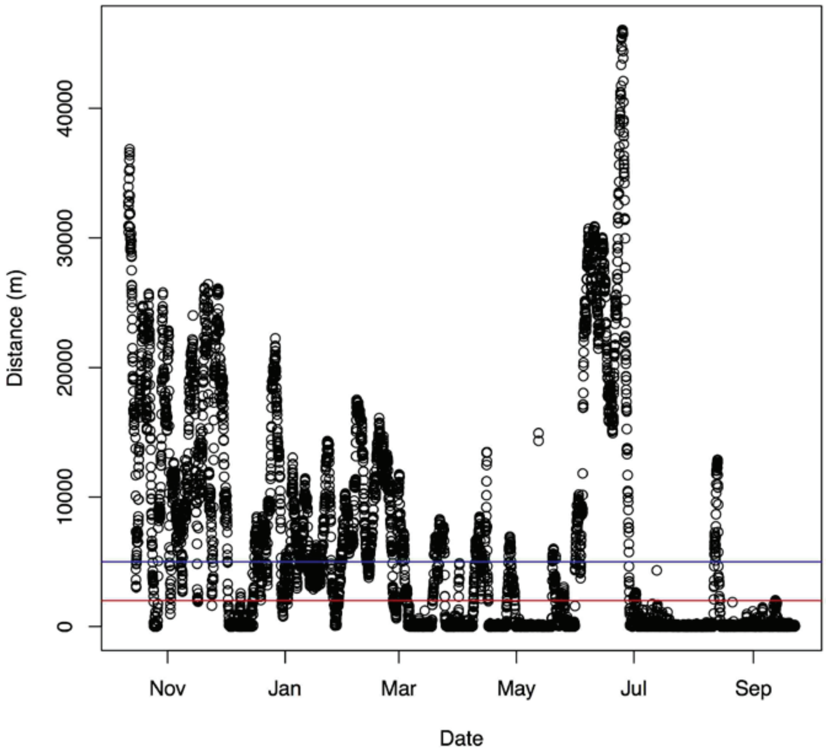

Figure 7.3 - Spatial proximity between 2 GPS collars at the same time of the day within the herd n°9 in 2010

B3 - La prédation naturelle et l'impact humain

Bien que le buffle, en raison de sa forte masse corporelle, soit peu susceptible d'être limité de manière descendante par la prédation naturelle (i.e. prédation par le lion), ce facteur nécessite d'être étudié plus en détail dans le futur. Nous avons toutefois tenté d'apporter des éléments de réponses en équipant de colliers GPS 6 femelles adultes dans deux troupeaux de buffles (i.e. troupeaux 4 et 10) situés dans une unité de gestion de la RNN (i.e. unité L5S, cf. Chapitre 3 Figure 3.2) dans laquelle 28 lions (18 mâles et 10 femelles) ont été équipés de colliers GPS entre 2005 et 2011. Pendant deux ans (2010 et 2011) il a été possible de comparer les déplacements de ces 6 femelles à ceux des 6 lionnes équipées par le "Niassa Carnivore Project". Malheureusement, les deux colliers GPS posés dans le troupeau n°10 ont cessé d'émettre après 9 mois et le succès des taux d'acquisition (i.e. nombre de localisations enregistrées par le collier en fonction de la fréquence d'acquisition initialement programmée) n'étaient que de 30%. Au final, le suivi d'un seul troupeau couplé au suivi de 6 lionnes n'était pas suffisant pour mener une analyse quant à l'impact global de la prédation naturelle du lion sur la population de buffles de la RNN. Qu'il s'agisse de la prédation directe (i.e. effet numérique) ou du risque associé à la prédation sur la sélection de l'habitat du buffle (i.e. le paysage de la peur, (Brown et al. 1999)), ce type d'analyses aurait nécessité l'établissement d'un protocole spécifique qu'il ne nous a pas été possible de réaliser au cours de cette thèse sur l'intégralité des troupeaux suivis. Certaines données étaient néanmoins disponibles et nous les discuterons dans la suite de ce chapitre (cf. C).

Pour ce qui est des impacts directs et indirects liés à la présence humaine, nous nous sommes heurtés à un manque de données spatiales sur le braconnage et les activités humaines au sein de la RNN. Les seules données disponibles pour nos analyses étaient les localisations géographiques des villages et des routes. Ces données n'étaient pas suffisantes pour identifier l'impact de la présence de l'homme sur les stratégies d'utilisation de l'espace des buffles. Bien que nous ayons essayé d'initier la récupération de ces données par les patrouilles de lutte anti-braconnage de la RNN, ainsi que la récolte directe lors de nos déplacements, l'effort d'échantillonnage n'était pas suffisant pour nous permettre de mener à bien une telle analyse. Nous avons néanmoins tenté de pallier ce problème à travers les interviews menées dans les villages de la RNN afin d'estimer ces impacts directs et indirects.

B4 - Les problèmes d'échelles

Afin de caractériser les stratégies d'utilisation de l'espace des buffles et les contraintes associées, nous nous sommes focalisés sur deux zones (i.e. zone Centrale et zone Est) qui présentaient les plus fortes densités d'herbivores de la RNN (Craig 2012). Ces deux zones représentent à elles seules environ 26,000 km^2 soit plus de 60% de la superficie de la RNN. A une telle échelle, certaines limites sont imposées par les instruments d'observation spatiale employés au cours de notre étude (i.e. résolution spatiale et résolution temporelle).

De plus, dans un environnement caractérisé par une saisonnalité prononcée, le domaine vital est défini comme la réalisation d'un processus de déplacement à une échelle temporelle relativement longue (saisonnière et annuelle). Dans ce type d'écosystème, une échelle intermédiaire est susceptible d'apparaître sous la forme de domaines vitaux sous-saisonniers. Cependant, isoler des segments stationnaires d'un jeu de données de localisations pose souvent des problèmes pratiques, notamment lorsque nous travaillons à une échelle spatiale comme celle de la RNN ou l'environnement présente une hétérogénéité spatiale et temporelle différente en fonction des zones considérées. Il aurait notamment été intéressant de disposer d'une meilleure résolution spatiale quant aux données météorologiques (e.g. nous disposions de données à 25 km de résolution spatiale pour la pluviométrie) afin de caractériser des sous-saisons et d'identifier si les stratégies d'utilisation de l'espace des buffles variaient en fonction de ces échelles intermédiaires, en saison sèche et en saison des pluies.

C - LE BUFFLE DANS LA RNN ET LES MECANISMES RESPONSABLES DE LA FAIBLE DENSITE DE LA POPULATION

C1 - Domaine vital

Plusieurs auteurs ont mis en évidence de large mouvement saisonniers chez le buffles du Cap (e.g. Sinclair 1977; Ryan et al. 2006) pouvant parfois même atteindre plus de 100 km (Naidoo et al. 2012b). Les variations de ces comportements migratoires s'expliquent par de nombreux facteurs, qu'il s'agisse des conditions environnementales (e.g. pluviométrie, feux de brousse, production primaire, type d'habitat), de la distance à la plus proche barrière (rivière, clôture, zone cultivée) ou de facteurs sociaux (âge, taille du troupeau). Une récente étude (Bennitt 2012) a montré des stratégies de déplacement contrastées dans le Delta de l'Okavango (Botswana) où la population de buffles présentaient des troupeaux résidents et des troupeaux migratoires. Selon l'auteur, ce contraste était probablement le résultat d'une différence de disponibilité des ressources et du niveau de dérangement humain. Différentes stratégies de déplacement ont également été observées dans la RNN (i.e. troupeaux de la zone Est VS troupeaux de la zone Centrale) et il semble que la disponibilité en eau en saison sèche en soit la principale cause.

Les écosystèmes de savanes sont généralement caractérisés par une forte ségrégation spatiale et temporelle des ressources (Estes 1991). Il en résulte que les buffles évoluant dans ce type d'écosystème présentent des tailles de domaines vitaux variables, de 50 à 350 km^2 en général (Cornélis et al. 2014), et pouvant parfois dépasser les 1,000 km^2 (Hunter 1996; Bennitt 2012). Les buffles évoluant dans des zones humides présentent généralement des domaines vitaux plus petits que ceux en zone sèche (Ryan et al. 2006) et les plus grands domaines vitaux sont observés lorsque les ressources sont fortement ségrégées ce qui induit des mouvements saisonniers (Cornélis et al. 2011; Naidoo et al. 2012b). Les domaines vitaux observés dans la RNN sont, à notre connaissance, parmi les plus grands jamais observés chez le buffle du Cap avec un domaine vital maximal de 2,070 km^2 (cf. Chapitre 5 - Table 5.3) et plus de 50% des troupeaux suivis présentant des domaines vitaux supérieurs à 1,000 km^2. En raison de communautés végétales de type *miombo* peu productives (Campbell 1996; Chidumayo 1997) et d'une forte ségrégation spatiale des ressources dans la RNN, la population de buffles est contrainte à réaliser d'importants déplacements au cours des saisons afin de satisfaire ses besoins alimentaires journaliers.

Les différences dans la taille des domaines vitaux saisonniers varient elles aussi en fonction des études. Par exemple, dans le Parc National du Serengeti (Tanzanie), la taille des domaines vitaux était plus faible en saison sèche en raison de la contrainte spatiale induite par l'eau disponible à cette période de l'année (Sinclair 1977). Le même phénomène a également été observé au Botswana (Halley et al. 2002) et en Namibie (Naidoo et al. 2012a). A l'inverse, un phénomène opposé a été observé en Afrique du Sud (Ryan et al. 2006; Winnie et al. 2008). Dans la RNN, les troupeaux de la zone Centrale, bien qu'ils réalisaient une migration en saison sèche ne présentaient pas une différence marquée dans la taille des domaines vitaux saisonniers. En revanche, dans la zone Est ou la rivière Lugenda est l'unique source d'eau disponible, les domaines vitaux saisonniers étaient plus petits en saison sèche. Il semblerait donc que la disponibilité en eau et son arrangement spatial dans le paysage soient responsables des tailles de domaines vitaux plus réduites en saison sèche à travers les différentes études menées en Afrique australe.

Plusieurs monographies sur le buffle du Cap ont suggéré que les domaines vitaux étaient stables sur le temps (Sinclair 1977; Prins 1996). De plus, plusieurs études ont montré que le pourcentage de chevauchement des domaines vitaux de troupeaux voisins est faible chez le buffle du Cap. Ces derniers ont tendance à utiliser des domaines vitaux exclusifs comme cela a été observé par Prins (1996), Halley et al. (2002) et Ryan et al. (2006) alors que Grimsdell (1969), Conybeare (1980) et Mloszewski (1983) ont observé des chevauchements entre les domaines vitaux de troupeaux voisins. La quasi absence de contacts dans la RNN entre troupeaux voisins suggère que les domaines vitaux ne sont pas défendus activement et que les buffles de la RNN exploitent leur domaine vital exclusivement, sans pour autant dépenser une énergie substantielle à leur défense. Néanmoins, les troupeaux de la zone Est présentaient un niveau de ségrégation spatiale plus marqué que ceux de la zone Centrale. Là encore, l'arrangement spatial des sources d'eau peut être responsable de ce phénomène. Les troupeaux de la zone Est utilise la Rivière permanente Lugenda en saison sèche alors que les troupeaux de la zone Centrale utilisent des poches d'eau résiduelles dans les lits de rivières asséchées ainsi que des trous d'eau naturels. Défendre un réseau de sources d'eau dispersées dans le paysage peut s'avérer plus consommateur en énergie que la défense d'un système linéaire (i.e. d'une rivière). De plus, l'eau disponible dans des poches résiduelles est sujette à des variations interannuelles et constitue donc un environnement moins prévisible que celui d'une rivière permanente. De ce fait, le buffle devrait montrer un partage de l'espace plus important lorsque la disponibilité des ressources (ici l'eau) est moins prévisible.

C2 - Sélection de l'habitat

Les buffles de savanes se trouvent majoritairement dans des habitats qui présentent une importante biomasse herbacée. La disponibilité en eau de surface et le couvert végétal sont généralement cités comme les contraintes principales à l'utilisation de l'habitat par le buffle. Le buffle doit boire au moins tous les deux jours et n'est pas capable de survivre en utilisant uniquement l'eau contenue dans son alimentation (Prins and Sinclair 2013). Cette contrainte à l'accès à l'eau est régulièrement citée dans les études sur l'utilisation de l'habitat par le buffle. Plusieurs études ont également montré une préférence pour les habitats de forêt riveraines, du moins en saison sèche. Ces zones de bas-fonds fournissent à la fois l'eau, le fourrage et le couvert nécessaire à satisfaire les besoins alimentaires du buffle et à assurer sa protection contre les prédateurs (Sinclair 1977; Redfern et al. 2003; Ryan et al. 2006; Cornélis et al. 2011). Les buffles de le RNN ont montré une sélection pour les habitats ouverts à forte production primaire qui sont caractérisés par une biomasse herbacée importante aux échelles inter- et intra-saisonnières. En saison sèche comme en saison des pluies, les buffles ont également sélectionné des habitats proches des rivières. En saison sèche, la proximité à l'eau est vitale et en saison des pluies, les buffles peuvent avoir tendance à pâturer à proximité des rivières en raison d'une meilleure qualité et quantité de fourrage, d'une teneur en humidité plus forte et d'espèces herbacées présentant une meilleure palatabilité, associées à ce type d'habitat.

L'un des résultats les plus remarquables de notre étude est la contrainte des feux de brousse sur l'utilisation de l'espace par la population de buffle de la RNN. Les avancées technologiques quant aux données satellitaires disponibles sur les feux de brousse à une échelle temporelle fine (i.e. journalière) couplées à la technologie GPS nous ont permis d'étudier les réponses comportementales des buffles à une échelle rapide. Bien que les feux puissent générer une repousse herbacée de qualité en début de saison sèche (van de Vijver et al. 1999), les feux de milieu et fin de saison sèche réduisent considérablement la quantité de fourrage disponible à la population de buffles. Les buffles sont ruminants et capables de subsister sur des pâtures de faibles qualité à l'inverse d'autres herbivores (Bothma et al. 2002). Qualifiés de paisseurs au sens large, ils ingèrent environ 2.2% de leur masse corporelle quotidiennement ce qui représente environ 15 kg de fourrage pour un buffle de 700 kg. Se sont des paisseurs efficaces, capables de devenir très sélectifs en saison sèche, voir de partiellement modifier leur régime alimentaire (i.e. brouteurs), et plusieurs études détaillées sur l'alimentation du buffle du Cap ont montré qu'il était confronté au compromis à réaliser entre la qualité et la quantité de fourrage ingérées afin de satisfaire ses besoins alimentaires (Redfern et al. 2006; Ryan et al. 2012). Il n'était pas rare d'observer des buffles se nourrir de pailles complètement sèches en saison sèche dans la RNN. L'importante étendue des feux de brousse sur la RNN (i.e. plus de 50% de la zone brûle chaque année) a donc un impact considérable sur la survie de la population en réduisant de manière considérable la quantité de fourrage disponible. Déjà fortement contraint dans l'espace par l'eau disponible à cette période de l'année, cette réduction de fourrage peut potentiellement fortement limiter l'accroissement de la population.

C3 - Pourquoi des faibles densités de buffle dans la RNN ?

Nous nous trouvons donc dans un environnement de type *miombo* caractérisé par des communautés végétales peu productive. Le climat tropical caractérisé par deux grandes saisons induit une ségrégation des ressources importantes, particulièrement en saison sèche où la contrainte associée à la disponibilité en eau influence fortement les stratégies d'utilisation de l'espace par la population de buffles de la RNN. Viennent s'ajouter à cela des feux brousse non contrôlés qui limitent considérablement la quantité de fourrage disponible aux buffles en fin de saison sèche. De ce fait, si nous considérons que les populations d'herbivores sont dépendantes pour leur survie et leur reproduction de zones de ressources clés en fin de saison sèche (Illius and O'Connor 2000), nous comprenons aisément que dans un tel contexte la densité de la population de buffles de la RNN puisse se trouver bien en dessous d'autres aires protégées de savanes sur sol pauvre et aux pluviométries voisines.

De plus, viennent s'ajouter aux contraintes liées à la ressource, l'impact de la prédation naturelle (i.e. le lion) et humaine. Outre le dérangement associé à ces deux types de prédations (Brown et al. 1999), nous avons montré que l'effet numérique direct sur l'effectif de la population était important. Nous avons estimé très largement qu'environ une centaine de buffles étaient prélevés chaque années par la chasse illégale. S'ajoute à cela une estimation, très large également, de près de 800 buffles prédatés naturellement par le lion. Ces chiffres cumulés représentent environ 14% de la population de buffles. Le taux de recrutement d'une population de buffles varie en fonction des études et oscille entre 5% et 12% (Jolles 2007) en fonction des conditions environnementales, notamment de la pluviométrie. Bien que nous ayons des incertitudes quant aux estimations de l'effectif de la population de buffles sur la RNN et que les estimations du nombre d'individus prédatés (naturellement et par l'homme) soient grossières, ces facteurs, associés à des contraintes fortes du milieu, semblent être responsables de la faible densité de buffles observées dans la RNN, en effet l'équivalent de l'intégralité du recrutement pourrait être consommé par les prédateurs (villageois inclus).

Les principaux facteurs responsables de la faible densité de buffles de la RNN sont résumé Figure 7.4 à partir du schéma général présenté en Introduction (Chapitre 1) ainsi que les études qu'il serait important de mener afin d'améliorer notre compréhension du système. En résumé, améliorer l'accès et la disponibilité des ressources en saison sèche (i.e. gestion des feux de brousse) et limiter la prédation humaine (même si cette dernière apparaît comme potentiellement bien inférieure à la prédation naturelle) permettrait à la population de buffles de la RNN d'améliorer son taux de recrutement.

D - IMPLICATION POUR LA GESTION DE LA RNN

Les populations de buffles sont susceptibles d'être impactées par une large gamme de facteurs, parmi lesquels les changements dans l'utilisation de l'habitat, la compétition avec le bétail, le braconnage, la sécheresse et les maladies. Les deux guerres qui ont ravagé le Mozambique entre 1964 et 1992 ont fortement impacté les populations animales afin de nourrir les groupes armés. L'ouverture de routes à travers les écosystèmes naturels ont également facilité la chasse illégale et fragmenté les habitats. L'augmentation de la population humaine, l'intensification de l'agriculture, la déforestation, ont progressivement contribué à la dégradation d'habitats favorables pour le buffle et les autres mammifères, à la fois à travers une compétition directe et en raison de l'impact sur les sols et leur érosion.

Dans le contexte de la RNN, une immensité sauvage en plein reconstruction, incluant des populations locales ainsi que des zones de chasse, la faible densité de buffles observées est logiquement devenue une priorité de gestion pour la RNN, notamment en raison de la forte valeur commerciale du buffle dans l'industrie du trophée de chasse. Le buffle est une espèce emblématique du continent africain et s'intéresser à sa faible densité dans la RNN sous-entend de s'intéresser à toute la communauté d'herbivores, dans une grande aire protégée faiblement productive, et où l'abondance au mètre carré est faible et où la diversité dépend donc beaucoup de la superficie de la zone. S'intéresser au buffle ici c'est s'intéresser à la ressource mais aussi à la gestion de l'homme dans une aire protégée.

Bien que nous nous trouvions dans un écosystème où les contraintes environnementales sont fortes, avec une ségrégation spatiale et temporelle marquée, plusieurs contraintes se sont ajoutées à la liste des mécanismes potentiellement responsables de la faible densité de buffle observée. Ces contraintes sont souvent associées à la présence humaine.

Tout d'abord, notre étude a montré qu'il était nécessaire de mettre en place une politique de gestion des feux sur la RNN. Le climat et la qualité des sols ont pendant longtemps été considéré comme les seuls facteurs à considérer lors qu'il s'agissait d'expliquer la distribution de la faune et de la flore. Mais il est de plus en plus mis en évidence que les feux jouent un rôle clé dans les écosystèmes (Pausas and Keeley 2009). Historiquement, l'écologie du *miombo* est en étroite association avec le feu mais l'accroissement de la population humaine contribue fortement à modifier les impacts des feux de brousse comme leur étendue dans un écosystème. Dans la RNN, les raisons d'initier des feux de brousse sont multiples : les locaux brûlent dès qu'ils le peuvent en saison sèche afin de "nettoyer" les zones ce qui procure une facilité de déplacement (i.e. à pied ou en vélo) ainsi qu'une augmentation de la sécurité (i.e. meilleure visibilité). Les braconniers brûlent également afin de faciliter la traque des animaux ou bien pour les diriger vers des pièges préalablement posés. Ces derniers peuvent également mettre le feu lorsqu'ils sont pistés par une patrouille de lutte anti-braconnage afin d'effacer leurs traces. De même les pêcheurs, qui sont très actifs sur la Rivière Lugenda en saison sèche, brûlent le long des rivières dans le but de faciliter leurs déplacements à vélo, notamment lorsqu'ils se rendent sur les lieux de ventes chargés de sacs de plusieurs dizaines de kilos. Les chasseurs de miel utilisent des fétus de paille auxquels ils mettent feu pour enfumer les abeilles avant la collecte du miel. Ces fétus sont négligemment jetés au sol et entrainent souvent d'importants feux. De plus, les techniques agricoles dans la RNN sont liées au feu car après le défrichement d'une zone, les locaux y mettent le feu pour améliorer la fertilité du sol. Ces feux sont souvent incontrôlés et débordent au delà de la zone considérée. Enfin, les opérateurs de chasse de la RNN brûlent également leurs zones afin d'améliorer la visibilité et de faciliter le pistage des animaux. De part toutes ces raisons, c'est environ 50% de la RNN qui brûle chaque année, ce qui correspond à une zone de plus de 20,000 km^2.

Je souhaiterais donner ici une anecdote pour comprendre l'ampleur de la situation : les village de Matondavela et Mecula sont reliés par une piste de 60 km. A la fin du mois d'août, j'ai emprunté cette piste et observé des départs de feux tous les 2 kilomètres environ. Vers la fin de la piste, je suis tombé sur un vieil homme, seul à vélo. Bien que la loi au Mozambique interdise d'initier des feux, cette dernière est très peu respectée. J'ai demandé au vieil homme pourquoi avait-il brûlé tout le long de son trajet. Il m'a simplement répondu, "pour nettoyer". En plein mois d'août, ces feux ont duré une quinzaine de jours et ont "nettoyé" une zone d'environ 2,000 km^2.

La gestion des feux de brousse n'est pas aisée. Néanmoins, il faudrait favoriser l'initiation de feux précoces en début de saison sèche. La végétation n'est pas encore totalement sèche à cette époque et les feux sont donc lents, de mauvaise qualité et ne durent pas plus d'une journée. De plus, en raison de l'humidité encore présente, notamment sous forme de rosée le matin, ces feux donnent une excellente repousse nutritive pour les populations d'herbivores. Ces feux précoces permettent également de constituer des barrières aux passages éventuels de feux tardifs en fin de saison sèche. La création de routes permet également de gérer l'étendue des feux, notamment en début de saison sèche. Les feux tardifs sont trop puissants pour être arrêté par la simple création d'une route. De plus, en fin de saison sèche, les vents augmentent dans la RNN et favorisent le passage des peux d'un côté à l'autre d'une route. Il a été montré que les feux favorisent la diversité végétale des communautés de type *miombo*. La diversité maximale est atteinte sous un régime de feux tous les 4 ans environ (Campbell 1996; Chidumayo 1997). Si cela est envisageable, les opérateurs de chasse devraient tenter de réaliser des rotations dans les zones qu'ils brûlent afin de toujours conserver des zones "refuges" chaque année. Idéalement, une même zone ne devrait pas être brûlée deux années consécutives. Si une zone a pu être maintenue non-brûlée pendant plusieurs années, le départ d'un feu en fin de saison sèche (i.e. feu chaud rapide) serait alors bénéfique et permettrait à la communauté végétale de repartir sur un même pied d'égalité et de favoriser ainsi sa richesse en terme de diversité. La gestion des feux doit également passer par une éducation des populations locales quant à ce phénomène. Certains départs de feu pourraient être éviter si les populations se donner les moyens de contrôler le feu, lorsqu'ils brûlent une zone défrichée par exemple. La gestion des feux devra également se faire par une méthode répressive et une application de la loi mozambicaine qui interdit à tout villageois d'initier un feu.

La RNN est à notre connaissance la seule aire protégée d'Afrique australe présentant des populations humaines officiellement reconnues au sein de ses limites. C'est la plus grande originalité de la RNN mais c'est également sa plus grande contrainte. Nous avons vu au cours de cette thèse que le niveau de dépendance des populations locales aux ressources naturelles était très fort. La RNN présente un large éventail de contraintes socio-écologiques qui inclut une longue saison sèche, une faible fertilité des sols, une prévalence de la mouche *tse-tse*, un empiètement des activités humaines sur l'écosystème et des conflits entre l'homme et la faune sauvage, ce qui induit une faible sécurité alimentaire sur la zone. Les populations locales ont montré une préférence pour la viande domestique. Des actions devraient aller dans ce sens avec le développement d'élevage et la production de viande bon-marché afin de satisfaire les besoins protéiques de la population humaine. De plus, le poisson est une source importante de protéine dans le régime alimentaire de la population. A l'heure actuelle, les informations disponibles sur la pêche dans la RNN et les quantités de poissons prélevés chaque année dans l'écosystème sont très faibles. Il me semble essentiel de prévoir une étude pour améliorer ces connaissances. Si les densités de poissons viennent à diminuer fortement dans la RNN, comme cela a déjà été montré (Brashares et al. 2004), l'impact se fera directement sur la viande de brousse et une augmentation de sa consommation.

Les gestionnaires de la RNN ont besoin de comprendre les relations des populations locales avec leur environnement. Il est nécessaire d'incorporer ces connaissances, ces expériences et ces attitudes dans les actions de gestion. Comme Bill Adams l'a observé (2004) :

> *"The challenge is not to preserve (or restore) 'the wild', but peoples' relationships with the wild. Without contact with nature, people's capacity to understand it and engage with it withers. The future of conservation will turn on the extent to which a strong individual connection to nature and natural processes is maintained."*

Les gestionnaires de la RNN doivent comprendre les interactions qui existent entre l'environnement et les populations et identifier la différence entre l'utilisation des ressources naturelles et le niveau de dépendance à ces ressources. Nos analyses ont permis d'illustrer que les activités humaines et les attitudes envers la faune sauvage variaient spatialement en fonction de la situation géographique des villages. De ce fait, les populations humaines de la RNN de doivent pas être considérer dans leur globalité par les gestionnaires mais différents profiles doivent être pris en compte.

Enfin, il m'apparait nécessaire de mettre en place une zonation de la RNN. Un exemple de ce qui a pu être fait en France est dans le Parc National des Cévennes. Ce Parc, d'une superficie de 93,500 ha, abrite une population de près de 76,000 habitants, essentiellement des exploitants agricoles. L'originalité du Parc est que la pratique de la chasse y est autorisée. L'objectif est de maintenir et préserver un équilibre agro-sylvo-cynégétique. Comme dans le Parc National des Cévennes, il me semble nécessaire d'identifier une/des zone(s) de protection intégrale dans la RNN, dans la ou lesquelles aucune utilisation des ressources naturelles ne pourra être envisagée, ou bien sous certaines conditions très contrôlées, et des zones intermédiaires (i.e. des zones "d'adhésion" dans le Parc National des Cévennes) dans lesquelles des politiques de gestion communes sont établies avec les populations locales. La mise en place d'un plan de zonation restera un des plus important défi pour les gestionnaires de la RNN. Il ne pourra néanmoins se faire sans que les populations locales perçoivent l'identité "Réserve Nationale" et surtout les bénéfices, notamment financier, qui découlent de la conservation.

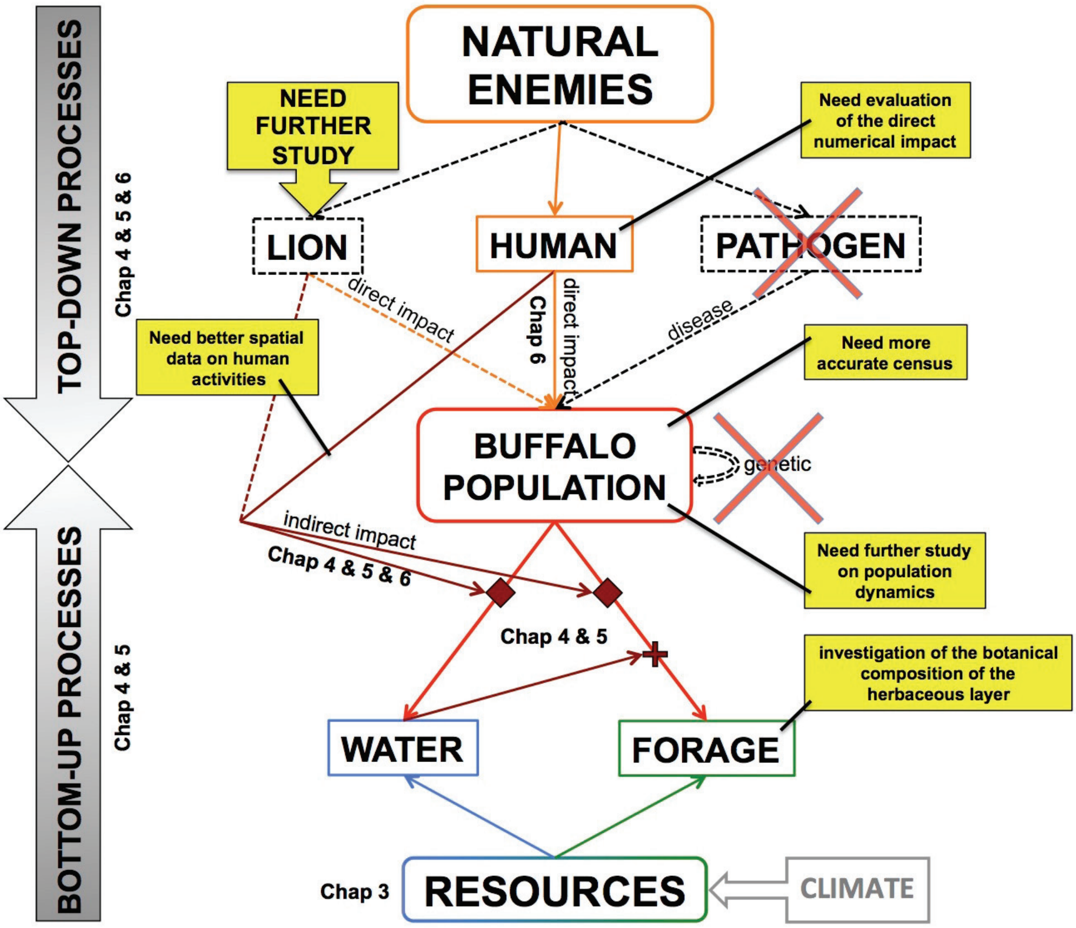

Figure 7.4 - Schematic representation of our results to explain the low buffalo population density in NNR and the needs for further engagements

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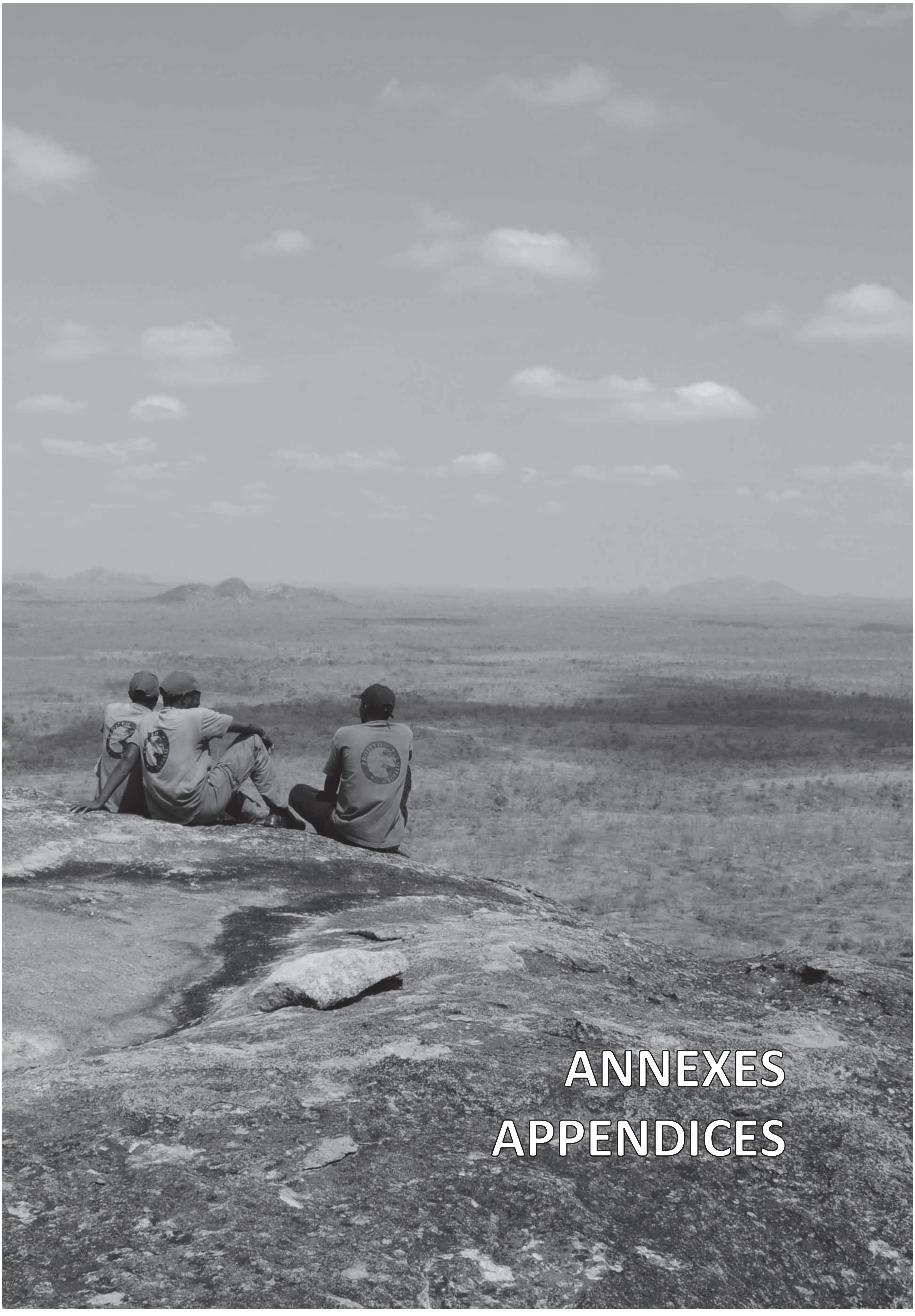

ANNEXES
APPENDICES

ANNEXE I - APPENDIX I

MAPS

A - Main villages, management blocks and road network

B - Vegetation map

C - Topography

D - River system subdivided in four classes

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H - Mean NDVI in 2010

I - Time series of NDVI in 2010

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K - Mosaic of four LANDSAT 5 ETM scenes of May and June 2008

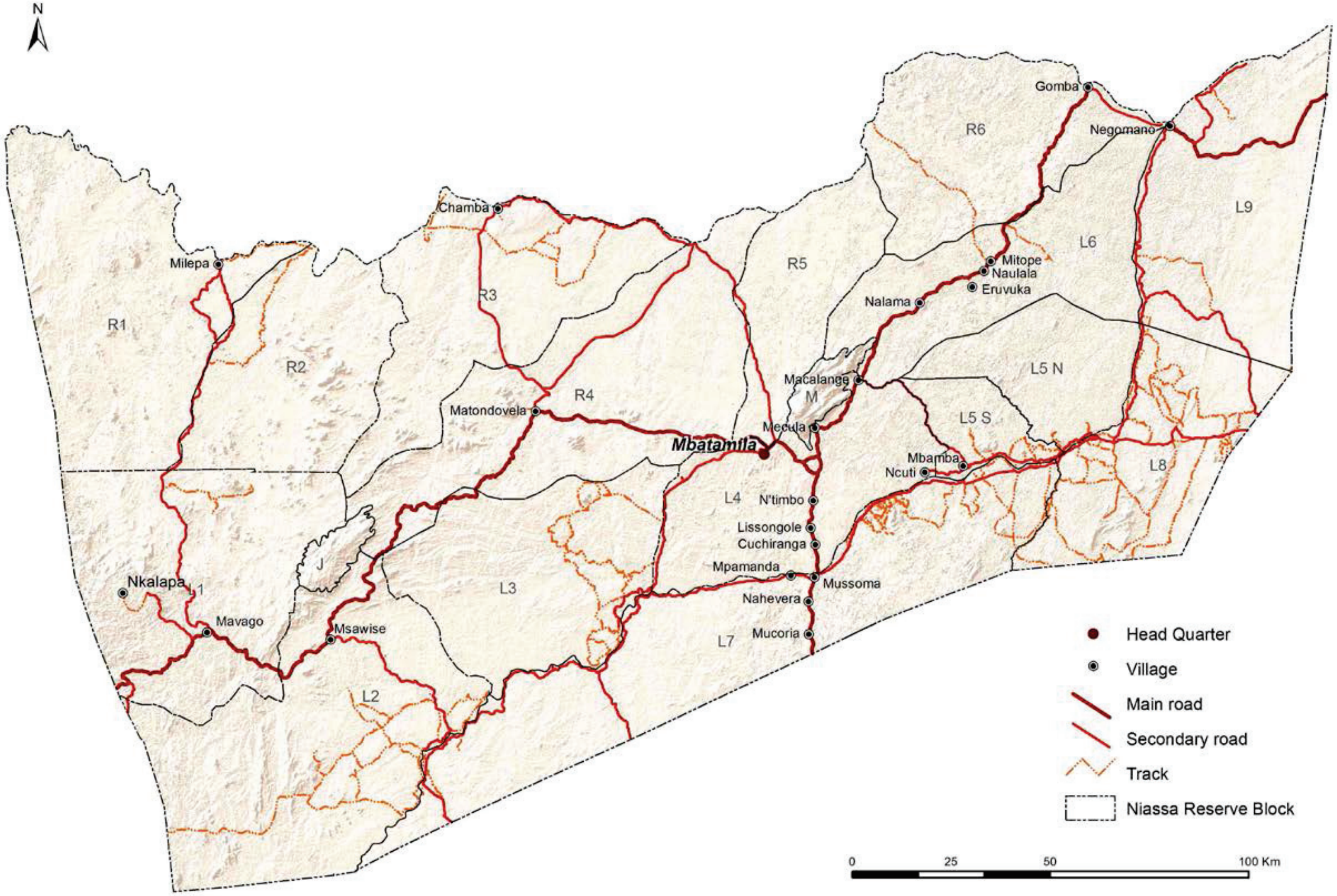


Figure I.A - Main villages, management blocks and road network in the NNR

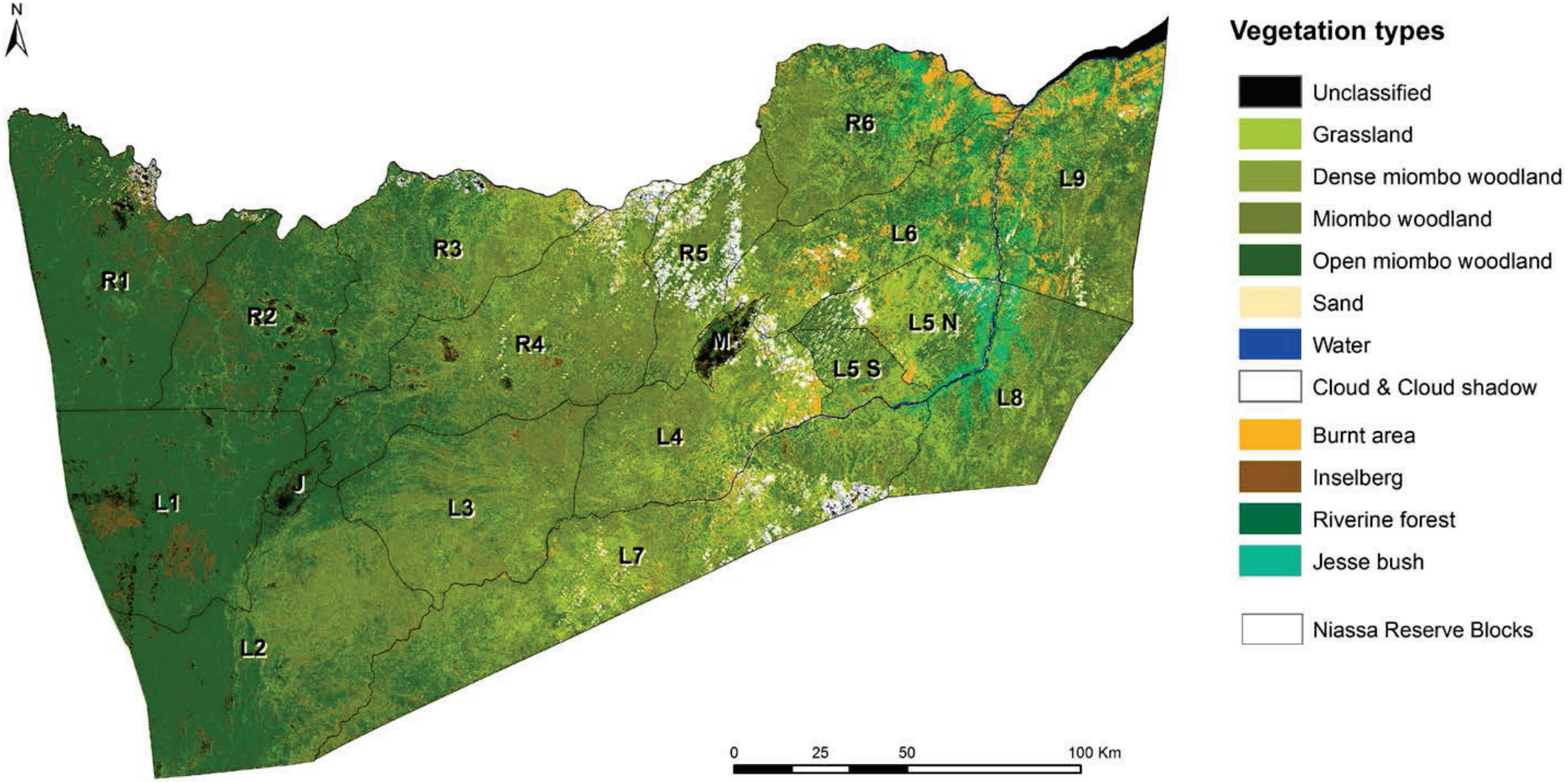


Figure I.B - Vegetation map of the Niassa National Reserve obtained from supervised classification of Landsat 5 ETM imagery of May-June 2008

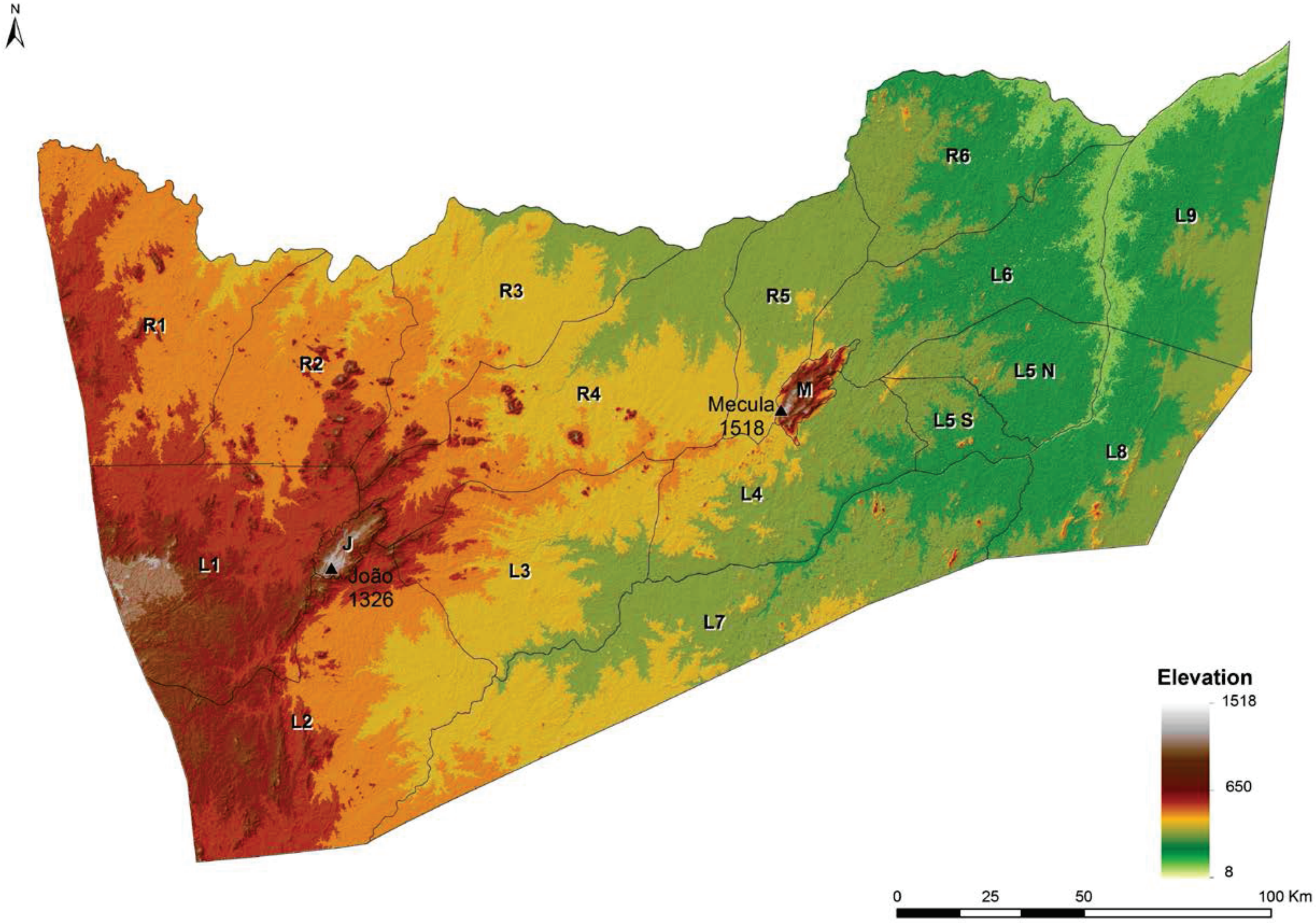


Figure I.C - Topography of the Niassa National Reserve

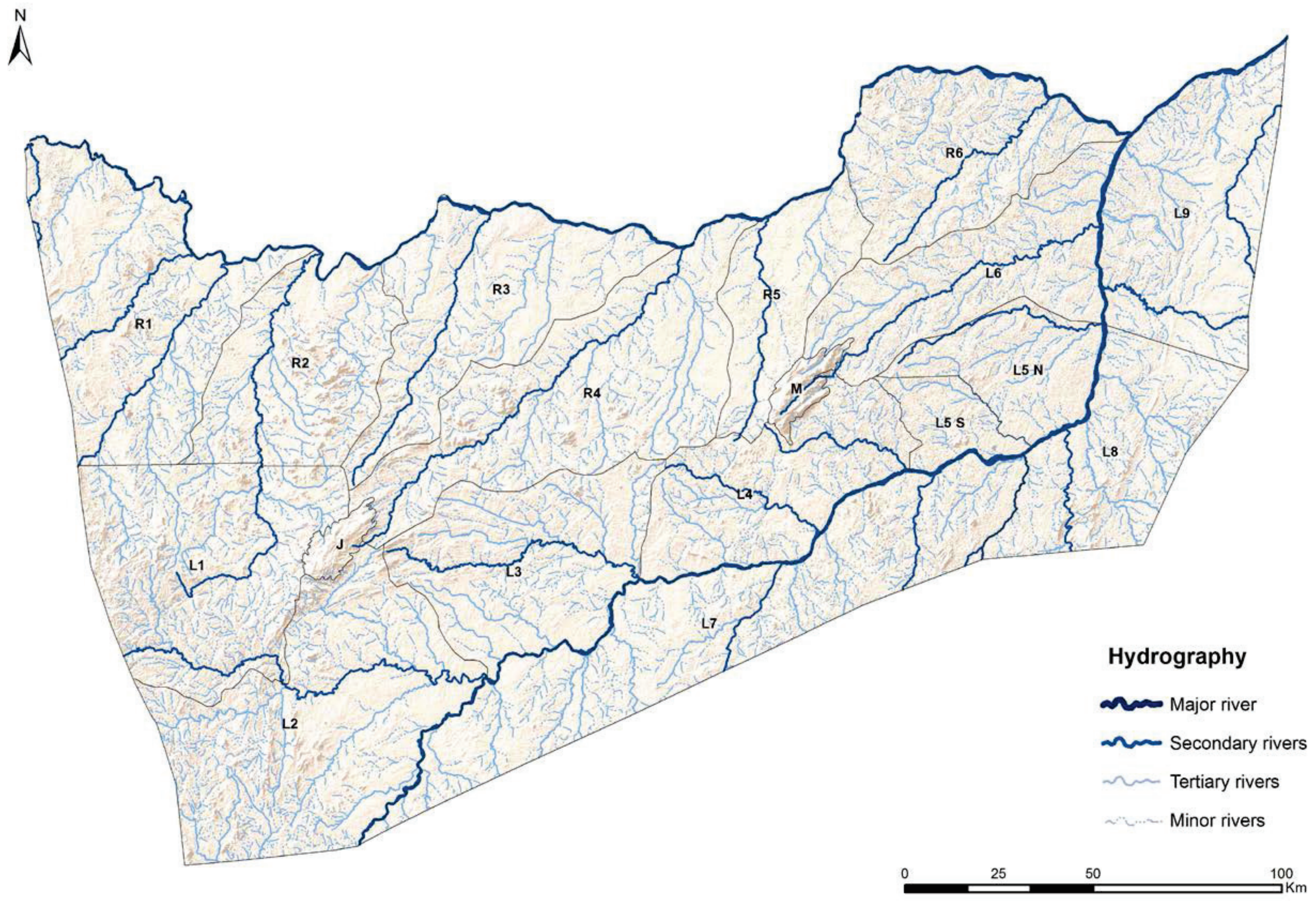


Figure I.D - River system in the Niassa National Reserve subdivided in 4 classes

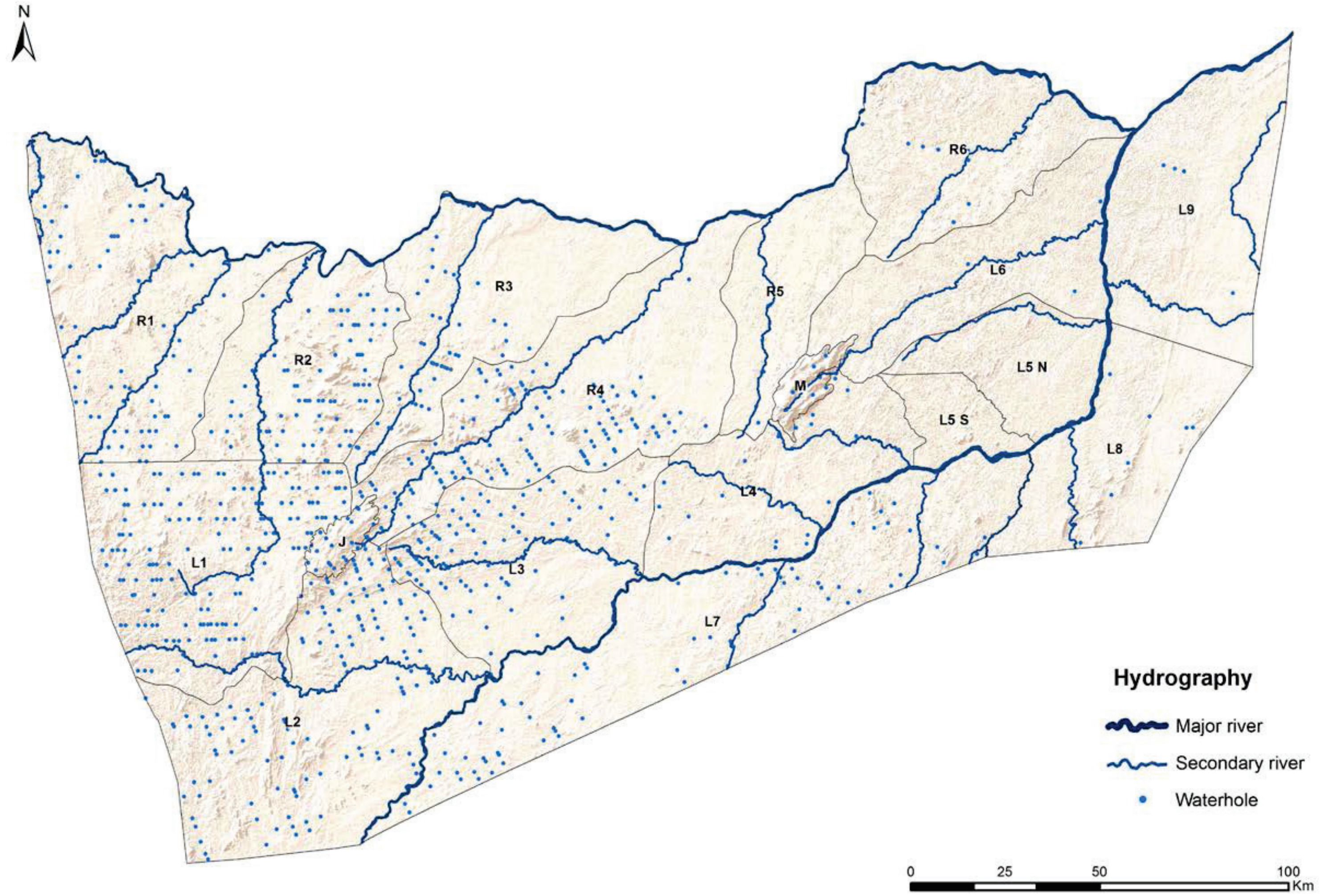


Figure I.E - Available water in the Niassa National Reserve in the dry season

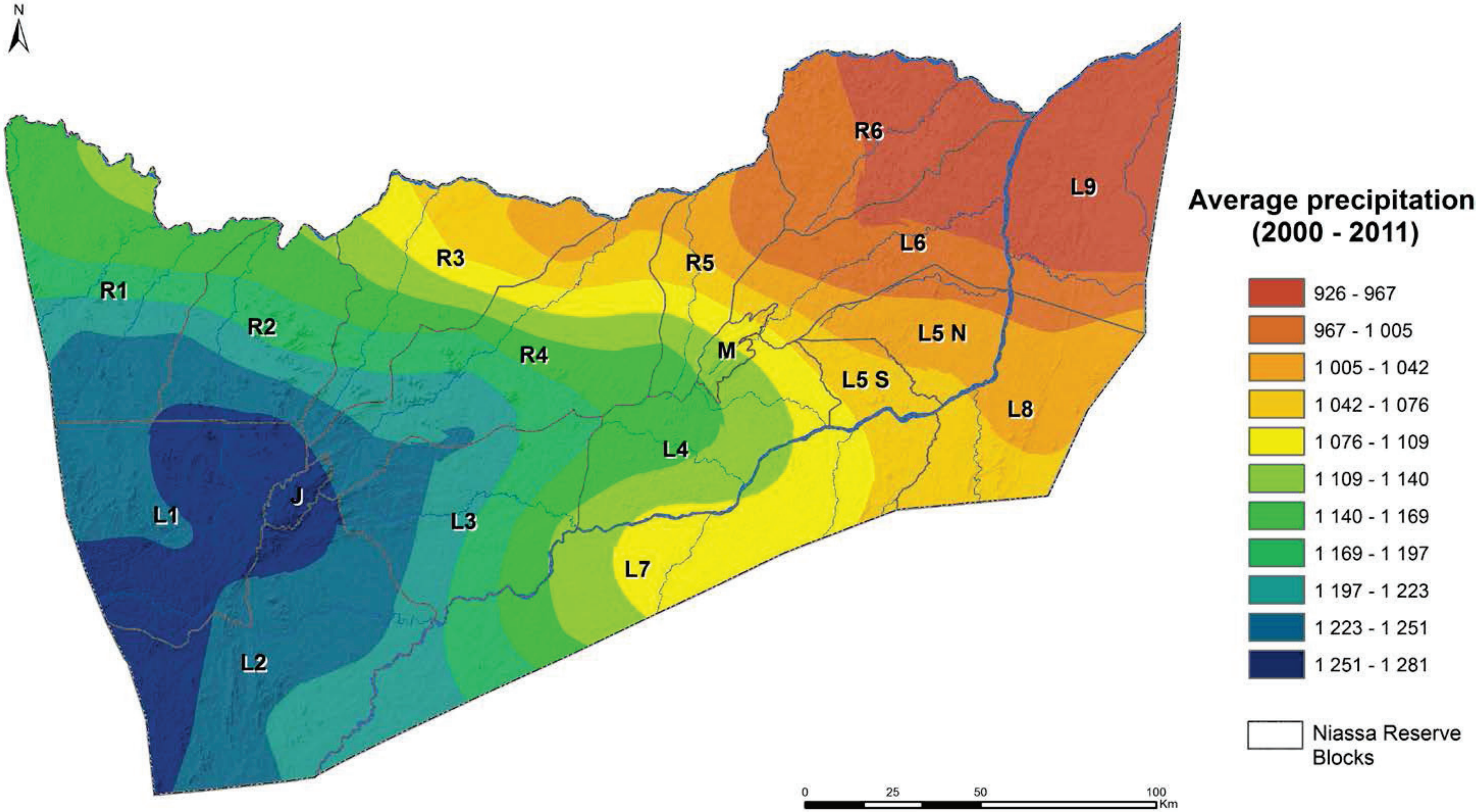


Figure I.F - Mean annual rainfall in the Niassa National Reserve between 2000 and 2011

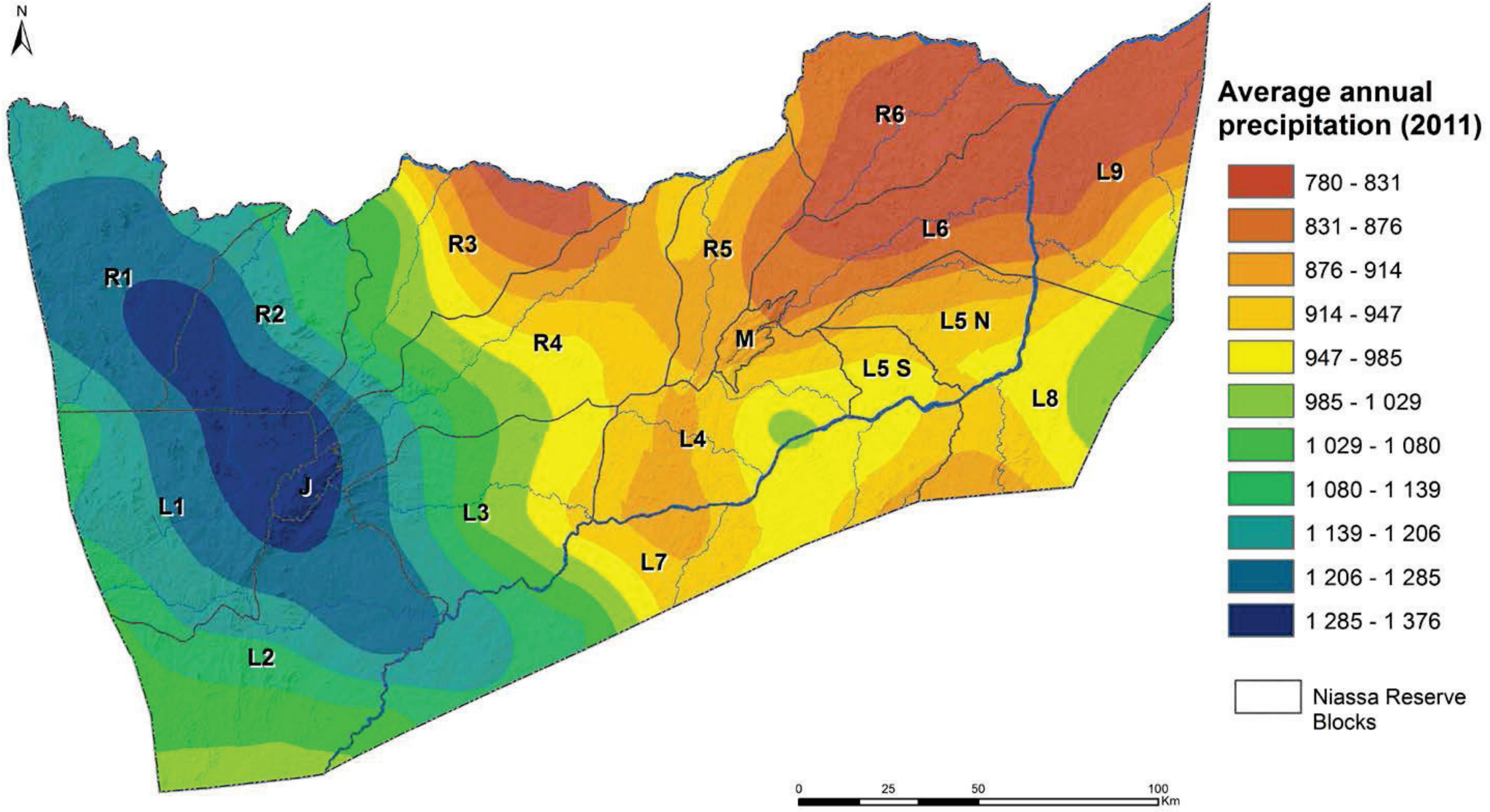


Figure I.G - Mean annual rainfall in the Niassa National Reserve in 2011

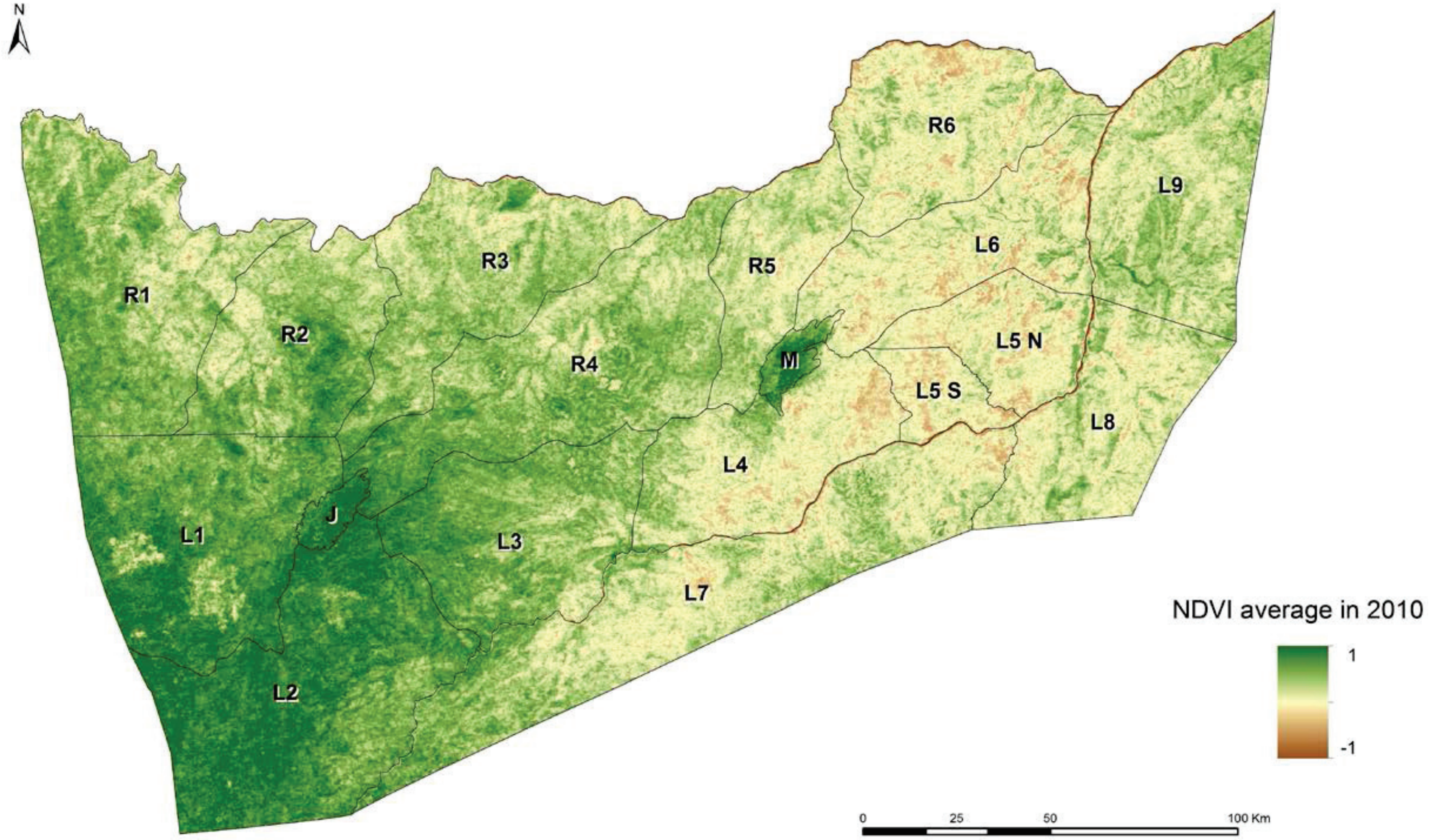
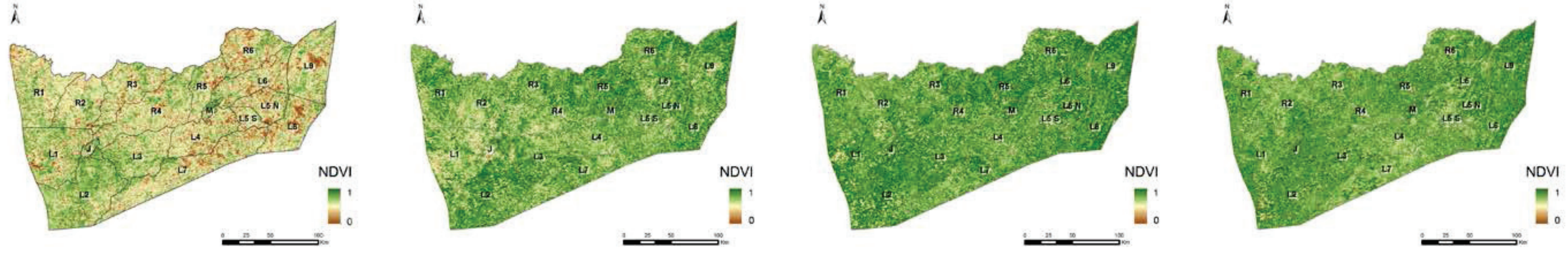
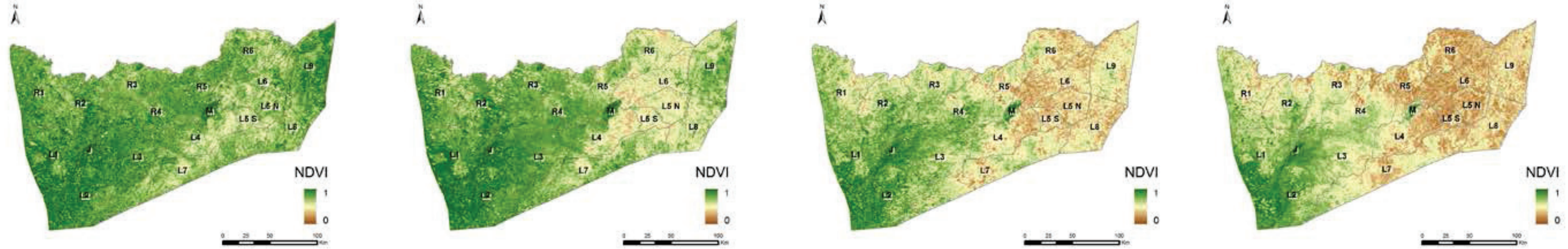


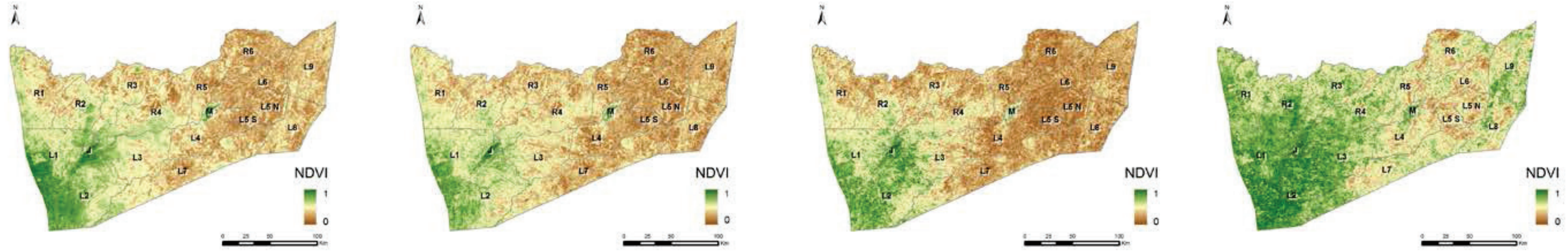
Figure I.H - Mean NDVI in the Niassa National Reserve in 2010



January, 2010 February, 2010 March, 2010 April, 2010

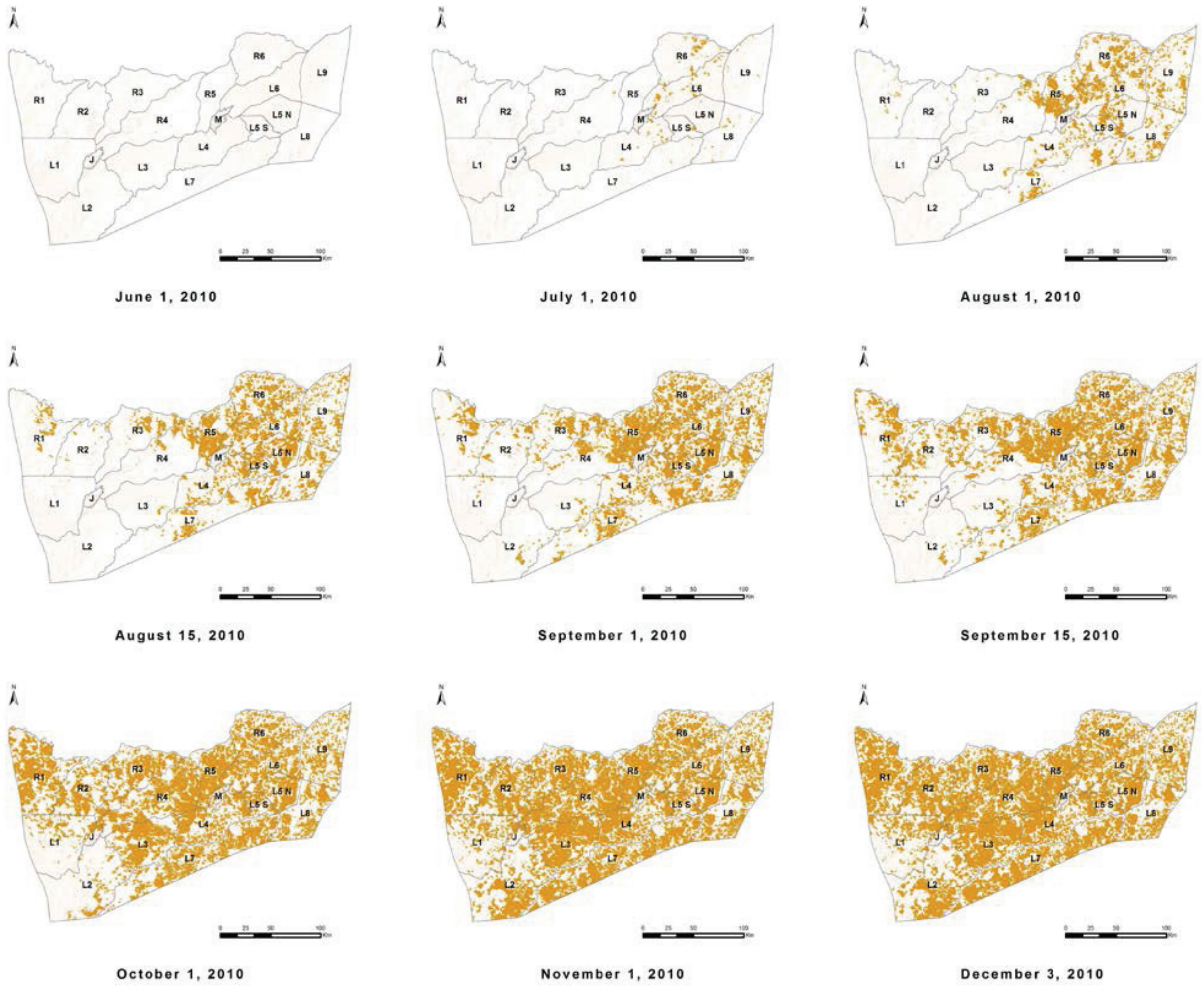


Mai, 2010 June, 2010 July, 2010 August, 2010



September, 2010 October, 2010 November, 2010 December, 2010

Figure I.I - Time series of NDVI in the Niassa National Reserve in 2010



June 1, 2010

July 1, 2010

August 1, 2010

August 15, 2010

September 1, 2010

September 15, 2010

October 1, 2010

November 1, 2010

December 3, 2010

Figure I.J - Time series of bushfires in the Niassa National Reserve in 2010

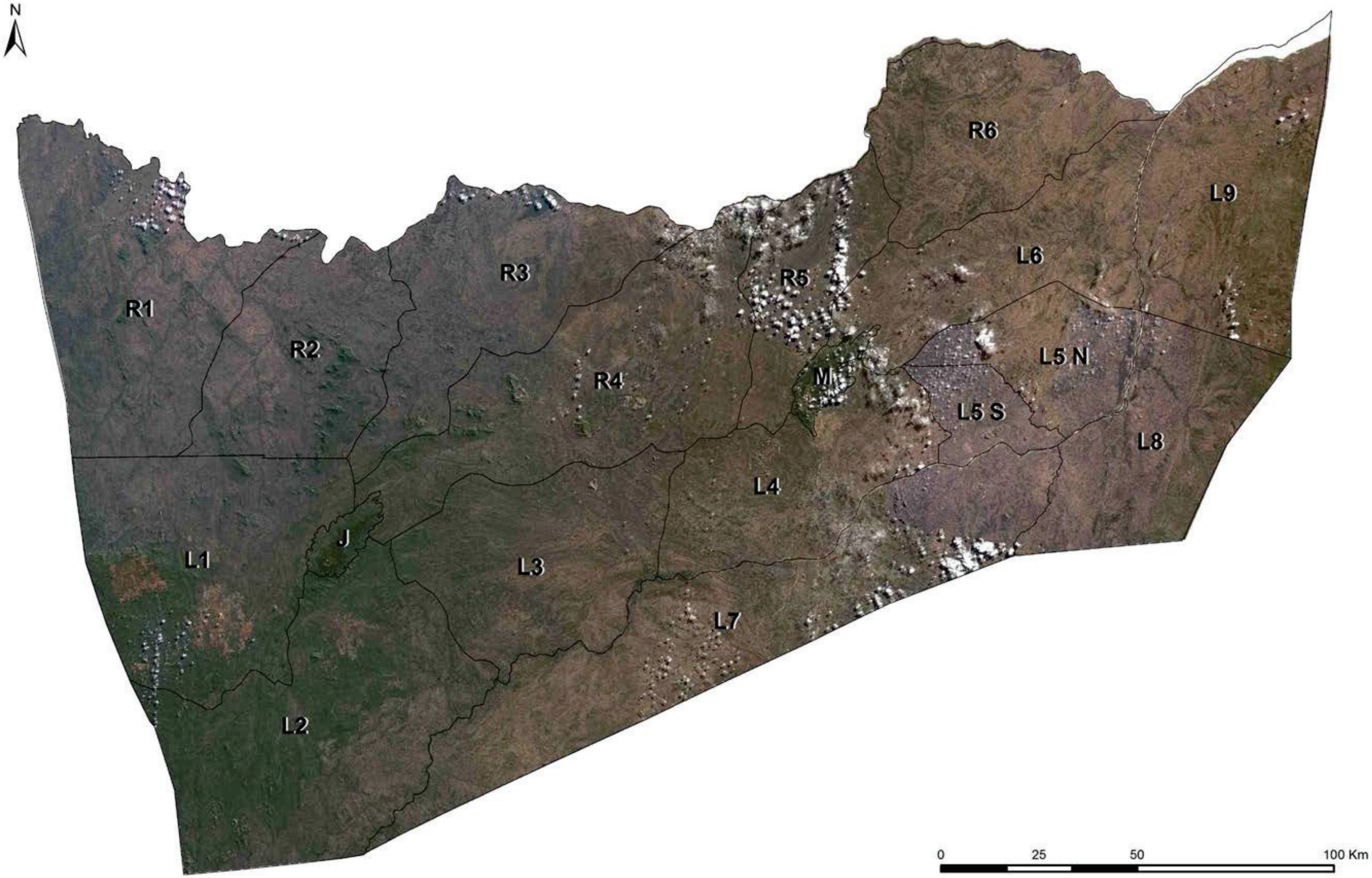


Figure I.K - Mosaic of four Landsat 5 ETM scenes from May and June 2008

ANNEXE II - APPENDIX II

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ECOLOGY, EVOLUTION AND BEHAVIOUR OF WILD CATTLE

Edited by Mario Melletti & James Burton

Part III - Chapter 20 - pp. 326-372
African buffalo Syncerus caffer (Sparrman, 1779)

Daniel Cornélis, Mario Melletti, Lisa Korte, Sadie J. Ryan,
Marzia Mirabile, Thomas Prin and Herbert H. T. Prins

Chapter

20

African buffalo *Syncerus caffer* (Sparrman, 1779)

Daniel Cornélis, Mario Melletti, Lisa Korte, Sadie J. Ryan, Marzia Mirabile, Thomas Prin and Herbert H. T. Prins

Names

Genus: *Syncerus* Hodgson, 1847

Species: African buffalo *Syncerus caffer* (Sparrman, 1779)

Subspecies: Cape buffalo *Syncerus caffer caffer*

Names in other languages: **French**: Buffle du Cap; **German**: Kaffernbüffel; **Spanish**: Búfalo cafre; **Italian**: Bufalo cafro.

Subspecies: West African savanna buffalo *Syncerus caffer brachyceros* (Gray, 1837)

Names in other languages: **French**: buffle de savane d'Afrique de l'Ouest; **German**: Savanne Westafrika Büffel; **Spanish**: Búfalo de Sabana de África Occidental; **Italian**: Bufalo di savana dell'Africa Occidentale

Subspecies: Central African savanna buffalo *Syncerus caffer aequinoctialis* (Blyth, 1866)

Names in other languages: **French**: buffle de savane d'Afrique Centrale; **German**: Savanne Zentralafrika Büffel; **Spanish**: Búfalo de Sabana de África Central; **Italian**: Bufalo di savana dell'Africa Centrale, Bufalo equinoziale.

Other common names: Nile buffalo.

Subspecies: Forest buffalo *Syncerus caffer nanus* (Boddaert, 1785)

Names in other languages: **French**: buffle de forêt; **German**: rotbüffel; **Spanish**: bùfalo de bosque; **Italian**: Bufalo di foresta; **BaAka**: Mboko; **Swahili**: Nyati.

Other common names: dwarf buffalo, red buffalo.

Ecology, Evolution and Behaviour of Wild Cattle: Implications for Conservation, ed. M. Melletti and J. Burton. Published by Cambridge University Press.

Taxonomy

The name *Bos caffer* was attributed by Sparrman in 1779. Since then, 92 species names have been given to the African buffalo. Taxonomists initially thought that each buffalo form represented a distinct species. Brooke (1873, 1875), who established the first classification of the African buffalo, reduced the number to three. Later, Blancou (1935) described up to 12 subspecies of buffalo.

Haltenorth (1963), Ansell (1972) and Grubb (1972) summarized the first classifications of Christy (1929), Schouteden (1945) and Blancou (1935, 1954), concluding that all forms should be considered as monospecific. Although there are considerable morphological variations in body size, fur colour, horn shape and size throughout the range of distribution, the African buffalo is currently considered as a single species by various authorities (IUCN 2013; Prins & Sinclair 2013), with a subdivision into four subspecies: Cape buffalo (*S. c. caffer*), forest buffalo (*S. c. nanus*), West African savanna buffalo (*S. c. brachyceros*), and Central African savanna buffalo (*S. c. aequinoctialis*). Additionally to those four subspecies, a mountain form (*S. c. mathewsi*) was also described in East Africa and may be distinct (Kingdon 1982).

A recent work of Groves & Grubb (2011), based on morphological measures, separates the African buffalo into four species, including the *mathewsi* form. In contrast, recent work of Smitz *et al.* (2013) conducted over the whole geographical range of the African buffalo, analysing mitochondrial D-loop sequences, revealed the existence of two lineages in the species, matching with the *caffer* subspecies of East and South Africa, and the *nanus* subspecies of West and Central Africa. These lineages seem to have diverged between 132and 286 kya (for further insight into the evolutionary history of the African buffalo, see Chapters 1 and 25). On the basis of the evolutionary history of both lineages, the authors suggest that the most prudent treatment of the African buffalo would be a subdivision into two subspecies, or management units, namely *S. c. caffer* (East-Southern Africa's lineage), and *S. c. nanus* (West Central Africa's lineage), which then should be extended to comprise *S. c. brachyceros* and *S. c. aequinoctialis* subspecies following standard nomenclature rules (*S. c. nanus*: Boddaert 1785; *S. c. brachyceros*: Gray 1837; *S. c. aequinoctialis*: Blyth 1866; for more details see Chapter 25). Further investigation using microsatellites may reveal finer-scale population structuring in West-Central and East-Southern Africa, which may be attributed to evolutionary significant units (ESUs) appropriate in terms of conservation management (Moritz 1994).

Hybrids *caffer* x *nanus* have been described in captivity (Cribiu & Popescu 1980). Although the different forms seem to be able to interbreed, the existence of hybridization in wild populations has yet to be conclusively demonstrated by molecular work. The occurrence of red calves in, for instance, the Queen Elizabeth National Park is often quoted as evidence for hybridization, but proof has never been provided. In Lake Manyara National Park, some 800 km further to the east, about 30% of the calves are red when young.

Subspecies and distribution

Historical distribution

Rainfall is the main biophysical factor limiting the distribution and abundance of African buffalo at a large geographical scale. Prior to the nineteenth century, the range of buffalo extended to most sub-Saharan ecosystems with annual rainfall above 250 mm (thus excluding the Horn of Africa and Namib/Kalahari deserts). The African buffalo is essentially a grazer, so its distribution strongly depends on the availability of herbaceous forage. As a consequence, core areas of the closed rainforests in Central Africa (i.e. areas without herbaceous cover) did not historically provide suitable conditions for buffalo (Sinclair 1977; Mloszewski 1983; Prins 1996; Melletti *et al.* 2007a). Buffalo did not colonize islands such as Zanzibar or Mafia, although they colonized Bioko Island (Equatorial Guinea), where they are now extinct (extirpated from Bioko Island sometime between 1860 and 1910 (Butynski *et al.* 1997)).

There is no palaeontological evidence of the presence of the African buffalo in North Africa or in the Nile Valley to the north of Khartoum (Prins & Sinclair 2013). In North Africa, aurochs (*Bos primigenius*; wild ancestor of domestic cattle) occupied a similar niche (Gautier 1988), perhaps preventing the buffalo's spread to the north (for more details on Bovini evolution, see Chapter 1). Buffalo could have expanded their range in eastern and southern Africa during the last Ice Age due to the extinction of possible competitors, such as *Pelorovis antiquus* and *Elephas recki* (for more details on evolution, see Chapter 1; Klein 1988, 1994; Prins 1996). Drawings of buffalo are rare in cave paintings, although representations can be seen in Kondoa in Northern Tanzania (Leakey 1983).

We present below the distribution and abundance of each of the four subspecies. For consistency and comparison purposes, this presentation is based on the geographical contours of the IUCN (Plate 11). Actually these contours are not defined by geographic boundaries, but are gradual and diffuse. For example, the occurrence of two subspecies (*S. c. caffer* and *S. c. aequinoctialis*) in Ethiopia or in the Democratic Republic of Congo is somewhat arbitrary.

Present distribution

Large discontinuities have emerged in the historical distribution range of African buffalo in areas of high human population densities, such as Nigeria or Central Ethiopia (Plate 11) African buffalo populations have undergone a severe reduction in size and geographical distribution since the nineteenth century, as a result of the combined effects of anthropogenic impacts such as land conversion, poaching, disease outbreaks and climatic events such as droughts. At present, around 70% of the savanna buffalo population is confined to a patchwork of protected areas and well-managed surrounding hunting zones, mostly loosely connected to one another (East 1998). Figure 20.1 shows the distribution of the four buffalo

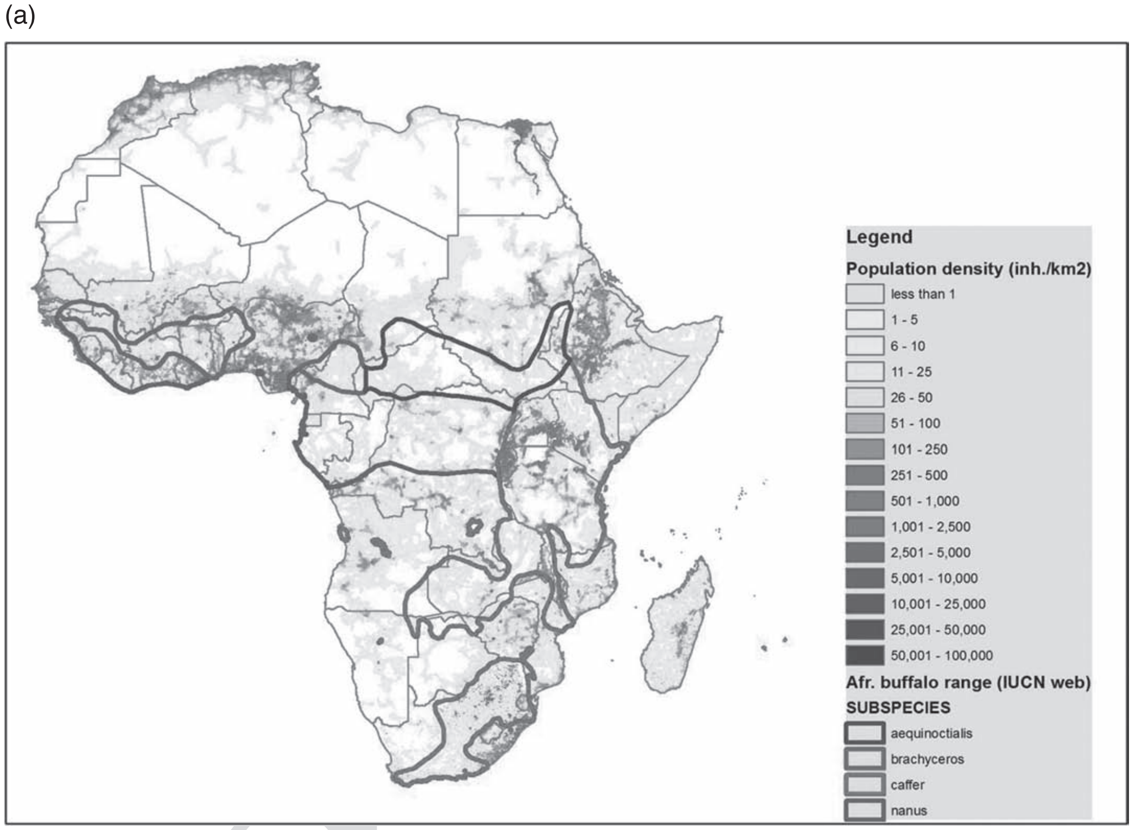

Figure 20.1 Distribution of the four African buffalo subspecies in relation to: (a) human population density; (b) average rainfall and (c) protected areas (source: IUCN SSC 2008). A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

subspecies in relation to human population density, rainfall and protected areas (East 1998; IUCN SSC 2008).

The expansion of livestock production gradually generated direct competition for space and resources and led to large and destructive epidemics in native African buffalo populations. Rinderpest was historically the most devastating disease for buffalo populations throughout Africa, leading to extreme reductions in population densities, and local extinctions. The most severe population collapse occurred in the 1890s, with mortality rates estimated at 90–95% across the continent (Sinclair 1977; Prins & van der Jeugd 1993; Winterbach 1998). This was followed by other episodes throughout the twentieth century. Rinderpest was declared eradicated in Africa by the World Animal Health Organization in 2011. During the twentieth century, the geographic distribution of buffalo has been actively reduced in several countries by large-scale culling operations and veterinary fences, in efforts to limit the transmission of several pathogens, such as foot-and-mouth disease (FMD) and trypanosomiasis, to cattle (Taylor & Martin 1987).

Recent climate fluctuations such as the drought that affected Sahelian and Sudanese regions at the end of the 1960s and Southern Africa in 1992 (Dunham 1994; Mills *et al.* 1995) have also strongly impacted buffalo populations over the past few decades. Last but not least, armed conflicts, the feeding of armies and labourers during peace time, the trafficking of weapons and bushmeat trade have strongly contributed to the reduction of buffalo populations.

Cape buffalo (*S. c. caffer*)

Cape buffalo occurs in southwestern Ethiopia (particularly Omo National Park), southern Somalia and northern Kenya southwards to South Africa. This subspecies is patchily distributed throughout East Africa, southwards to Zambia, Malawi, some parts of Mozambique (small populations south of the Zambezi river with the bulk of it in the north of the country, Niassa Reserve and Cabo Delgado areas; Skinner & Chimimba, 2005), northeastern Namibia (mainly eastern and western Caprivi, Mamili National Park and an introduced population in the Waterberg

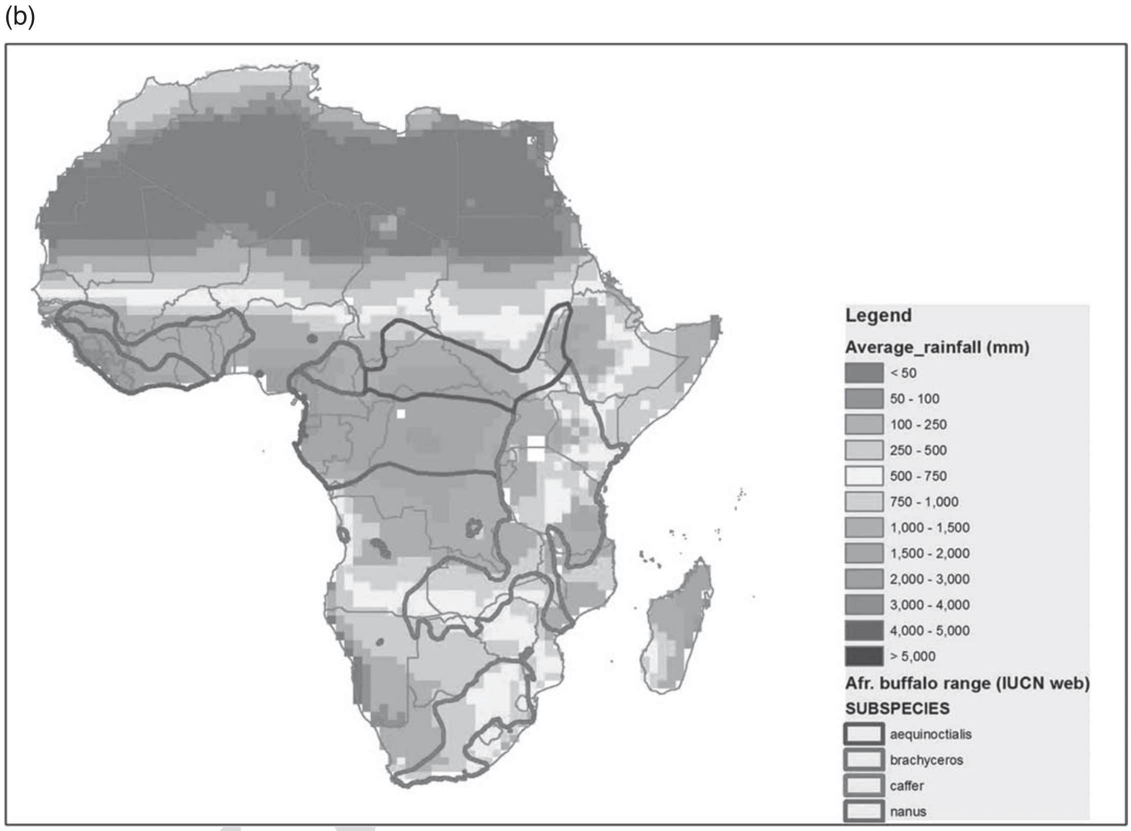

Figure 20.1 (*cont.*)

Plateau Park, central Namibia), Botswana (north of 20° S, Okavango Delta area, Moremi Game Reserve and the Chobe National Park) and Zimbabwe (Hwange National Park; Matabeleland, Zambezi Valley, south Lake Kariba and Gonarezhou National Park; Skinner & Chimimba 2005). Small populations of Cape buffalo still survive in some areas of southeast Angola bordering Zambia and Namibia. In South Africa, Cape buffalo have been reintroduced to some areas from which they were formerly extirpated. They are currently widely distributed in Kruger National Park and smaller populations persist in KwaZulu-Natal (Winterbach 1998) and in many private reserves. The current population in Swaziland was also reintroduced after extirpation.

West African savanna buffalo (*S. c. brachyceros*)

This subspecies still occurs locally in western countries within the Sahelo-Sudanian band (savannas and gallery forests), including southeastern Senegal, northern Ivory Coast, southern Burkina Faso, Ghana, northern Benin, extreme south of Niger, Nigeria (very locally), northern Cameroon and a small part in the Central African Republic (East 1998).

Central African savanna buffalo (*S. c. aequinoctialis*)

This subspecies still locally populates Central African countries within the Sahelo-Sudanian band (savannahs and gallery forests): southeast Chad, northern Central African Republic (East of Chari River), northern Democratic Republic of Congo, southeast Sudan and western Ethiopia (Ansell 1972; East 1998). The subspecies is now extinct in Eritrea.

Forest buffalo (*S. c. nanus*)

This subspecies occurs in two disjoint distribution ranges in West and Central Africa, respectively in the relict coastal rainforest belt and in the large basin of the Congo River. The distribution ranges are mainly located in areas with an annual rainfall of more than 1500 mm, in transition areas between dense tropical forests and savanna ecosystems, for instance in Gabon and Uganda (East 1999). In West Africa, forest buffalo is distributed from Guinea-Bissau to southwestern Ghana. In Central Africa, forest buffalo persist in south Nigeria, south Cameroon, Equatorial Guinea (extinct on Bioko Island), south and southwest Central African Republic, western Uganda,

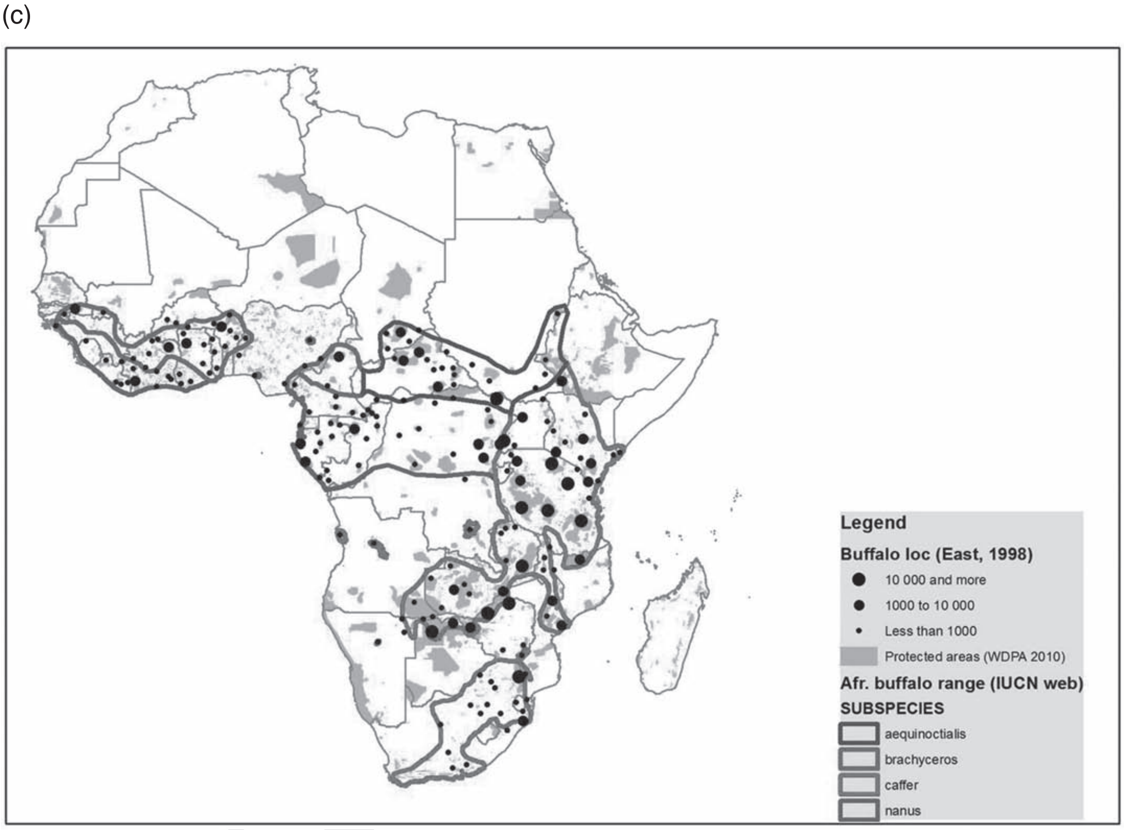

Figure 20.1 (*cont.*)

western Rwanda and possibly northwest Burundi, the Democratic Republic of Congo, the Republic of Congo and Gabon. The greatest part (i.e. 75%) of the population lives in and around protected areas in Cameroon, Central African Republic, Gabon, Democratic Republic of Congo and Republic of Congo (Wilson & Mittermeier 2011). In both distribution ranges, numbers have declined substantially due to poaching and deforestation (East 1999), but their status is generally poorly known (Blake 2002; Melletti *et al.* 2007a, 2007b; Korte 2008a).

Abundance

Over the past 60 years aerial counts have been widely used to estimate population sizes of savanna buffalo. As with any estimation technique, these methods are subject to potentially important biases (Jachmann 2002; Redfern & Viljoen 2002). During aerial counts, significant numbers of animals may be missed due to obstruction by vegetation canopy cover (e.g. high grass, forest galleries), and due to lower probability of detecting small herds. Furthermore, estimates from aerial sampling counts (ASCs) are generally less accurate (especially for small populations and low sampling rates) than aerial total counts (ATCs). Despite these limitations, aerial counts remain the most reliable approach to estimate buffalo populations in savanna ecosystems. We cite the animal numbers from the original reports, in the text, in a rounded-off form, and report to the closest 100 individuals for all figures larger than 200, while we report reserve size to the closest 10 km^2 so as to prevent reporting non-significant digits.

In the following sections and Table 20.1, we present an update of buffalo abundance and distribution per country and protected area, based on the most recent and available census data. The total estimated numbers per country are presented in Table 20.2 and compared with the last update (East 1998) in the section ‘Status in the wild’.

Cape buffalo

In **Ethiopia**, the population of Omo National Park and surrounding buffer zone (7850 km^2) was estimated at 700 individuals, based on an ASC carried out in 2007 (Renaud 2007);

Table 20.1 Abundance and distribution of the four African buffalo subspecies per country and protected area based on the most recent and available census data. Original data are presented.

Subspecies	International PA complex	Country	Protected area/ hunting blocks	Date	Method	Sampling effort[a]	Number obs.	Estimated population	Error	Error statistics	Area (km^2)	Density (ind/ km^2)	Source
S. c. aequinoctialis	/	Central African Republic	Bamingui-Bangoran NP, Manovo-Gounda-St. Floris NP and adjacent PAs	2010	ASC	7%	738	4048	± 27%	CV	94 962	0.04	Bouché 2010
	/	Chad	Zakouma NP	2012	ATC	100%	8091	8091	/	/	3026	2.67	Potgieter *et al.* 2012
	/	Democratic Republic of Congo	Garamba NP	2012	ATC	100%	5980	5980	/	/	4920	1.22	Bolanos 2012
	/	Ethiopia	Gambella NP Akobo block	2010	ASC	6%	91	1378	± 2641	SE	20 000	0.07	EWCA 2010
S. c. brachyceros	WAPOK complex (Burkina Faso, Bénin, Niger, Togo)	Benin	W NP	2003	ATC	100%	21	424	/	/	5872	0.07	Bouché *et al.* 2003
		Benin	Pendjari NP	2003	ATC	100%	124	3421	/	/	2827	1.21	
		Benin	Hunting zones (Djona, Pendjari, Konkombri and Mékrou) + Goungoun Classified Forest	2003	ATC	100%	715	715	/	/	5243	0.14	
		Burkina Faso	W NP	2003	ATC	100%	1400	1400	/	/	2412	0.58	
		Burkina Faso	Arli NP	2003	ATC	100%	399	399	/	/	485	0.82	
		Burkina Faso	Hunting zones (Tapoa djerma, Kourtiagou, Koakrana, Pagou-Tandougou, Ougarou, Pama, Singou and Konkombouri)	2003	ATC	100%	3031	3031	/	/	8124	0.37	
		Niger	W NP and Tamou Reserve	2003	ATC	100%	1170	1170	/	/	3083	0.38	
		Togo	Keran NP & Oti-Mandori Reserve	2003	ATC	100%	0	0	/	/	2886	0.00	
		Burkina Faso	Comoé-Léraba complex	2005	ATC	100%	90	90	/	/	1847	0.05	Bouché 2005
		Burkina Faso	Ponasi Complex (Nazinga GR, Kabore-Tambi NP and adjacent hunting zones)	2004	ATC	100%	145	145	/	/	3105	0.05	Bouché *et al.* 2004

Table 20.1 *(cont.)*

Subspecies	International PA complex	Country	Protected area/ hunting blocks	Date	Method	Sampling effort^a	Number obs.	Estimated population	Error	Error statistics	Area (km^2)	Density (ind/ km^2)	Source
		Cameroon	Bouba Ndjida, Faro, Benoue NPs + hunting blocks	2008	ATC	100%	630	(4000)	/	/	22 137	0.18	Omondi *et al.* 2008
		Ghana	Mole NP	2006	ATC	100%	700	700	/	/	4500	0.16	Bouché 2006
		Ivory Coast	Comoé NP	2010	ASC	6%	56	899	± 905	SD	11 945	0.08	N'Goran *et al.* 2010
		Nigeria	Yankari NP	2011	ATC	100%	174	174	/	/	2244	0.08	Bergl *et al.* 2011
		Senegal	Niokolo Koba NP	2006	ASC	40%	15	457	± 447	SE	9130	0.05	Renaud *et al.* 2006
		Senegal	Niokolo Koba NP	2003	ASC	7%	68	957	± 864	95% IC	9130	0.10	Mauvais & Ndiaye 2004
S. c. caffer		Botswana	North country (Moremi GR, Chobe National NP, Makgadikgadi Nxai Pan NP and surrounding WMAs in the Ngamiland, Chobe and Central districts)	2010	ASC	14% [5–22]	7958	39 579	± 27%	95% CI	73 478	0.54	Chase 2011
		Democratic Republic of Congo	Virunga NP	2010	ASC	?	?	2154	?	?	7823	0.28	Plumptre *et al.* 2010
		Ethiopia	Chebera Churchura NP	2005–2006	Pedestrial (LT)	5%	130	2617	± 426	SE	1215	2.15	Megaze *et al.* 2012
		Ethiopia	Omo NP and buffer zone	2007	ASC	40%	330	675	± 31%	SE (%)	7853	0.09	Renaud 2007
		Kenya	Laikipia/Samburu ecosystem	2002	ATC	100%	2012	2012	/	/	10 000	0.20	Omondi *et al.* 2002
		Kenya	Masai Mara NR/ community areas	2010	ATC	100%	4649	4649	/	/	4716	0.99	Kiambi *et al.* 2010
		Kenya	Meru Conservation Area	2007	ATC	100%	2288	2288	/	/	12 000	0.19	Mwangi *et al.* 2007
		Kenya	Nasolot/south Turkana/Rimoi/ Kamnarok	2010	ATC	100%	0	0	/	/	4551	0.00	Edebe *et al.* 2010
		Mozambique	Chipanje Chetu	2011	ASC	11%	10	/	/	/	6641	/	Craig 2011b
		Mozambique	Niassa Reserve	2011	ASC	10%	644	6214	[3462–8967]	95% CI	42 296	0.15	Craig 2011a

Mozambique	East Musengezi River (south Lake Cabora Bassa)	2010	ASC	25%	41	143	± 177%	95% CI	13 962	0.01	Dunham 2010
Mozambique	West the Musengezi River (south Lake Cabora Bassa)	2010	ASC	12%	587	4483	± 107%	95% CI	2621	1.71	Dunham 2010
Mozambique	Banhine NP	2009	ASC	19%	16	/	/	/	1192	/	Stalmans & Peel 2009
Mozambique	Quirimbas NP	2011	ASC	10%	0	0	/	/	20 834	0.00	Craig 2011c
Mozambique	Marromeu Complex	2010	ATC	100%	10 300	10 300	/	/	11 270	0.91	Beilfuss *et al.* 2010
Mozambique	Zinave NP and surrounding area	2010	ASC	15.2% [6–21]	0	0	/	/	9 231	0.00	Dunham *et al.* 2010
Namibia	Caprivi River Systems	2007	ATC	100%	5971	5971	/	/	1778	3.34	Chase 2007
Rwanda	Akagera National Park	2010	SRF		?	?			1120		Viljoen *et al.* 2010
South Africa	Kruger NP	2011	ATC	100%	40 922	40 922	/	/	20 000	2.05	Ferreira *et al.* 2012
Tanzania	Selous ecosystem	2002	ASC	?	?	280 701	± 61 278	SE	94 009	2.99	Debonnet & Wilson 2008
Tanzania	Selous ecosystem	2006	ASC	?	?	113 463	± 25 613	SE	80 883	1.40	Debonnet & Wilson 2008
Tanzania	Selous-Niassa Wildlife Corridor	2006	ASC	5%	94	1456	± 949	SE	9096	0.16	Tawiri 2006
Tanzania	Selous-Niassa Wildlife Corridor	2009	ASC	10%	418	4095	± 2116	SE	9096	0.45	Tawiri 2009
Tanzania	Serengeti Ecosystem (Serengeti NP, Maswa and Ikorongo-Grumeti GRs, Ngorongoro CA, Liliondo GCA and adjacent areas)	2009	ATC	100%	32 068	32 068	/	/	26 827	1.20	Tawiri 2010
Tanzania	Katavi-Rukwa ecosystem	1988–2002	ATC	?	?	39 557	?	?	8 494	4.65	Caro 2008
Uganda	Murchison Falls PA (Murchison Falls NP, Bugungu & Karuma WRs)	2010	ATC	?	356	9192	± 3789	SE	5044	1.82	Rwetsiba & Nuwamanya 2010
Uganda	Kidepo NP	2008	ATC	100%	3643	3643	/	/	1128	3.23	WCS Flight Programme 2008

Table 20.1 *(cont.)*

Subspecies	International PA complex	Country	Protected area/ hunting blocks	Date	Method	Sampling effort^a	Number obs.	Estimated population	Error	Error statistics	Area (km^2)	Density (ind/ km^2)	Source
		Uganda	Queen Elizabeth NP	2010	ATC	100%	10 282	10 282	/	/	2113	4.87	Plumptre *et al.* 2010
		Zambia	Kafue Ecosystem	2011	ASC	3–12%	/	4566	± 687	SE	70 000	0.07	Frederick 2011
		Zambia	Luanga Valley ecosystem	2008	ASC	12%	1540	17 155	± 3,673	95% CI	49 700	0.35	WCS Flight Programme 2009
		Zimbabwe	Gonarezhou complex (Gonarhezou NP, Malipati SA and surrounding CLs)	2010	ASC	15.2% [6–21]	558	2742	± 75.8%	95% CI	7112	0.39	Dunham *et al.* 2010
		Zimbabwe	Sebungwe Region (Chizarira and Matusadona NPs, Chiziza/Chete SAs, P&W Estate, Sajarira FA, North Gokwe, Binga Kariba CLs)	2006	ASC	15%[7–23]	1771	10 395	± 37.6%	95% CI	15 622	0.67	Dunham *et al.* 2006
		Zimbabwe	Hwange-Matetsi complex and adjacent areas (Zakuma NP, Deka SA, Ngamo and Sikumi Forest Areas and Tsholotsho and Maitengwe CL)	2007	ASC	8%[3–15]	1461	24 500	±120%	95% CI	24 570	1.00	Dunham *et al.* 2007
	Amboseli-West Kilimanjaro/ Magadi – Natron (Kenya, Tanzania)	Kenya/ Tanzania	Amboseli NP	2010	ATC	100%	235	235	/	/	8797	0.03	WCS Flight Programme 2010
			Namanga-Magadi	2010	ATC	100%	62	62	/	/	5513	0.01	
			Lake Natron	2010	ATC	100%	37	37	/	/	7047	0.01	
			West Kilimanjaro	2010	ATC	100%	0	0	/	/	3014	0.00	

	Tsavo/ Mkomazi ecosystem	Kenya	Tsavo East and West, Chyulu NP, South Kitui NR, Galana, Taita and Rombo blocks	2011	ATC	100%	7281	7281	/	/	45 126	0.16	Ngene *et al.* 2011
		Tanzania	Mkomazi NP				121	121			3193	0.04	
	Zambezi Heartland (Mozambique, Zambia, Zimbabwe)	Mozambique	Lake Cabora Bassa	2003	ASC	15%	265	1561	± 90%	95% CI	6329	0.25	Dunham 2004
		Zambia	Lower Zambezi NP, Chiawa and Rufunsa GMAs/Tonga-Sikongo CL		ASC		844	6658	± 102%	95% CI	11 954	0.56	
		Zimbabwe	Mana Pools NP, Hurungwe, Sapi, Charara, Dande, Chewore SAs and part of Guruve District		ASC		3537	19 527	± 37%	95% CI	13 373	1.46	
S. c. nanus		Cameroon	Campo Ma'an NP	2000–2002	Pedestrial (LT)	/	/	20	/	95% CI	650	0.01	Bekhuis *et al.* 2008
		Central African Republic	Dzanga-Ndoki NP (Dzanga sector)	2002–2004	Pedestrial (RT)	5%	32	40	/	/	495	0.08	Melletti 2005; Melletti *et al.* 2007a
		Gabon	Lope´ NP (northeast sector)	2002–2004	Ground survey	/	/	342	/	/	72	5	Korte 2008b
		Gabon	Réserve de Faune de Petit Loango	2006	Ground survey	/	/	/	/	/	500	1.70	Morgan 2007
		Republic of Congo	Noubale-Ndoki NP	1993–2000	Pedestrial (LT)	/	/	/	/	/	3920	0.01	Blake 2002
		Republic of Congo	Odzala NP	1990s	Ground survey	/	/	500	/	/	13 600	0.04	Chamberlan *et al.* 1995

ASC: aerial sampling counts; **ATC**: aerial total counts; **CA**: conservation area; **CL**: communal land; **FA**: forest area; **GCA**: game controlled area; **GR**: game reserve; **LT**: line transect; **NP**: national park; **NR**: national reserve; **RT**: recce transect; **SA**: safari area; **SRF**: systematic reconnaissance flight; **WMA**: wildlife management area; **WR**: wildlife reserve.

[a] Sampling efforts generally are weighted means of several block counts sampled at different intensities

Table 20.2 The total estimated numbers of three African buffalo savanna subspecies per country are presented and compared with the last update of East (1998)

		East (1998)	**Cornélis, Melletti, Korte, *et al*. (this study)**
S. c. aequinoctialis		**>59 000**	**>23 000**
	Central African Republic	19 000	4050
	Chad	1020	8090
	Democratic Republic of Congo	39 180	5980
	Eritrea	Ex	Ex
	Ethiopia	x	4380
	Sudan	>100	(8900)
S.c. brachyceros		**>20 000**	**> 17 000**
	Benin	>2000	4560
	Burkina Faso	1620	5070
	Cameroon	3210	4000
	Gambia	Ex	Ex
	Ghana	C	700
	Guinea	V	V
	Guinea Bissau	x	?
	Ivory Coast	8330	900
	Mali	120	Ex?
	Niger	500	1170
	Nigeria	>200	>170
	Senegal	>4000	460
	Togo	U/R	x
S. c. caffer		**> 548 000**	**> 473 000**
	Angola	<500	x
	Botswana	26 890	39 580
	Burundi	500	Uk
	Democratic Republic of Congo	No data	2150
	Ethiopia	2330	3600
	Kenya	>19 560	>16 560
	Malawi	>3150	Uk
	Mozambique	9570	23 310
	Namibia	1000	6000
	Rwanda	1200	R
	Somalia	U	Uk
	South Africa	30 970	>77 800
	Swaziland	U	Uk
	Tanzania	>342 450	>189 230
	Uganda	>20 220	23 120
	Zambia	>40 090	>28 330
	Zimbabwe	50 330	63 000
Total		**>627 000**	**>513 000**

-: absent; **?**: may occur but current presence not confirmed; **Ab**: abundant; **C**: Common; **Ex**: Extinct; **Ex?**: probably extinct; **R**: rare; **U**: uncommon; **Uk**: unknown; **V**: occurs only as a vagrant; **x**: definitely present but abundance unknown

this represents a 64% decrease since an ASC conducted in 1996 (Graham *et al.* 1996). At most 300 individuals are estimated to range within Mago National Park and Tama Wildlife Reserve (respectively 1940 and 1670 km^2, east of Omo National Park; Ludwig Siege, EWCA, personal communication). Further north, in Chebera Churchura National Park (1220 km^2), the buffalo population was estimated (line transect; LT) in 2006 at 2600 individuals (Megaze *et al.* 2012).

In **Uganda**, data from the 2010 ASC of Murchison Falls Protected Area estimated a population of 9200 buffalo within an area of 5040 km^2 (Rwetsiba & Nuwamanya 2010). In Kidepo National Park and surrounding areas (1130 km^2) the last ATC estimated a total population of 3600 individuals, primarily located inside the park (WCS Flight Programme 2008). In Queen Elizabeth National Park (2110 km^2), the most recent ATC reported 10 300 buffalo (Plumptre *et al.* 2010).

In the Akagera National Park (**Rwanda**), the buffalo population was estimated at 7800 individuals in the late 1970s (Monfort 1979). During civil unrest in the 1990s, their population was severely reduced. In 1997 Akagera National Park was reduced in size from more than 2500 km^2 to its current extent of 1120 km^2 (East 1999). An aerial survey (SRF; systematic reconnaissance flight) was carried out in 2010 and small numbers of buffalo were sighted in Akagera National Park (average group size 23; individuals $n = 38$) and Gabiro area (average group size 39; individuals $n = 9$), but no reliable population estimate is available (Viljoen *et al.* 2010).

In Virunga National Park (Democratic Republic of Congo, 7820 km^2), an ASC carried out in 2010 reported 2100 buffalo

(Plumptre *et al.* 2010). In the south of the country (Katanga province), the buffalo population in Upemba National Park (10 000 km^2) and Kundelungu National Park (2200 km^2) is on the brink of extinction with just 15 individuals observed in 2008 surveys (Vanleeuwe *et al.* 2008). In these parks wildlife was abundant throughout the 1980s but then rapidly declined in the 1990s and 2000s due to economic and political instability, and subsequent insecurity (Vanleeuwe *et al.* 2008).

In **Kenya**, the status of buffalo varies with the locality considered. In the northern part of the country (Nasolot, south Turkana, Rimoi and Kamnarok region; 4550 km^2) no buffalo were recorded during an ATC conducted in 2010 (Edebe *et al.* 2010). In Laikipia/Samburu ecosystem (an area covering about 10 000 km^2), 2002 aerial surveys reported 2000 buffalo, with an estimated 30% decrease between 1999 and 2002; the largest reported decline (55%) was in Samburu area (Omondi *et al.* 2002). In Meru Conservation Area (4010 km^2, covering Meru National Park, Kora National Park, Bisinadi, Mwingi and North Kitui National Reserves), there were 1800 individuals (wet season), and 2300 (dry season) (Mwangi *et al.* 2007). In Masai Mara National Reserve and community areas (4720 km^2), the buffalo population was estimated at 4600 individuals in 2010 (Kiambi *et al.* 2010).

In Amboseli-West Kilimanjaro/Magadi-Natron protected areas (Kenya/Tanzania border, 24 370 km^2) an ATC estimated the population at 300 individuals (90% in the Kenya section) (WCS Flight Programme 2010). In Tsavo/Mkomazi ecosystem (Kenya/Tanzania border, 48 320 km^2) the last three ATCs reported estimates of 9400 (2005), 5600 (2008) and 7400 (2011) individuals (Ngene *et al.* 2011). During the last ATC, 98% of the buffalo (7300 individuals) were observed in the Kenyan section of the Tsavo/Mkomazi ecosystem.

Tanzania has the largest African buffalo population, with over 342 000 individuals recorded in the last update (East 1998). Buffalo are common in most of the country's major wildlife areas, e.g. Selous Game Reserve, Serengeti, Tarangire and Katavi National Parks, the Ruaha ecosystem and the Katavi-Rukwa and Kilombero Game Controlled Areas. The Selous ecosystem (over 90 000 km^2, southern Tanzania) certainly has the largest buffalo population in Africa and over half of Tanzania's. Recent ASCs reported a population estimate of 280 700 individuals in 2002 (94 000 km^2) and 113 500 (80 890 km^2) individuals in 2006 (Debonnet & Wilson 2008). In Selous-Niassa Wildlife Corridor (9100 km^2), a region bordering Mozambique, dry season ASCs conducted in 2006 and 2009 reported 1500 and 4100 buffalo, respectively (Tawiri 2006, 2009). In the Serengeti ecosystem (north Tanzania), ATCs conducted in 2008 and 2009 (covering 26 830 km^2) recorded 32 900 and 32 100 buffalo, respectively. The population numbers for 2008 and 2009 surveys were the highest for the Serengeti ecosystem in 14 years (Taiwiri 2010). In Katavi-Rukwa ecosystem (8500 km^2, Tanzania) the buffalo population was estimated at 39 600 individuals (surveys 1988–2002; Caro 2008). A review of aerial census data collected during the late 1980s to early 2000s in eight large census zones of Tanzania suggests that buffalo populations globally remained stable in Tarangire census zone, but declined in Burigi Biharamulo, Greater Ruaha, Katavi and Moyowosi-Kigosi census zones during the time period considered (Stoner *et al.* 2006).

In **Mozambique**, buffalo populations occurred throughout the country until the 1970s, but suffered greatly from the former civil conflict (1977–1992). In Niassa Reserve (42 300 km^2) buffalo were successively estimated at 2300 (2006), 6800 (2009) and 6200 (2011) individuals (Craig 2011a). In Quirimbas National Park and adjacent areas, an ASC undertaken in 2011 over 20 830 km^2 reported no buffalo observations (Craig 2011c). In Chipanje Chetu area, an ASC conducted in 2011 (area surveyed: 6640 km^2) reported the observation of a single herd (ten individuals; Craig 2011b). In southern Cabora Bassa region (northwest Mozambique), an ASC undertaken in 2010 estimated the buffalo population at 4600 individuals (area surveyed: 16 590 km^2) (Dunham 2010). In Gilé National Reserve, no buffalo observation was reported by the ASC conducted in 2007 (Mesochina *et al.* 2008), but a reintroduction programme is currently ongoing (20 buffalo reintroduced from Gorongosa National Park in 2012). Central Mozambique hosts residual populations of buffalo, except the open floodplains of the Marromeu Complex (11 270 km^2), with an estimated population >10 300 individuals (Beilfuss *et al.* 2010). Buffalo were extinct in Gorongosa National Park (4000 km^2) and the population (360 individuals; 2010 estimate) was restocked (2006–2011) with 186 buffalo from Kruger and Limpopo National Parks (Carlos L. Pereira, personal communication). In south Mozambique, 16 individuals were recorded by ASC in Banhine National Park (1190 km^2) in 2009 (Stalmans & Peel 2009). In the Limpopo National Park (11 230 km^2) an ASC conducted in 2007 estimated the buffalo population at around 200 (Swanepoel 2007).

In **Zambia**, aerial surveys were conducted in the Kafue ecosystem (Kafue National Park and surrounding game management areas combined). In 2008, 6300 buffalo were recorded in an area of 48 000 km^2, and in 2011, 4600 individuals were recorded in an area of 70 000 km^2. The 2011 survey used a combination of total and sample counts and was more accurate than the previous 2008 survey (Frederick 2009, 2011). In Luanga Valley ecosystem (49 700 km^2; eastern Zambia), an ASC conducted in 2008 reported an estimation of 17,200 buffalo (WCS Flight Programme 2009).

A transfrontier ASC conducted in 2003 in the Zambezi Heartland between Lakes Kariba and Cabora Bassa (Zimbabwe, Mozambique and Zambia; 31 660 km^2) estimated the buffalo population at 27 700 individuals (Dunham 2004). In Zimbabwe, the buffalo population estimate was 19 500 (13 373 km^2, including Mana Pools National Park, Hurungwe, Sapi, Charara, Dande, Chewore Safari Area and part of Guruve District). In Mozambique the estimate was 1 600 (6330 km^2; communal lands south and north of Lake Cabora Bassa and east of the Luangwa River). No buffalo were observed north of Lake Cabora Bassa. In Zambia the buffalo population estimate was 6700 (11 950 km^2, including Lower Zambezi National Park, Chiawa and Rufunsa Game Management Areas and Tonga-Sikongo communal land).

In **Zimbabwe**, an ASC conducted in 2006 in the Sebungwe region (15 620 km^2, including Chizarira and Matusadona National Parks, Chiziza and Chete Safari Areas, P&W Estate, Sajarira Forest Area and North Gokwe, Binga Kariba communal lands) reported an estimate of 10 400 buffalo (Dunham *et al.* 2006). A 2007 ASC conducted in Hwange-Matetsi complex and adjacent areas (24 570 km^2, including Zakuma National Park, Deka Safari Area, Ngamo and Sikumi Forest Areas and Tsholotsho and Maitengwe communal lands) estimated 24 500 buffalo (Dunham *et al.* 2007). In Gonarezhou complex (7110 km^2, including Gonarhezou National Park, Malipati Safari Area and surrounding communal lands), an ASC conducted in 2010 reported 2700 buffalo (Dunham *et al.* 2010). Other substantial buffalo populations also occur in several conservancies in southeast Lowveld, among which are Save Valley (3340 km^2, 1900 individuals in 2002), Bubye Valley (3430 km^2, about 3000 individuals) and Nuanetsi Conservancies (1490 km^2, about 1000 individuals) (Chris Foggin, personal communication).

In **Angola**, buffalo have been wiped out by uncontrolled hunting and poaching throughout the country, including Kissama National Park, where East (1998) reported a declining population of the transitional 'red' buffalo. Residual populations may still range in the areas north of Luanda, in Cabinda and Cangandala National Park. In the southeast, typical Cape buffalo may still occur in Quando Cabando (Wouter Van Hoven, personal communication), but the numbers are unknown.

In **Botswana**, buffalo are found only north of 20° S in the Okavango-Chobe region. In 2010, an ASC covering northern Botswana, (73 480 km^2, including Moremi Game Reserve, Chobe National Park, Makgadikgadi Nxai Pan National Park and surrounding wildlife management areas) estimated the population at 39 600 individuals (Chase 2011).

In **Namibia**, buffalo were largely eradicated as part of a veterinary campaign. The construction of the veterinary cordon fences along the international border with Botswana is thought to be a factor responsible for buffalo decline (Martin 2002). An ATC conducted in 2007 on the Caprivi River systems (area covered: 1780 km^2) reported 5900 buffalo (Chase 2007). A small population (about 50 buffaloes) was introduced in Waterberg Plateau Park (400 km^2) between 1981 and 1991 and increased to 200 in 2000, and a relict population of 70 animals still occurs in Bushmanland (Tsumkwe area; 24 km^2; Martin 2002).

In **South Africa**, buffalo were extirpated from their former range except for a few areas such as Kruger National Park (20 000 km^2), where the country's major population now occurs (37 500 in 2009 and 40 900 in 2011; Ferreira *et al.* 2010, 2011, 2012). About 4000 buffalo persist in Hluhluwe-Imfolozi Park (900 km^2; Jolles 2007). Buffalo from Hluhluwe-Imfolozi and Kruger National Park are known carriers of diseases transmissible to cattle and thus cannot be translocated from one region of South Africa to another. The buffalo population in Mokala National Park (270 km^2) was estimated at 400 in 2012. In Addo Complex area (1640 km^2) 300 were counted in 2011. In Karoo National Park (770 km^2) only four individuals were observed from 2010 to 2012. In Mountain Zebra National Park (280 km^2) 77 individuals were counted in 2012. Mount Camdeboo Game Reserve (140 km^2) presented stable numbers at 30–36 in 2010–2011 surveys (Ferreira *et al.* 2012). There are approximately 32 000 disease-free buffalo in South Africa. Six thousand of these are in national or provincial parks, while the remaining 26 000 are privately owned and resident on approximately 2700 private game ranches or reserves (South African Private Buffalo Owners Association, personal communication).

West African savanna buffalo

In West Africa, buffalo numbers have declined alarmingly during the last decade. Since East's (1998) assessment, populations larger than 1000 individuals persist in only two of five sites. In West Africa, more than anywhere else in Africa, savanna buffalo populations are restricted within the borders of a limited number of protected areas.

In **Senegal**, the last buffalo population is located in Niokolo Koba National Park (9130 km^2). This population was estimated by ASC at 1000 and at 500 in 2003 and 2006, respectively (Mauvais & Ndiaye 2004; Renaud *et al.* 2006). An estimation dating from the early 1990s by pedestrian sampling count (PSC) was of 11 000 individuals (Galat *et al.* 1992).

This subspecies is now extinct in the **Gambia** (Jallow *et al.* 2004).

In **Mali**, the buffalo is extinct in the Boucle de la Baoulé National Park, but a relict population may still occur along the border with Senegal in the riverine forest of the Faleme Hunting Zone, and maybe in Bafing National Park (Bourama Niagate, personal communication).

In **Guinea Conakry**, Sudanian savannas still locally host small populations in protected areas (Kankan Forest reserve, Bakoun classified forest or Bakoy sector), but no population estimate is available (Brugière 2012).

In **Ivory Coast**, savanna buffalo still range in Comoé National Park (11 950 km^2), where the population was estimated (ASC) at 900 individuals in 2010, representing an 80% decline since the 1970s (N'Goran *et al.* 2010).

The largest buffalo population of West Africa is located in WAP Regional Park (28 350 km^2)in **Benin**, **Burkina Faso** and **Niger**. This complex comprises three national parks ('W', Arly and Pendjari) and several hunting zones, containing a buffalo population estimated by ATC in 2003 at 10 600 individuals (Bouché *et al.* 2003). Of these, about one-third (3400) were located in Pendjari National Park (2 830 km^2). Counts have not been repeated for the entire area since 2003. However, recent counts conducted at Pendjari National Park suggest a decreasing trend in population (Sinsin *et al.* 2008), while the 'W' National

Park population has remained fairly stable or increased (Bouché 2012).

In **Burkina Faso**, ATCs conducted on Ponasi (3100 km^2) and Comoé-Leraba (1850 km^2) protected area complexes estimated the buffalo population at 145 and 90 individuals, respectively (Bouché *et al.* 2004; Bouché 2005).

In Mole National Park (4500 km^2, **Ghana**), 500 and 700 individuals were counted in 2004 (ASC) and 2006 (ATC), respectively (Mackie 2004; Bouché 2006), whereas the population was estimated (ASC) at 1700 individuals in 1993 (Wilson 1993), suggesting an overall decline in numbers. The presence of buffalo has been reported in 2013 in Kyabobo National Park along the Togo border (Fazao Malfakassa National Park; D. Brugière, personal communication).

In **Togo** no buffalo were observed during the ATC carried out in Keran National Park (1400 km^2) and in Oti-Mandori Faunal Reserve (1800 km^2; Bouché *et al.* 2003).

In **Nigeria**, the West African savanna buffalo formerly occurred widely in the northern savannas, but has been extirpated from most of its former range. To our knowledge, a relict population remains in the National Parks of Yankari (2240 km^2; 170 individuals) (Bergl *et al.* 2011) and Kainji Lake (not estimated; Aremu *et al.* 2007).

In Northern **Cameroon**, an ATC conducted in 2008 in the complex of protected areas of Faro, Benoue and Bouba Ndjidda National Parks and their adjacent hunting blocks (22 140 km^2 in total) found 600 individuals (Omondi *et al.* 2008). It is likely that this figure is a gross underestimate due to inappropriate transect inter-distance (3–5 km). On the basis of empirical correction factors (effective bandwidth of 200–300 m), the size of the population can be estimated at around 4000 individuals.

Central African savanna buffalo

Most Central African savanna buffalo populations declined alarmingly during the last decades, and few protected areas still encompass significant (>1000) numbers. However, in contrast to West Africa, the savannas of Central Africa are less degraded overall, and still host diffuse (low density, small size) populations of buffalo in many areas.

One of the largest populations is located in **Chad** (Zakouma National Park; 3030 km^2), where the ATC carried out in 2012 reported an estimate of 8100 individuals (Potgieter *et al.* 2012). Interestingly, the Zakouma population is still increasing (due to intense conservation efforts), with a mean annual growth rate of 8% during the four last years.

A second important population is located in the northeast of the **Central African Republic**, in a complex of protected areas (94 960 km^2) comprising Bamingui-Bangoran National Park, Manovo-Gounda-St. Floris National Park and protected areas of diverse statuses. This complex includes a population estimate in 2010 (ASC) of 4000 individuals (Bouche 2010). The comparison with prior ASCs emphasized a population decline of 31% between 1985 and 2005 (Douglas Hamilton *et al.* 1985) and a drastic decline (76%) between 2005 and 2010 (Renaud 2005). In 2010 most herds were found in hunting zones, while the national parks and reserves were occupied by transhumant cattle. No information currently exists from Bangassou Forest Reserve (12 080 km^2) where East (1998) reported a population greater than 1000 individuals.

In **South Sudan**, ASCs carried out in 2007 (Fay *et al.* 2007) in an area larger than 150 000 km^2 revealed sizeable buffalo population estimates (8900), mainly located in Boma National Park (22 800 km^2), but these figures may be inferred from very few sightings and thus strongly overestimated. However, comparison with an ATC conducted over the same area (using the same methods) in 1981 indicates that buffalo populations declined by at least 80% in 25 years. No buffalo were observed in 2007 in Southern National Park (23 000 km^2) although 60 000 were counted in 1981. In northern **Democratic Republic of Congo**, ATCs carried out in Garamba National Park (4 920 km^2) in 2007 and 2012 reported estimates of 5200 and 6000 buffalo, respectively (Bolanos 2012). In **Ethiopia**, an ASC conducted in 2010 in Gambella National Park (20 000 km^2) and adjacent areas reported 1400 individuals (EWCA 2010), but this inference was based on very few observations and is to be taken with precaution. Roughly 3000 buffalo are estimated to range in Dati area, north of Gambella (EWCA, unpublished).

Forest buffalo

Forest buffalo population estimates are available for only a few sites. At Lopé National Park (**Gabon**), the population is using a mosaic landscape of forest and equatorial savanna (70 km^2) in the northeast corner of the park, and is estimated to be 300 individuals, organized into 18 herds (Korte 2008b). In Odzala National Park, **Republic of Congo**, the population is estimated to be 500 buffalo subdivided mainly into three large herds (Chamberlan *et al.*, 1995).

Bekhuis *et al.* (2008) estimated a population of 20 buffalo in an area of 650 km^2 in **Cameroon** at Campo-Ma'an National Park. At the Dzanga sector of Dzanga-Ndoki National Park, **Central African Republic**, the population is estimated between 32 and 40 individuals in two herds in 500 km^2 of rainforest (Melletti 2005; Melletti *et al.* 2007a).

Density

Buffalo density is dependent on many factors, including the spatiotemporal distribution of resources (water, forage quality and quantity), and also in conjunction with epidemiological, conservation and management contexts.

Cape buffalo may locally reach very high densities (20 individuals/km^2) in optimal habitats such as Lake Manyara National Park (Tanzania), where both high-quality forage and water are available year-round (Prins 1996). In contrast, in the woodlands of the nearby Serengeti National Park, lower densities were reported (8 individuals/km^2; Sinclair 1977). In the northern section of Akagera National Park (Rwanda), high

Table 20.3 Main differences between the four African buffalo subspecies

African buffalo subspecies	Syncerus caffer caffer	Syncerus caffer brachyceros	Syncerus caffer nanus	Syncerus caffer aequinoctialis
Main habitat	Different types of woodland and open arid savannas, montane grassland	Different types of woodland and open savannas	Rainforest, natural forest clearings, equatorial savanna, forest logging roads, coastal forest	Different types of woodland and open savannas
Home range size (km^2)	Range 0.5–1537 [1]	Range 172–620	Range 2.3–8.0	
Herd size (individuals)	Range 10–1654 2000–4000 [2]	Range 19–150	Range 3–24	Range 2–800 Mean 24.8 [5]; 7.7 [4]
Density (individuals/km^2)	Range 0.7–20	Range 0.8 [4]–1.19 [5]	Range 0.01–7.4	Range 2.55 [5]; 1.75 [4] Mean 2.15
Daily movement (km)	Range 1–15 [1]	Range 5–15 [3]	Range 1–4 [3]	
Calving interval (months)	Range 12–36	~24	~24	~24
Herd structure	Many males in mixed herds; bachelor groups; lone males; fission–fusion patterns	Many males in mixed herds; bachelor groups; lone males; fission–fusion patterns	Only 1–2 males in mixed herds; no bachelor groups; few lone males; fission–fusion patterns	Many males in mixed herds; bachelor groups; lone males; fission–fusion patterns
References	Prins & Sinclair 2013; Bennitt 2012; Naidoo *et al.* 2012; Chase 2011; Ryan *et al.* 2007; Hunter 1996; Prins 1996, 1989b; Funston *et al.* 1994; Prins & Douglas-Hamilton 1990; Conybeare 1980; Sinclair 1977; Cobb 1976	Cornelis *et al.* 2011; Sinsin *et al.* 2008; Stark 1986	Korte 2008a, 2008b; Melletti 2008; Bekhuis *et al.* 2008; Melletti *et al.* 2007a; Morgan 2007; Van Der Hoeven *et al.* 2004; Tutin *et al.* 1997	

[1] Migratory subpopulation combined for different areas
[2] Possible temporary associations of two or more herds
[3] Mixed herds
[4] Dry season (Stark 1986)
[5] Wet season (Stark 1986)

densities were also reported (13 individuals/km^2) until the 1990s. To date, in well-managed protected areas such as Selous reserve (South Tanzania), Kruger National Park (South Africa), or Hwange National Park (Zimbabwe), the average density of Cape buffalo ranges between 1 and 3 individuals/km^2.

West and Central African savanna buffalo range on soils poorer in nutrients than those of Cape buffalo habitats and display lower densities (0.5–1.5 individuals/km^2) in the well-managed protected areas (e.g. within WAPOK complex). Historically, higher densities were observed in several large floodplains (e.g. South Sudan, north Central African Republic), but these areas are now dominated by cattle and crop production, or were heavily poached. At present, high buffalo densities are still observed in the floodplains of Zakouma National Park (Chad; 2.4 individuals/km^2).

In Campo Ma'an National Park (Cameroon) the density of forest buffalo is 0.01–0.04 individuals/km^2 in 650 km^2. Most of this forest has a closed canopy without grass in the understory (Bekhuis *et al.* 2008), leading to low buffalo densities. The same holds for Nouabalé-Ndoki National Park in adjacent Republic of Congo (Blake 2002) and the coastal rainforests of Gabon (Prins & Reitsma 1989). In Dzanga-Ndoki National Park (Dzanga sector, 490 km^2) in Central African Republic the density is between 0.06–0.08 individuals/km^2 (Melletti 2005). In Lopé National Park (Gabon), buffalo density is locally high (5 individuals/km^2; 70 km^2 of the northeast corner of the park) in the forest–savanna mosaic, but lower (0.4 individuals/km^2) in the surrounding forest (White 1992; Korte 2008b). In the Réserve de Faune de Petit Loango (Gabon) the density was locally estimated at 1.7 individuals/km^2 in a coastal habitat (Morgan 2007).

More details on density in different areas are summarized in Tables 20.1 and 20.3.

Descriptive notes

Among African mammals, the buffalo has (with the African elephant) a very marked polymorphism across its range. The size, pelage colour and shape of horns differ greatly by region.

The African buffalo is the largest and most massive bovid of the African continent, with a broad head and short, thick legs and neck. Horns are present in both sexes. The front hooves are larger than the hind to support the heavy weight of the trunk and the head. The muzzle is wide, with a wet nose, large eyes, and drooping fringed ears. Females have a small, rounded udder with two pairs of inguinal mammae. Adult males have a tufted penis. Buffalo have sweat glands but no specialized olfactory skin glands. The tail is tufted with dark hair, and adult males sometimes appear to have a beard. The sense of smell in the buffalo is highly developed. Buffalo also seem to have good eyesight, and can spot predators from a great distance (Prins & Sinclair 2013).

The deciduous dentition is: I 0/3, C 0/1, P 3/3 = 20; by the ninth month of age the temporary teeth have erupted. Crown height and enamel ridge pattern, together with stages of tooth eruption, can be used for ageing buffalo and results are identical for populations of Western, Eastern and Southern Africa (Grimsdell 1969, 1973a; Spinage & Brown 1988; Taylor 1988). The permanent molars erupt at about 3.5 years of age. The lower canines erupt between 4.5 and 5.5 years old. Each year, one cementum line develops, making dental analysis a useful tool for ageing buffalo. Dental formula is: I 0/3, C 0/1, P 3/3, M 3/3 (× 2) = 32. The structure and adaptation of the stomach is described in Chapter 6.

Cape buffalo

Body measurements: **Shoulder height**: 140–160 cm (Ansell 1972); **Head and body length**: 210–300 cm; **Tail length**: 75–120 cm; Body mass: females up to 500 kg, males from 650 kg (Ansell 1972) to 900 kg. Their skin can be thicker than 2–3 cm. The main morphological differences between the four buffalo subspecies are shown in Figure 20.2.

The world trophy record (horn span) comes from Lake Manyara (Tanzania): 165 cm (bull) and 150 cm (cow). The mean live mass of Southern African adult bulls is 753 kg. Muscular tissues represent 40.6% of the live mass and fat 5.6% of carcass mass (Du Toit 2005).

The Cape buffalo is the largest subspecies, heavily built, with the biggest horns, including strong development of bosses in the horns of the males (Prins & Sinclair 2013). Bulls have a hump above the shoulders that supports the heavy head and horns. The pelage colour varies from black to reddish-brown. Horns are large in both sexes. The body is covered by short hair, with some areas where it is absent. Juveniles have a denser coat than adults and may go through colour changes from yellowish-brown to dark brown before they attain the typical adult black. Red calves are also present up to 30% in some Cape buffalo populations (Prins 1996). Colour mutations have been described in two individuals from Luangwa valley (Zambia), with a white band around the body (Skinner & Chimimba 2005), considered partial albinism.

Cape buffalo males have laterally extending curved horns, large bosses, and when adult, little or no hair between the horns. Females have more slender horns, also laterally extending, with hair on the skin between the horns. The tips of the horns often show signs of breakage. Bosses are very variable in size and do not develop until males are 3–5 years old. There is no relation between the age of an adult male (older than five years) and the size of the boss (Prins & Sinclair 2013). Male's horns become conspicuously roughened after some 4–5 years. In particular in the southern savanna males, the basal horn sheaths expand medially and anteposteriorly across heavily roughened frontals that are up-arched to form prominent bosses (Klein 1994). These bosses are not formed in females. When bulls are sparring, they place their bosses against each other and push. Extensive bossing is a recently derived feature that developed only in the Late Quaternary (Gentry 1978, 1990). It does not occur in the *nanus* subspecies, where fights are infrequent (Kingdon 1997; Van Hooft *et al.* 2002). Since extensive bossing only occurs in adult males, it probably evolved through sexual selection; it occurs particularly in Cape buffalo in east and southern Africa, which are characterized by large group sizes. This suggests that bossing has evolved in the context of a complicated male hierarchy (for details see the section on behaviour; Prins & Sinclair 2013). The frontal bones under the bosses have a honeycomb structure. The height of the bony walls of the cells is about 15–20 mm, while cell diameter is about 7 mm. It is thought to be an adaptation to absorb strong hits and for moving the head in any direction to face attack. While the average weight of a dry skull (including horns) is 8 kg in Lake Manyara National Park, the heaviest skulls were 16 kg (Prins & Sinclair 2013). Horn size was studied as an indicator of health status in male and female Cape buffalo (Ezenwa & Jolles 2008). In both sexes, horn size was significantly negatively correlated with the number of different parasites infecting an individual. These findings support the idea that horn condition plays a role as an indicator of health in both sexes. In particular, Ezenwa & Jolles (2008) suggest that this is a possible role for sexual selection in the maintenance of horns in female ungulates; however, this hypothesis needs further research.

West and Central African buffalo

Body measurements: **Shoulder height**: 120–145 cm; **Head and body length**: 200–245 cm; **Tail length**: 55–70 cm; **Body mass**: 300–600 kg. Smaller than Cape buffalo and bigger than forest buffalo, these intermediate subspecies also have widely spread horns, but these are not curved down as are those of Cape buffalo. Horn span measures 56–103 cm and horn length along the curve is 53–94 cm. The skull measures 43–60 cm.

There are also populations that appear to be intermediate between *brachyceros* and *nanus* subspecies in South Nigeria, Central African Republic and North Cameroon (Wilson & Mittermeier 2011). The red forms of savanna buffalo may be found from Guinea to Chad until North Uganda in the Sahel-Soudan savanna (Grubb 1972; Mloszewski 1983; R. Kock, personal communication).

Forest buffalo

Body measurements: **Shoulder height**: 100–130 cm; **Head and body length**: 170–220 cm; **Tail length**: 60–90 cm; **Body mass**: 265–320 kg. Among the four *Syncerus* subspecies, forest buffalo is the smallest, at around half the size of Cape buffalo

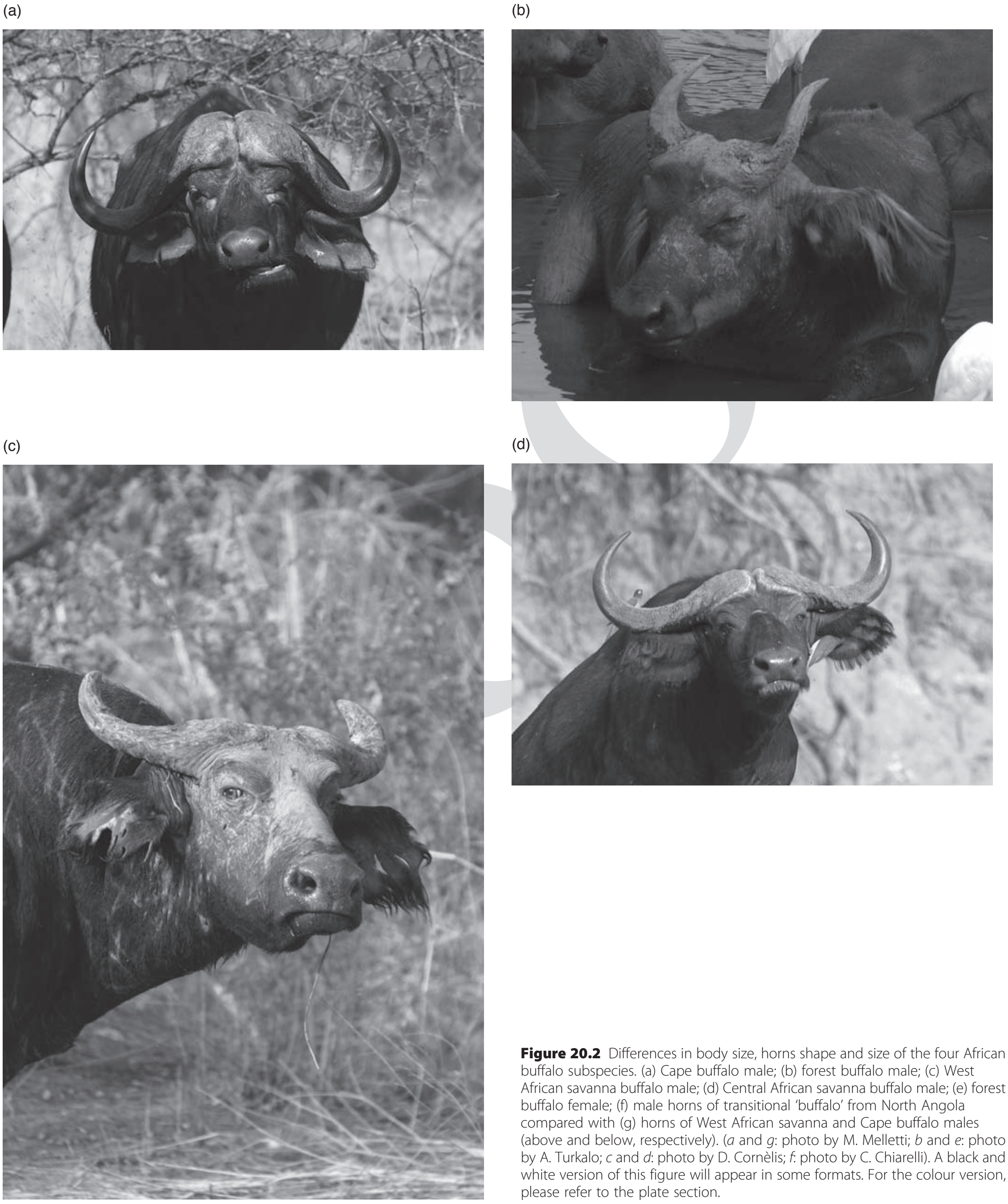

Figure 20.2 Differences in body size, horns shape and size of the four African buffalo subspecies. (a) Cape buffalo male; (b) forest buffalo male; (c) West African savanna buffalo male; (d) Central African savanna buffalo male; (e) forest buffalo female; (f) male horns of transitional 'buffalo' from North Angola compared with (g) horns of West African savanna and Cape buffalo males (above and below, respectively). (*a* and *g*: photo by M. Melletti; *b* and *e*: photo by A. Turkalo; *c* and *d*: photo by D. Cornèlis; *f*: photo by C. Chiarelli). A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

Figure 20.2 *(cont.)*

(Sinclair 1977; Mloszewski 1983; Prins 1996; Wilson & Reeder 2005; Figure 20.2).

Horns are oriented towards the rear in the same plane as the forehead. Horns span ranges of 34–65 cm and horn length along the curve is 41–69 cm and 35–63 cm, in Central and West African populations, respectively (Wilson & Mittermeier 2011). The skull is smaller than that of a savanna buffalo, but still short and wide. The skull length ranges between 39 cm and 49 cm (Wilson & Mittermeier 2011).

Morphological differences within forest buffalo populations are less pronounced than within other subspecies. In addition, the sexual dimorphism (e.g. horn shape and body size) is much less pronounced in the forest buffalo than in the other subspecies. In forest buffalo, the horns are much smaller, back swept and with no boss. These characteristics may reflect the infrequency of fighting, and instead, adaptation to dense rainforest (Kingdon 1997). It has been suggested that horn size tends to increase from West Africa to East and Southern Africa (Grubb 1972); this remains to be tested empirically.

The pelage colour ranges from shades of red and brown to black. Calves and juveniles can have a denser and redder coat than adults, although they may also display dark patterns. Adult bulls show variability in colour patterns even within the same herd. They may be almost all black or completely reddish-brown, with many intermediate shades possible. Females are generally red brown with different shades and show a less pronounced colour gradation than males, but can sometimes be black (L. Korte, personal observation). Another characteristic are the tufted hairs of the ears.

Habitat

African buffalo live in a wide range of habitats, from open grasslands to rainforests, including all intermediate vegetation types: scrublands, woodlands and deciduous forests. They appear not to be bounded by elevation constraints, and their altitudinal distribution ranges from coastal to the boundaries of forests on the highest mountains, except areas with annual rainfall less than 250 mm (e.g. Namib and the Sahara deserts). African buffalo persist in semi-arid environments, as long as surface water is available within 20–40 km, year-round (Naidoo *et al.* 2012; Prins & Sinclair 2013).

The carrying capacity of savanna ecosystems for large grazers such as buffalo is positively correlated with mean annual rainfall and the soil quality (Sinclair 1977; Grange & Duncan 2006; Winnie *et al.* 2008). In similar water regime conditions, the nutrient content of vegetation and primary production are much lower on poor than rich soils (Breman & De Wit 1983; Le Houérou 2008). The low carrying capacity of wild ungulates in savanna ecosystems of West Africa (compared to those of volcanic areas in East Africa) mainly results from poorer soil conditions (Bell 1982; East 1984; Fritz 1997; Hibert 2007).

Most of what we know today about the behavioural ecology of savanna buffalo comes from monographs focused on the Cape buffalo (e.g. Grimsdell 1969; Sinclair 1977; Mloszewski 1983; Prins 1996; Ryan 2006). To date, the ecology of West and Central African savanna buffalo remains poorly investigated and comes from sporadic publications (Boy 1958; Gillet 1969, Stark 1986; Cornelis *et al.* 2011). For this reason, and because several behavioural traits are similar within savanna buffalo subspecies, we present all savanna subspecies in one grouping.

Savanna (Cape, West and Central African) buffalo

Savanna buffalo are mainly found in habitats with a high herbaceous biomass. In the distribution range of Cape buffalo (Eastern and Southern Africa) suitable grasses are found in several types of woodland, such as mopane (*Colophospermum mopane*), miombo (*Brachystegia* spp.), Acacia (*Acacia* spp.) and *Baikiaea* spp. West and Central African savanna buffalo live in a variety of habitats ranging from typical Sahelian shrub savannas (*Combretum* spp., *Terminalia* spp., *Acacia* spp.) to Sudanian woodlands (e.g. *Isoberlinia doka*, *Daniellia oliveri*, *Burkea africana*).

The availability of surface water and cover are commonly cited as the main constraints on habitat use of savanna buffalo. Buffalo must drink at least every two days, taking in about 45 litres daily; they are unable to survive on the moisture content of their food alone (Prins 1996; Prins & Sinclair 2013). They have not evolved any water-saving mechanisms (buffalo sweat profusely, and their faeces comprise approximately 80% water (Taylor 1970; Prins 1996)).

This constraint of access to water is manifest in studies of buffalo habitat use. For example, a GPS-tracking protocol undertaken in West Africa showed that buffalo herds spend 95% of their time within 5.3 km of permanent water areas and around 50% of their time within 1.4 km (Cornelis *et al.* 2011). Many studies showed a preference for riverine habitats, at least during the dry season. These lowland areas (e.g. riparian galleries and surrounding grasslands) provide water, green grass and cover against climatic extremes and predators, simultaneously (Sinclair 1977; Redfern *et al.* 2003; Ryan *et al.* 2006; Cornelis *et al.* 2011). At first rains, the water constraint relaxes and buffalo generally (but not systematically) leave the depleted areas of the dry season and move to habitats located higher in the toposequence (e.g. plateaus), where both water and new green grass are temporary available (Sinclair 1977; Cornelis *et al.* 2011).

It is worth noting that buffalo are also good swimmers, and can forage underwater in floodplains (Chobe River, Okavango, Botswana; Prins & Sinclair 2013). Finally, savanna buffalo may also ascend and descend steep slopes, up to about 50° and may be found at high elevations (Prins & Sinclair 2013). They are known to regularly reach the alpine belt on Mount Kenya and are observed on Kilimanjaro, throughout the forest belt on the northern and western slopes, and tracks were observed up to 4200 m (Grimshaw *et al.* 1995).

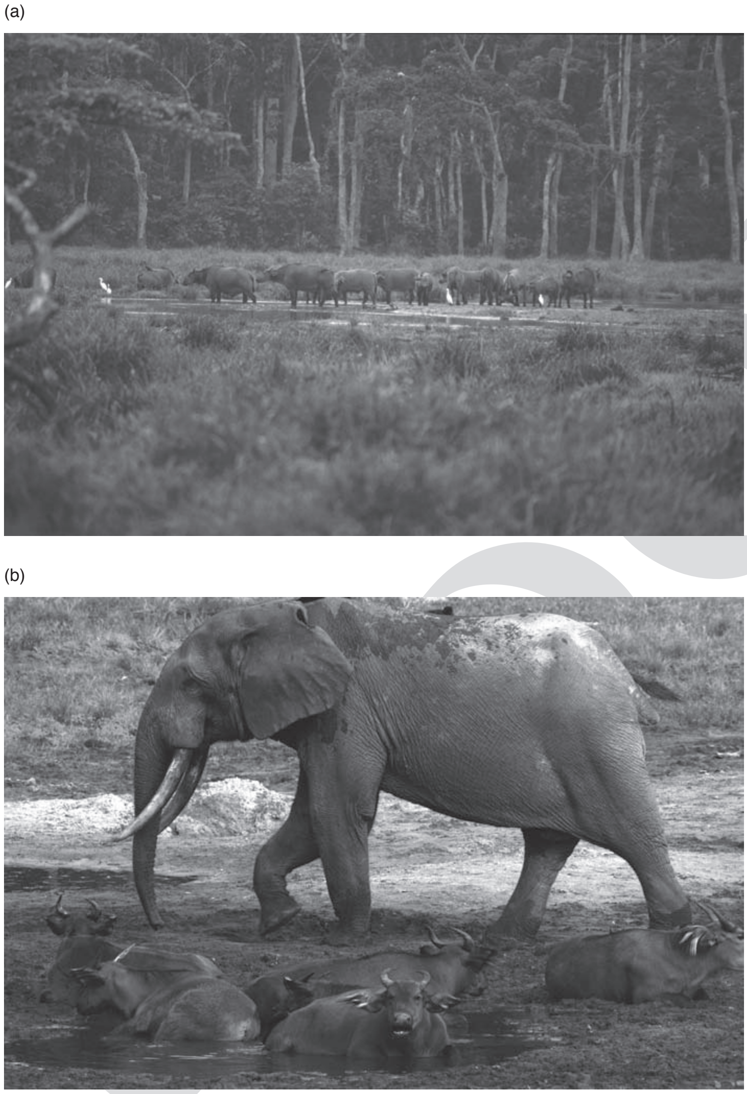

Figure 20.3 Forest buffalo are forest dwellers, inhabiting different habitats with: (a) grassy glades and watercourse areas in rainforest (photo by M. Melletti); (b) forest muddy areas (photo by A. Turkalo); and (c) coastal and equatorial savannas (photo by Mathieu Bourgarel, Cirad). A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

Forest buffalo

Forest buffalo are forest dwellers, inhabiting rainforests with grassy glades, watercourse areas and mosaics of equatorial forests and savannas (Figure 20.3). This subspecies is absent (or present at very low densities) in continuous forests (Prins & Reitsma 1989; Blake 2002; Melletti *et al.* 2007a, 2009; Melletti 2011).

Suitable habitats for forest buffalo are mosaics of forest with equatorial savannas or clearings, which consist of grassy vegetation and shrubs such as *Palisota* spp. (Reitsma 1988; Blake 2002; Tchouto 2004). Blake (2002) at Noubale-Ndoki National Park found high buffalo abundance close to open grassy areas with low abundance in the closed canopy forest, suggesting it is unsuitable for forest buffalo. Melletti *et al.* (2007a, 2007b, 2008, 2009) also found a significant relationship between buffalo and natural forest clearings at Dzanga-Ndoki National Park, where clearings were the centre of buffalo home ranges and no signs of buffalo presence were recorded more than 500 m from clearings (Figure 20.4; Melletti *et al.* 2007a). Buffalo positively selected these clearings, although the surface area of clearings represented only 1% of the total area. In Cameroon, buffalo rarely penetrated into the forest more than

Figure 20.3 *(cont.)*

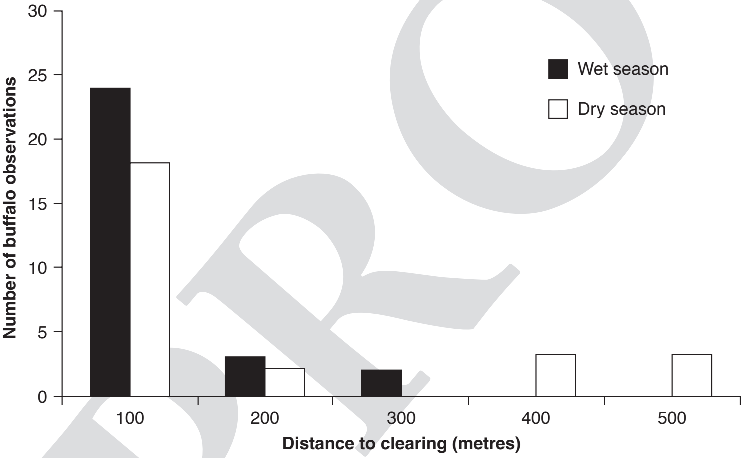

Figure 20.4 Forest buffalo: distribution frequency of the distances to clearings of buffalo observations as revealed by RECCE method in forest habitat during both the dry (from December to February) and wet (from March to November) seasons (Melletti *et al.* 2007a, with kind permission from John Wiley and Sons, *Journal of Zoology*, modified).

300 m from logging roads, which were the main feeding sites for buffalo (Bekhuis *et al.* 2008).

Sites with greater percentages of open areas report high densities of forest buffalo (Morgan 2007; Korte 2008b; Table 20.1). For example, forest buffalo density is 5 individuals/km^2 in the forest–savanna mosaic at Lopé National Park, but only 0.4 individuals/km^2 in the adjacent continuous forest (White 1992). In the coastal area of the Réserve de Faune de Petit Loango (Gabon), Morgan (2007) reports densities of 1.75 individuals per km^2, whereas sites with forest clearing have low densities (Van Der Hoeven *et al.* 2004; Melletti 2005; Bekhuis *et al.* 2008).

At Lopé National Park, Korte (2008a) used radio-tracking data of nine adult females from different herds to quantify habitat preference. Buffalo select proportionally more open habitat (marsh and savanna) and use forest less than would be expected based on available habitat at the landscape level. Habitat use within home ranges varied with season (Figure 20.5). Between March and August >60% of locations of individuals were in forest habitats that represented <50% of home range area. In addition, between the June and August dry season buffalo moved into burned savanna to feed on new grass. These results suggest that forest buffalo use forest fragments, galleries and corridors more often than continuous forest, and habitat preference changes with season based on food availability. Buffalo remained close to the forest clearing areas and did not penetrate deep into the forest, as confirmed

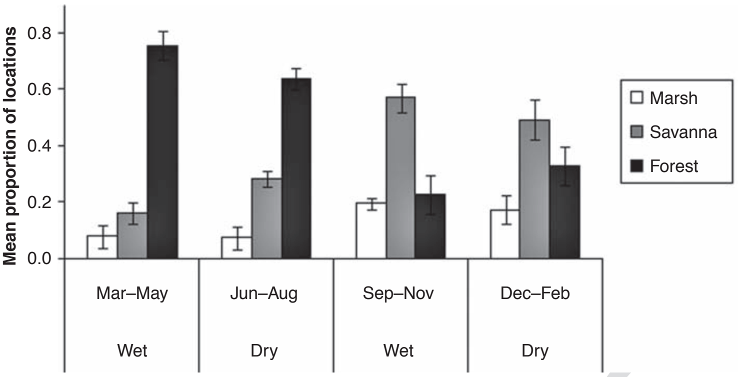

Figure 20.5 Mean proportion of locations (± SE) during daylight hours in each habitat by season for seven radio-collared adult female forest buffalo at Lopé National Park, Gabon, December 2002–December 2004 (Korte, 2008a; with kind permission of the American Society of Mammalogy, Allen Press, Inc).

by studies in other localities (Blake 2002; Melletti *et al*. 2007a; Bekhuis *et al*. 2008; see also Figure 20.4).

Very little information is available on foraging technique. At Dzanga-Ndoki National Park, buffalo use every place within a clearing for feeding, with intermediate areas between the forest edge and the centre of glades used more frequently (Melletti *et al.* 2007b; Melletti 2011). While feeding was mainly within the clearings in Dzanga-Ndoki National Park and in Noubale-Ndoki National Park (Maisels *et al*. 2002; Blake 2002; Melletti *et al.* 2007a; Melletti 2011), sites that lack of clearings in Cameroon and Ivory Coast report signs of feeding on the edges of roads and river banks (Hoppe-Dominik 1992; Bekhuis *et al*. 2008).

Differences in habitat use between age and sex classes are not pronounced. Males are generally permanent members of the herd and share the same habitat and home range with females. Finally, forest buffalo have been found making use of dry caves in the rainforest of Cameroon for resting (C. A. van der Hoeven *et al*., personal observation).

Movements and home range

The African buffalo is generally considered a sedentary species. In buffalo, both home range (HR) size and movements (either seasonal or daily) are related to habitat and to the spatiotemporal distribution of key resources. As pointed out previously, buffalo habitat use tends to be largely constrained by access to water in most study locations. Small HRs are generally observed in forested or high-rainfall regions, and large ones in open, drier habitats.

Savanna (Cape, West and Central African) buffalo

Large seasonal movements approaching migrations were reported by several authors. Large herds in the Serengeti National Park were shown to undertake seasonal movements (Sinclair 1977). Before the fencing in the 1960s, buffalo in Kruger National Park ranged westward in the dry season to take advantage of wetter areas with persistent forage (Witkowski 1983; Ryan 2006). Using GPS-tracking on Cape buffalo in the Caprivi Strip (northeastern Namibia), Naidoo *et al.* (2012) showed that part of the buffalo population undertook seasonal migrations ('partial migration'). The GPS-tracked animals moved up to 115 km from permanent rivers. This study also emphasized that some individuals behaved as dispersers. Variation in migratory behaviour was explained by a large set of factors: environmental conditions (rainfall, fires, woodland cover, vegetation, biomass), distance to the nearest barriers (rivers, fences, cultivated areas) and social factors (age, herd size). Buffalo in larger herds moved greater distances than those in small ones. A similar study undertaken in the south-eastern part of the Okavango Delta (Botswana) also emphasized contrasting movement strategies (Bennitt 2012). Buffalo formed two subpopulations with divergent migratory strategies (resident in the west of the study area and migrant in the east). According to the author, this contrast was probably driven by differing resource availabilities and levels of anthropogenically induced spatial restriction. Finally, in West Africa (WAP Regional Park), most GPS-tracked herds were shown to perform a large (35 ± 10 km) omnidirectional movement at the onset of the monsoon in response to a large-scale gradient of primary production (Cornelis *et al*. 2011).

At a daily scale, Cape buffalo may transit long distances between different grazing areas and often walk single-file. Buffalo herds can cover distances up to 8 km in a 24-hour period (Sinclair 1977; Stark 1986). Daily average distances of 3 km and 6 km have been reported in Zimbabwe (Conybeare 1980; Taylor 1985), and of 3.35 km in Kruger National Park (Ryan & Jordaan 2005). In contrast, bachelor herds were reported to move 1–2 km/day (Taylor 1985). While moving in the mixed herds, adult bulls are often located in the front and at the rear of the herd, but do not make decisions about where to move (Prins 1996).

Savanna ecosystems generally display strong spatial and temporal variations of resources (Estes 1991). As a result, savanna buffalo herds exhibit variable HR sizes across their continental distribution range. A compilation of the literature reveals that annual HR areas generally range between 50 km^2 and 350 km^2, but sometimes can exceed 1000 km^2 (Table 20.4). Buffalo living in wetter areas appear to have smaller HRs than those in drier habitats (Ryan *et al.* 2006). The larger ranges are generally observed in areas where resources are spatially segregated, which forces buffalo to undertake seasonal movements

(Cornelis *et al.* 2011; Naidoo *et al.* 2012). As in many ungulate species, sexual segregation occurs in herds, and some of the adult and subadult bulls temporarily leave the mixed herds to form bachelor groups (see the Behaviour section). Several studies suggest that bachelor groups form smaller (0.5 km^2 and 4 km^2) HRs (Grimsdell 1969; Sinclair 1977; Taylor 1985; Naidoo *et al.* 2012).

Seasonal differences in home range sizes also varied across studies. For example, in Serengeti National Park (Tanzania), the HR size of mixed herds was smaller in the dry season because space is constrained around water points at this point in the year (Sinclair 1977). In contrast, the opposite was observed in Benoue National Park (Cameroon), with an increase in HR size during the early dry season fires (61 km^2 versus 46 km^2) (Stark 1986).

Long-term longitudinal studies undertaken on buffalo mixed herds have suggested that HRs are stable over time (Sinclair 1977; Prins 1996). Interestingly, studies investigating space sharing between neighbouring mixed herds reported contrasting results. In the Cape buffalo, a tendency to use exclusive HRs was observed by Prins (1996), Halley *et al.* (2002) and Ryan *et al.* (2006), whereas Grimsdell (1969), Conybeare (1980) and Mloszewski (1983) reported overlaps between neighbouring HRs. Cross *et al.* (2005) found considerable exchange of individuals between apparent herds, and a flexible structure over time, suggesting that herd definition itself may vary. In West Africa, (WAP Regional Park), the GPS-tracking of adult females emphasized a marked spatial segregation between neighbouring herds (Cornelis *et al.* 2011). The quasi-absence of direct contacts in this study suggests that HRs were not actively defended. These herds found a way to exploit exclusive HRs without spending substantial energy in their defence. Several ongoing GPS-tracking studies implemented in different places (e.g. Zimbabwe, Mozambique, Botswana, South Africa, Namibia), should soon lead to a better understanding of the strategies of exploitation and sharing of space by this species.

Forest buffalo

Few studies investigated HRs and movements of forest buffalo. In Dzanga-Ndoki National Park (Central African Republic), a study of a single buffalo herd over two years identified a stable HR size of 8 km^2 (Melletti *et al.* 2007a). In this herd, daily distances travelled by buffalo were generally very short (i.e. 500–1500 m) and were mainly restrained to clearings and surrounding areas (Table 20.3). The maximum distance travelled during a 24-hour tracking period was about 4000 m (Melletti 2008). Forest buffalo males are permanent members of the herd and their HRs thus overlap completely with those of females range: 2–8 km^2; Melletti *et al.* 2007a).

In the mosaics of savanna and forest of Lopé National Park (Gabon), the average HR size was estimated at 5 km^2 (range: 2–8 km^2; $n = 7$ radio-collared adult females) and herds were shown to maintain stable HRs from year to year (Korte 2008a). In this area, the HR overlap was small between radio-collared buffalo belonging to neighbouring herds, suggesting a strong spatial segregation (Figure 20.6).

Table 20.4 Home ranges size in different African buffalo populations

Study area	Home range size (km^2), mixed herds	Reference
Okavango Delta (Botswana)	359–1537 [1]; 159–818 [2]	Bennitt 2012
Caprivi strip (Namibia)	50–448 (0.6–125 male herds)	Naidoo *et al.* 2012
Klaserie Private Nature Reserve (South Africa)	170–327	Ryan *et al.* 2006
Botswana	920–1455	Hunter 1996
Lake Manyara National Park, Tanzania	50	Prins 1996
Sabi Sand Game Reserve (South Africa)	40–120	Funston *et al.* 1994
Matusadona National Park, Lake Kariba (Zimbabwe)	60–110 (0.5–3.0, male herds)	Taylor 1989, 1985
Kenya, Zambia (Busanga swamp), Zimbabwe	126–1075	Mloszewski 1983
Sengwa Wildlife Research Area (Zimbabwe)	207–286	Conybeare 1980
Hwange National Park (Zimbabwe)	286	Conybeare 1980
Akagera National Park (Rwanda)	35–60	Monfort 1980
Serengeti (Tanzania)	222	Sinclair 1977
Momella Lakes, Arusha National Park (Tanzania)	10.9	Vesey-Fitzgerald 1974
Rwenzori National Park (Uganda)	9.4–9.6	Eltringham & Woodford 1973
Tsavo National Park (Kenya)	85–350	Leuthold 1972
W Regional Park (Niger, Burkina Faso, Benin)	172–620	Cornélis *et al.* 2011
Benove National Park (Cameroon)	46–61	Stark 1986
Lopé National Park (Gabon)	2–8	Korte 2008a
Dzanga-Ndoki National Park (Central African Republic)	2–8	Melletti *et al.* 2007a

[1] Migratory population
[2] Resident population

Long-term observations in the Central African Republic and in the Republic of Congo support the assumption that the same herds occupy the same clearings for long periods (Turkalo & Fay 2001; Blake 2002; Breuer 2008; Geßner 2008).

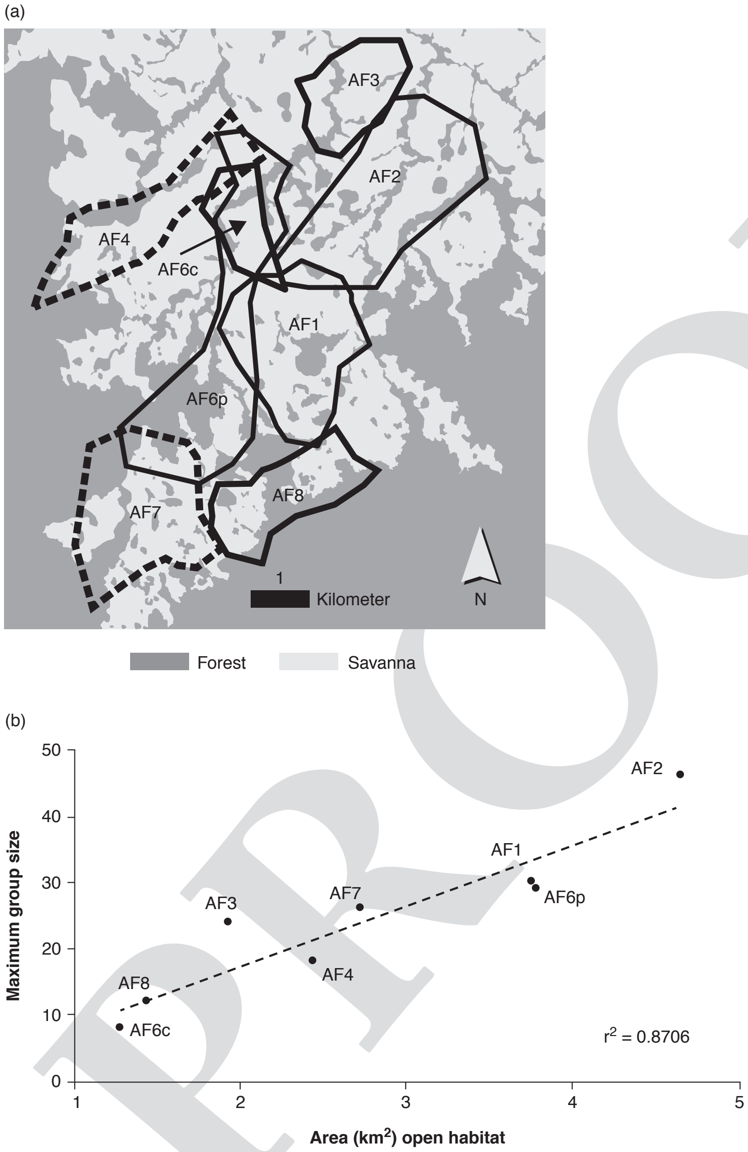

Figure 20.6 (a) Home range of each radio-collared buffalo in the study area at Lopé National Park, Gabon (December 2002 to December 2004); (b) maximum size of group based on observations that included a radio-collared adult female (AF) forest buffalo in relation to the area of open habitat in the home range of those females. Each data point represents maximum group size ($n = 8$) defined by the presence of radio-collared buffalo. Positive correlation between maximum group size and area of open habitat is significant (Korte, 2008b; with kind permission from John Wiley and Sons, *Journal of Zoology*).

Forest buffalo HRs are much smaller than those of the typical savanna subspecies. It is likely that this pattern, common to all studies, primarily results from the spatial arrangement of suitable resources in dense tropical forest, but also to less pronounced seasonality of the environment. Accessible and palatable food for buffalo is scarce in dense tropical forest, except in ecotone areas (e.g. forest clearings, glades, marshes, included savannas, logging roads, etc.: see Bekhuis *et al.* 2008), which often are small in size, patchily distributed and distant from each other (i.e. beyond the locomotion capacity of buffalo). The forest buffalo may thus have adapted several ecological traits to this environment, such as HRs small in size centred on 'islands' of profitable resources, small herds and a lower body mass.

Activity patterns

African buffalo display a large array of activity modes, including feeding, resting/ruminating, relocating between foraging areas (transit), checking for predators (vigilance), wallowing

Table 20.5 Percentages of daytime grazing, resting and ruminating activities for different populations of Cape buffalo

Study area	Grazing	Resting	Ruminating	Reference
Chebera Churchura National Park (Ethiopia)	50%	39%		Megaze *et al.* 2012
Okavango Delta (Botswana)	~40%	~30%		Bennitt 2012
Huhluwe-Umfolozi Game Reserve (South Africa)	21–28% adult females 14–28% adult males	66% adult females 70% adult males		Turner *et al.* 2005
Kruger National Park (South Africa)	37%	26%	29%	Ryan & Jordaan 2005
Willem Pretorius Game Reserve, Free State (South Africa)	40%	34%	34%	Winterbach & Bothma 1998
South Africa	48%			Whyte 1996
Lake Manyara National Park (Tanzania)	22–56%	25% adult females 29% adult males	10–50%	Prins 1996; Prins & Iason 1989
Matusadona National Park (Zimbabwe)	51% bachelor males[1] 47% herds[1]		25% bachelor males[1] 41% herds[2]	Taylor 1989
Western Zambia- Zimbabwe	44–52%[2]	53%[1]	36%	Mloszewski 1983
Serengeti (Tanzania)	38–44%			Sinclair 1977

[1] Mean for dry and wet seasons
[2] Dry season
Males, females and mixed herds are indicated. The range of percentage represents minimum and maximum values.

and drinking. Their respective proportion in both daily and seasonal activity budgets is mainly influenced by spatiotemporal changes in resources quality and availability, interspecific competition, weather conditions and predation pressure (Sinclair 1977; Prins 1996; Ryan & Jordaan 2005; Valeix *et al.* 2009a; Owen-Smith *et al.* 2010). Ruminant ungulates such as buffalo spend large proportions of their time feeding, and must additionally allocate time to ruminating, which results in an overall total time (feeding plus ruminating) of 70–80% (Beekman & Prins 1989; Prins 1996).

Savanna (Cape, West and Central African) buffalo

In Cape buffalo, most studies report feeding time accounting for 35–45% of the 24-hour activity budget (Table 20.5; Grimsdell & Field 1976; Sinclair 1977; Mloszewski 1983; Prins 1996; Winterbach & Bothma 1998; Ryan & Jordaan 2005; Bennitt 2012).

Grazing most often takes place in the early morning and late afternoon, and during the first half of the night, suggesting that buffalo cease feeding during the hottest part of the day and during the coolest part of the night for thermoregulation purposes. Note that an exception to this feeding pattern was observed at Lake Manyara National Park (Tanzania), with the main grazing bout occurring between 10.00 and 14.00 hours (Prins 1996). In most studies, buffalo herds appear to spend an equal or greater proportion of time feeding at night than during the day (Sinclair 1977; Taylor 1985; Prins & Iason 1989; Ryan & Jordaan 2005). At a seasonal scale, most authors reported a trend toward more time spent feeding in the dry season than the wet in response to lower vegetation quality and quantity and decreased intake rates. Other modes of activity, such as resting, rumination and vigilance, are not mutually exclusive, thus making it hard to individualize ratios and to compare across studies. Most studies reported average rumination times of around 30–35% of the 24-hour activity budget (Sinclair 1977; Prins 1996; Winterbach & Bothma 1998; Ryan & Jordaan 2005). Seasonal trends in rumination time are the subject of debate; Sinclair (1977) reported that buffalo spend more time ruminating during the dry season, whereas Beekman and Prins (1989) found the opposite. Buffalo must drink at least every two days, but when they drink appears to vary by study site. Ryan and Jordaan (2005) found two main periods of diurnal drinking (the early morning and mid-morning) and their observations suggest more time devoted to drinking during the day than at night. In contrast, Winterbach and Bothma (1998) found that buffalo drank in the early afternoon, and Grimsdell and Field (1976) found that they drank in the mid-morning. In one study, buffalo were shown to modulate hourly drinking patterns according to the risk of predation by preferentially avoiding waterholes during high-risk hours of the day (dawn and dusk), when lions were likely to be in their vicinity (Valeix *et al.* 2009b). To our knowledge, no seasonal trend in drinking frequency was reported in literature. Mud wallowing is frequent in buffalo males, contrary to females and young. Males generally wallow during the hottest

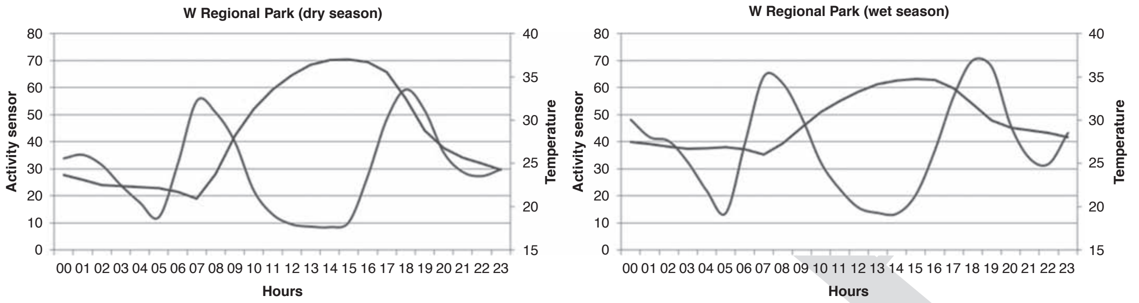

Figure 20.7 Daily bigeminus activity pattern of a buffalo cow tracked in WAP transfrontier conservation area (Burkina Faso, Benin, Niger) from March 2007 to February 2008 (using temperature and activity sensors). The first peak of activity started at dawn and the second finished after dusk, both lasting on average about 3–4 hours. This daily bigeminus pattern was particularly marked during the dry season, with the occurrence of a major resting period between 09:00 and 15:00, corresponding to the hottest hours of the day (Cornelis, 2011).

period of the day for periods lasting up to three hours. This practice is less effective in temperature regulation than the use of shade, which mixed herds generally seek at this time of the day (Sinclair 1977).

Fewer studies investigated the activity patterns of West and Central African buffalo. In Central Africa (Benoue National Park, Cameroon), observations over a 24-hour period conducted during the dry season suggested that buffalo graze approximately 33% of the time, with temporal patterns similar to those of Cape buffalo. In West Africa (WAP Regional Park), the seasonal and daily activity patterns of buffalo herds were explored using biorhythm indices derived from GPS location data and activity sensors (Cornelis 2011). Results suggest that the herds moved faster and were more active when food conditions were most favourable (beginning of the wet season). At a daily scale, herds were equally active during night and day, and were mostly crepuscular, with two main active periods per day (Figure 20.7). However, one herd locally facing a risk factor (daytime human disturbance) clearly switched to a nocturnal activity mode.

Forest buffalo

Observations of forest buffalo activity show similar patterns to those recorded for savanna buffalo: both usually alternate periods of grazing with resting/ruminating throughout the day and the night. At Dzanga-Ndoki, Melletti *et al.* (2007b) recorded higher figures of resting and ruminating time in the dry season than in the wet season and, for this activity, the differences between seasons were statistically significant. At Dzanga-Ndoki, around 50% of the time spent in the clearings by buffalo was dedicated to resting and ruminating activities (both sexes). Observations performed in clearings also suggest than females spent more time feeding (50%) than males (20%). The proportion of grazing individuals increased with increasing group size. Forest buffalo do not show an increase in grazing during the dry season, suggesting that season does not influence grazing activity. A decrease in grazing rate followed by resting in the middle of the day, when temperatures were highest, was observed both in CAR (Melletti *et al.* 2007b) and in Gabon (Molloy 1997).

Korte (2008a) observed similar patterns of feeding activity at Lopé National Park, where buffalo spent >30% of the time feeding. Feeding varied with the habitat and time of the day. Buffalo were most active in savanna habitat during the late morning (09:30–12:30). Periods of inactivity also varied with habitat and period of the day (Korte 2008a). Inactive behaviours were most often observed in marshes in the late afternoon. During daylight hours, the herds spent >38% of their time inactive. Buffalo were relatively inactive during the day between March and August, when >60% of their locations were recorded in forest habitat. Korte (2008a) found that the proportions of time spent in different behaviours did not differ between years or among seasons. However, activity varied significantly among individuals. Forest buffalo wallow in mud and water during the hottest daylight hours mainly in the dry season (December–March; Melletti *et al.* 2007a). Korte (2008a) recorded similar mud and water wallowing within marsh habitat, especially between September and February. Buffalo feed in the savanna areas in the early morning, retire to a wallow and rest in marsh areas until sunset.

Feeding ecology

Buffalo are ruminants, essentially feeding on grass and roughage. This species is capable of subsisting on pastures too coarse and too tall for most other herbivores (Bothma 2002), and as a ‘bulk grazer’ they ingest around 2.2% of their body mass daily. This represents, on average, 6.5 kg for a forest buffalo of 300 kg, 11 kg for a West or Central African buffalo of 500 kg, and 15 kg for a Cape buffalo of 700 kg.

Buffalo are very efficient grazers (adapted dentition and mobile tongue allowing the ingestion of high quantities of grass in a short time). Optimal feeding conditions for buffalo prevail when the grass forms swards and leaf heights reach and exceed 10 cm, as in flood plains or in forest glades (Prins

1996). However, buffalo cannot cut pastures as short as other species. The African buffalo thus occupies an important niche, opening up habitats that are preferred by short-grass grazers (Estes 1991; Prins 1996). Their primary competitors are cattle, *Bos taurus*, African elephant, *Loxodonta africana*, plains zebra, *Equus quagga*, and wildebeest, *Connochaetes taurinus* (Sinclair 1977; De Boer & Prins 1990; Plumptre 1995; Prins 1996).

Savanna (Cape, West and Central African) buffalo

In savanna buffalo, optimal dietary conditions occur during the rainy season, while the end of the long dry season is a period of food scarcity (both in quantity and quality) (Prins & Sinclair 2013). Detailed diet studies conducted in Eastern and Southern Africa indicate that buffalo are resource-limited and constrained by a minimum dietary protein concentration of 7–8% to make fermentation in the rumen possible (Sinclair 1977; Prins 1996). In such a situation, buffalo thus face a tradeoff of quality and quantity in obtaining an appropriate protein-to-fibre ratio in their diet (Redfern *et al.* 2006; Ryan *et al* 2012). During the dry season, savanna buffalo are generally constrained to become more selective, and to partially switch their diet to browse (see below). Despite this, buffalo were reported to live at or below nitrogen requirements for prolonged periods, accounting for visibly losing body condition (Prins 1989b; Ryan 2006; Ryan *et al.* 2012). In natural ungulate communities, the regulation of populations is driven by two processes: a control by available food resources on the one hand ('bottom-up regulation') and a control by predation ('top-down' regulation) on the other (Hunter & Price 1992). In the case of savanna buffalo, most authors agree that resources play a dominant role in the regulation of populations (Sinclair *et al.* 2003; Hopcraft *et al.* 2010).

There is moderate consensus in feeding studies on Cape buffalo about the preferred grass species (Sinclair 1977). Usually species that are avoided contain low nutritious quality or presence of aromatic oils (Prins 1996). During the dry season, usual food resources are of poor quality, due to lignifications and high standing biomass. During this period, floodplain species (e.g. *Leersia hexandra*) and riverine forest species (e.g. *Setaria sphacelata*) become important. In areas with upwelling groundwater, species such as *Cyperus laevigatus* may also form a mainstay in the dry season (Prins & Sinclair 2013). Buffalo prefer grasses such as *Cynodon dactylon*, but may also eat broadleaved grasses such as *Panicum maximum*. Sinclair (1977), in the Serengeti, reported that buffalo preferred soft, nutritious grass such as *Digitaria macroblephora*. Although there is little information on seasonal changes of diet, Sinclair (1977) analysed stomach contents and showed that Cape buffalo select more grass leaf at the end of the rainy season. Finally, Taylor (1985) found that grasslands dominated by *Panicum repens* were the best habitat on the shores of Lake Kariba (Matusadona National Park, Zimbabwe). In Cape buffalo, the diet of the different age and sex classes does not appear to differ, and dry matter food intake ranges between 1.2% and 3.5% of body mass, similar to other ruminants, but subject to food quality (Sinclair 1977; Prins & Beekman 1989).

Few studies have investigated the feeding ecology of West and Central African buffalo. In West Africa (WAP Regional Park), habitat selection analysis emphasized the importance of perennial grasses (e.g. *Andropogon gayanus*; Cornelis *et al.* 2011). In this study, a gradient in primary production appeared to determine large-scale movements of herds at the onset of the wet season, but its action clearly was modulated by the proportion of perennials available. Buffalo herds were shown to establish early wet season HRs at locations where this proportion reached a 9% threshold. At Benoue National Park (Cameroon), Stark (1986) similarly reported a very high proportion of grasses in the diet, particularly *Andropogon gayanus*, which represented 51% of the volume ingested in the dry season, versus 40% in the wet season. At Zakouma National Park (Chad), Gillet (1969) noted a preference for *Setaria anceps* (particularly new shoots after fire) and *Andropogon gayanus*, but also *Vetiveria nigritana*. In the dry season, the unburned straws of *Echinochloa obtusiflora* appeared to be preferred.

For more details on grass species eaten by savanna buffalo in different locations, see Table 20.6.

The savanna buffalo are primarily grazers, but partially switch to browse when grasses become tall and lignified (Field 1972; Leuthold 1972; Sinclair 1977; Mloszewski 1983; Hashim 1987; Prins 1996). Shrub and tree leaves have been shown to contain higher protein (nitrogen) content than dry grasses during the dry season (Kone *et al.* 1990; Prins 1996). As mentioned above, the contribution of nitrogen from browse facilitates the fermentation of fibrous grass in the rumen, which they eat in high quantities during the dry season. According to Estes (1991), the browse can represent up to 5% of the total diet, but higher figures were reported in several sites (e.g. 26% in the dry season in Cameroon; Stark 1986). A wide range of species of shrubs and trees are consumed throughout the African savanna, including *Grewia* spp., *Heeria* spp., *Combretum* spp., *Capparis* spp., *Piliostigma* spp. (Field 1968; Pienaar 1969; Jarman 1971; Graaff *et al.* 1973; Ryan 2006). In drier habitats in the Eastern Cape, buffalo appear to be adapted to eat woody species because grassy vegetation is scarce. In this particular habitat, during the dry season, up to 33% of their diet comprises species such as *Acacia* sp., *Plumbago* sp. and *Grewia* sp.

In some areas buffalo can maintain or create 'grazing lawns' if the feeding interval is short enough (Prins 1996). Evidence of this 'returning' behaviour has also been described for buffalo in Kruger National Park and Klaserie Private Nature Reserve in South Africa (Bar-David *et al.* 2009). They may also create favourable lawns in conjunction with other large herbivores such as elephant at Lake Rukwa, Tanzania (Vesey-FitzGerald 1960) or hippopotamus in Uganda (Eltringham 1999) and Benoué National Park in central Cameroon (H. H. T. Prins, personal observation).

Geophagy has been reported at several sites, where clay or substrates rich in iron also may explain this preference. On

Table 20.6 Main grass species recorded in the diet of savanna buffalo in different locations

Okavango Delta, Botswana[15]	**Serengeti, Tanzania[1]**	**Lake Manyara National Park, Tanzania[2,5]**	**Tsavo NP, Kenya[3]**	**Gonarezhou National Park, Zimbabwe[4]**	**Mount Meru, Tanzania[1]**	**Ruwenzori Uganda[6]**	**Kafue National Park, Zambia[4]**	**Zambezi Valley, Zimbabwe[4]**
Aristida. adscensionis	*Cynodon dactylon*	*Chloris gayana*	*Digitaria macroblephora*	*Cenchrus ciliaris*	*Cynodon dactylon*	*Capparis tomentosa*	*Andropogon gayanus*	*Eragrostis rigidior*
Cenchrus ciliaris	*Panicum coloratum*	*Cynodon dactylon*	*Panicum coloratum*	*Chloridum cameronii*	*Cyperus laevigatus*	*Cynodon dactylon*	*Cenchrus ciliaris*	*Hyparrhenia filipendula*
Cynodon dactylon	*Panicum maximum*	*Cynodon plectostachyus*	*Panicum maximum*	*Colophospermum mopane*	*Themeda trianda*	*Hyparrhenia filipendula*	*Chloridum cameronii*	
Dactyloctenium giganteum	*Panicum infestum*	*Cyperus laevigatus*		*Eragrostis rigidior*		*Sporobolus pyramidalis*	*Cynodon dactylon*	
Eragrostis rigidior	*Setaria chevalieri*	*Leptocarydion vulpiastrum*		*Heteropogon* sp.			*Heteropogon contortus*	
Panicum repens	*Sporobolus spicatus*	*Sporobolus spicatus*		*Hyparrhenia filipendula*			*Hyparrhenia filipendula*	
Panicum maximum	*Sporobolus pyramidalis*	*Sporobolus helvolus*		*Panicum maximum*			*Panicum maximum*	
Stipagrostis uniplumis	*Themeda triandra*	*Sporobolus cordofanus*		*Schizachyrium sanguineum*			*Parinari capensis*[a]	
Sporobolus fimbriatus		*Sporobolus pyramidalis*		*Schmidtia bulbosa*			*Sporobolus pyramidalis*	
Tragus berteronianus		*Urochloa mosambicensis*					*Themeda trianda*	
Urochloa trichopus							*Vossia cuspidata*	

Kruger National Park, South Africa[7,13,14]	**Hwange National Park, Zimbabwe[8]**	**Lake Kariba, Zimbabwe[9]**	**Sabi Sand Wildtuin, South Africa[10]**	**Akagera National Park Rwanda[11]**	**Huhluwe-Umfolozi G.R. South Africa[12]**	**Zakouma National Park, Chad[16]**	**Benoue National Park, Cameroon[17]**
Andropogon gayanus	*Andropogon gayanus*	*Panicum repens*	*Panicum maximum*	*Chloris gayana*	*Panicum deustem*	*Andropogon gayanus*	*Andropogon gayanus*
Cenchrus ciliaris	*Cynodon dactylon*		*Themeda trianda*	*Cynodon dactylon*	*Panicum maximum*	*Echinochloa obtusiflora*	*Andropogon tectorum*
Digitaria eriantha	*Cyperus laevigatus*			*Hyparrhenia filipendula*	*Themeda trianda*	*Setaria anceps*	*Chloris robusta*
Euclea sp.	*Schizachyrium sanguineum*			*Panicum maximum*		*Vetiveria nigritana*	*Digitaria* spp.
Heteropogon contortus				*Sporobolus pyramidalis*			*Echinochloa* spp.
Panicum coloratum				*Themeda trianda*			*Hyparrhenia* spp.
Panicum maximum							*Loudetia* spp.
Schmidtia bulbosa							*Panicum* spp.
Themeda trianda							
Urochloa mosambicensis							

[1] Sinclair 1977; [2] Prins 1996; [3] Leuthold 1972; [4] Mloszewski 1983; [5] Vesey-Fitzgerald 1969; [6] Field 1968; [7] Pienaar 1969; [8] Wilson 1975; [9] Taylor 1985;
[10] Funston *et al.* 1994; [11] Monfort 1979; [12] Perrin & Brereton-Stiles 1999; [13] Macandza *et al.* 2004; [14] Bowers 2006; [15] Bennitt 2012; [16] Gillet 1969; [17] Stark 1986
[a] Fruit also eaten

Mount Kenya, geophagy is reported in the bamboo belt (2100–3000 m), where clay soils are rich in iron and aluminium (Grimshaw *et al.* 1995). This rare activity is carried out mainly by solitary individuals on Mount Kenya (Mahaney 1987). In Lent Valley in Kilimanjaro, buffalo enter into caves rich in sodium bicarbonate and chew off the soda deposits.

Forest buffalo

Few data exist on forest buffalo feeding ecology because direct observations are rarely feasible in rainforest habitats. Blake (2002) and Melletti (2008) observed buffalo feeding mainly on Poaceae and Cyperaceae within clearings, in particular on *Rhyncospora corymbosa*, *Kyllinga* sp. and *Cyperus* sp., in Noubale-Ndoki National Park and in Dzanga-Ndoki National Park. Blake (2002) also recorded several species of Marantaceae, including *Marantochloa purpurea*, *M. cordifolia*, *M. filipes* and *Halopegia azurea*. In addition, species of Commelinaceae family such as *Commelina diffusa*, *Palisota brachythyrsa* and a species of algae (*Spirogyra* sp.) were recorded. Melletti (2008) also found indirect signs of feeding activity on *Commelina* and *Palisota* sp. in the understory of *Gilbertodendrum dewevrei* mono-dominant forest.

Bekhuis *et al.* (2008) used micro-histological faecal analysis in a two-month study to determine the diet of forest buffalo at Campo-Ma'an National Park (southern Cameroon). They found that the most important part of the diet was composed of graminoids (43%, with *Leptochloa caerulescens* representing 15% of the total diet), non-graminoid monocots (21%, mainly Commelinaceae such as *Palisota* spp.), dicotyledonous plants (33%, mainly leaves) and cryptogamous plants (3%). The composition of the diet suggests that buffalo fed mainly along logging roads and river banks (Bekhuis *et al.* 2008). Using a similar method at Lopé National Park (Gabon), Lustenhouwer (2008) and Van der Hoek *et al.* (2012) found that the majority of plants consumed by forest buffalo were monocotyledons, primarily grasses (*Poaceae*) and sedges (*Cyperaceae*), with a low proportion of dicotyledonous plants in the diet. In the same study area, Van der Hoek *et al.* (2012) emphasized the importance of savanna habitat, noting that controlled burning is a key tool for maintaining open areas.

Details of forage species composition and percentage identified in buffalo dung are shown in Table 20.7.

So far, no evidence of the existence of grazing lawns was found in the different studies focused on the feeding ecology of forest buffalo, even in areas of high density, such as Lopé National Park (L. Korte and M. Melletti, personal observations).

Table 20.7 Major diet categories of forest buffalo (Campo Ma'an National Park, Cameroon)[1]

Major categories[2]	Percentage
Graminoids	42.9
Leptochloa	15.1
Other graminoids	27.8
Non-graminoid monocots	21.3
Commelinaceae	18.2
Other non-graminoid monocots	3.1
Dicotyledons	32.1
Dicotyledon leaves	26.5
Dicotyledon stems	6.2
Cryptogamous plants	3.1

[1] Bekhuis *et al.* (2008)
[2] Data refers to April–May 2002
Kind permission John Wiley and Sons, *African Journal of Ecology*, modified.

Reproduction and growth

Savanna (Cape, West and Central African) buffalo

In most of the Cape buffalo range there is a birthing peak during the wet season; however, in the more mesic conditions of Lake Manyara National Park (Tanzania) such a peak is not apparent (Prins 1996). In Matusadona National Park (Zimbabwe), conceptions occurred between December and May, with births between November and April, of which almost two-thirds of them were in January/February (Taylor 1985). These patterns have also been observed in northern Botswana (Carmichael *et al.* 1977), Kruger National Park and neighbouring Klaserie Private Nature Reserve in South Africa (Fairall 1968; Pienaar 1969; Ryan *et al.* 2007). In the Serengeti there is a clear calving peak, with about 50% of all calves born within seven weeks (Sinclair 1977). This peak may be tied to differences in social organization among bulls (see above). In Klaserie Private Nature Reserve, South Africa, births were quite highly synchronized, and the birthing peak was found to be correlated to the highest protein content of grass, which mostly coincided with the month of January (Ryan *et al.* 2007).

Experiments on captive buffalo males in South Africa showed a seasonal cycle in testosterone levels, endocrine function and seminal quality; but this pattern is not clear enough to explain a breeding or calving season (Brown *et al.* 1991). More recently Skinner *et al.* (2006) found a calving period in January for captive buffalo, similar to what was observed in wild populations (Ryan *et al.* 2007). Pro-oestrus may last two or three days and oestrus one day in captive Cape buffalo, and the oestrous cycle from 18 to 22 days (Knechtel 1993). The gestation period is about 340 days (Vidler *et al.* 1963; similar in captivity; Knechtel 1993). Buffalo give birth of a single calf, which weighs 30 kg, and twins are extremely rare. Suckling bouts of calves last about ten minutes when they are four weeks old, decreasing to five minutes when they are six months old (Prins 1996). Calves suckle from the rear; when the female starts walking with the herd the calf can continue receiving milk and the mother does not lose the protection of the herd. The age of weaning depends on many factors, including population density and intraspecific competition. In Lake Manyara National Park, where the buffalo density was high and the population stationary, many calves were still not weaned at

18 months old, while in Serengeti, where the density was much lower and the population increasing, fast weaning took place at the age of ten months. The calving interval in Manyara was therefore about 36 months (Prins 1996) and in Serengeti only 15 months (Sinclair 1977). Considering these patterns, birth rates seem to be density dependent.

Buffalo young are called 'calves' until they reach the inguinal fold at its highest point on the flank of the cow (Pienaar 1969). Juveniles are defined as weaned, but younger than three years (if testicles are not observable it is difficult to sex a juvenile in the field). Subadults begin to show secondary sexual characteristics and horn shape begins to diverge in males and females. For example, in Cape buffalo, the horns of cows start extending laterally whereas those of males curve strongly, upwards, and bosses start to develop. Subadult savanna buffalo bulls still have skin covered with hairs between the bosses, while adult bulls normally do not. Ovulating in females starts after three years of age, and the age at first breeding is five years (Grimsdell 1973b; Sinclair 1977; Taylor 1985). Males reach sexual maturity at 5–6 years of age, but usually do not breed until seven years or older, at which time the horns are fully developed.

Foetal sex ratio is approximately 1:1 in Kruger National Park and Lake Manyara National Park, Tanzania, and appears to be independent of rainfall, maternal lactation status or density (Visscher *et al.* 2004). In Manyara National Park, with increasing age, the sex ratio in herds becomes increasingly slanted in favour of females (Prins 1996). Van Hooft *et al.* (2007, 2010) found that during dry years, calves are sired by bulls with haplotypes that differ from bulls that sire calves during wet years (Van Hooft *et al.* 2007 2010). Bulls spend considerable amounts of time outside herds, which may partly explain the differentiation in fatherhood of calves. Life tables show that mortality patterns across ages in males and females are similar (Grimsdell 1969; Sinclair 1977); the average age of death (excluding calf mortality because remains of calves are too rare to find) is about 12 years. Maximum longevity in the wild is about 20 years and in captivity 29.5 years (Jones 1993).

Forest buffalo

What is known on reproduction and growth in forest buffalo is largely based on incidental observations during field studies of habitat, home range or behavioural activities rather than comprehensive studies focused on reproduction or growth. These initial observations give an indication of trends, but we lack long-term data on forest buffalo reproduction and growth.

It is difficult to ascribe a breeding season to forest buffalo because observations of mating are rare and births do not, so far, seem seasonally limited (Melletti *et al.* 2007a, 2007b; Korte 2008a, 2008b). At Lopé National Park in Gabon, Korte (2008a, 2008b) reported just one observed mating among nine radio-collared buffalo during a two-year study. The mating was observed in August 2003, with a calf born in June 2004. This June birth preceded the September through November wet season, when the lactating female would have access to a seasonal flush of new grass. Other collared females were also observed with new calves during this period, suggesting a possible calving season in the June through August dry season. Two of the buffalo had calves with them when collared in December 2002, two other animals birthed in July 2004, and a fourth female birthed in August 2004. In 1996 at Lopé, new calves were reported in August, September and December, during a six-month study of three herds. However, Korte (2008a, 2008b, 2008c) observed new calves in March 2003 and April 2003, ruling out a definitive calving season.

Sites in the Central African Republic and Cameroon report births during the wet season (Melletti 2008; Geßner 2008). At the Dzanga-Ndoki National Park, Melletti (2008) observed mating three times between June through August in 2002 and 2003. Although the same months as observations at Lopé National Park (Korte 2008a, 2008b), at Dzanga this period is the wet season with a light decreasing of rainfall. Also during the April through August wet season, Melletti (2008) reported new calves; however, no new calves were reported during the December through February dry season. Two births, one on 20 April and a second on 25 June, were reported at Ikwa Bai in Cameroon during a four-month study between 2 April and 6 July 2007 (Geßner 2008). Although calves were born during the wet season when food availability is probably at its peak, small sample size and short study period limit conclusions for calving seasons in Cameroon.

To the best of our knowledge, the literature reports births of only a single calf. During two years of observation of a population of about 342 buffalo at Lopé National Park in Gabon, no multiple births were observed (Korte 2008b). Melletti *et al.* (2007b) report a herd growing from 16 to 24 individuals with the addition of eight calves over a two-year period with no twins. Calving intervals are about two years, with a gestation of at least ten months (Melletti *et al* 2007b; Korte 2008b). Calves remain with cows for at least two years (Korte 2008b). Only adult female buffalo are observed with calves, suggesting that age of first reproduction is at least three years of age, if not older (Melletti *et al.* 2007b; Korte 2008b).

Studies of forest buffalo have followed guidelines developed for Cape buffalo to age individuals (i.e. calves: <12 months; juveniles: 12–36 months; subadults: 3–5 years; adults: >5 years; Pienaar 1969; Sinclair 1977). Little has been done to develop methods for ageing forest buffalo using cementum lines, tooth wear or tooth eruption sequences, to validate or calibrate ageing methods. Tooth wear is not found to be constant within species, differing with factors such as heredity, nutrition, habitat and the severity of the seasons (Hillson 1986). Thus, forest buffalo may have a different tooth wear pattern than Cape buffalo, given their very different habitat, i.e. forest versus savanna. Although horn size can be used as an indication of sex for individuals, visual observation of testicles is the most reliable method to determine a male individual. Adult females can have similar horns and body size to subadult males, so it is best to not rely solely on horn size and/or shape to sex individuals (Molloy 1997). When herds are observed over several months, it is possible to identify distinct individuals using horn morphology, scars and pelage characteristics to consistently record individuals (Prins 1989a; Melletti *et al*. 2007b; Korte 2008a, 2008b; Geßner 2008).

Behaviour

Savanna (Cape, West and Central African) buffalo

African savanna buffalo are gregarious animals living in mixed herds, and core members include adult females, subadults, juveniles and calves. Young females are known to maintain post-weaning bonds with their mother until the birth of their first calf, and certainly longer. In contrast, young males gradually become independent, and are likely to form subadult male groups within the mixed herd. At the age of about 4–5 years (and occasionally earlier), the males temporarily leave the herd to form bachelor groups. The elder males (from about ten years) sometimes permanently leave the herd, but this behaviour is not systematic (Sinclair 1977; Prins 1996).

Herd size in Cape buffalo varies across their distribution, from as few as 20 to as many as 2000 individuals in the floodplains of eastern and southern Africa (Sinclair 1977, Prins 1996). In West Africa (WAP Regional Park), the mean herd size was about 45 individuals when excluding bachelor males, and the largest herds were estimated to contain about 150 individuals (Cornelis *et al*. 2011). Similar figures were reported for Central African savanna buffalo, except in floodplain areas such as Zakouma National Park (Chad), where herds of up to 800 individuals were observed. Within savanna buffalo populations, differences in herd sizes were also observed, and herd sizes tend to be smaller where food resources are poor (Winnie *et al*. 2008).

Mixed herds were shown to be long-lasting social structures displaying a high degree of fidelity to their home range (Sinclair 1977; Prins 1996). The herd as a social unit has a much longer life span than any individuals, and recognizable herds were known to have existed for over 50 years (Prins 1996). Although adult females generally exhibit a high degree of philopatry to their native herd, herd switching was reported by a telemetry study in northern Botswana, where 7 of 45 adult cows switched herds, covering distances up to 133 km (Halley *et al*. 2002). In Cape buffalo, the migration rate per generation between herds was estimated by a genetic approach to be 5–20% for females and close to 100% for males (Van Hooft *et al*. 2003).

Fusion–fission group dynamics operate within mixed herds, meaning that herds may temporarily split into sub-herds and then merge again. Contrasted patterns of splitting and merging were described across studies. In the Serengeti, Sinclair (1977) reported that mixed herds tend to split into sub-herds when resources are fragmented, i.e. during the dry season. In contrast, Bothma (2002) reported that the herds tend to congregate during the dry season in areas where water and forage are abundant, and split into sub-herds during the wet season to exploit the available habitat more efficiently. Halley *et al*. (2002) made the same observation in Chobe National Park (Botswana), where buffalo were shown to range in herds of more than 1400 individuals during the dry season. Such large herds might in fact be temporary associations of two or more mixed herds.

At Lake Manyara National Park (Tanzania), where herds are less constrained by resources, the pattern of fusion–fission appears related to herd size: large herds split more frequently than smaller ones (Prins 1996). In Kruger National Park, South Africa, a longitudinal monitoring of multiple radio-collared individuals showed that herds were far less discrete than in previous studies (Cross *et al*. 2005). New herds may arise from these fusion–fission processes, comprising mixed subsets of previous herds, or single subsets.

As described above, bulls can be found within herds or smaller groups called 'bachelors' (Sinclair 1977; Prins 1989a, 1996). This sexual segregation operated by males is related to the energy cost of reproduction activities, which occur at the expense of the time normally allocated to foraging. Males competing for females are forced to leave the herd once their body condition decreases (Prins 1996; Turner *et al*. 2005). Individuals living in bachelor groups thus can spend more time foraging, but also utilize patches of habitat too small for the herd. The temporal patterns of sexual segregation appear contrasted between study areas. In Serengeti, where buffalo display a clear peak in calving, males join the mixed herds during the wet season (about eight months) and form stable bachelor groups during the dry season (Sinclair 1977). Bachelor herds in Serengeti comprise, on average, 5–10 individuals, the largest ones up to 50 (Sinclair 1977). They have a stable membership and there is evidence of linear dominance hierarchies in both bachelor and herd males (Sinclair 1977). In contrast, in more profitable areas such as Manyara (Tanzania), where buffalo are able to cover maintenance costs year-round, calving (and thus rutting) does not show a clear seasonal pattern, and adult males move in and out of mixed herds at a higher frequency (the so-called 're-entrant consecutive polygyny system'; Prins 1996). In this situation, buffalo males do not form stable associations, do not show fidelity to the same herd and do not have a particular home range. In the re-entrant consecutive polygyny system, the average size of bachelor groups is 3.5 individuals, and the largest groups comprise as many as 50 individuals (Prins 1996). These differences in patterns of sexual segregation depend on the seasonal patterns in resources availability. These two reproductive states may also explain the great differences in testosterone level between bulls during a season (Brown *et al*. 1991).

Cows, juveniles and calves stay together in large to very large herds, and even subadults of both sexes stay within their maternal herd. When the herd moves between feeding areas one or more adult males may precede it. However, adult cows are quite often in the lead as well. Buffalo leaders may stop an entire herd by not moving on or by giving a stopping signal, which involves standing and blocking the direction of movement. These 'individuals' are not to be viewed as 'true leaders' – for example, taking the decision of where to drink. It seems to be a communal decision taken by the adult cows in a procedure that has been called 'voting' (Prins 1996). Communal decision making seems to take place also in other mammals, and may be linked to information exchange. 'Voting' in buffalo takes place after a long resting bout, typically at the end of the afternoon when almost all individuals lie down. In this case females rise and elevate their head as if staring in a particular direction. Prins (1996) describes the voting posture as when the head position is halfway between a resting position and full alert, when the individual has the head elevated at a height as if gazing over its nostrils. The voting posture is maintained for a few minutes, after which the cow beds down again. We can distinguish two patterns of voting postures: (1) when we have a short vector that implies little consensus within the herd of voting females; and (2) where a long vector means a high degree of consensus (i.e. all heads were pointing in the same direction). Little consensus is often followed by a splitting of the herd and the resulting sub-herds then merge again after a few days (Prins 1996).

Social interactions between subadult cows are quite rare and restrained. Subadult bulls show intense sparring behaviour, similarly to adult bulls. During sparring, horns, and especially the bosses, are placed against each other, after which the animals start pushing. The 'winner' often is able to hook the other buffalo. Sparring may function as testing dominance between individuals, although it looks as if both contestants enjoy the game. Most interactions between adult bulls appear to be limited to evaluating the size of each other, often observed by other bulls. A more intense form of 'sizing each other up' is the parallel walk. Fights only happen when both contestants are equally strong and large. They are exceptionally rare and can result in fatal injuries to both bulls. Buffalo calves seldom play.

Females and their offspring have a rather fixed location inside a herd, which may vary with age and sex classes. Such a location may be inherited, because female offspring stay with their mothers up to maturity (Prins 1989b). Aggressive (agonistic) behaviour may also play a role in determining position within the herd. Agonistic behaviour consists of hooking and butting with the horns; among females this is typically aimed at the flanks or the rump of other adult females (Prins & Sinclair 2013; a summary of the main behaviours recorded are shown in Table 20.8).

Among males there is a distinct ritualized threat and submissive behaviour. Dominant males threaten by standing with the head up but muzzle pointing down, thus emphasizing the shoulders, a posture characteristic also of other bovine species, including the gaur (*Bos gaurus*), banteng (*Bos javanicus*) and bison (*Bison bison*, *B. bonasus*). A submissive male, when threatened, approaches the dominant with head held low and parallel to the ground and will often place the muzzle between the hind legs of the dominant one. At the same time the subordinate animal utters a loud and long bellow, sometimes continuing for the entire duration of the submissive display. The behaviour is similar to that of small calves when suckling or searching for their mother. This ritualized submission seems unique to African Buffalo; it is not shown by water buffalo. Buffalo are generally silent. They occasionally grunt, especially when a cow is hooked by another animal. They snort and cough when alarmed and when they start running. Bulls that are injured or about to die can make very loud bellows. Other bulls may or may not react to the sound. In about one-third of the instances that a bull is wounded by lions or hunters another adult bull will try to help him. Buffalo that are badly wounded may also seek the protection of the herd. They do not have an alarm call, but have a very efficient warning system, especially at night, by becoming silent (Prins & Sinclair 2013).

Mating depends on degree of willingness of a cow to be mounted. When the female is receptive, bulls show extensive tending behaviour ('consorting'); only adult bulls exhibit tending. Bulls show flehmen when testing urine of receptive females. When receptiveness increases the bull tries to lay his chin on her tail base. In general she then walks away, after which the bull tries again. When the cow is willing to stay put, the tending bull is often supplanted by a more dominant one who then mates with the cow. Other bulls may attempt intromission during mating, but females start running away, making copulation impossible. Mounting and ejaculation usually take a few seconds only. Females mating with more than one male has not been reported, but given the interrupted tending behaviour described above, this is a possibility (see Van Hooft *et al.* 2010). The cow remains with the herd to calve, although if the herd moves the females and their calves may be left behind temporarily. Calves may associate with age mates, and these associations are especially noticeable in females and may last for many years (Prins 1996), similarly to zebu cattle (Reinhardt 1983). Sometimes these coalitions result in coincident death at a much older age, when both 'friends' perish in so-called 'multiple kills' by lions; in Lake Manyara National Park multiple kills comprised about 6% of kills (H. H. T. Prins, personal observation).

Buffalo exhibit quite aggressive behaviour when attacked by predators, chasing and sometimes killing lions. In particular, they may respond to calf distress calls by chasing off the predators (Sinclair 1977). Buffaloes can reach 48–55 km/hr at top speed, and they can jump about 1.5 m in height. They also defend themselves against lions quite well in dense thickets, standing with their hindquarter to trees and bushes. Buffalo in open habitats adopt the antipredator strategy of forming large herds – predator swamping (Sinclair 1977; Melletti *et al.* 2007b; Prins & Sinclair 2013).

Lions use terrain features as cover to stalk buffalo herds (Prins & Iason 1989; Mugangu *et al.* 1995). Lions may take buffalo from the middle of a herd, sometimes without other

Table 20.8 Main behaviours recorded in the African buffalo

Agonistic behaviour	Vocal communication	Sexual behaviour	Parent/juvenile behaviour	Antipredator behaviour
High horn presentation[1]	Signal to move[9]	Urine testing by bulls	Calf croaking[19]	Alert posture[20]
Submissive bellow[2]	Direction giving signal[10]	Licking vulva by bulls[18]	Pushing off calf	Head tossing[4]
Wallowing[3]	Water call[11]	Cow head on bull rump		Wheeling and flight
Circling[4]	Position signal[12]	Cow pushing belly of bull		Individual/herd attack
Rolling (mud/dust)	Warning call[13]			
Horning (vegetation)[4]	Aggressive call[14]			
Head tossing[4]	Mother to calf call[15]			
Rubbing face and neck in mud[4]	Calf distress call			
Lateral display[5]	Danger call[16]			
Head low posture[6]	Grazing vocalizations[17]			
Flight/alarm posture				
Charging – chin raised[7]				
Front-pressing[7]				
Sparring[8]				

[1] The head is held at shoulder level, associated with head tossing
[2] Mouth is opened and the tongue is curled
[3] Mud and dust baths mainly carried out by dominant males (social significance)
[4] Dominance, threat and aggressive displays
[5] Head is held at or above shoulders, chin pulled, tossing and hooking movements, means of asserting dominance
[6] Defensive and submissive displays performed by a low-ranking male
[7] During fighting
[8] No charge, milder exercise, little horn-tangling and half-hearted pushing, mainly performed by subadults
[9] Call given for herd coordination during movements
[10] Intermittent sound given by leaders at the beginning of herd movement
[11] Call emitted many times during movement to drinking places
[12] Sound emitted by a high-ranking buffalo within a herd that announces its presence and location
[13] Sound given to an encroaching submissive individual
[14] Grunt given by a dominant bull after a stampede
[15] Croaking call emitted by cows seeking their calves
[16] When lions are detected
[17] Variety of sounds during grazing
[18] Bulls can prompt cows to urinate
[19] Call emitted when losing contact with mothers
[20] Advancing to investigate the presence of a possible predators, etc. Alert behaviour mainly performed by adult females in forest buffalo

Sources: Sinclair 1977; Mloszewski 1983; Estes 1991; Prins 1996; Melletti *et al.* 2007b

buffalo paying attention, while in other instances buffalo chase lions and sometimes kill them. It seems that large numbers make buffalo safer, and adult bulls seem invulnerable when in prime condition. However, lions often kill males in bachelor groups (Schaller 1972). In the Serengeti, predation by lions accounted for 44 males, versus six females, six young and six indeterminate sex (Wilson & Mittermeier 2011). Usually, two or more lions attack from the rear, and they have to take the buffalo down quickly, otherwise he can drive them off. Lions unable to take down a standing buffalo have been seen perched on top of the standing buffalo (H. H. T. Prins, personal observation). Sometimes buffalo will try to push lions against *Acacia* thorns. If lions successfully put down the buffalo they try to suffocate it by holding the muzzle because they cannot break the neck.

The main predators of Cape buffalo are lions, but predation by spotted hyena (*Crocuta crocuta*) and leopard (*Panthera pardus*), has been recorded, usually targeting young animals (Kruuk 1972; Schaller 1972; Prins & Iason 1989; Ruggiero 1991; Funston *et al.* 2003). In forest areas such as Mount Meru, Tanzania, predation is insignificant. In the Serengeti National

Park, predation by lions accounts for only 25% of mortality (Sinclair 1977). In Lake Manyara National Park lion predation is very high, up to 85%, in the absence of major diseases. Thus, the population regulatory effect of predation depends strongly on location. Other infrequent (less than 5%) causes of natural mortality include getting stuck in mud, falling down cliffs or fights with other buffalo (Prins & Sinclair 2013). Mass mortality of buffalo has been reported in Zambia when they were stampeded over cliffs by lions on two occasions (63 and 42 buffalo, respectively), and also by mass entanglement in floating grass while trying to cross a lagoon (Prins & Sinclair 2013).

Forest buffalo

Forest buffalo herds are small, stable groups with relatively little switching between herds (Melletti *et al.* 2007b; Geßner 2008; Korte 2008b, 2009). Adult cows and their offspring live in herds that vary between about 3 and 25 individuals in the forest buffalo (Happold 1973; Melletti *et al.* 2007a; Korte 2008a, 2008b). Herds comprise several adult females with their young and with one or two bulls (Dalimier 1955; Blake 2002; Melletti *et al.* 2007a; Korte 2008a). This may be the best reproductive strategy when females occur in small herds that are widely scattered in grassy patches within a rainforest that is otherwise unsuitable to forest buffalo. The ratio of adult males to adult females at Lopé National Park in Gabon is 1:6, with an overall ratio of 1:2 for adults and subadults to juveniles and calves (Korte 2008a). At Bai-Hokou of the Dzanga-Ndoki National Park in the Central African Republic, a herd of 24 individuals included one adult male, nine adult females, six juveniles and eight calves (Melletti *et al.* 2007b). Geßner (2008) reported a stable herd of at least 23 buffalo, including an adult male, at least one subadult male, two subadult females and ten adult females with at least three juveniles and four calves at Ikwa Bai at Nki National Park in Cameroon. Forest buffalo herds split into smaller subgroups and not all individuals are together at all times.

Herd size appears stable within herds, but can vary widely across herds (Korte 2008b). During a two-year study at Lopé National Park in Gabon, the mean group size for 18 herds was 12 (range of means 3–24), considerably smaller than Cape buffalo herds. Although mean group size varied little with time of day, across season or between savanna and marsh habitat, herd size varied widely across herds, from fewer than ten individuals in the smallest herds to more than 20 in the largest herds. Melletti *et al.* (2007b) also report that herd size did not vary with season or food availability. This herd at Dzanga-Ndoki National Park in the Central African Republic increased from 16 to 24 due to the birth of eight calves during the two-year study, with no immigration or emigration. Although the herd remained small, individuals split into smaller subgroups with fission patterns lasting 1–3 days before the herd merged again (Melletti *et al.* 2007b; Melletti 2008). This trend seemed more frequent when the herd grew to 24 individuals at the end of the study period (Melletti 2008). Melletti *et al.* (2008) also report that group size was smaller and individuals were more dispersed within the same forest clearing during the wet season.

Although this subspecies is forest-dwelling, forest buffalo are dependent on open areas adjacent to continuous forest (Melletti *et al.* 2007a, 2007b; Bekhuis *et al.* 2008; Geßner 2008; Korte 2008a, 2008b). At a local level, the quantity and dispersion of food resources appear to influence group size (figure 20.6a,b from Korte 2008b). For eight radio-collared buffalo at Lopé National Park there was a significant positive correlation between maximum group size and the area of open habitat in each collared animal's home range. These open habitats are savannas and marshes, where food resources are abundant. Thus, aggregation patterns appear to be linked to food resources. At other forested sites, buffalo depend on forest clearings or grassy areas along roads, where food resources are present (Hoppe-Dominik 1992; Melletti *et al.* 2007a; Bekhius *et al.* 2008; Geßner 2008; Korte 2008b).

Antipredator strategies in forest buffalo seem to consist of moving and resting together (Melletti *et al.* 2007b). At Dzanga-Ndoki National Park, buffalo were closer to each other when moving compared to distance between individuals when grazing. In addition, an adult female always led the group in flight with the adult male often (i.e. in over 90% of cases) the final individual, possibly an antipredator strategy. Melletti *et al.* (2007b) also report larger group size when buffalo are a greater distance from forest edges, noting that every individual was surrounded by other buffalo, probably indicating an antipredator strategy. In addition, the adult male was commonly closer to the females than to juveniles (Melletti *et al.* 2007b). Melletti *et al.* (2007b, 2008) also report observations of the herd standing in alert postures for a few minutes and then fleeing a few hundred metres within the same clearing (i.e. when the herd smelled the observers or a predator), but on some occasions the buffalo moved to another clearing, with an adult female always leading the group.

Leopard predation on buffalo is rarely observed in the rainforest; however, at Lopé National Park, Gabon, where buffalo density is high in the savanna areas, buffalo make up over 10% of the biomass consumed (Henschel *et al.* 2005).

Geßner (2008) reports that forest buffalo displayed increased vigilance at the start of her three-month study when an observation mirador was constructed at the forest clearing. Vigilance decreased during the study as animals adjusted to the presence of observers; however, levels of vigilance increased when a non-herd subadult female visited the clearing and at the births of two calves. At Dzanga-Ndoki National Park levels of vigilance increased when buffalo were approached by lowland gorillas feeding in the same clearing (Melletti 2008).

Forest buffalo are more often observed as part of a herd than as individuals (Melletti *et al.* 2007b; Korte 2008b; Geßner 2008). For example, solitary males and females are observed at Lopé National Park, but the majority of observations are of two or more buffalo (Korte 2008a, 2008b). Although solitary adult males are observed more often than solitary adult females, adult males were not observed leaving herds to form bachelor groups, and males consistently stayed with the same herds. During two years of field work, Melletti *et al.* (2007b) encountered neither solitary adult males nor bachelor groups. Solitary adult females and juveniles were observed on a few occasions, but they joined the herd after a few days. Geßner (2008) reports a solitary subadult male at the Ikwa Bai in Cameroon, but did not observe bachelor herds. Thus, so far, field studies have produced little evidence for bachelor herds in forest buffalo, unlike Cape buffalo studies.

Forest buffalo herds usually include more than one generation of young. Calves stay with their mothers for at least two years and juveniles will often stay with their mothers after the birth of the next calf (Melletti *et al.* 2007b; Korte 2008a, 2008b). Calves stay close to the females after birth and integrate into the herd with little attention from other herd members (Geßner 2008). Melletti (2008) observed females leaving their herd for a few days at the time of birth, returning to the herd when the new calves are able to walk properly. During these periods, females remained apart from the herd and concealed their calves in tall grass or bushes when grazing. Cape buffalo can display similar behaviour when calves are born (Sinclair 1977; Mloszewski 1983; Prins 1996). Forest buffalo are attentive to calves, but the literature reporting on births of calves does not describe specific care of calves by females (Melletti *et al.* 2007b; Geßner 2008; Korte 2008c).

Few observations of agonistic behaviours are reported for forest buffalo (Molloy 1997; Melletti *et al.* 2007b; Geßner 2008; Korte 2008a, 2008b). Geßner (2008) defined the sequence of a buffalo placing it nose between the hind legs of a second individual and jumping away as a submissive behaviour. This is similar to the appeasement ceremony observed in Cape buffalo (Estes 1991). At Ika Bai in Cameroon, subadult buffalo males displayed submissive behaviour to the adult male of the group; adult females from different subgroups also displayed submissive behaviour when the subgroup joined; and juveniles displayed submissive behaviour to adult buffalo, establishing hierarchy within the group. Geßner (2008) also reports a peak of chasing between the adult male and subadult male in June, when the adult male is establishing his position in the herd. Melletti (2008) also reports submissive behaviour when a subadult or juvenile approached the herd. Defensive displays are rare, with Melletti *et al.* (2007b) reporting the most frequent interaction as adult females displacing juveniles from resting areas at Bai-Hokou (Dzanga-Ndoki National Park) in the Central African Republic. Despite distinct home ranges and the occasional encounters of different herds, territorial defence was not observed at Lopé National Park (Korte 2008a). Field studies report a limited number of behavioural displays among forest buffalo. Melletti (2008) at Bai-Hokou in the Central African Republic observed the only adult male performing urine testing just before copulation on a few occasions. He also reported short vocal signals when the herd was moving from one clearing to another, during grazing, while resting and with all activities associated with the displacement of young by adults at Dzanga-Ndoki National Park.

There are few data on intraspecific and interspecific competition for food resources in forest buffalo. This buffalo lives in smaller herds than savanna buffalo, which could facilitate better inter-individual tolerance and reduce competition for food resources. However, this hypothesis is not supported by the strong spatial segregation of home ranges observed at all study sites (see above). Melletti *et al.* (2007b) observed that most frequent interaction between the members of the herd during feeding and resting was the driving off of other individuals, mainly initiated by adult females and usually directed towards a juvenile. The authors conclude that this kind of interaction could be due to competition for the best feeding and resting spots. Within a clearing these social interactions between buffalo were relatively common. Moreover, several other large mammals use this habitat type and can congregate in the same clearing. During feeding, buffalo, sitatunga, red river hogs, gorillas, bongos and even forest elephants may tolerate each other even within a few metres. Among these, sometime elephants are less tolerant, mainly towards buffalo, driving them off or simply annoying them.

Spatial aggregation patterns in forest buffalo have been studied by Melletti *et al.* (2008, 2010) at 45 resting sites of a single herd in Dzanga-Ndoki National Park, where both habitat structure and season influenced these patterns. In open habitats such as clearings, groups cover a larger area when resting and are more rounded in shape compared to group properties noted in forest during the wet season. Forest buffalo also have a more aggregated spatial distribution when resting in clearings than when in the forest. Individual positions within the herd in the clearing habitat varied with age and sex. In the clearings, the adult male was on most occasions located in the centre of the herd ($n = 20/24$ observations). In contrast, females occupied intermediate ($n = 57/80$), peripheral ($n = 14/80$) and central positions ($n = 9/80$) within the group. Juveniles also occurred in intermediate ($n = 64/77$) and peripheral positions ($n = 13/77$). Although these results are limited by small sample size (one herd), it can give an indication that habitat characteristics and social behaviour can have relevant effects on the spatial distribution of animals within a group.

Parasites and diseases

Savanna (Cape, West and Central African) buffalo

The savanna buffalo is susceptible to several infectious diseases of importance in Africa. Some diseases (hereafter referred to as indigenous) originated in Africa and co-evolved with African buffalo populations while others (hereafter referred to as alien) have been introduced by imported cattle breeds. The savanna buffalo is known to be a reservoir for foot-and-mouth disease (FMD), corridor disease (theileriosis), bovine tuberculosis (BTB) and bovine brucellosis. The role of savanna buffalo in the epidemiology of pathogens such as anthrax, Rift Valley fever and lumpy skin disease is still unclear and requires more investigation (Prins & Weyerhaeuser 1987; de Garine-Wichatitksy *et al.* 2012; Caron *et al.* 2013).

The transmission of infectious diseases between individuals can occur though different routes, including direct inter-individual contact (e.g. sperm, milk, aerosols), indirectly by contaminated material (e.g. faeces, saliva) released on food and in water, or by haematophagous vectors (e.g. ticks, mosquitoes). In buffalo, several ecological traits (e.g. highly gregarious behaviour, fusion–fission group dynamics, dispersal and mating strategies) are conducive to the transmission and the diffusion of pathogens.

Rinderpest, an alien disease imported in the Horn of Africa in the 1890s, had a devastating effect on many African cloven-hoofed ungulate species and is thought to have caused up to 95% mortality of savanna buffalo populations throughout Africa in the early twentieth century. Subsequent rinderpest epizootics caused major die-offs throughout the twentieth century (until the mid 1980s), but the disease was recently declared eradicated (Morens *et al.* 2011). The extreme pathogenicity of rinderpest and high mortality prevented the development of a wildlife reservoir (De Vos & Bengis 1994). In contrast, BTB and bovine brucellosis successfully established themselves in buffalo, which act as a maintenance host. Bovine tuberculosis is a chronic, progressively wasting disease with prevalence rates up to 60% in buffalo herds (Jolles 2004). Although BTB-infected buffalo can suffer declines in body condition (Caron *et al.* 2003), adult survival and fecundity (Jolles *et al.* 2005), longitudinal studies undertaken in a high-prevalence area such as the Kruger National Park (South Africa) suggest little demographic impact (Cross *et al.* 2009). Similarly, current knowledge of the impact of bovine brucellosis (a chronic disease also known as ‘contagious abortion’) does not indicate an immediate threat to buffalo survival at the population level (Michel & Bengis 2012). However, the impacts of these chronic diseases may be a non-linear function of environmental conditions such that they are only detectable in stressful periods (e.g. prolonged droughts) (Cross *et al.* 2009). For example, anthrax outbreaks were locally shown to cause mass mortalities in buffalo during drought periods (Prins & Weyerhaeuser 1987; De Vos & Bryden 1996).

Indigenous diseases (e.g. FMD, corridor disease and African trypanosomiasis) generally do not pose a threat to the survival of buffalo populations because of the evolutionary development of unique coping mechanisms (Michel & Bengis 2012). These diseases are generally carried asymptomatically by buffalo, which act as biological reservoirs of transmission to cattle, thus posing particularly severe problems at wildlife–domestic interfaces (Miguel *et al.* 2013; see Chapter 26 for more details). In Southern Africa, diseases transmitted from buffalo to cattle have contributed greatly to the eradication of buffalo from cattle production areas and to the confinement of buffalo to well-fenced areas, thus strongly limiting their movements and distribution range (Laubscher & Hoffman 2012). Due to their known or perceived role in the epidemiology of many infectious diseases, buffalo populations have been the target of control measures by veterinary services to protect cattle populations, crucial livelihood assets for most African national economies, but also for poor small-scale farmers living in the periphery of protected areas.

Finally, savanna buffalo are known to be hosts of a long list of endoparasites, including trematodes, cestodes, nematodes and pentastomids (Penzhorn 2000; Belem & Bakoné 2009). These infections do not normally result in pathogenic symptoms or mortality, although co-infection by gastrointestinal worms and bovine tuberculosis was shown to generate synergistic effects (increased mortality) (Jolles *et al.* 2008).

Forest buffalo

The susceptibility of forest buffalo to infectious diseases is expected to be similar to the savanna buffalo due to their phylogenetic relatedness. However, forest buffalo have not been reported to be infected by diseases of importance such as FMD and BTB. Forest buffalo sustain little exposure to alien infectious diseases compared to savanna buffalo because habitat within its distribution range is not suitable for cattle production. Interspecific contacts are thus rare. However, the recent increase in human encroachment in rainforest habitat (e.g. the logging industry) is currently boosting cattle production along the forest block of the Congo Basin, thus potentially leading to higher risks of disease transmission.

Ectoparasites in the forest buffalo have been recorded from an adult male found dead in the Nouabale-Ndoki National Park, Republic of Congo (Deem *et al.* 2005). This individual was affected by ticks of genus *Amblyomma* sp., *Rhipicephalus* sp., trematodes *Carmyerius gregarius* and oocysts of *Eimeria* spp. Intestinal schistosomes can also heavily infest buffalo, especially old bulls that spend considerable time around water. At Lopé National Park in Gabon, Lustenhouwer (2008) reported that forest buffalo used moist areas despite the risk of exposure to endoparasites. A genus of rumen fluke, *Paramphistomum* sp., was the most common parasite based on dung sampling.

Status in the wild

IUCN: Least Concern

African buffalo is considered a species of Least Concern according to the IUCN Red List (IUCN SSC 2008), not qualifying for Critically Endangered, Endangered, Vulnerable or Near Threatened status; buffalo are not a listed CITES species (UNEP-WCMC 2012). Though African buffalo appear to be widespread and abundant, many countries recognize the need to protect forest buffalo at the national level (Djeukam 2007). For example, buffalo are a protected species in Gabon, with no hunting allowed, and in Cameroon buffalo are a partially protected species with regulations on hunting (Kamdem-Toham *et al.* 2003; Djeukam 2007).

Savanna (Cape, West and Central African) buffalo

Savanna buffalo populations are likely to be impacted by a large array of factors, among which are land use changes, competition with livestock, poaching, drought and disease. Buffalo numbers suffered their most severe collapse during the great rinderpest epidemic of the 1890s, and subsequent outbreaks that have spread from cattle to wildlife during the twentieth century (Winterbach 1998). As above mentioned ('Parasites and diseases' section), local eradication programmes, corridor barriers and fencing of protected areas have further fragmented the initial meta-population.

During the last decades, civil wars (e.g. Angola, Sudan, Ivory Coast, Central African Republic, Mozambique, Democratic Republic of Congo, etc.) and national policies allowing armies to exploit bushmeat largely contributed to locally decimate buffalo populations. Opening roads through natural ecosystems facilitates uncontrolled hunting, fragments populations and generates barriers to dispersal (Blom *et al.* 2004). Poaching is not only conducted to support a local demand, but is often carried out by informal but well organized market channels delivering meat to towns (Dublin *et al.* 1990; FitzGibbon *et al.* 1995; Mduma *et al.* 1998). Increasing agricultural activities, high livestock numbers, deforestation (e.g. charcoal production) and increasing human population densities progressively contribute to the degradation of areas suitable for buffalo. In many locales, livestock overgrazing makes the habitat unsuitable for the buffalo and other large mammals, both through straightforward competition and due to impacted soils and erosion. Protected areas thus increasingly become isolated and disconnected, and buffalo subpopulations are left vulnerable to local extinction due to disease outbreaks, hunting or fires. In much of rural Africa, programmes for livestock vaccination have come to a complete standstill. In many regions a combination of disease and lawlessness is likely to present a major threat to the future survival of buffalo populations (Prins & Sinclair 2013).

Buffalo have a high commercial value as trophies throughout Africa, a value enhanced by their reputation of being one of the most dangerous African animals. For example, in 2013 the price of a two-week safari including the opportunity to shoot one buffalo globally amounts to €7000–35 000 (depending on the region, quality of service, trophy size, etc.; for more details on buffalo hunting, see Table 20.9). In Southern Africa, many private ranches and communal 'game conservancies' have been stocked with disease-free buffalo and make a good profit (e.g. Hearne & McKenzie 2000; Du Toit 2005 – see also the section 'Status in captivity'). Most hunting areas, if well managed, play an important role in conserving habitats, species richness, employment and income for local people around protected areas. Buffalo also have an unrealized potential value due to their resistance (both apparent and inherent) against many tropical diseases compared to livestock.

The conservation prospects of the three savanna subspecies of buffalo are quite different. Summation of the country estimates given above (Tables 20.1–20.2) gives a total population of >513 000 for the three subspecies of savanna buffalo, a figure slightly lower than the last global estimate (627 000; East 1998). As mentioned above, these estimates are likely to be conservative, for two main reasons. The first is that aerial surveys tend to underestimate buffalo populations due to detection bias from the air. The second is that population estimates are unavailable for some parts of these subspecies' ranges. Although comparisons between estimates are complex in areas presenting a dissimilar level of information (e.g. Sudan), global trends emerge from this exercise. The Cape buffalo (*S. c. caffer*) population globally appears stable and even increasing in countries such as Mozambique or South Africa. The slight decrease in the overall number of Cape buffalo mainly results from an apparent decrease of the total estimate in Tanzania, the country hosting the largest population. The situation of the West African savanna buffalo (*S. c. brachyceros*) also appears globally stable at the scale of the distribution range, but marked contrasts appear by country. In Burkina Faso, Niger and Benin, sustained efforts brought to several protected areas by the international community (e.g. the European Commission) during the last decade seem to bear fruit. In contrast, the West African savanna buffalo population of Senegal (Niokolo National Park) and Ivory Coast (Comoe National Park) has alarmingly dropped by 90%. Most worrying is the future of the Central African savanna buffalo (*S. c. aequinoctialis*) population, which has faced an estimated decrease of 60% during the last 15 years. Although uncertainties remain about the status of the population in Sudan, the large population previously observed in Democratic Republic of Congo and the Central African Republic fell sharply due to internal problems of governance (civil war, civil unrest).

Forest buffalo

The forest buffalo is declining across its geographic range (IUCN SSC 2008). Based on only a few population estimates, East (1999) estimated a total population of 60 000 forest buffalo with about 75% of the population in nominally protected areas, including Lobeke National Park (Cameroon), Dzanga-Ndoki National Park (CAR), Nouabalé-Ndoki-Kabo (Congo-Brazzaville), Lopé National Park, Wonga-Wongue and Gamba (Gabon), Odzala National Park (Congo-Brazzaville) and Maiko National Park (Congo-Kinshasa).

The future of this subspecies depends on well-managed protected areas and hunting zones with special attention to forest clearings and mosaics of forest and savannas, where critical food resources are abundant (Blake 2002; Melletti 2008; IUCN SSC 2008). In addition to habitat loss, poaching is a major threat to forest buffalo populations (IUCN SSC 2008). Buffalo are hunted for their meat and many rural populations depend on bushmeat for protein (Foerster *et al.* 2012). For example, in the Gamba Protected Areas Complex, Gabon, forest buffalo is a target species in the bushmeat trade, and is the fourth highest species present in the markets (Thibault & Blaney 2003). Thus, appropriate hunting regulations

Table 20.9 The range of costs for a single buffalo hunt in different African countries where the species is legally hunted

	Guinea[1]	Burkina Faso	Benin	Cameroon	Central African Republic	Ethiopia	Uganda	Tanzania	Mozambique	Zambia	Zimbabwe	Botswana	Namibia	South Africa (RSA)
Trophy fees	1120	€430–480	€600	800–1800 €1500–2000[1]	€800–2000	1000–3300	2000–4000[2]	2500–3900	3000–5000	3000–3500	2600–4500	5000	3250–8500	6500–30 000[3]
Daily rates	?	€850	€1000–1300	944–1300 €2230[1]	€1900	1950–3584	1200–1500	2000	1000–1550	1000–1500	850–1250	3900	1650–2000	200–640
Total hunter days	8	7–10	7	7–13	7–10	16	10	10	7–10	7–10	10	10	8	5–10
All-inclusive hunting cost per buffalo	10 000	€6380–8930	€7600–9700	7408–10 900 ~€17,110[1]	~€14 100	~17 950	~14 000	15 000–22 000	10 000–14 500	10 000–18 500	10 000–17 000	~14 000	11 500–14 000	9750–48 000

Buffalo are a key species in the safari hunting industry. The economic activity that can be generated around a buffalo hunt is much higher than only the buffalo trophy fee. This activity creates also jobs, recruiting people from local communities such as drivers, trackers, skinners, cooks, cleaning ladies, etc.
All hunts are considered to be carried out by a single hunter, with one buffalo bull included.
All prices are in US dollars unless otherwise specified.
The trophy fees and daily rates listed come from the websites of the main hunting outfitters. These values may change by a small percentage from year to year.
Daily rates depend on the kind of accommodation, service, quality of hunting areas, logistics and so on and vary from country to country.
A buffalo hunt starts from a minimum of five to a maximum of 16 days.
A percentage of trophy fees and total hunting cost go to local communities and to the government. This percentage varies from country to country.
[1] Trophy and daily fees and total hunting cost are related to the forest buffalo (*Syncerus caffer nanus*).
[2] 75% of trophy fees goes to local communities and 25% to the Ugandan government (source: Uganda Wildlife Authority).
[3] The trophy fees are determined by trophy size (horns size measured in inches) and location. This is mainly applied in private, fenced reserves.
Both the government reserves and private fenced lands are included.

and enforcement of these regulations are also critical for maintaining forest buffalo populations (Wilkie *et al.* 2011).

Status in captivity

Savanna (Cape, West and Central African) buffalo

In South Africa, numerous disease-free buffalo breeding projects have been supported by the government since 1996, with the objective of restocking areas where buffalo populations were not viable anymore, or disappeared due to disease or exclusion by cattle farmers (Laubscher & Hoffman 2012). Disease-free animals were produced using calves taken at birth from captive mothers and fostered by surrogate disease-free dairy cows (mainly Jersey cows due to their good mothering abilities and high milk yield). The initial stocks were built from the Kruger National Park population, offering the best gene pool, but animals (record-class trophies) were also imported from Tanzania. These projects rapidly had a snowball effect through the involvement of the private sector (mainly driven by trophy hunting businesses) and buffalo breeding is now part of a wholly commercial system. Around 26 000 buffalo are privately owned and resident on approximately 2700 private game ranches or reserves in 2013 (South African Private Buffalo Owners Association, personal communication). In recent years, the increasing demand for disease-free buffalo has gradually led to an increase of their price in South Africa. In 2008 disease-free buffalo were being sold for just over ZAR 160 000 (ZAR 1 ≈ $0.11), while in 2010 this price increased to over ZAR 325 000 per buffalo at the same farmers' auctions (Cloete 2011). In 2012, ZAR 20 million was paid for a buffalo cow and her bull calf, as well as a record price of ZAR 26 million for a buffalo bull (Laubscher & Hoffman 2012). The buffalo cow that fetched the 2012 record price had a horn spread of 109 cm, making it the biggest of any cow in captivity. In this buffalo breeding system, bulls are selected on temperament and semen quality as well as horn length, and cows are primarily selected on reproductive performance. Although game farmers argue that selective breeding is restoring what years of culling has eliminated, a selection process based on specific traits (here trophy quality) and implemented at an industrial scale may have unexpected consequences for the genetic integrity of the species.

In 2012 there were 166 Cape buffalo in captivity across five regions of the world. In Africa, 48 (22 males, 24 females, 2 unknown) are kept in different zoos (ISIS: www2.isis.org/Pages/Home.aspx). Furthermore in Africa there are hundreds of Cape buffalo that are sold as game annually. For example, if we only look at the data from www.gamefarmnet.co.za/veiling.htm in 2012, about 350 Cape buffalo were sold.

Europe has 62 (17 males, 45 females), North America 26 (7 males, 19 females), Asia 18 (9 males, 9 females) and Latin and Central America report 12 (4 males, 8 females) (ISIS: www2.isis.org/Pages/Home.aspx; see also Chapter 27 and, in particular, Table 27.1). These numbers reflect individuals managed in cooperation with zoological breeding collections, and therefore are likely an underrepresentation of the total number of buffalo in captive collections.

Forest buffalo

In 2012 there were 135 forest buffalo in captivity across four regions and 26 institutions of ESB (EAZA) (see also Chapter 27). In Africa, six buffalo (two males, four females) are in two zoological gardens. In Australia there are four males and one female forest buffalo in two institutions. Europe has the greatest number of forest buffalo with 32 males, 84 females and 4 undetermined housed across 20 institutions. In the United States there are just four females in two different institutions. San Diego Zoological Society reports high calf mortality and a decision to no longer maintain forest buffalo due to little hope for maintaining high genetic diversity (G. P. Carmi & R. G. Rieches, personal communication).

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ANNEXE III - APPENDIX III

MAPS

A - Global home ranges in the Central zone

B - Global home ranges in the Eastern zone

C - Seasonal home range Herd 1

D - Seasonal home range Herd 2

E - Seasonal home range Herd 3 - I

F - Seasonal home range Herd 3 - II

G - Seasonal home range Herd 4 - I

H - Seasonal home range Herd 4 - II

I - Seasonal home range Herd 4 - III

J - Seasonal home range Herd 6 - I

K - Seasonal home range Herd 6 - II

L - Seasonal home range Herd 9

M - Seasonal home range Herd 10

N - Seasonal home range Herd 11

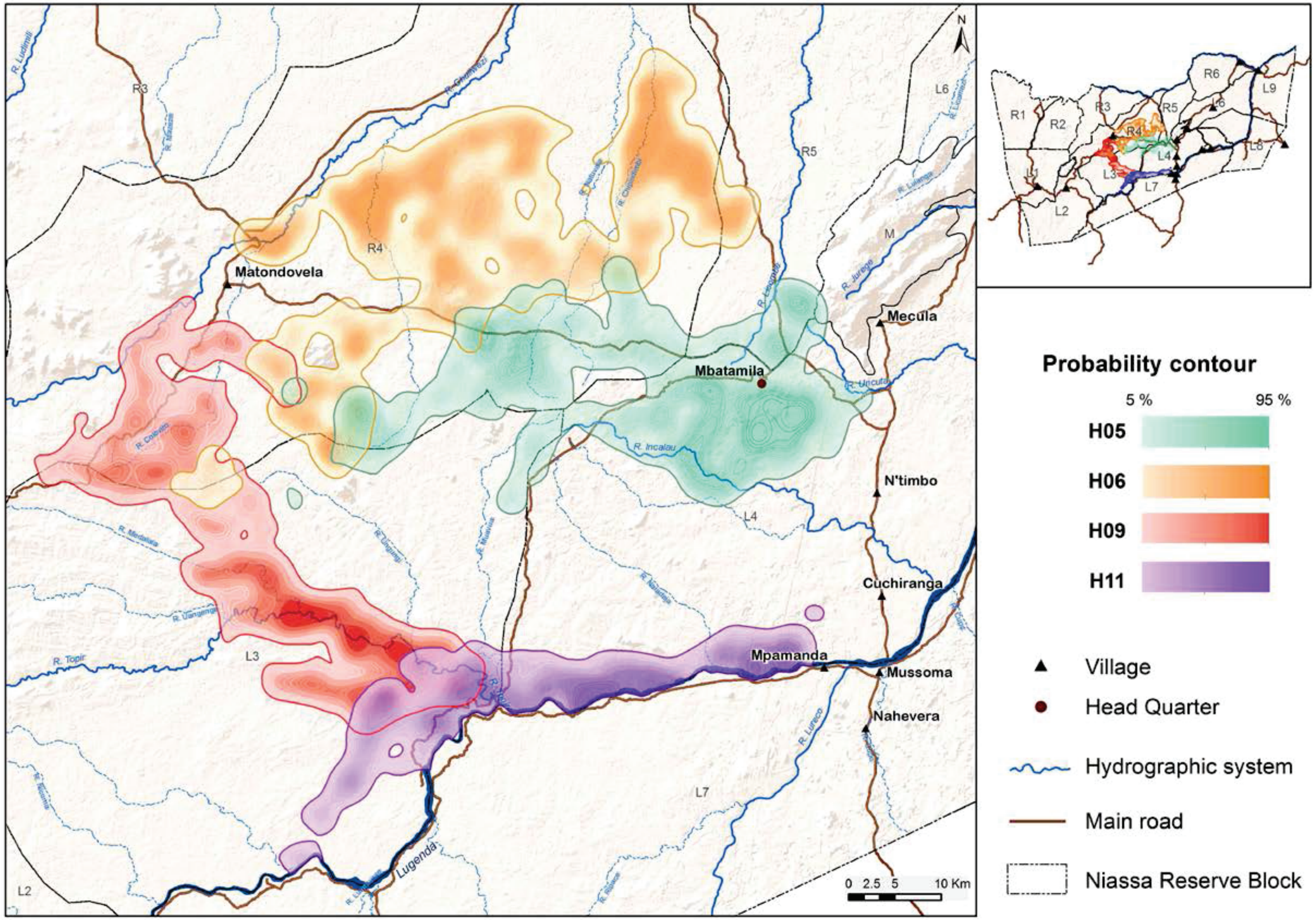


Figure II.A - Global home ranges of 4 herds in Niassa National Reserve in the Central zone from 2009 to 2013 using location-based kernel density estimation (LKDE)

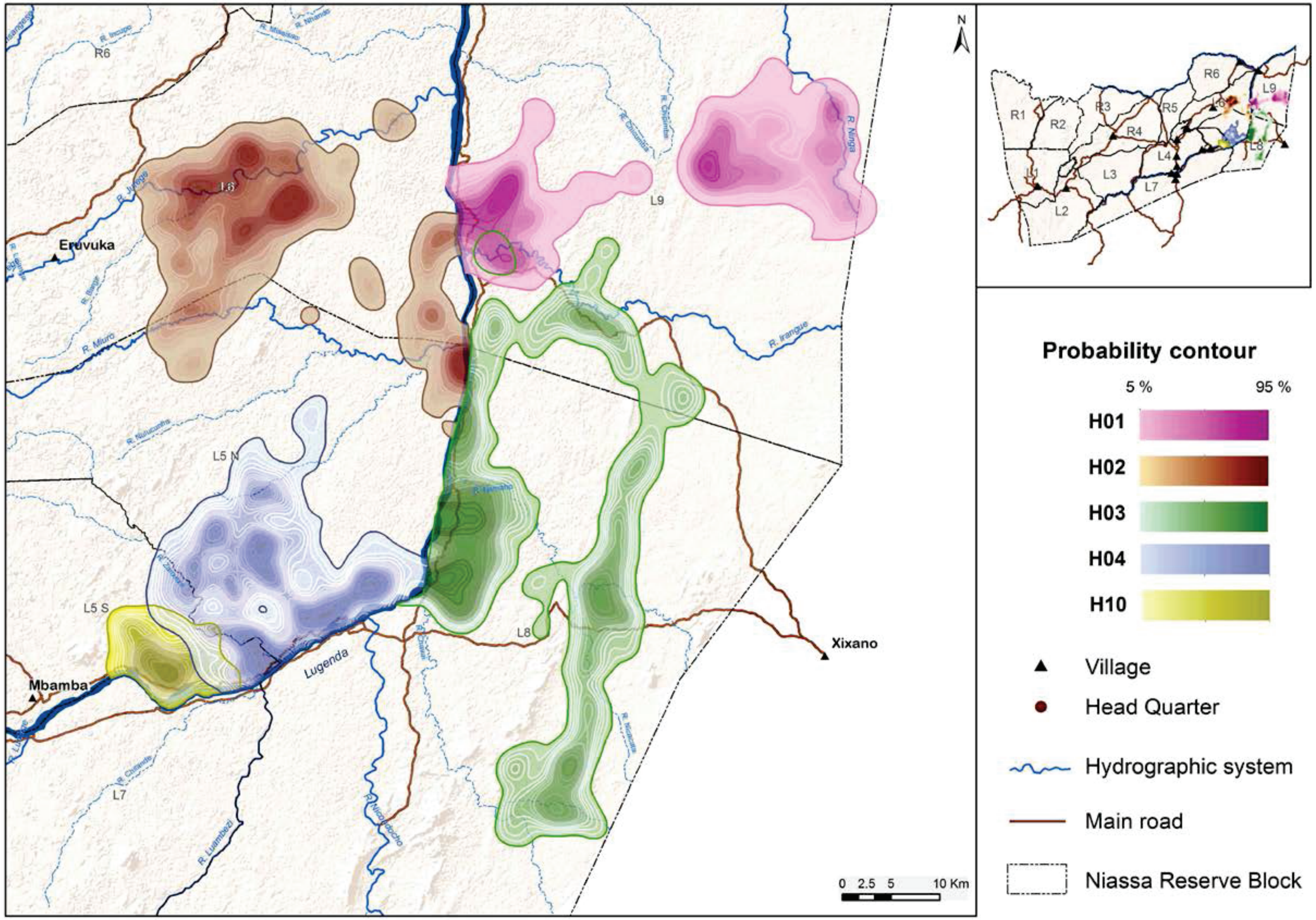


Figure II.B - Global home ranges of 5 herds in Niassa National Reserve in the Eastern zone from 2009 to 2013 using location-based kernel density estimation (LKDE)

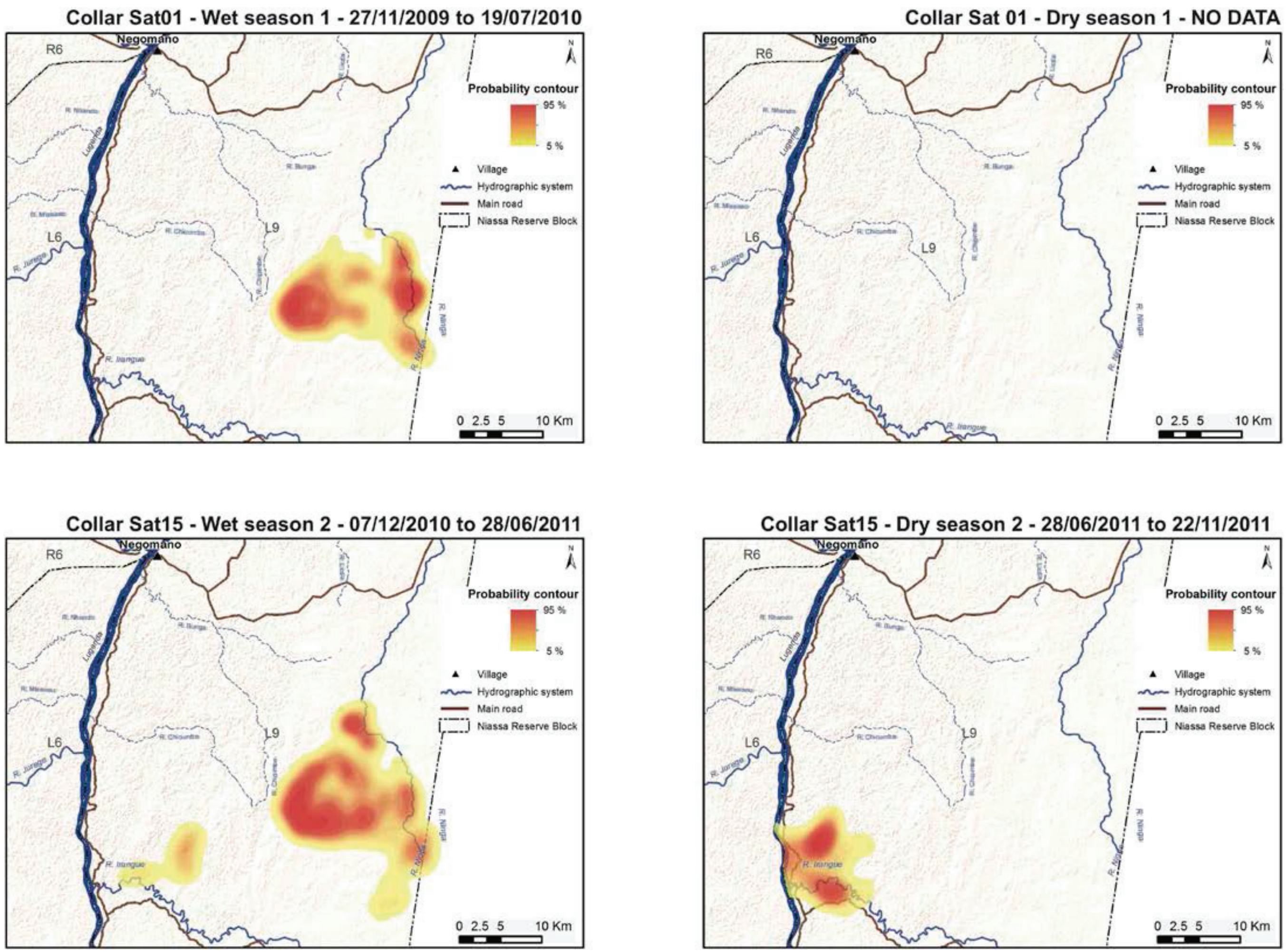
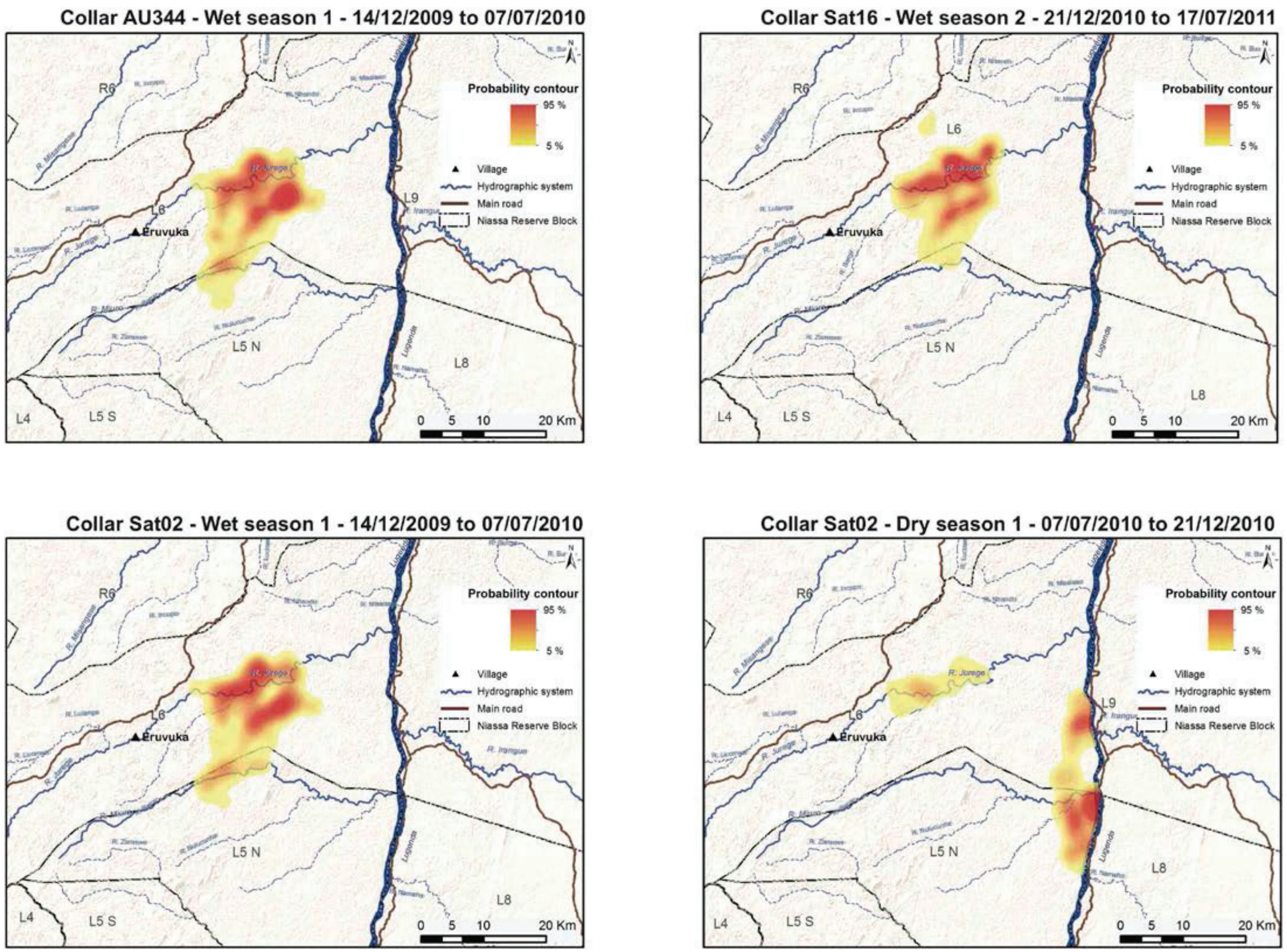


Figure II.C - Seasonal home range of buffalo cows Sat01 and Sat15 (Herd 1) from November 2009 to November 2011 (1 dry season / 2 wet seasons) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit block L9)



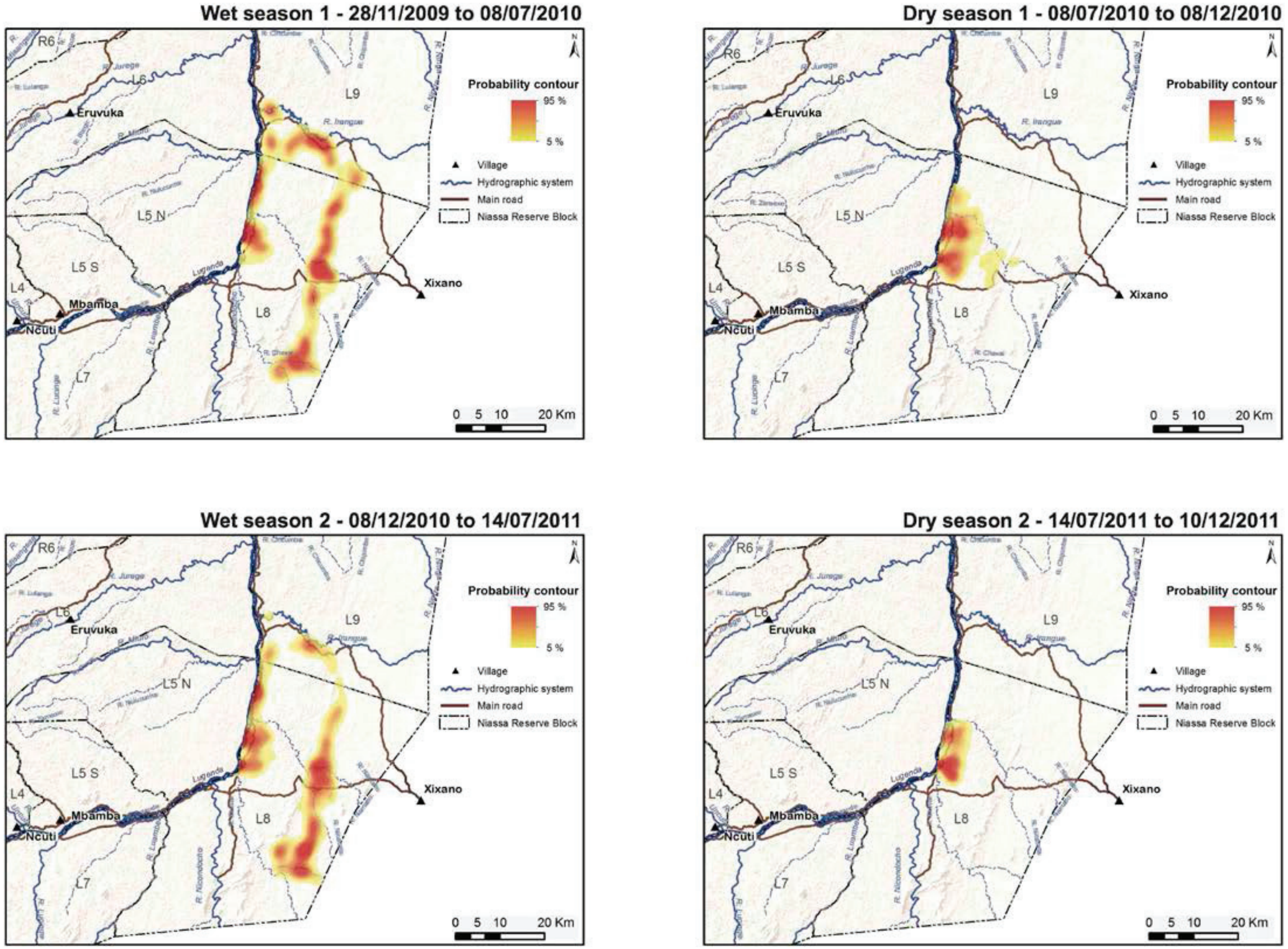
Collar AU344 - Wet season 1 - 14/12/2009 to 07/07/2010

Collar Sat16 - Wet season 2 - 21/12/2010 to 17/07/2011

Collar Sat02 - Wet season 1 - 14/12/2009 to 07/07/2010

Collar Sat02 - Dry season 1 - 07/07/2010 to 21/12/2010

Figure II.D - Seasonal home range of buffalo cows AU344, Sat02 and Sat16 (Herd 2) from November 2009 to July 2011 (1 dry season / 2 wet seasons) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L6-L5N)


Wet season 1 - 28/11/2009 to 08/07/2010

Dry season 1 - 08/07/2010 to 08/12/2010

Wet season 2 - 08/12/2010 to 14/07/2011

Dry season 2 - 14/07/2011 to 10/12/2011

Figure II.E - Seasonal home range of buffalo cow AU347 (Herd 3) from November 2009 to December 2011 (2 dry seasons / 2 wet seasons) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L8-L9)

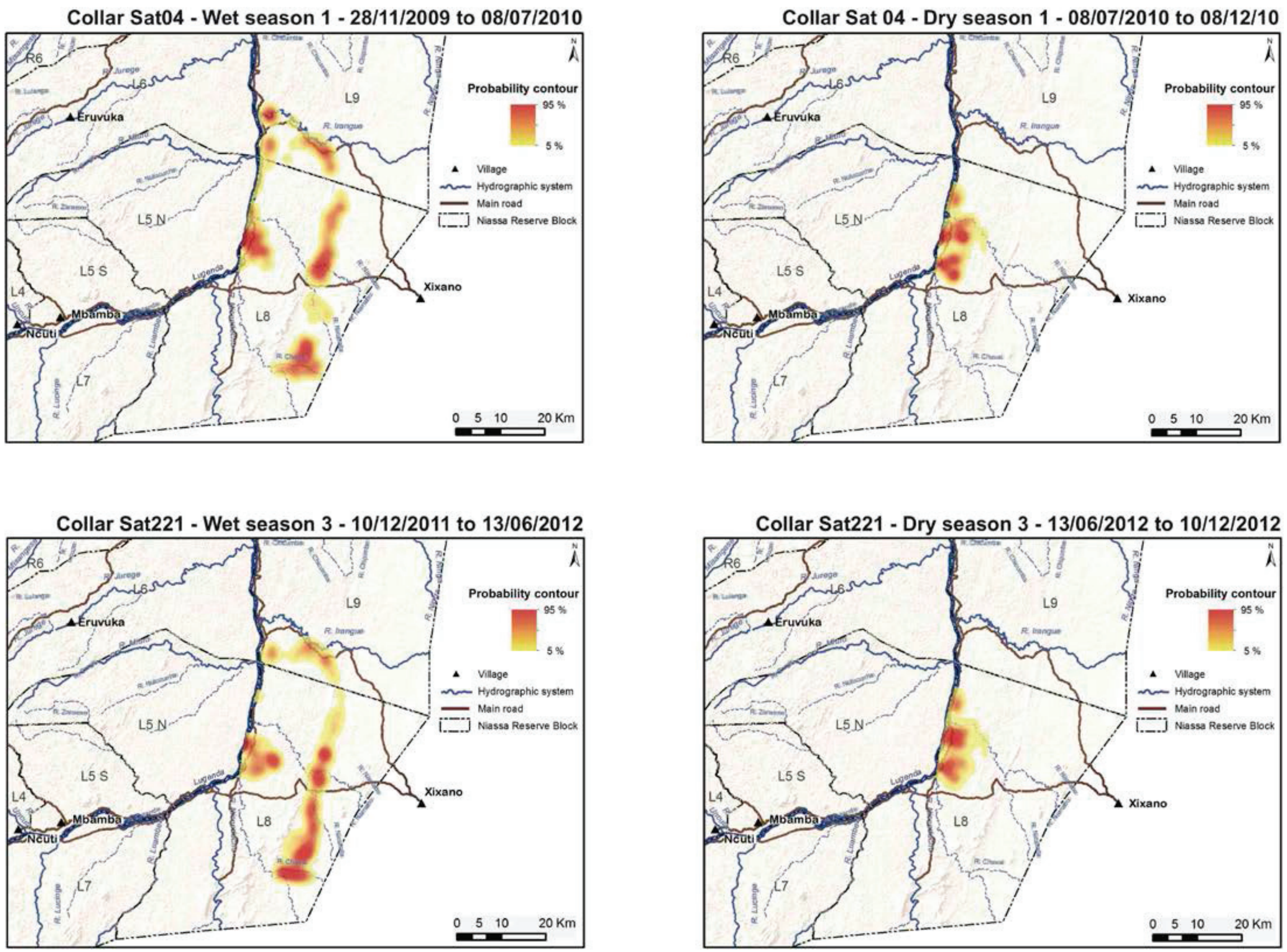


Figure II.F - Seasonal home range of buffalo cows Sat04 and Sat221 (Herd 3) from November 2009 to December 2012 (2 dry seasons / 2 wet seasons) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L8-L9)

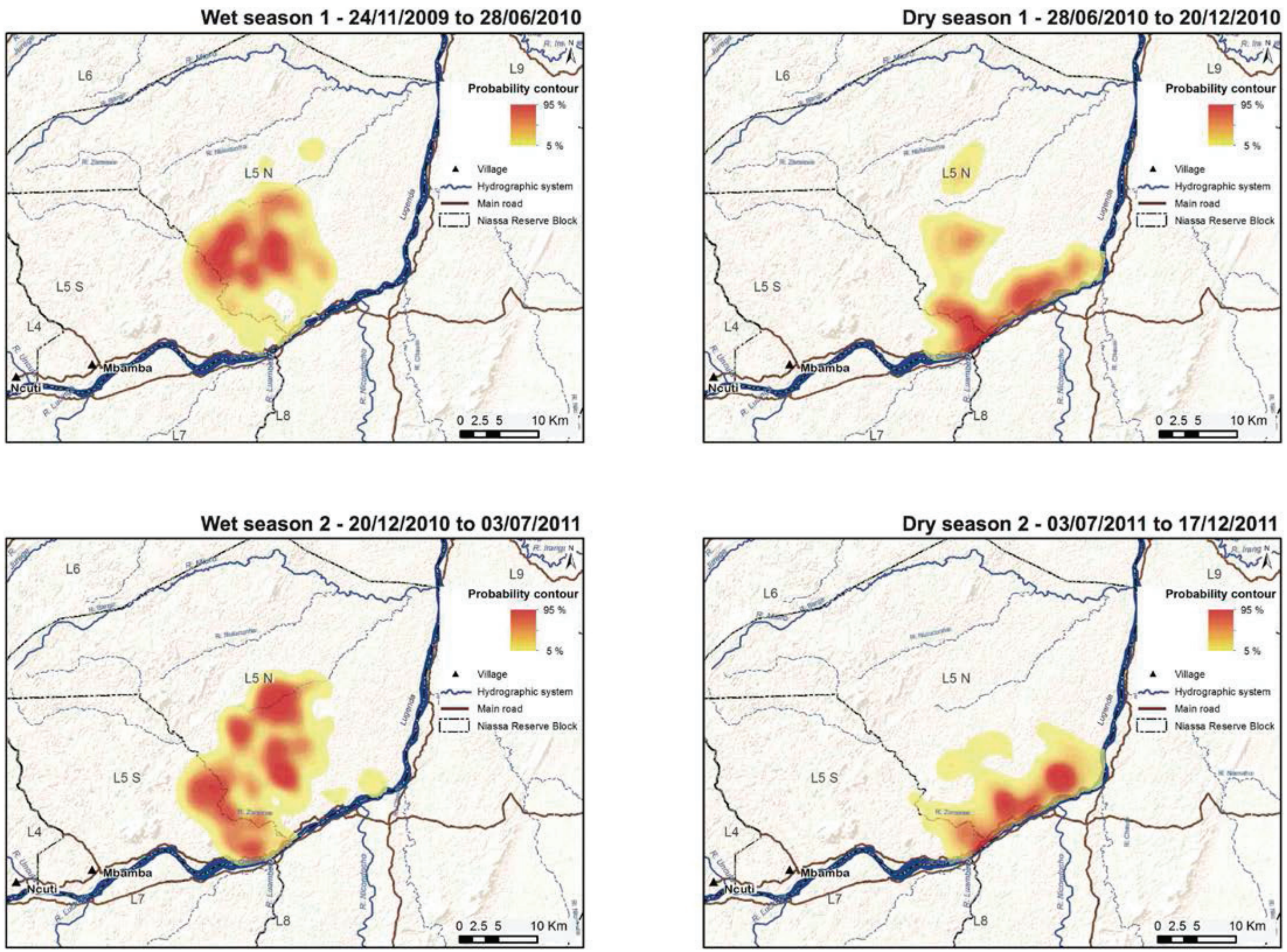
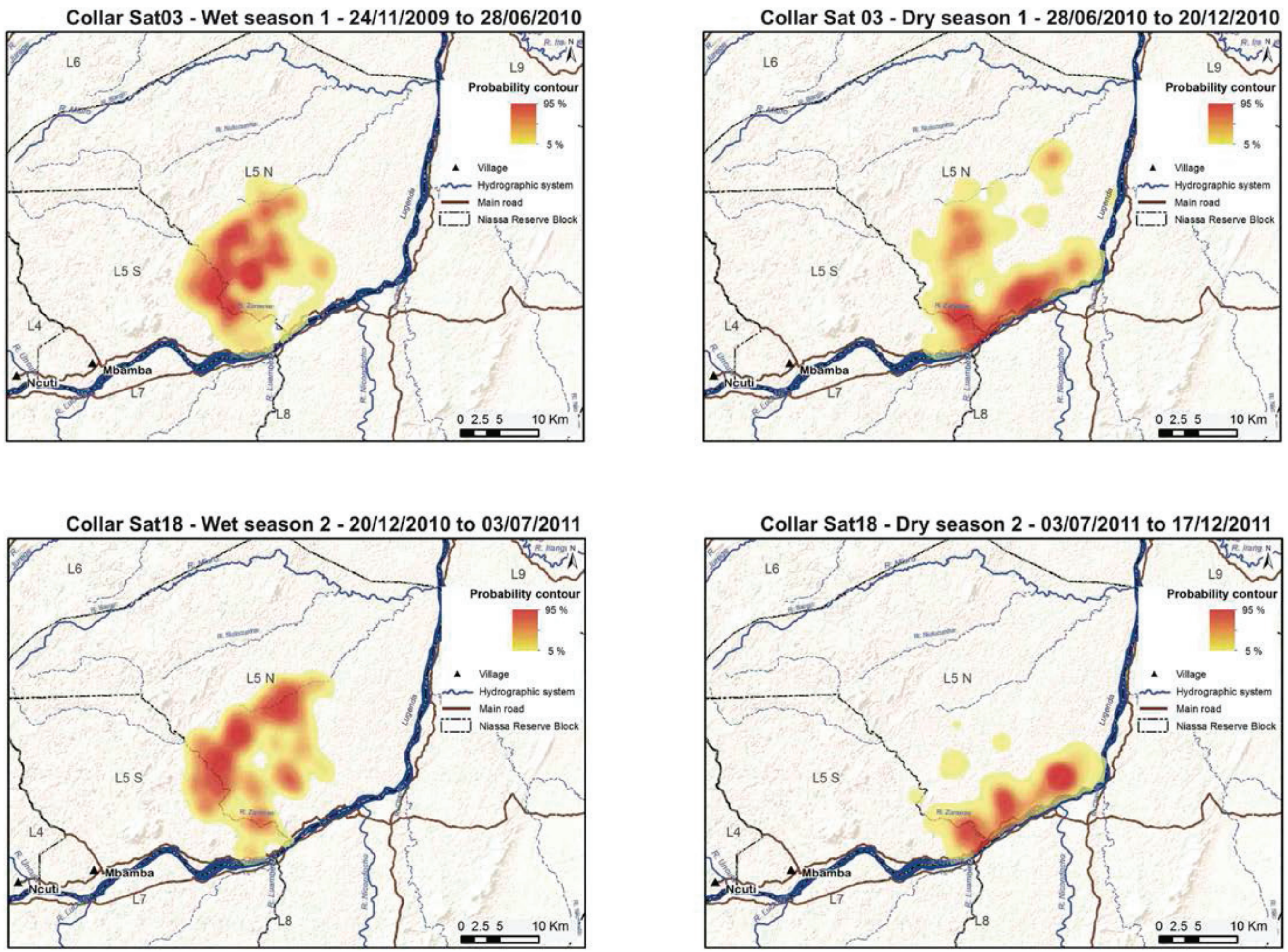


Figure II.G - Seasonal home range of buffalo cow AU346 (Herd 4) from November 2009 to December 2011 (2 dry seasons / 2 wet seasons) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L5N-L5S)



Collar Sat03 - Wet season 1 - 24/11/2009 to 28/06/2010

Collar Sat 03 - Dry season 1 - 28/06/2010 to 20/12/2010

Collar Sat18 - Wet season 2 - 20/12/2010 to 03/07/2011

Collar Sat18 - Dry season 2 - 03/07/2011 to 17/12/2011

Figure II.H - Seasonal home range of buffalo cows Sat03 and Sat18 (Herd 4) from November 2009 to December 2011 (2 dry seasons / 2 wet seasons) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L5N-L5S)

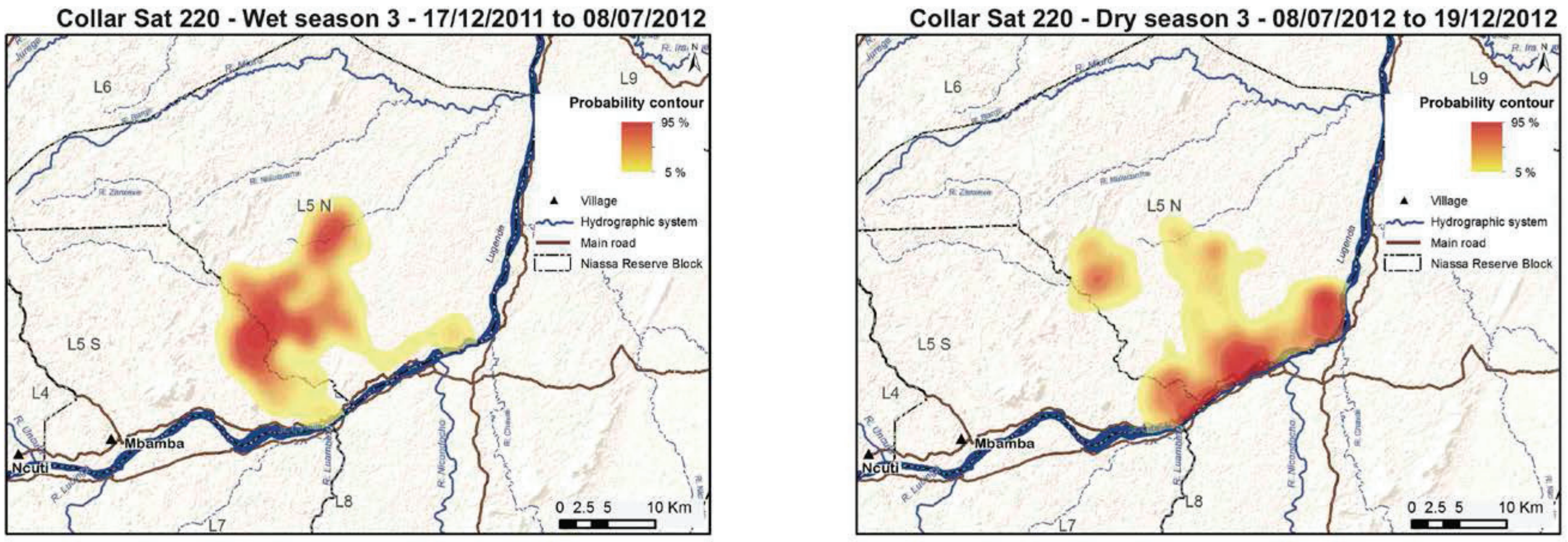


Figure II.I - Seasonal home range of buffalo cow Sat220 (Herd 4) from December 2011 to December 2012 (1 dry season / 1 wet season) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L5N-L5S)

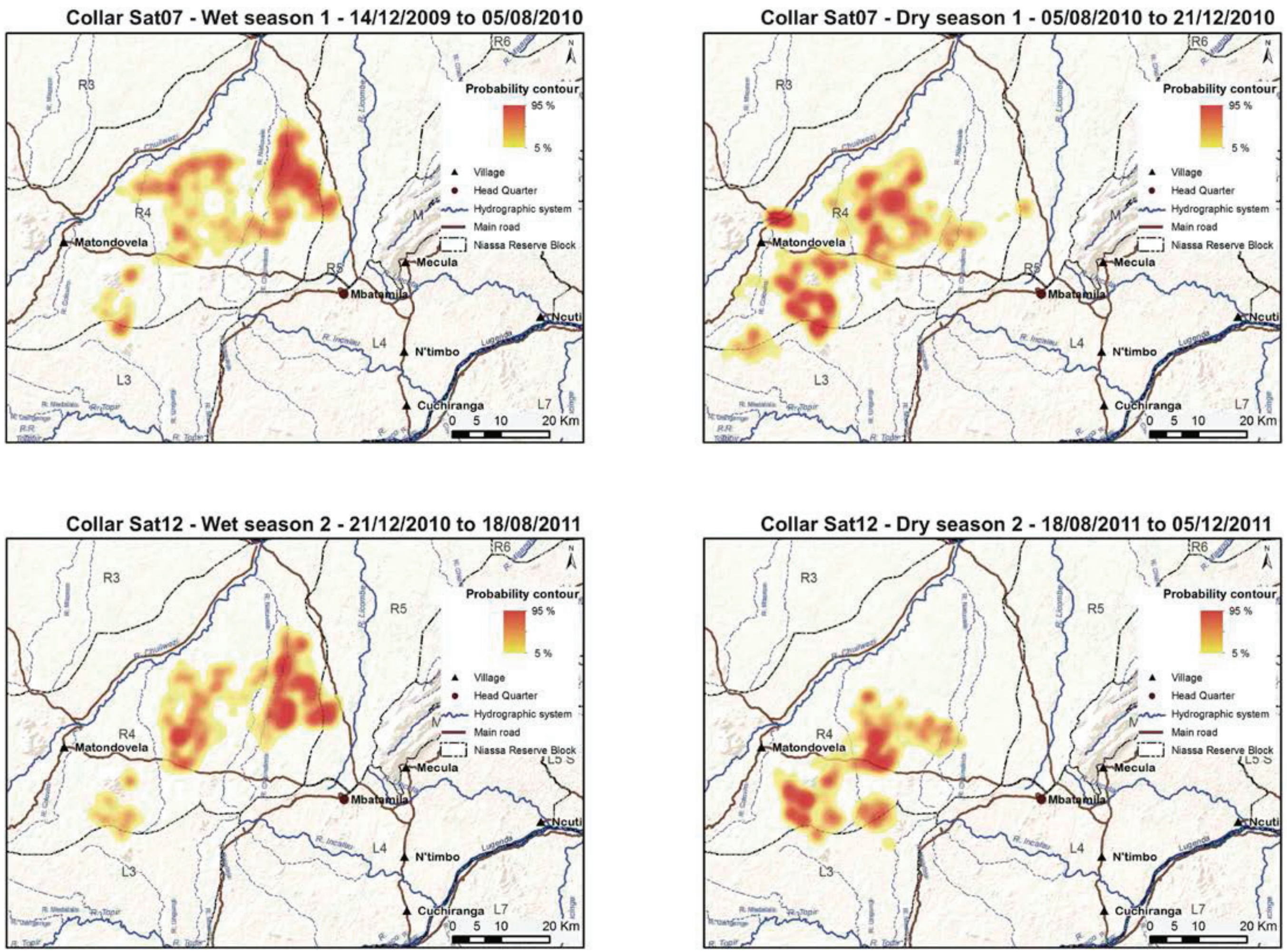


Figure II.J - Seasonal home range of buffalo cows Sat07 and Sat12 (Herd 6) from December 2009 to December 2011 (2 dry seasons / 2 wet seasons) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L3-R4-R5)

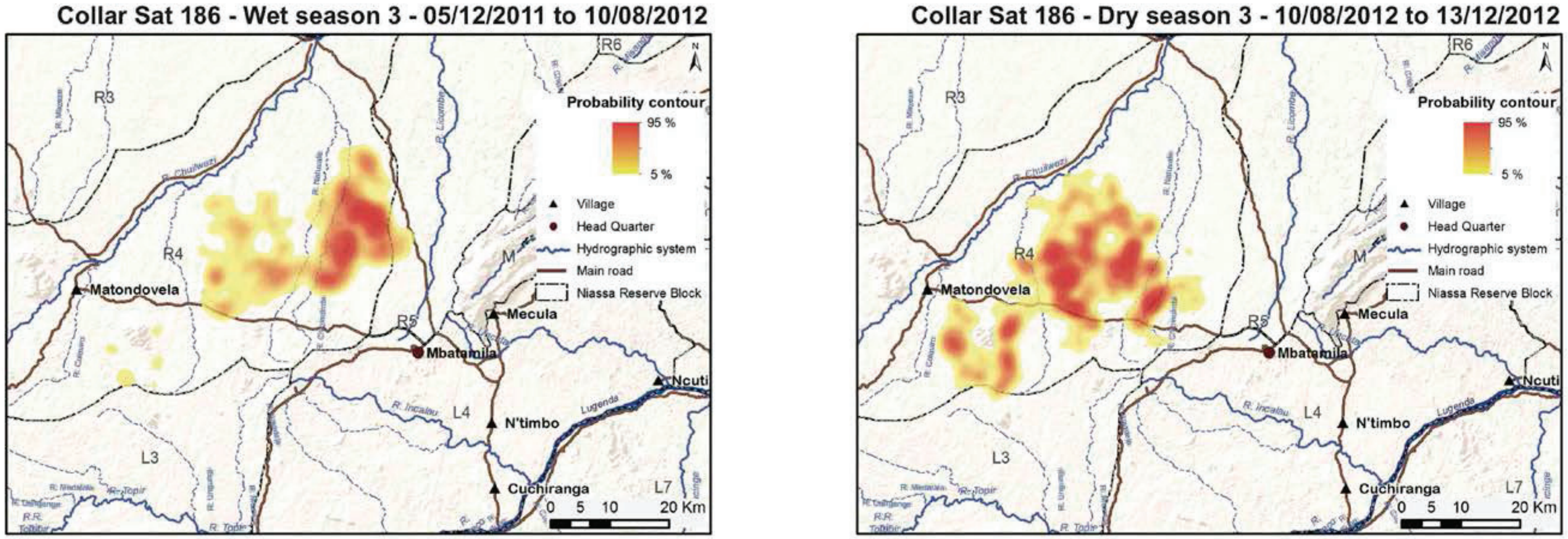
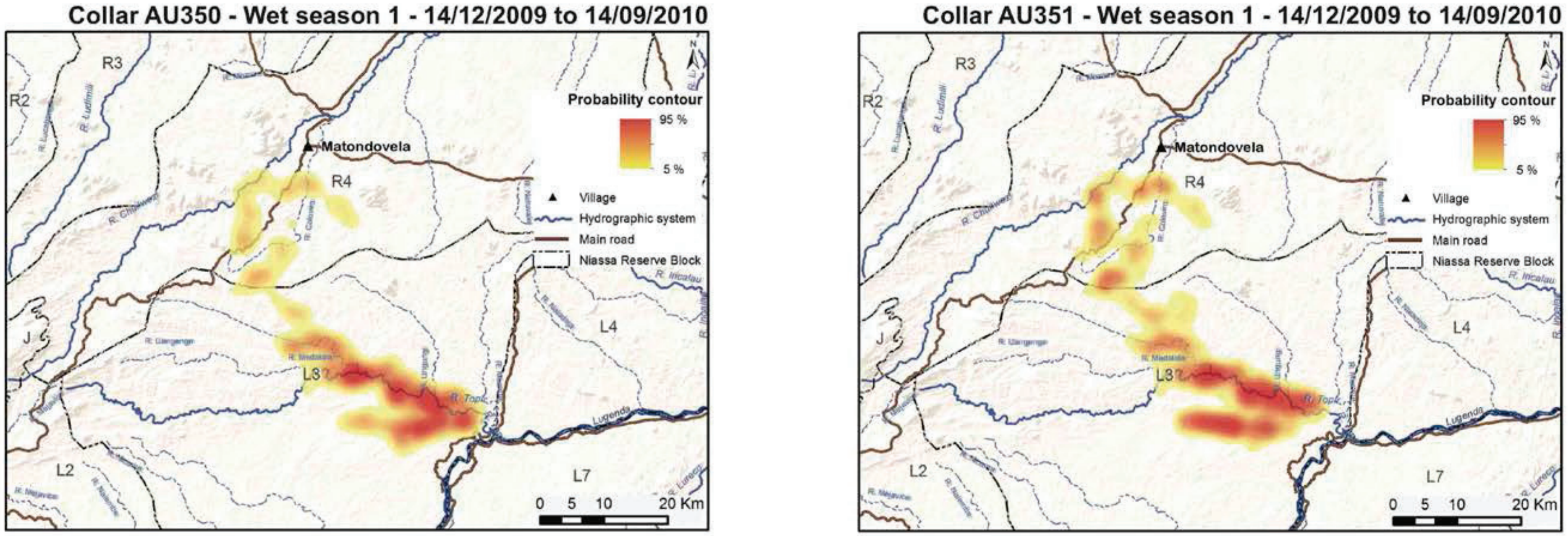


Figure II.K - Seasonal home range of buffalo cow Sat186 (Herd 6) from December 2011 to December 2012 (1 dry season / 1 wet season) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L3-R4-R5)



Collar AU350 - Wet season 1 - 14/12/2009 to 14/09/2010

Collar AU351 - Wet season 1 - 14/12/2009 to 14/09/2010

Figure II.L - Seasonal home range of buffalo cows AU350 and AU351 (Herd 9) from December 2009 to September 2010 (1 wet season) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L3-R4)

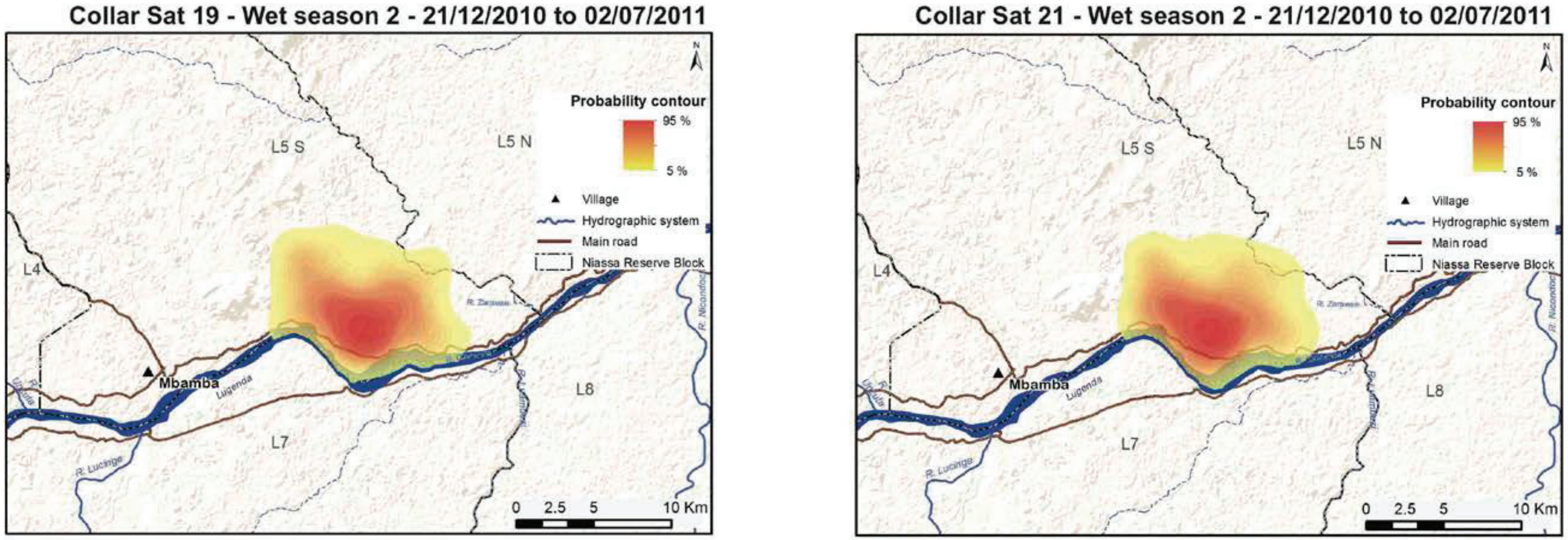


Figure II.M - Seasonal home range of buffalo cows Sat19 and Sat21 (Herd 10) from December 2010 to July 2011 (1 wet season) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L5N-L5S)

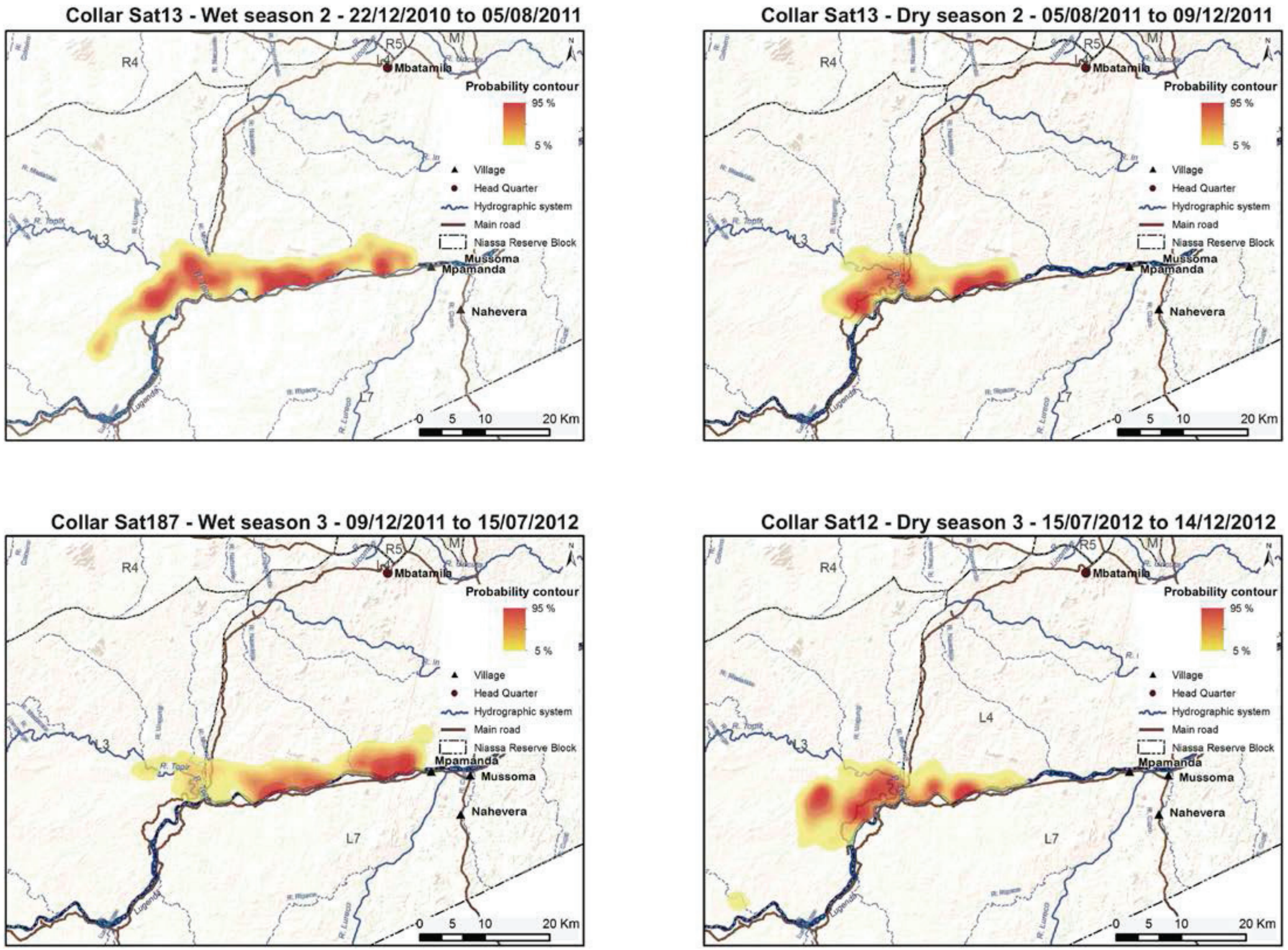
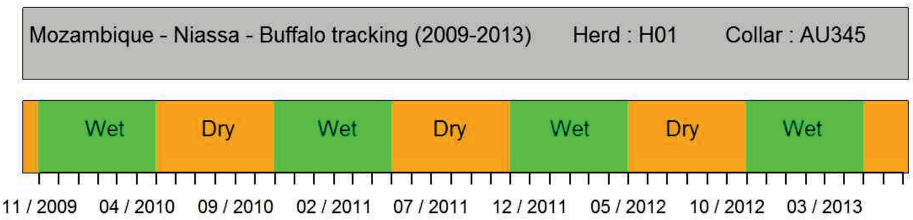


Figure II.N - Seasonal home range of buffalo cows Sat13 and Sat187 (Herd 11) from December 2010 to December 2012 (2 dry seasons / 2 wet seasons) using location-based kernel density estimation (LKDE) in Niassa National Reserve (eastern zone / Management unit blocks L3-L4)

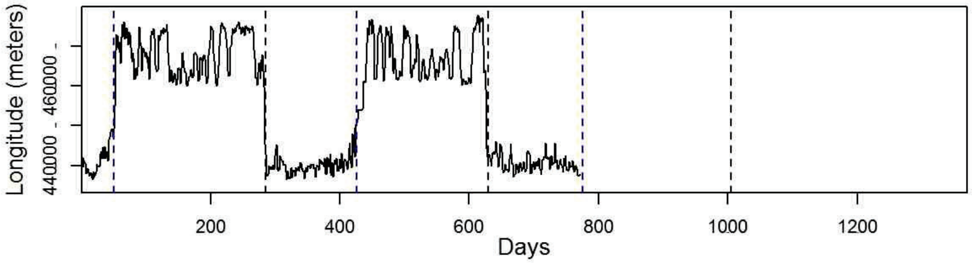
ANNEXE IV - APPENDIX IV

A - SYNOPTIQUES DES COLLIERS GPS SATELLITES ET UHF PRESENTES PAR ORDRE D'IDENTIFICATION DES TROUPEAUX ET COUPLES A LA PLUVIOMETRIE JOURNALIERE ET AU POURCENTAGE DE BRULE AU SEIN DE L'ENVELOPPE DU DOMAINE VITAL (LKDE 95%)

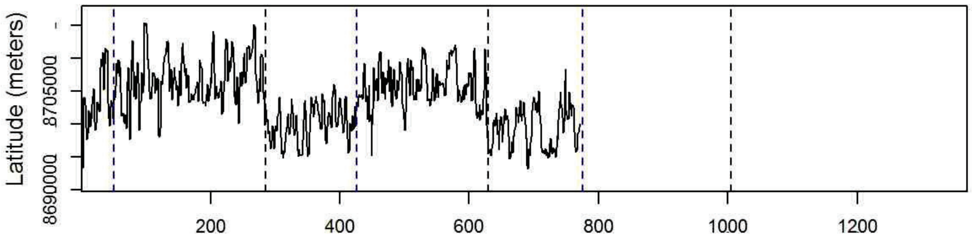
B - SYNOPTIQUE GENERAL DU TRACKING GPS ET DU TAUX DE REUSSITE D'ACQUISITON DES COLLIERS



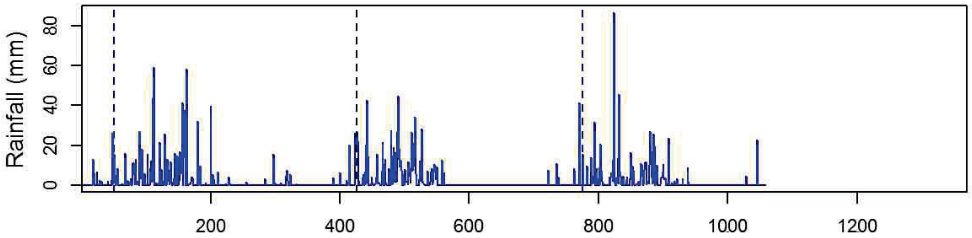
(a) Herd location as a function of time - Longitude



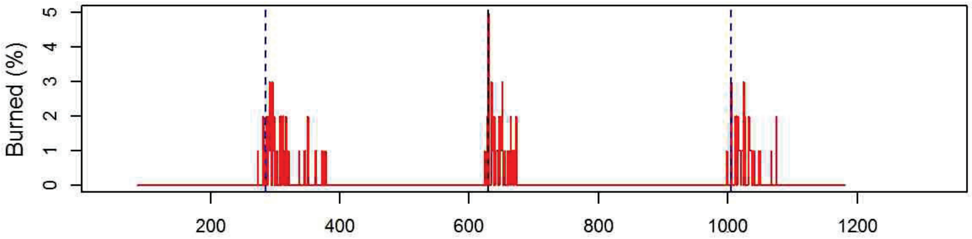
(b) Herd location as a function of time - Latitude



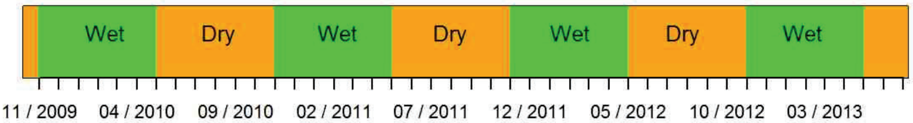
(c) Daily rainfall within annual home range contours (TRMM data)



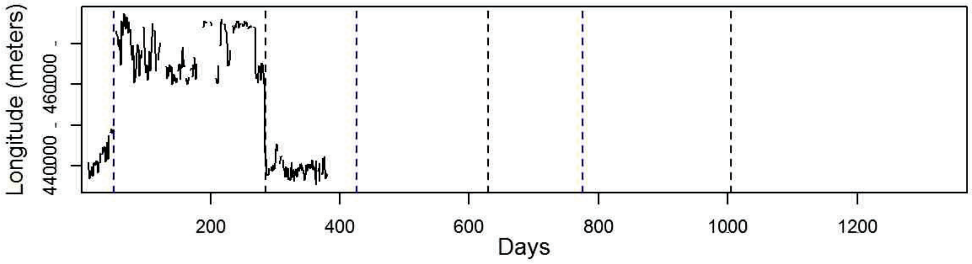
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



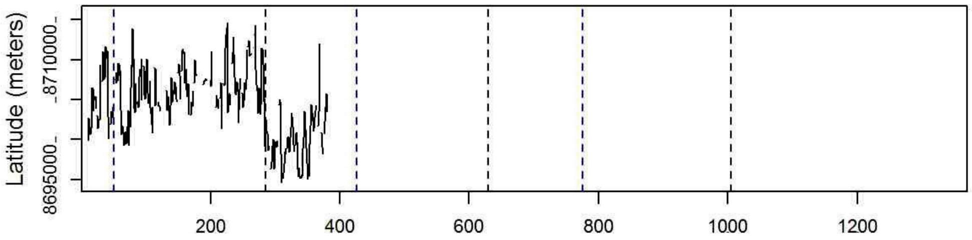
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H01 Collar : Sat01



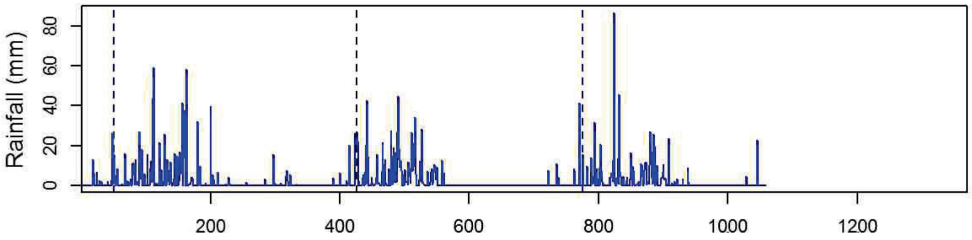
(a) Herd location as a function of time - Longitude



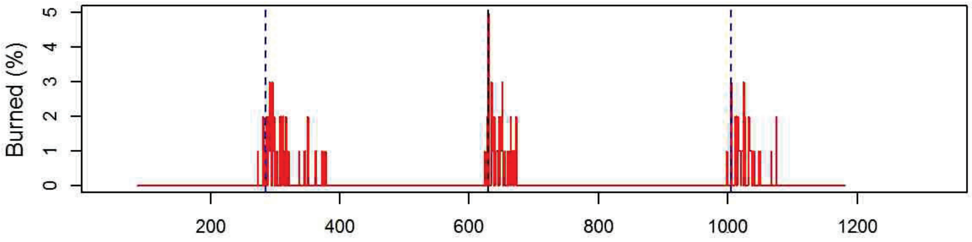
(b) Herd location as a function of time - Latitude



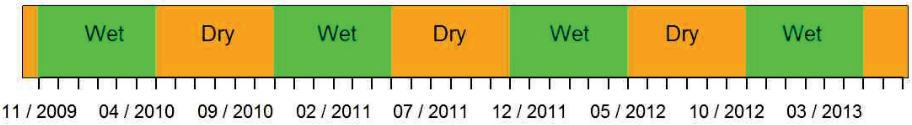
(c) Daily rainfall within annual home range contours (TRMM data)



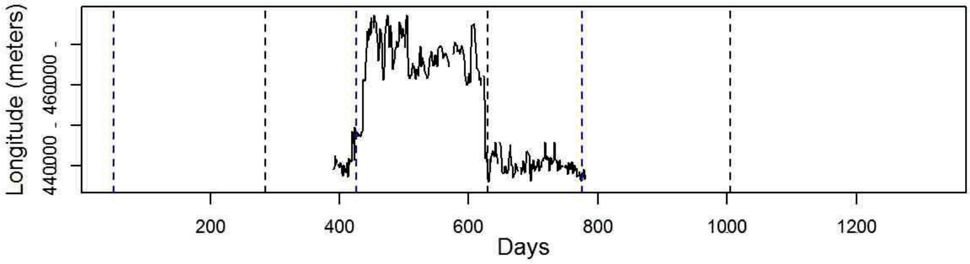
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



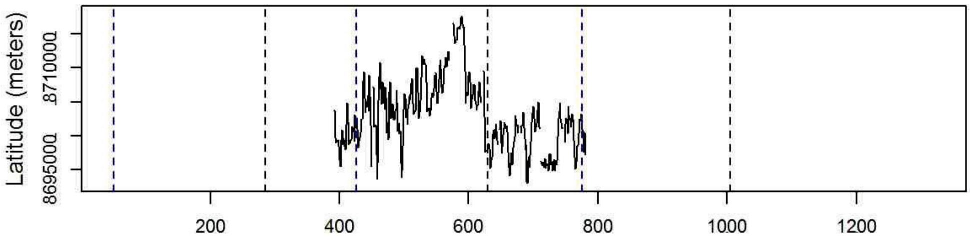
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H01 Collar : Sat15



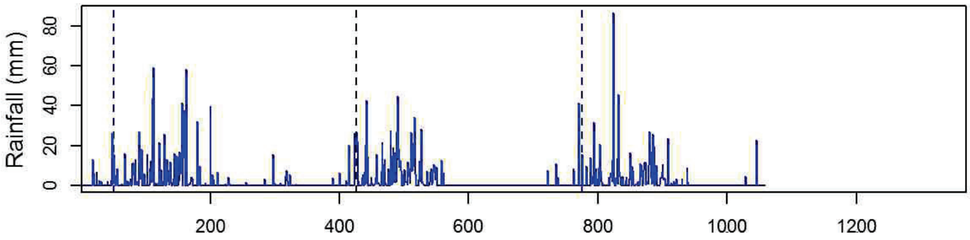
(a) Herd location as a function of time - Longitude



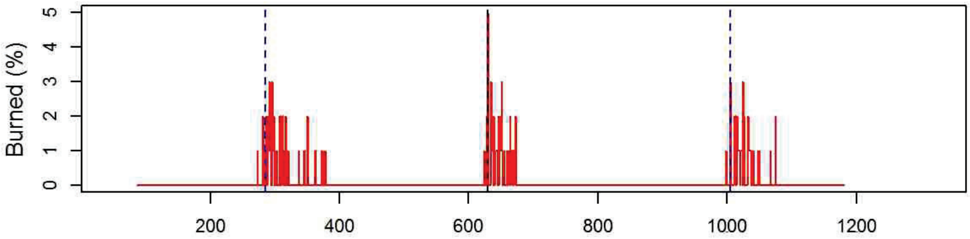
(b) Herd location as a function of time - Latitude

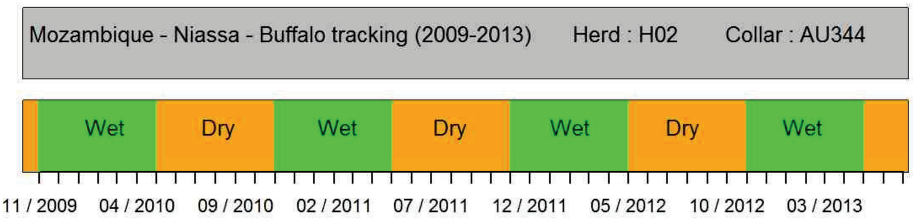


(c) Daily rainfall within annual home range contours (TRMM data)

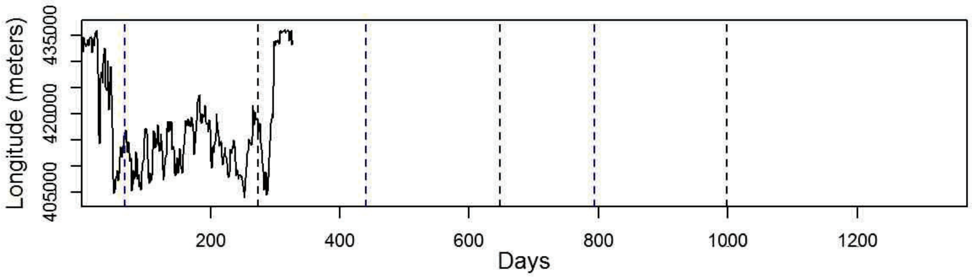


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

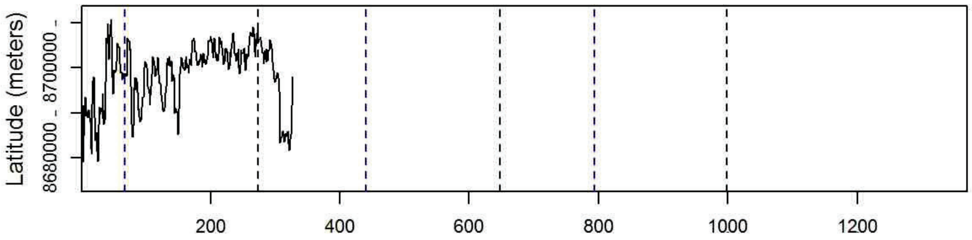




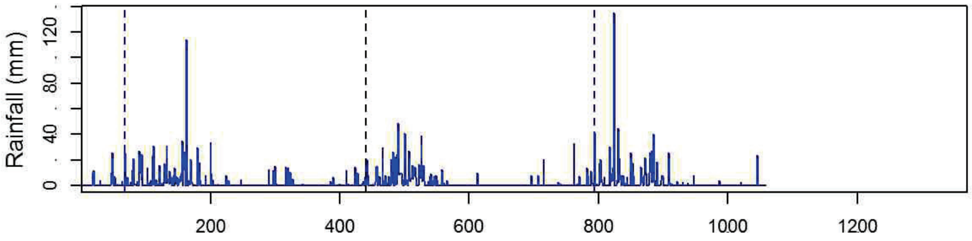
(a) Herd location as a function of time - Longitude



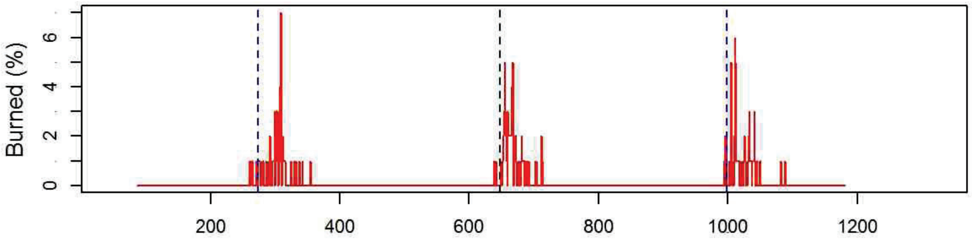
(b) Herd location as a function of time - Latitude

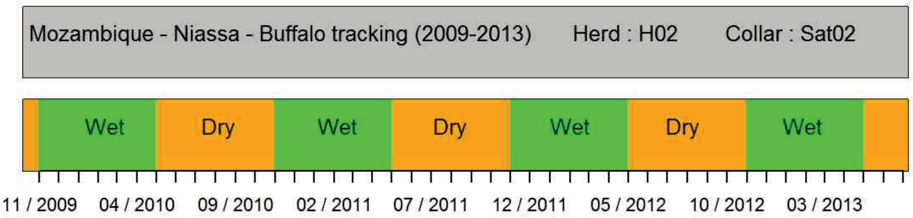


(c) Daily rainfall within annual home range contours (TRMM data)

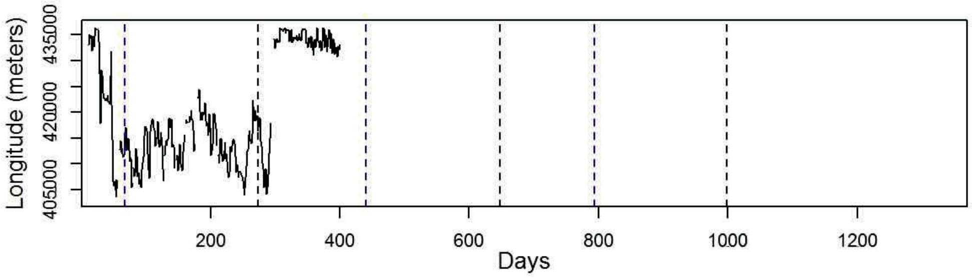


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

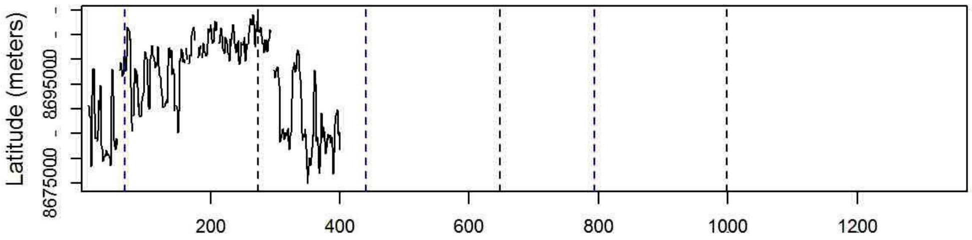




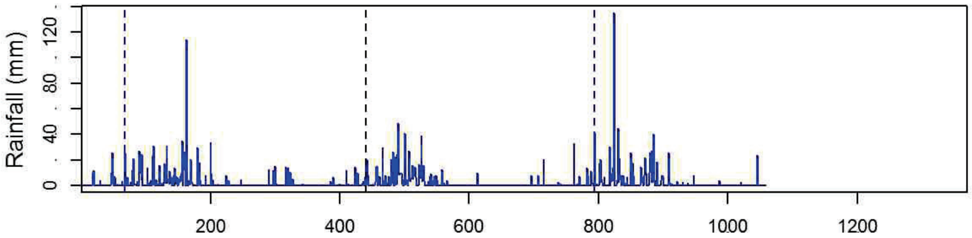
(a) Herd location as a function of time - Longitude



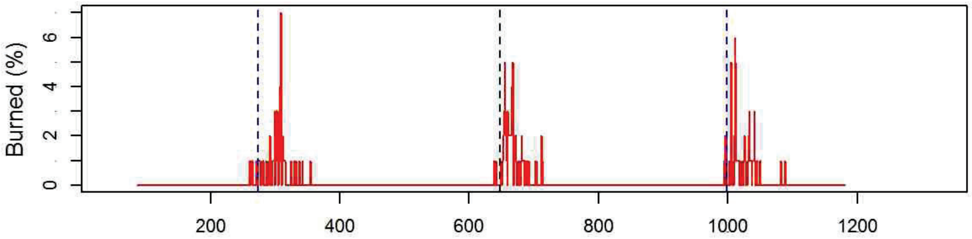
(b) Herd location as a function of time - Latitude



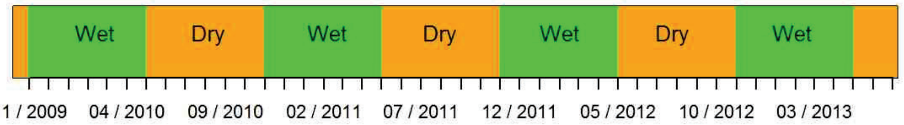
(c) Daily rainfall within annual home range contours (TRMM data)



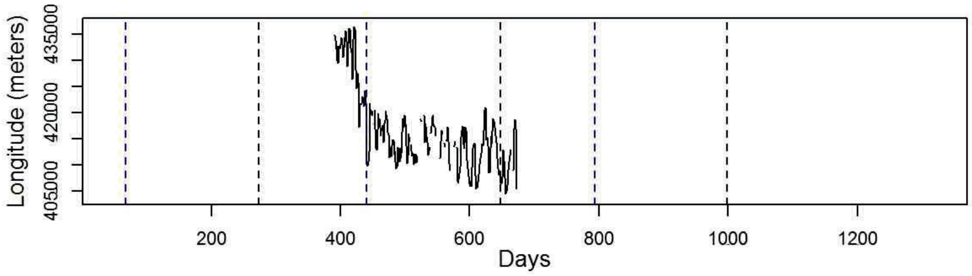
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



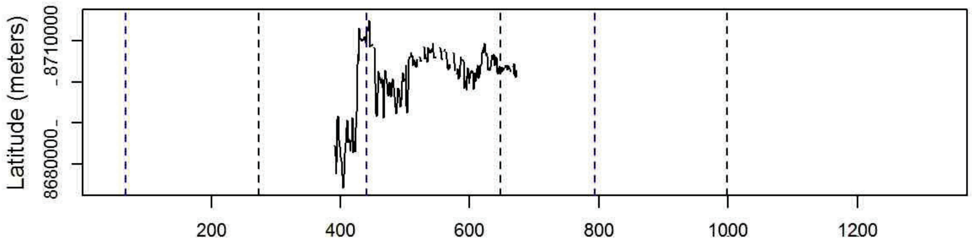
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H02 Collar : Sat16



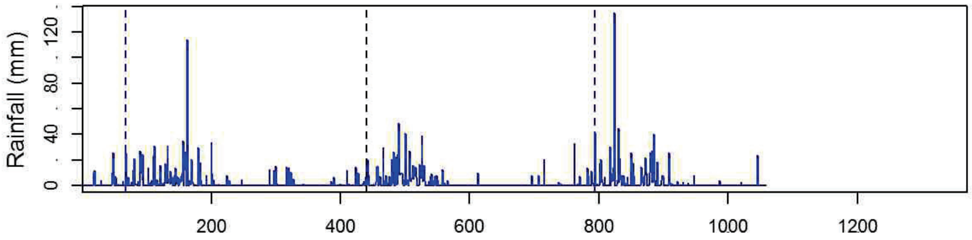
(a) Herd location as a function of time - Longitude



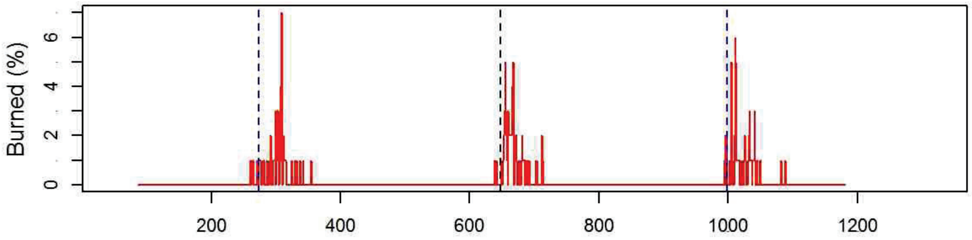
(b) Herd location as a function of time - Latitude

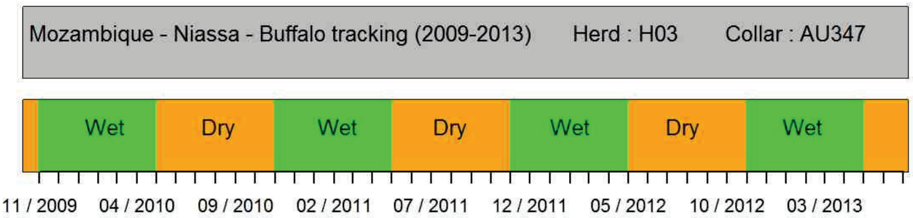


(c) Daily rainfall within annual home range contours (TRMM data)

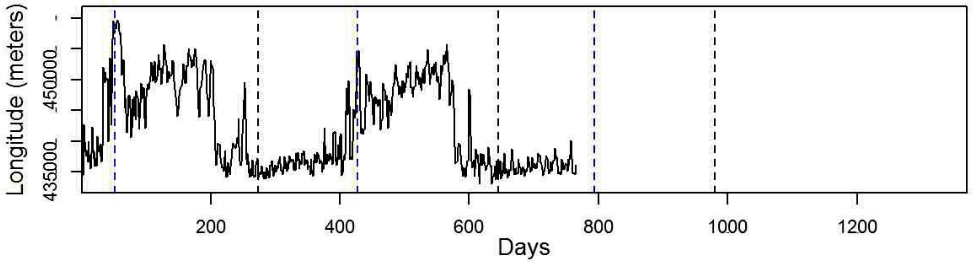


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

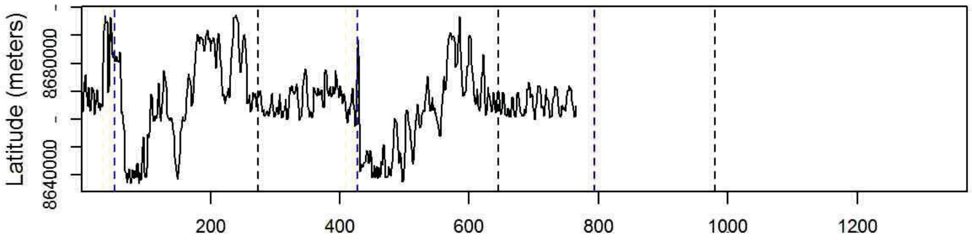




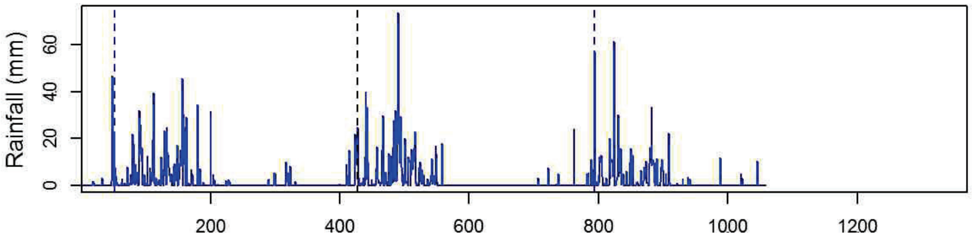
(a) Herd location as a function of time - Longitude



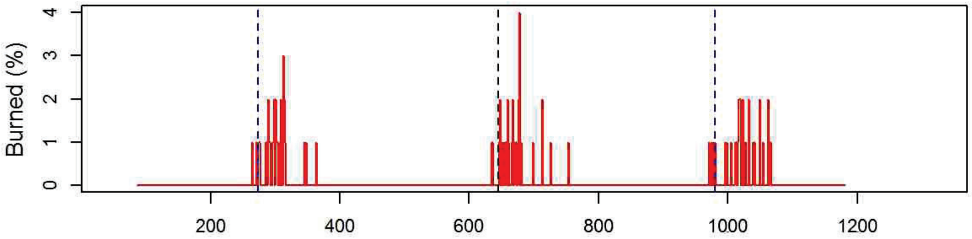
(b) Herd location as a function of time - Latitude

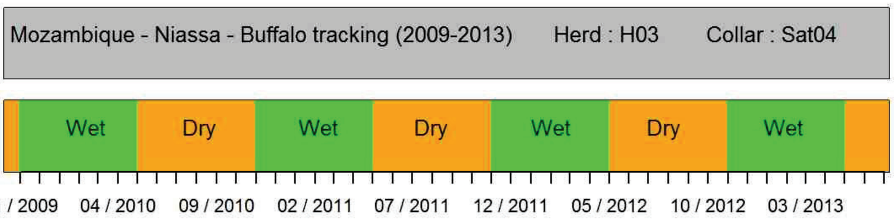


(c) Daily rainfall within annual home range contours (TRMM data)

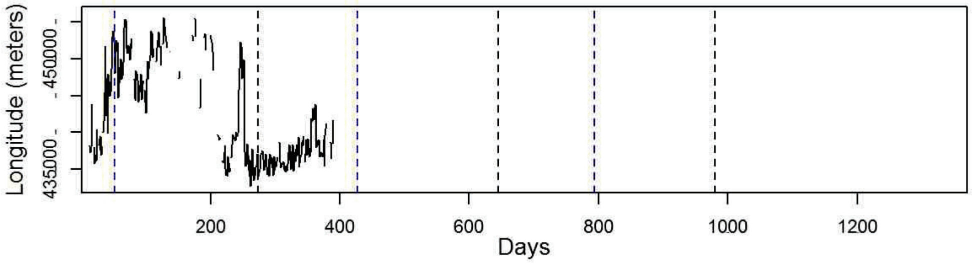


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

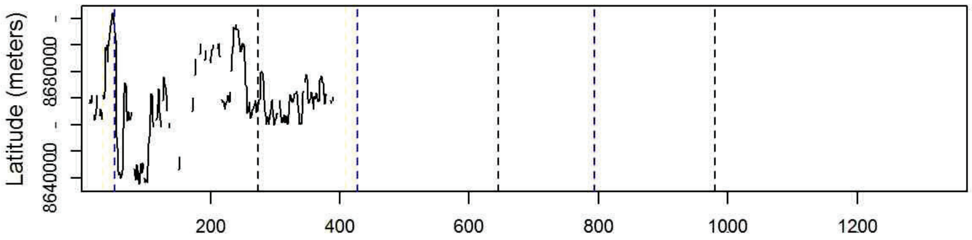




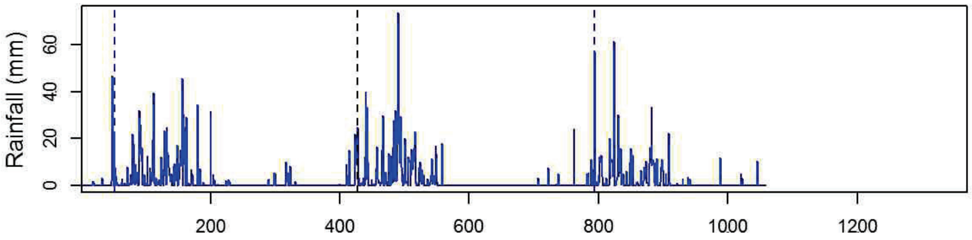
(a) Herd location as a function of time - Longitude



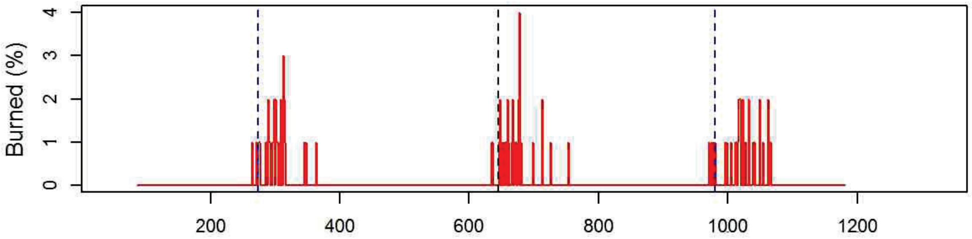
(b) Herd location as a function of time - Latitude



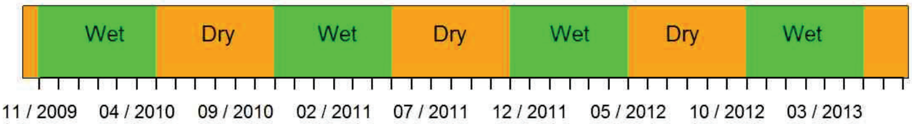
(c) Daily rainfall within annual home range contours (TRMM data)



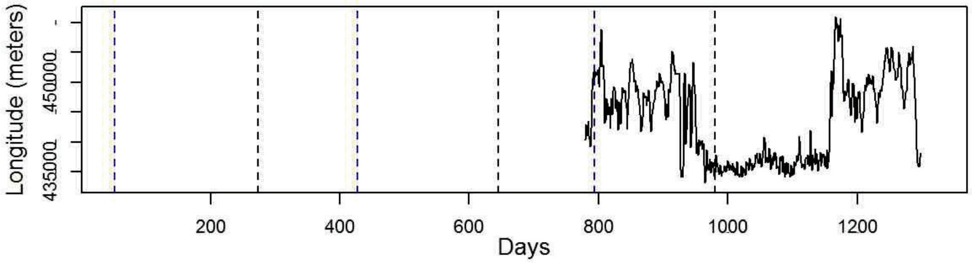
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



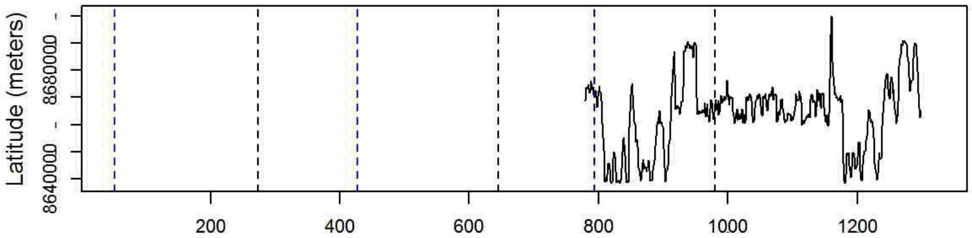
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H03 Collar : Sat221



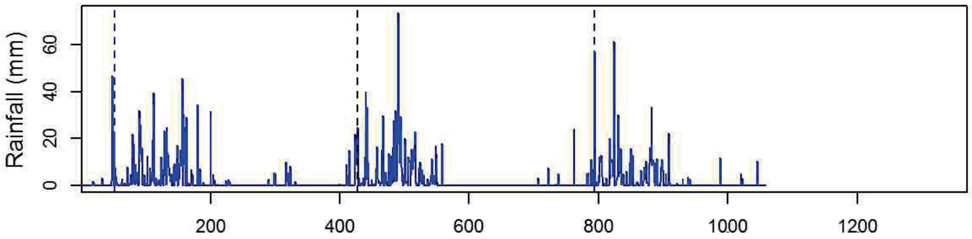
(a) Herd location as a function of time - Longitude



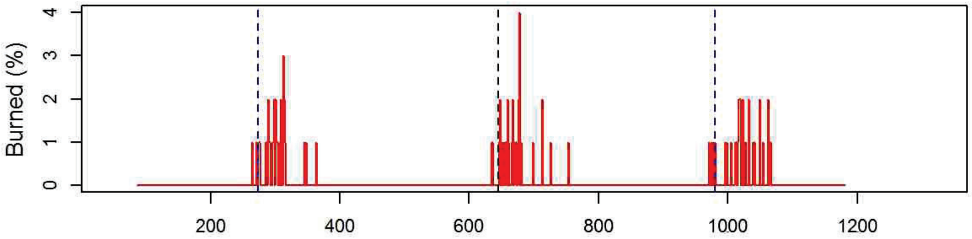
(b) Herd location as a function of time - Latitude



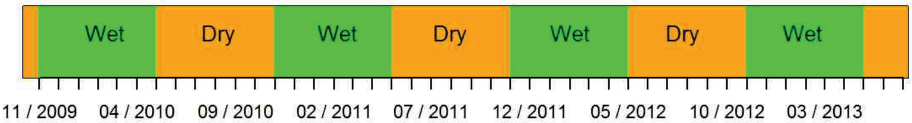
(c) Daily rainfall within annual home range contours (TRMM data)



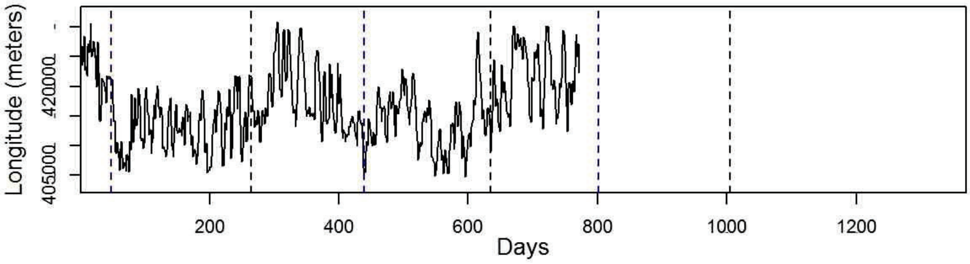
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



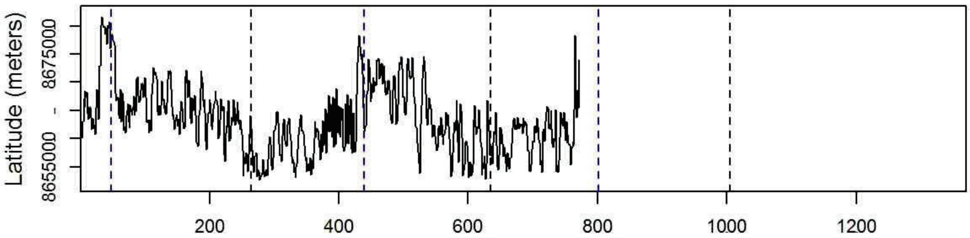
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H04 Collar : AU346



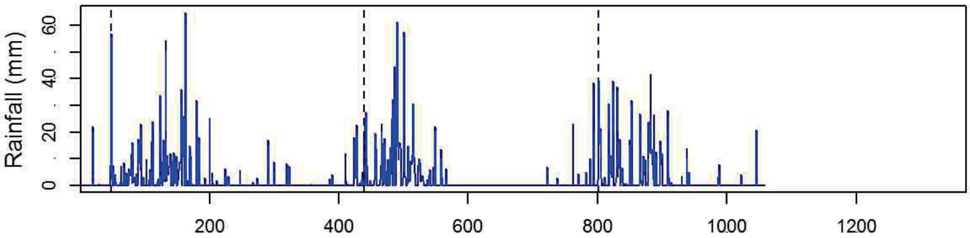
(a) Herd location as a function of time - Longitude



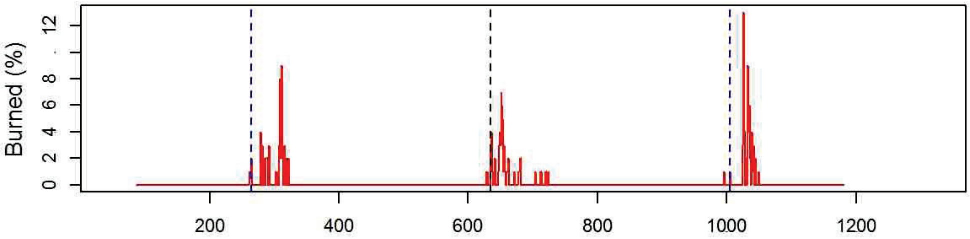
(b) Herd location as a function of time - Latitude

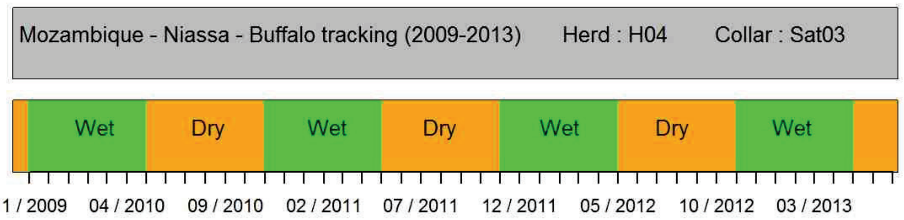


(c) Daily rainfall within annual home range contours (TRMM data)

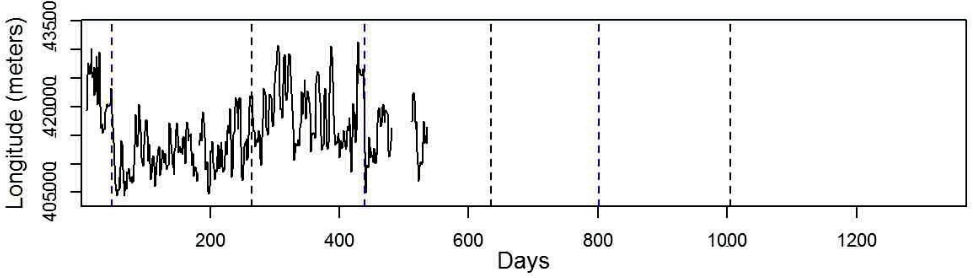


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

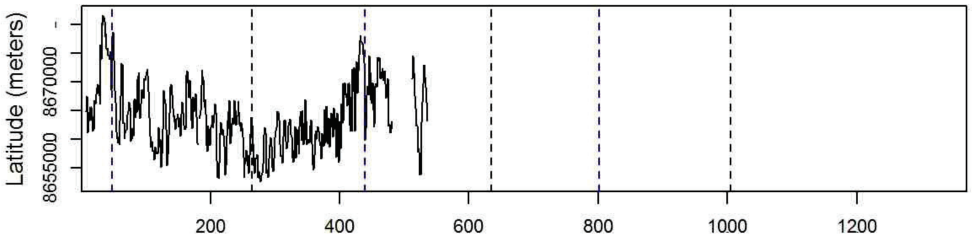




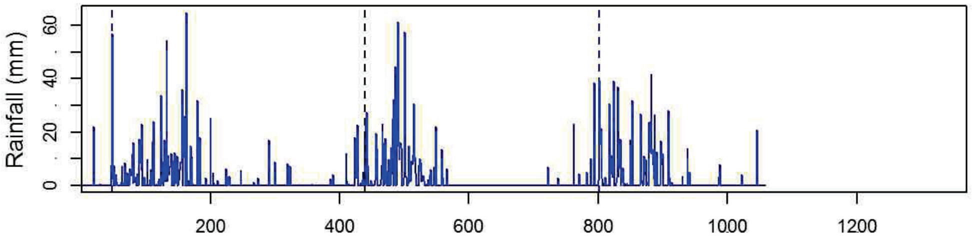
(a) Herd location as a function of time - Longitude



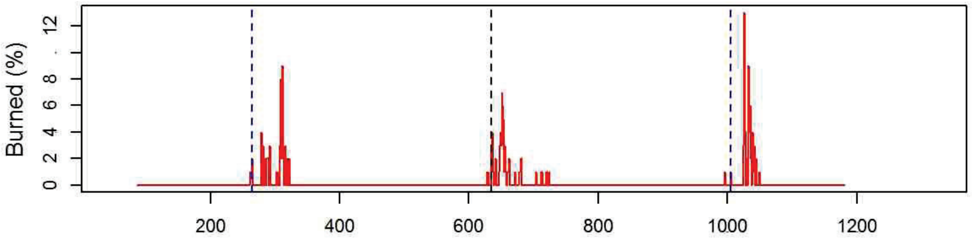
(b) Herd location as a function of time - Latitude



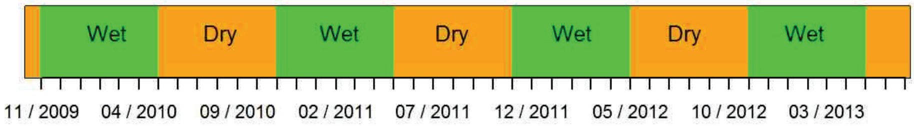
(c) Daily rainfall within annual home range contours (TRMM data)



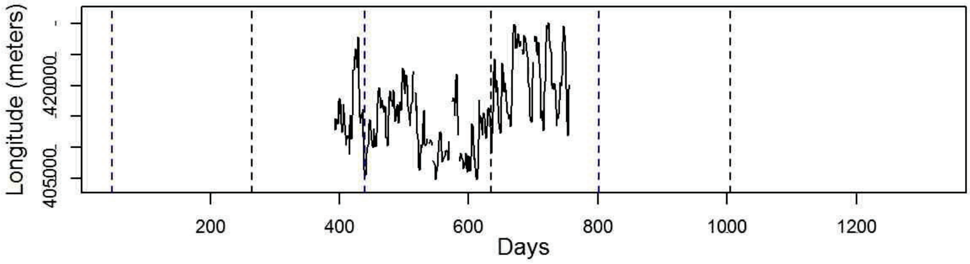
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



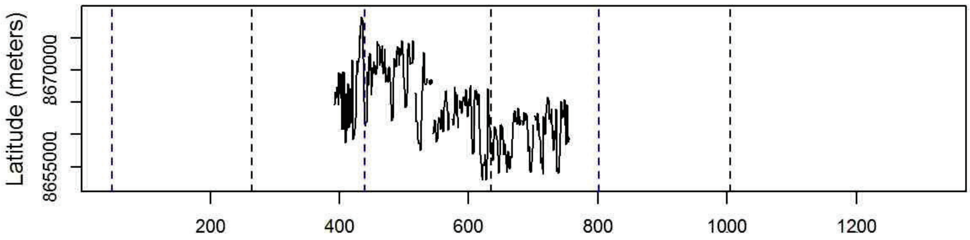
Mozambique - Niassa - Buffalo tracking (2009-2013)   Herd : H04   Collar : Sat18



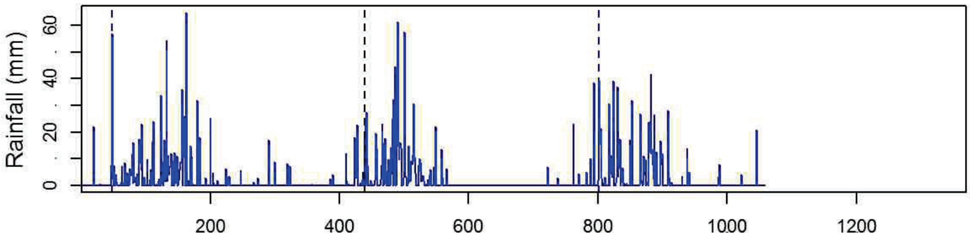
(a) Herd location as a function of time - Longitude



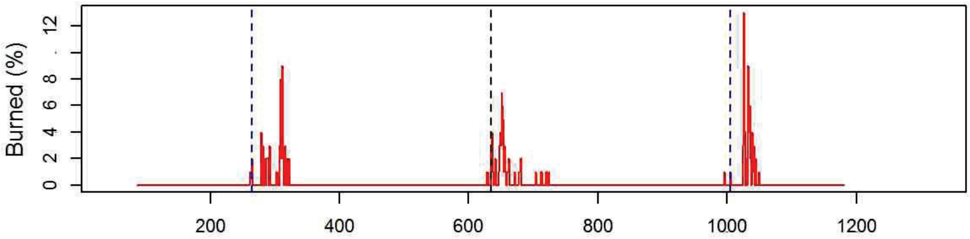
(b) Herd location as a function of time - Latitude

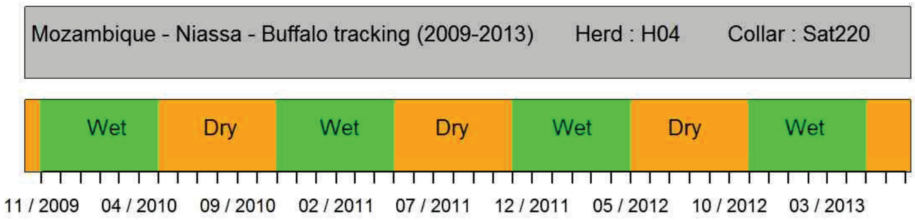


(c) Daily rainfall within annual home range contours (TRMM data)

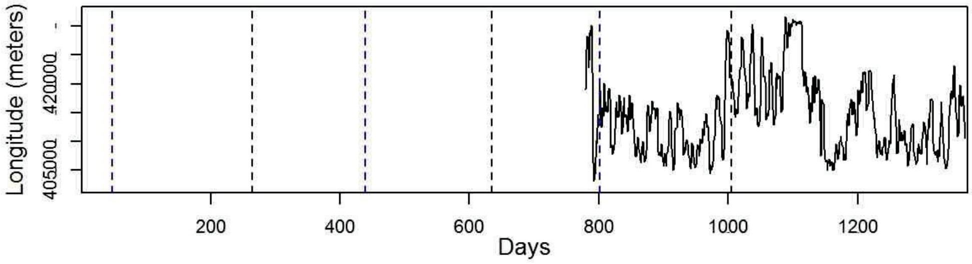


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

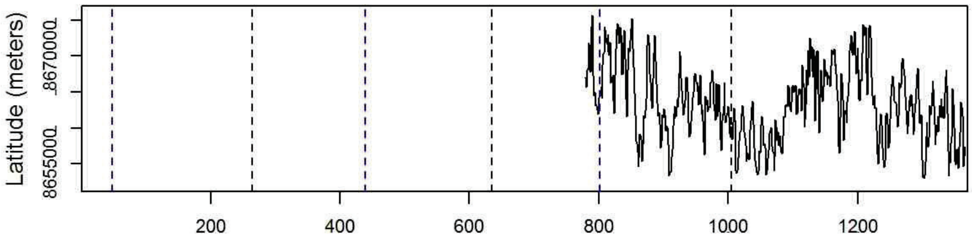




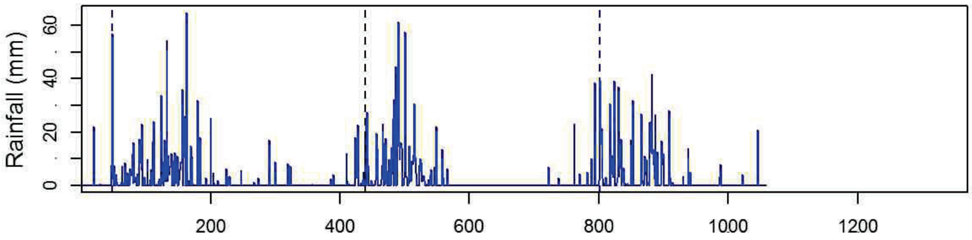
(a) Herd location as a function of time - Longitude



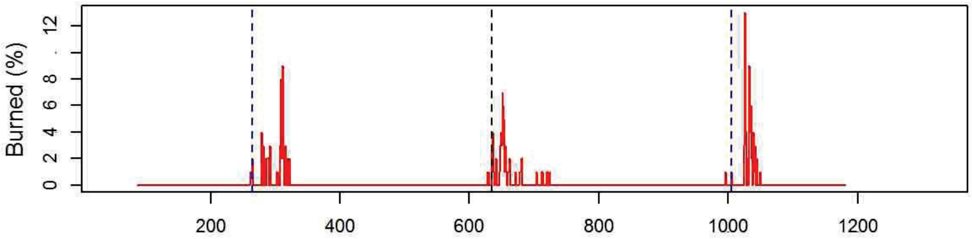
(b) Herd location as a function of time - Latitude



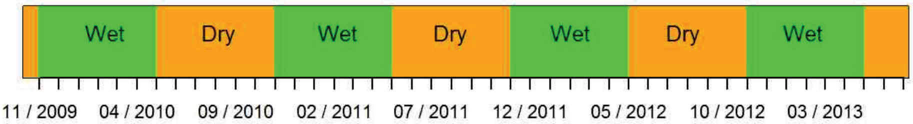
(c) Daily rainfall within annual home range contours (TRMM data)



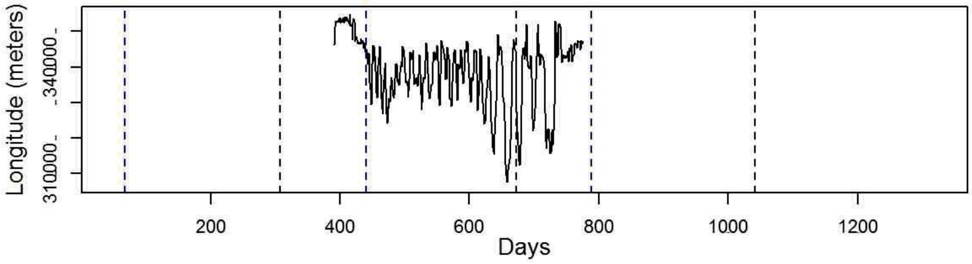
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



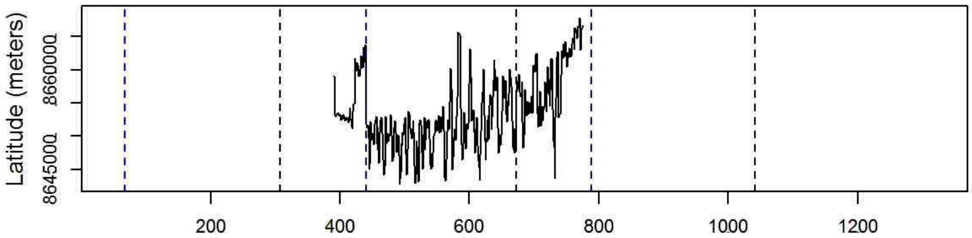
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H05 Collar : AU509



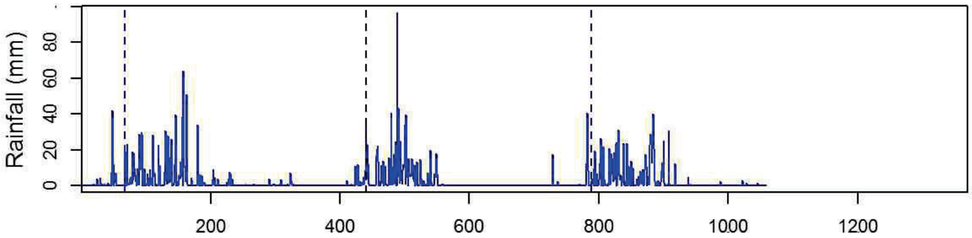
(a) Herd location as a function of time - Longitude



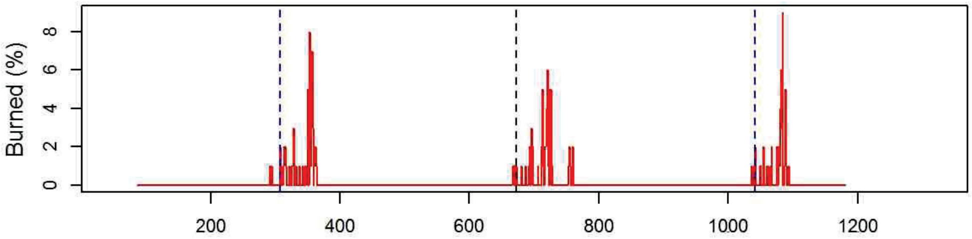
(b) Herd location as a function of time - Latitude



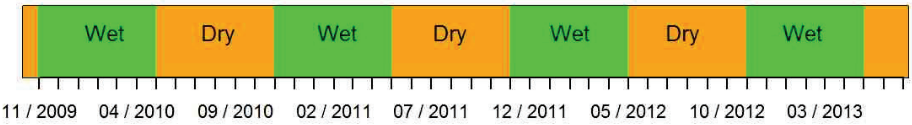
(c) Daily rainfall within annual home range contours (TRMM data)



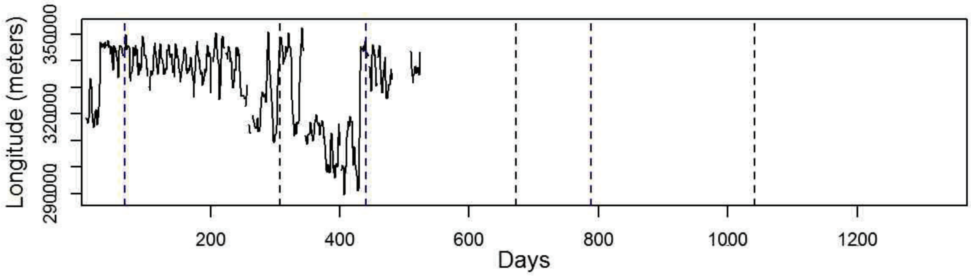
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



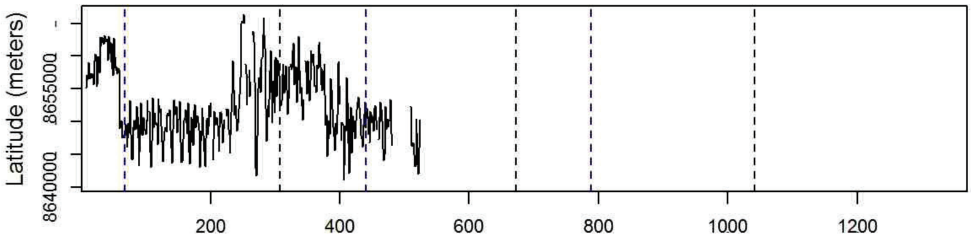
Mozambique - Niassa - Buffalo tracking (2009-2013)   Herd : H05   Collar : Sat06



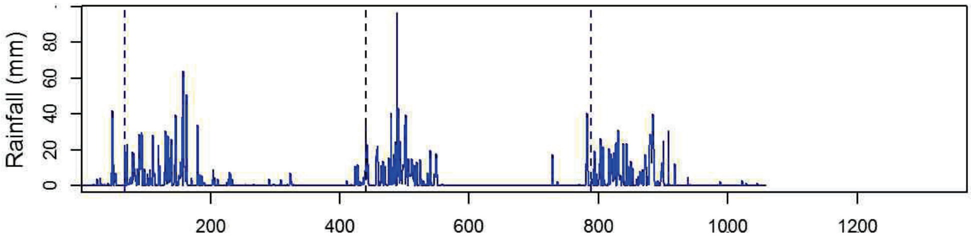
(a) Herd location as a function of time - Longitude



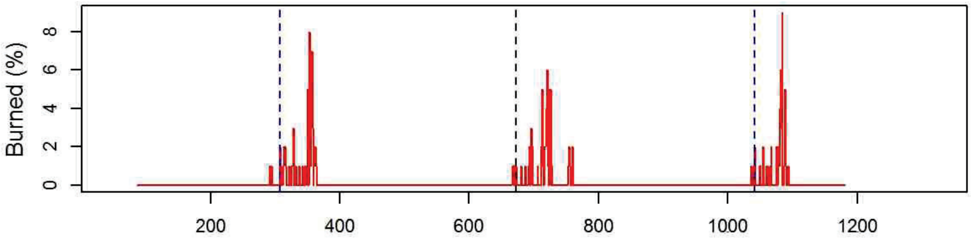
(b) Herd location as a function of time - Latitude



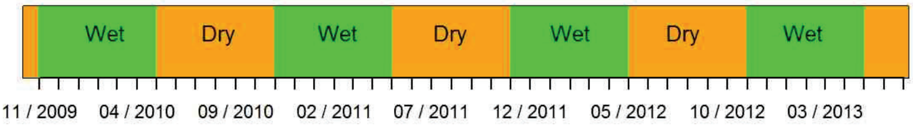
(c) Daily rainfall within annual home range contours (TRMM data)



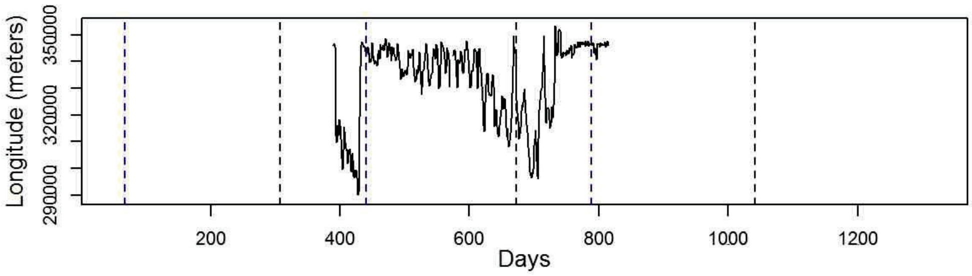
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



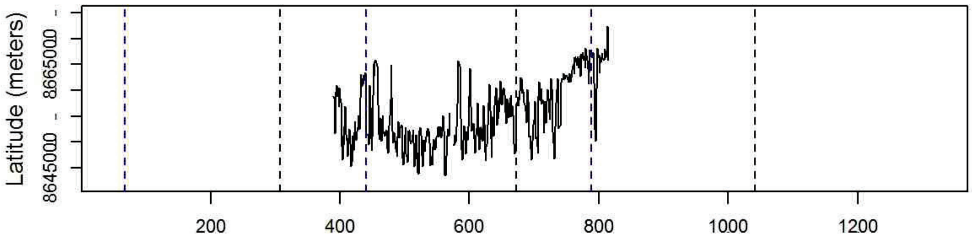
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H05 Collar : Sat14



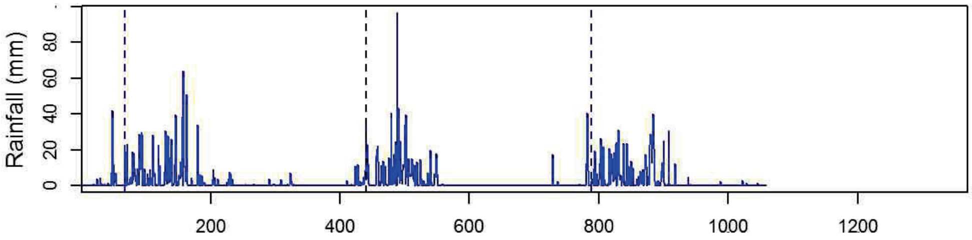
(a) Herd location as a function of time - Longitude



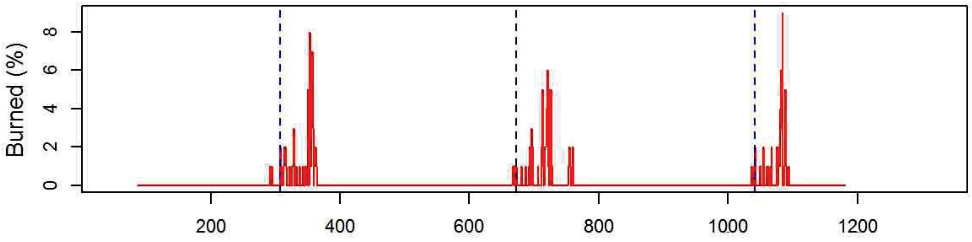
(b) Herd location as a function of time - Latitude



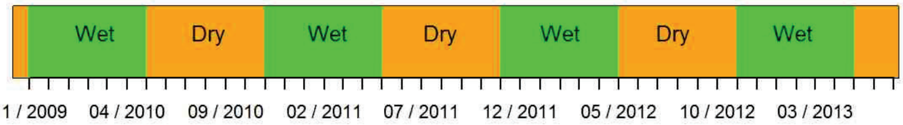
(c) Daily rainfall within annual home range contours (TRMM data)



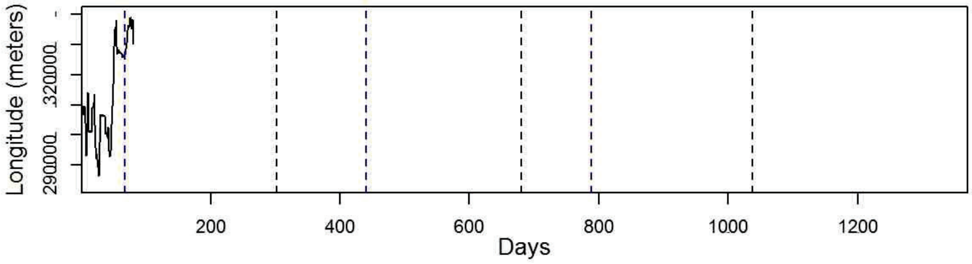
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



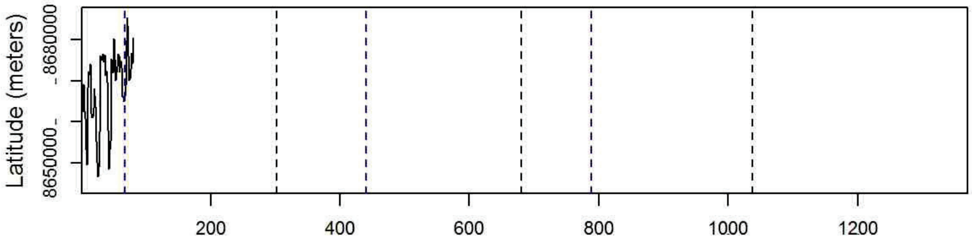
Mozambique - Niassa - Buffalo tracking (2009-2013)   Herd : H06   Collar : AU349



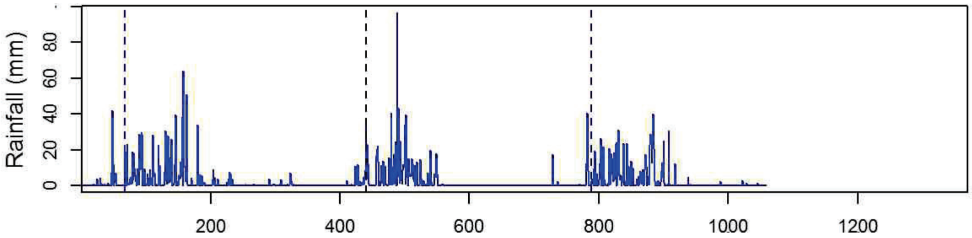
(a) Herd location as a function of time - Longitude



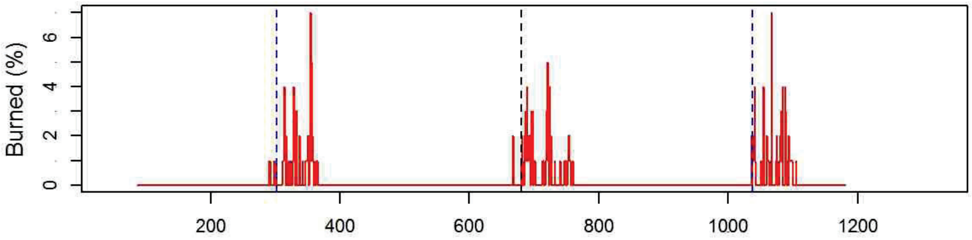
(b) Herd location as a function of time - Latitude



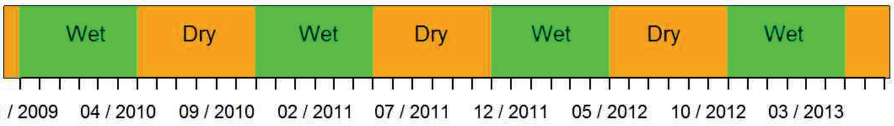
(c) Daily rainfall within annual home range contours (TRMM data)



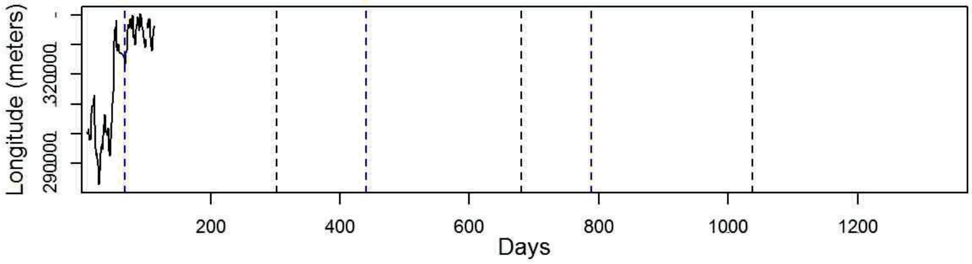
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



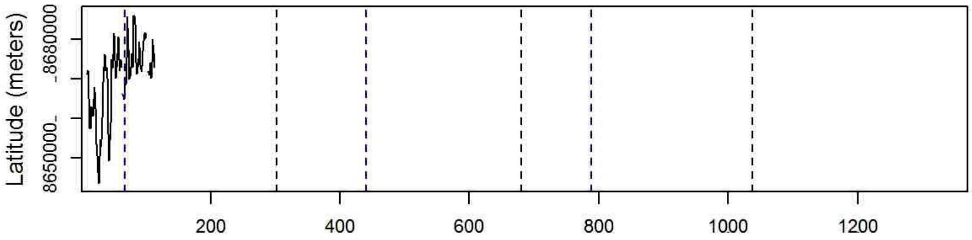
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H06 Collar : Sat05



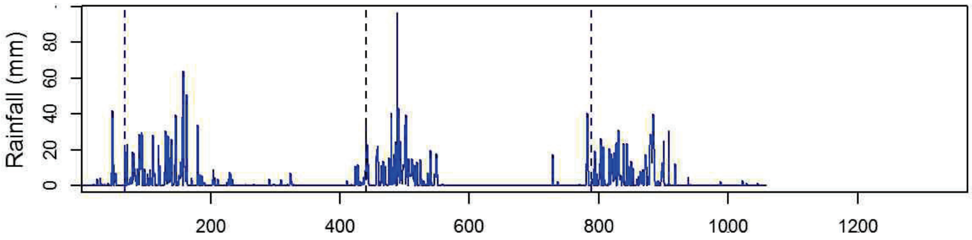
(a) Herd location as a function of time - Longitude



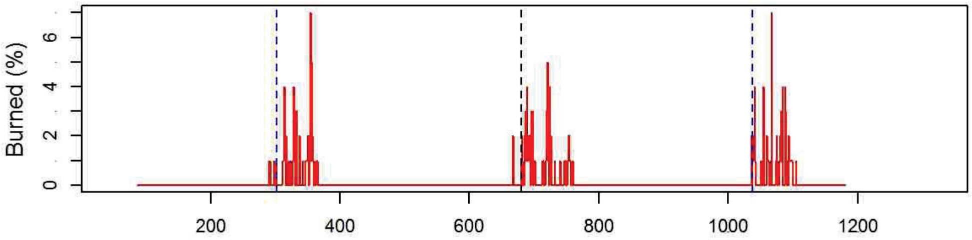
(b) Herd location as a function of time - Latitude

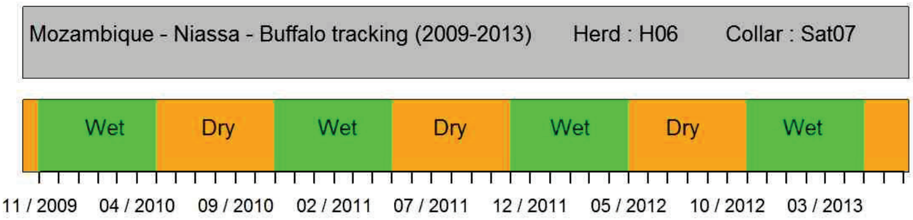


(c) Daily rainfall within annual home range contours (TRMM data)

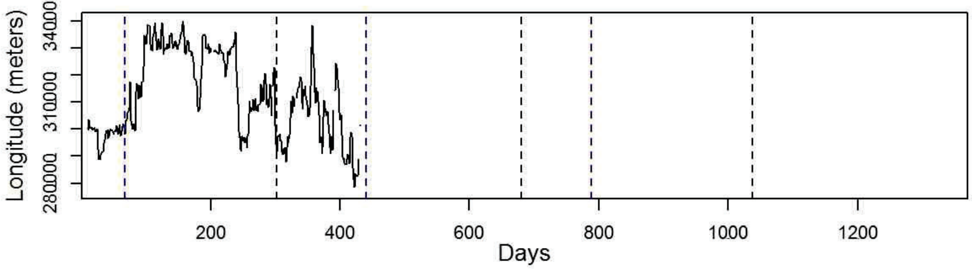


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

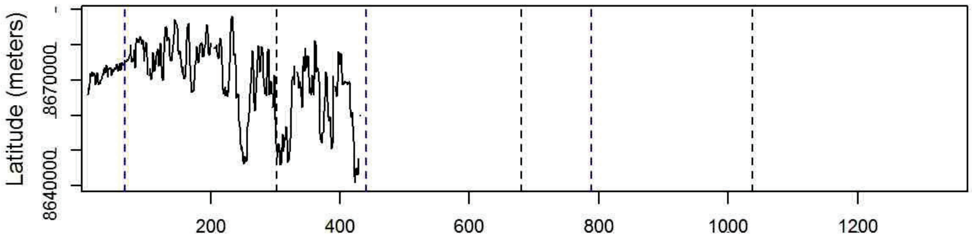




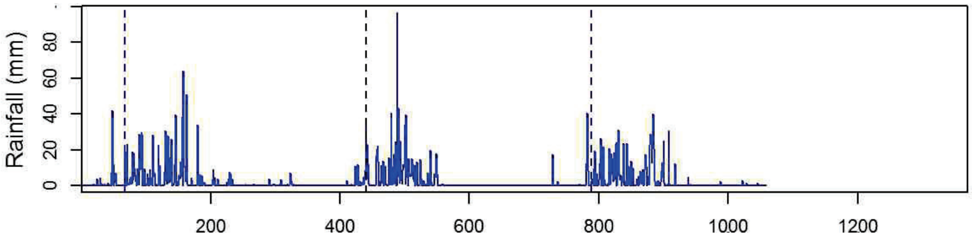
(a) Herd location as a function of time - Longitude



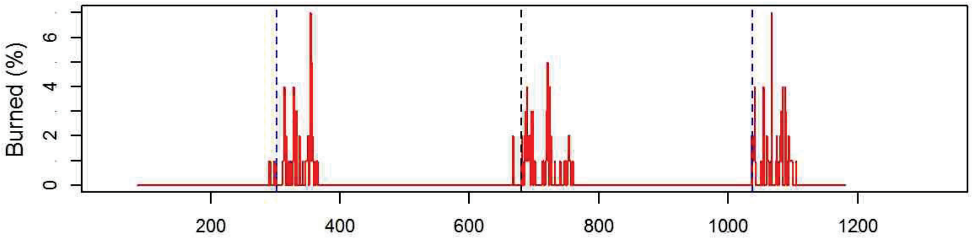
(b) Herd location as a function of time - Latitude



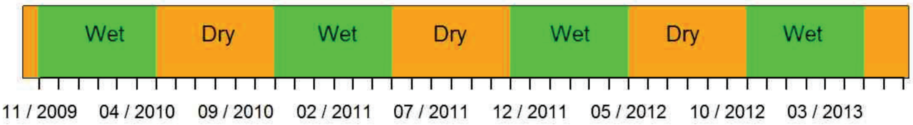
(c) Daily rainfall within annual home range contours (TRMM data)



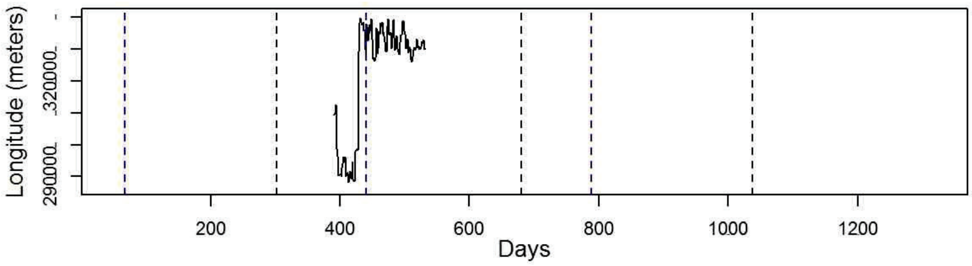
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



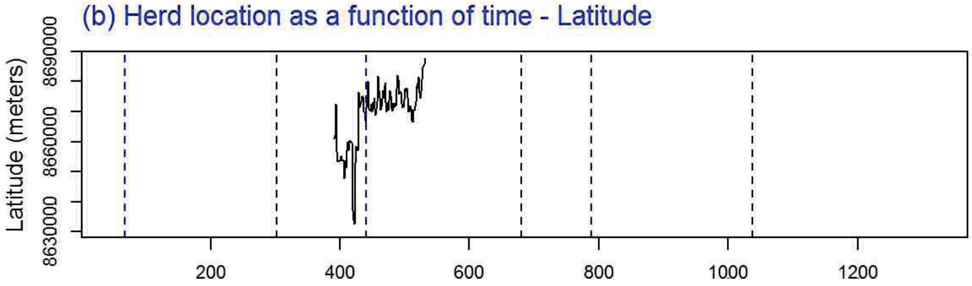
Mozambique - Niassa - Buffalo tracking (2009-2013)   Herd : H06   Collar : Sat11



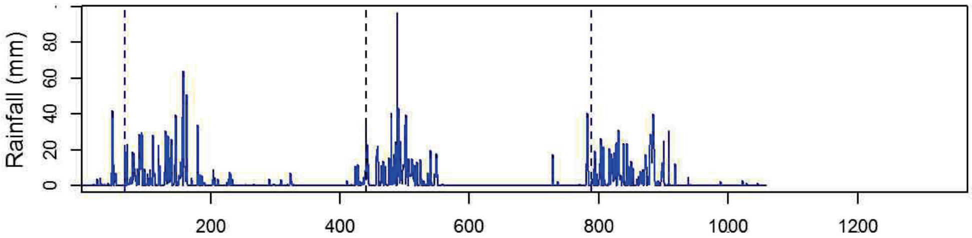
(a) Herd location as a function of time - Longitude



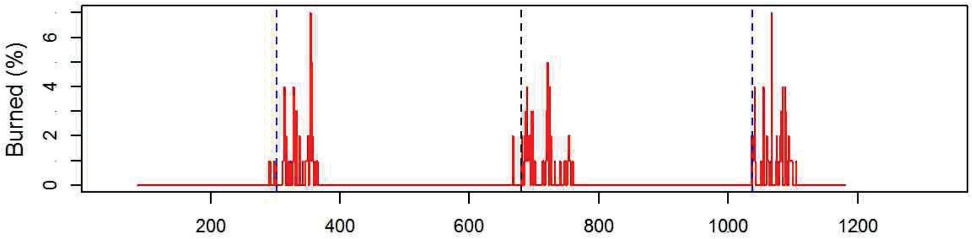
(b) Herd location as a function of time - Latitude



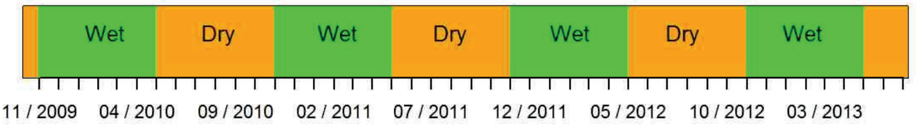
(c) Daily rainfall within annual home range contours (TRMM data)



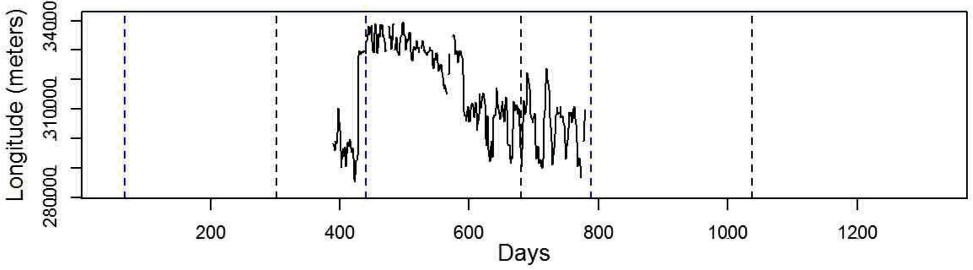
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



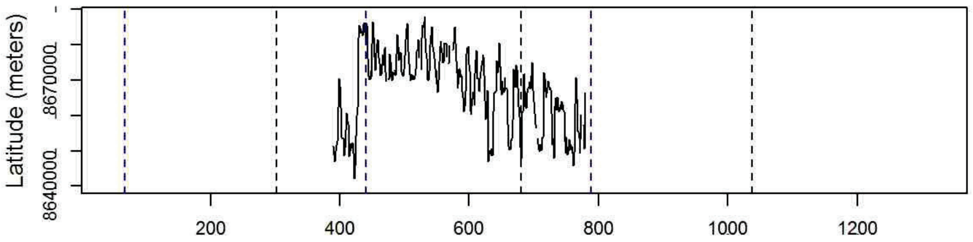
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H06 Collar : Sat12



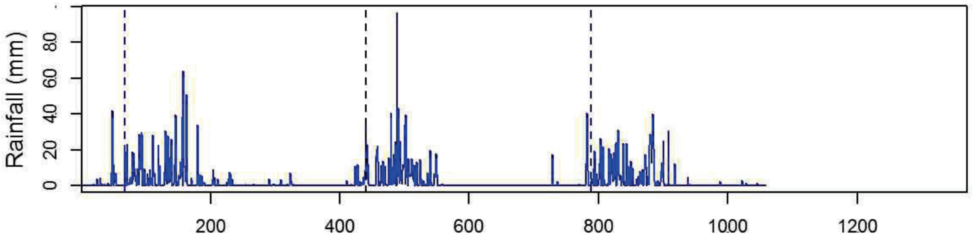
(a) Herd location as a function of time - Longitude



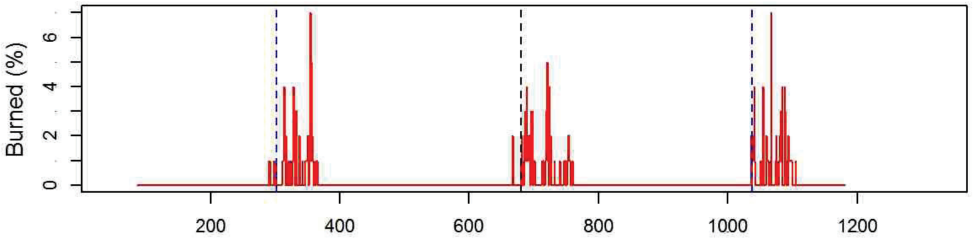
(b) Herd location as a function of time - Latitude



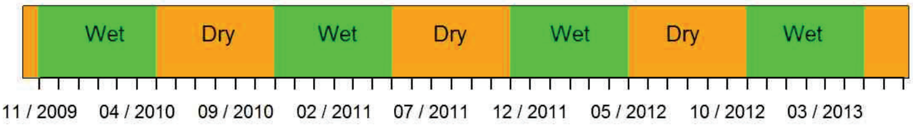
(c) Daily rainfall within annual home range contours (TRMM data)



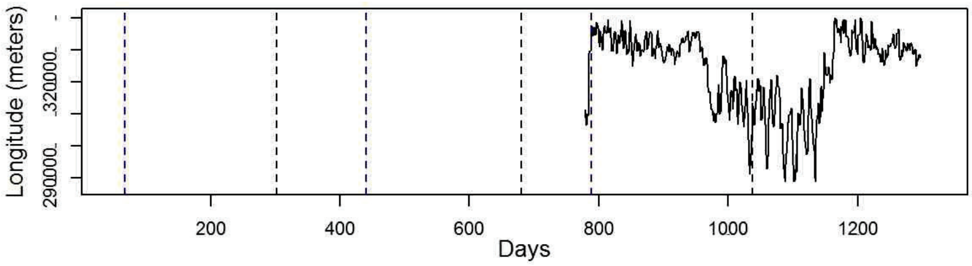
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



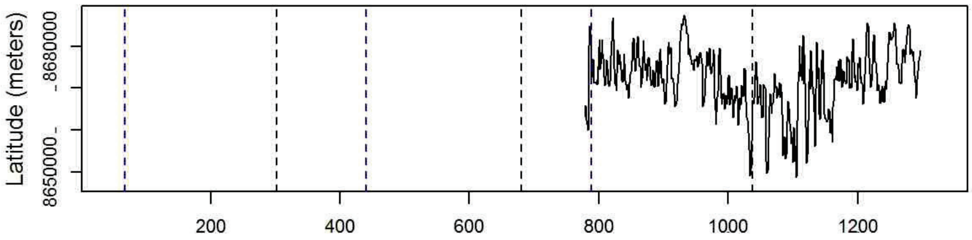
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H06 Collar : Sat186



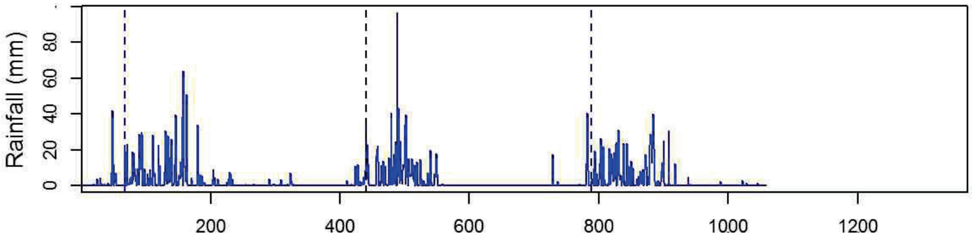
(a) Herd location as a function of time - Longitude



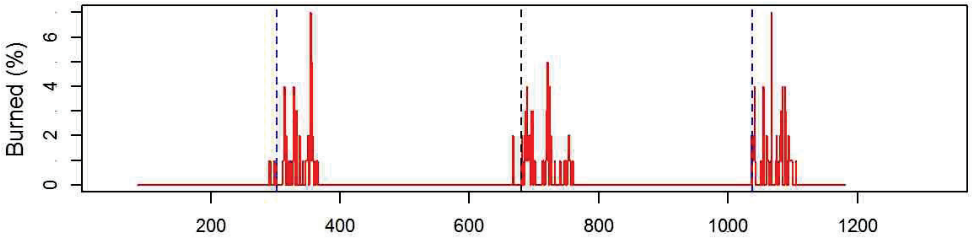
(b) Herd location as a function of time - Latitude

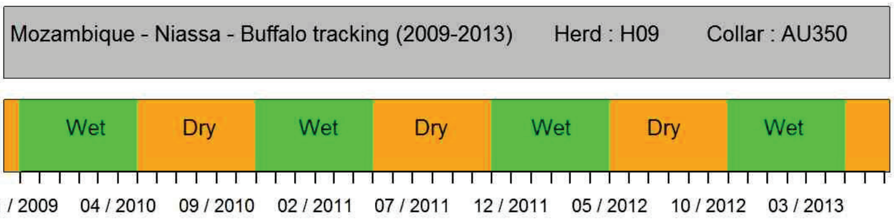


(c) Daily rainfall within annual home range contours (TRMM data)

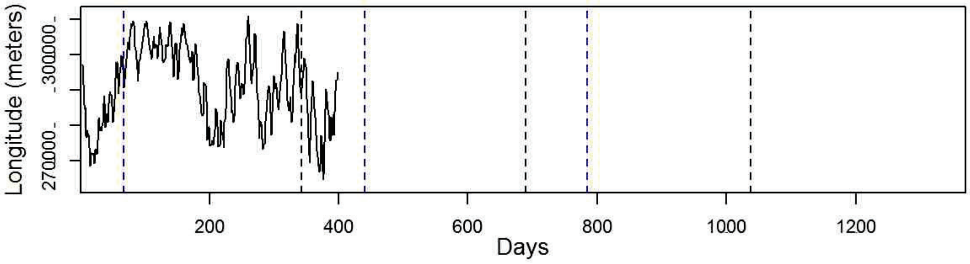


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

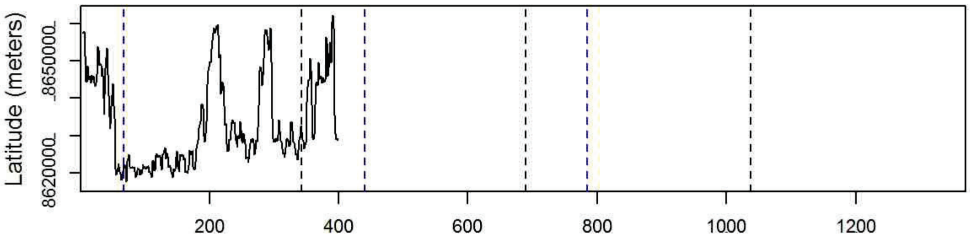




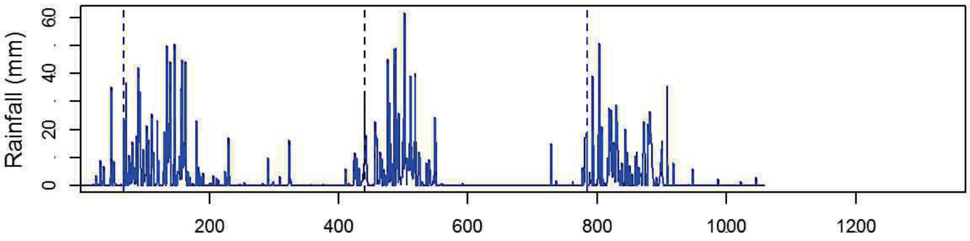
(a) Herd location as a function of time - Longitude



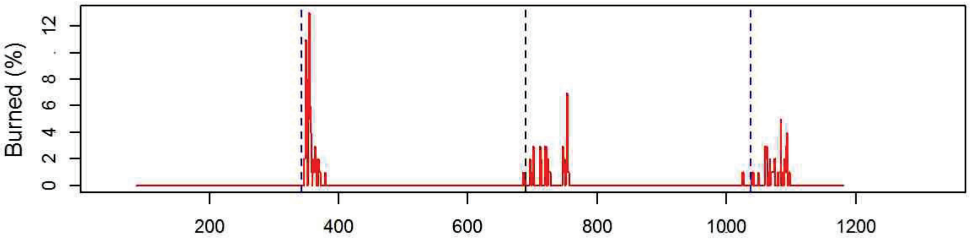
(b) Herd location as a function of time - Latitude

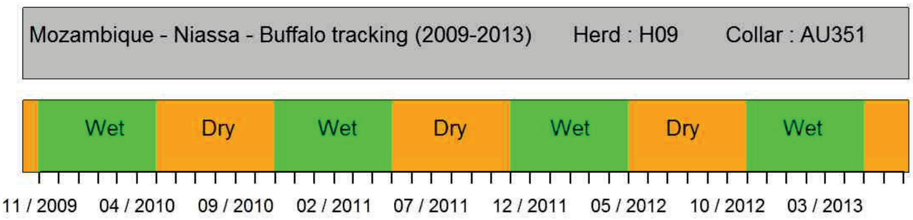


(c) Daily rainfall within annual home range contours (TRMM data)

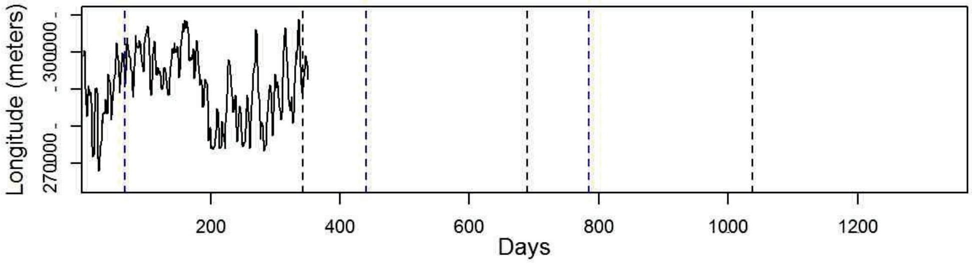


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

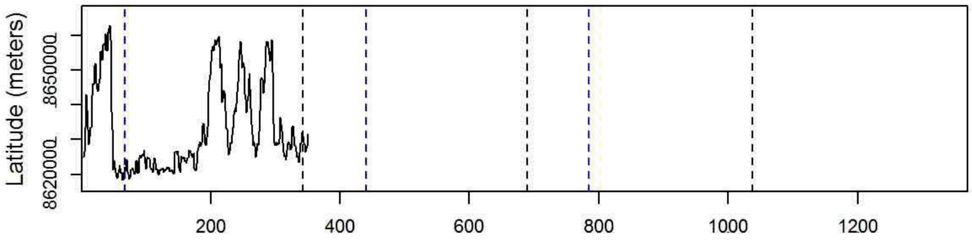




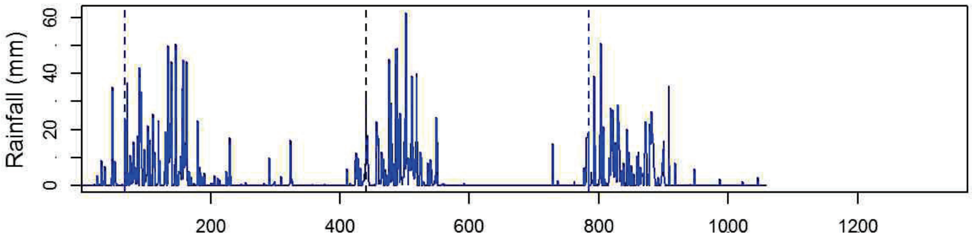
(a) Herd location as a function of time - Longitude



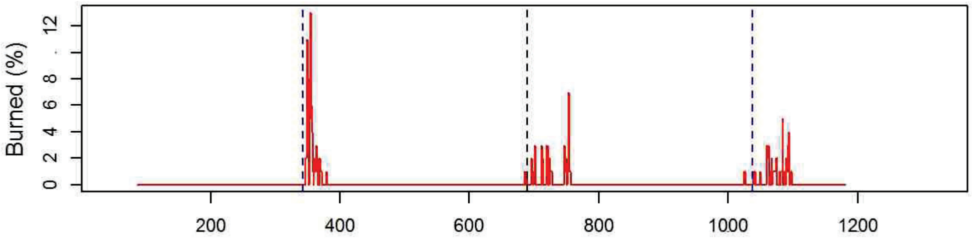
(b) Herd location as a function of time - Latitude

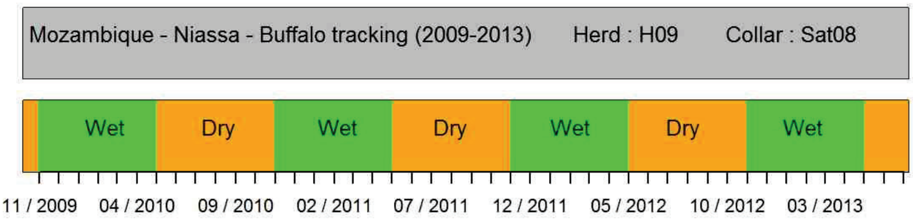


(c) Daily rainfall within annual home range contours (TRMM data)

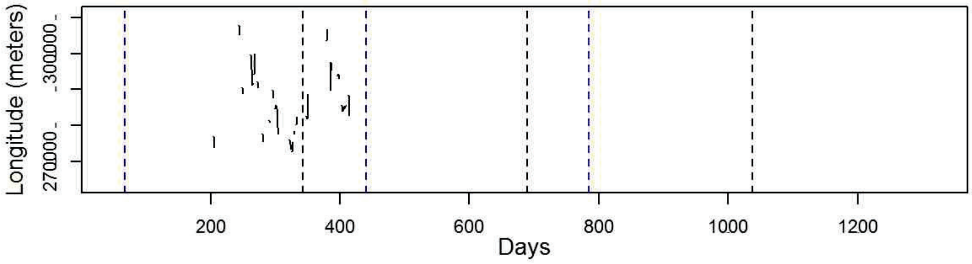


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

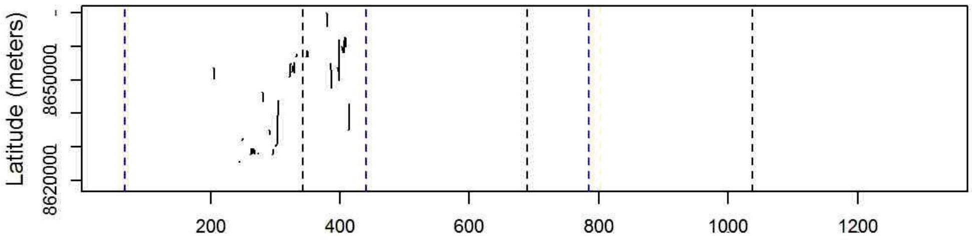




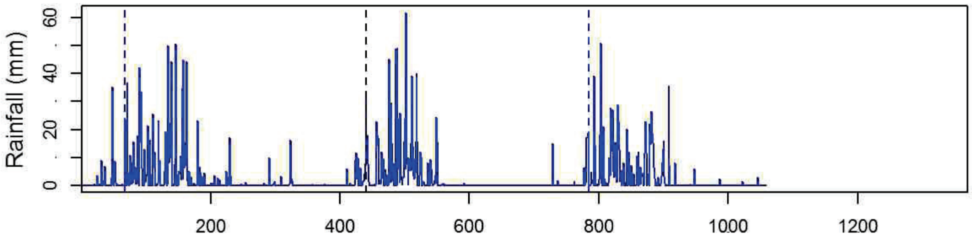
(a) Herd location as a function of time - Longitude



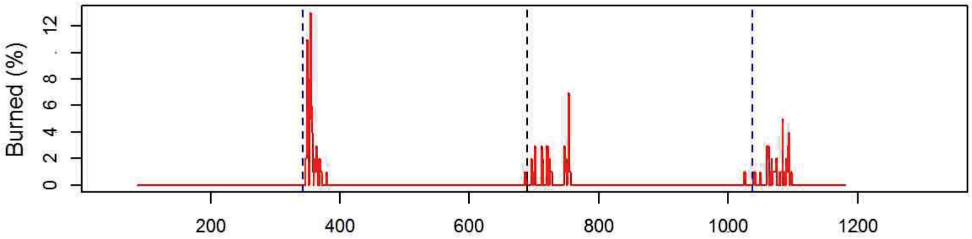
(b) Herd location as a function of time - Latitude



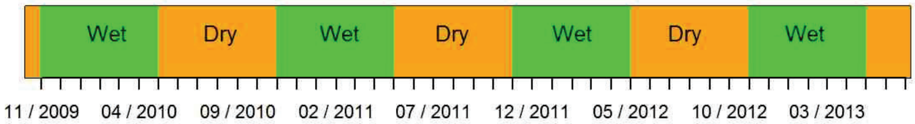
(c) Daily rainfall within annual home range contours (TRMM data)



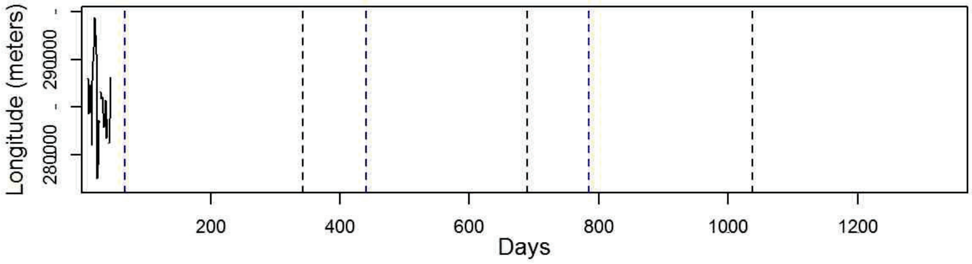
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



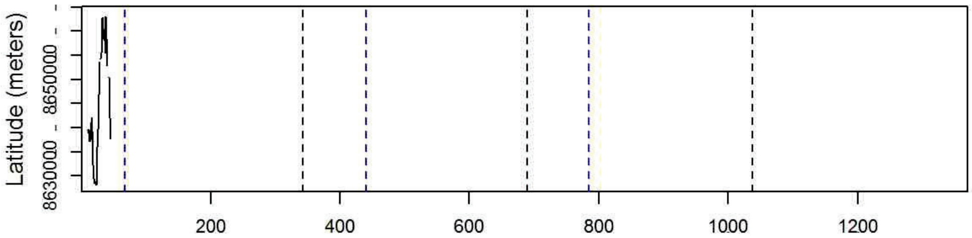
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H09 Collar : Sat09



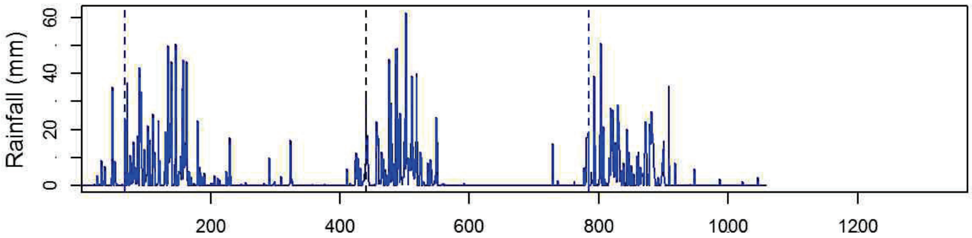
(a) Herd location as a function of time - Longitude



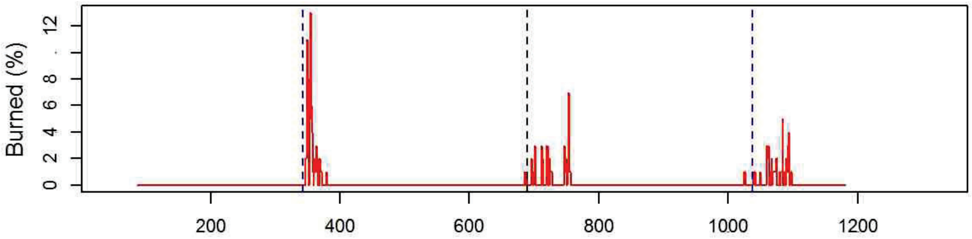
(b) Herd location as a function of time - Latitude

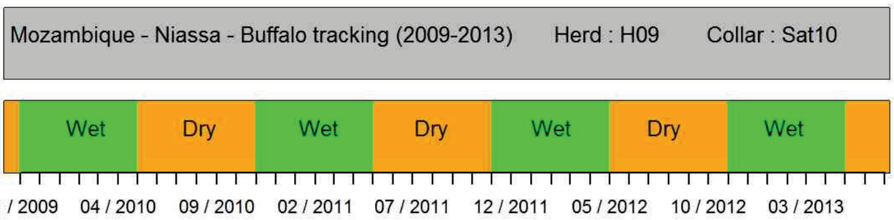


(c) Daily rainfall within annual home range contours (TRMM data)

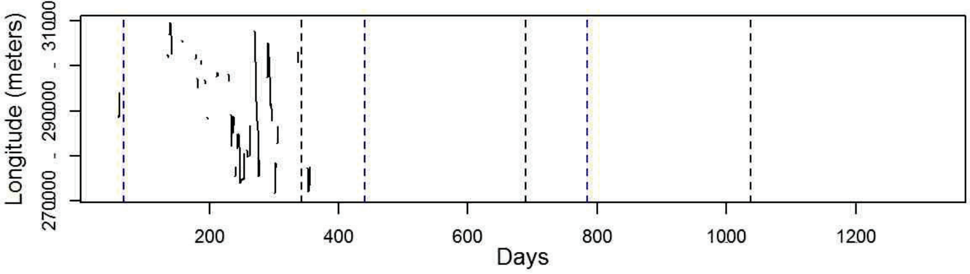


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

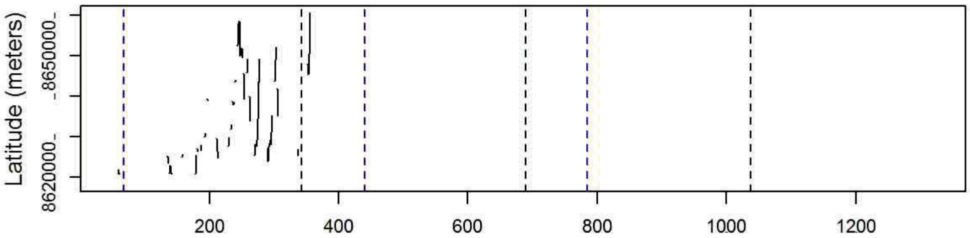




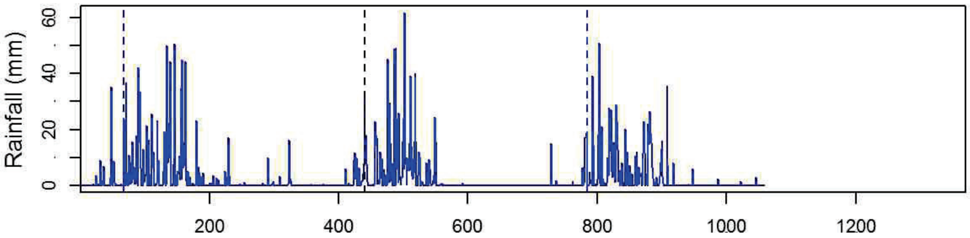
(a) Herd location as a function of time - Longitude



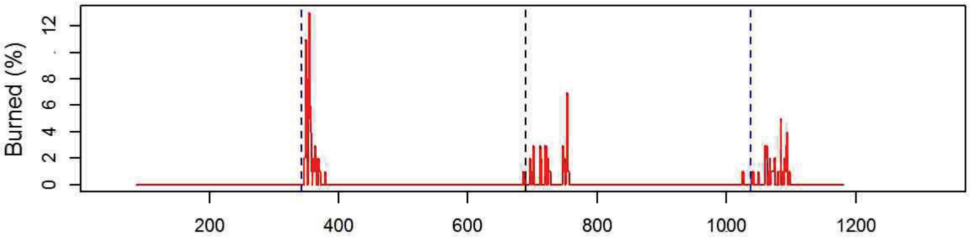
(b) Herd location as a function of time - Latitude

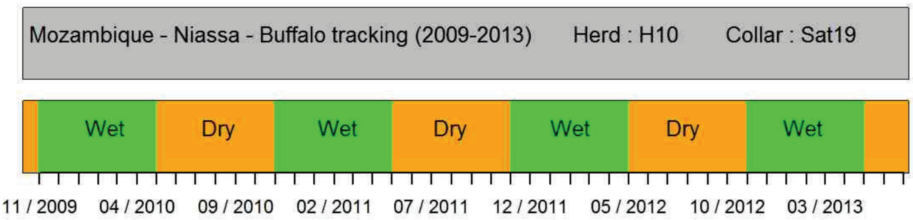


(c) Daily rainfall within annual home range contours (TRMM data)

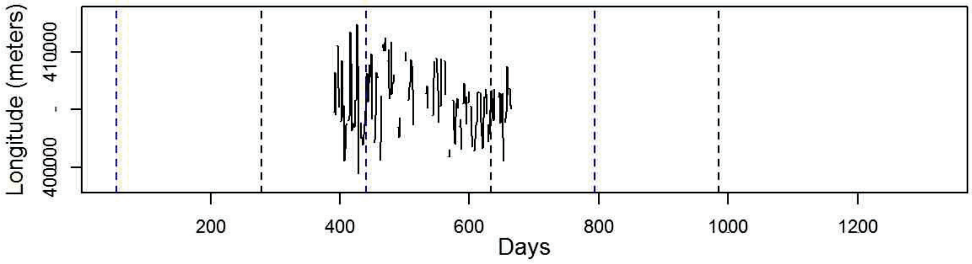


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

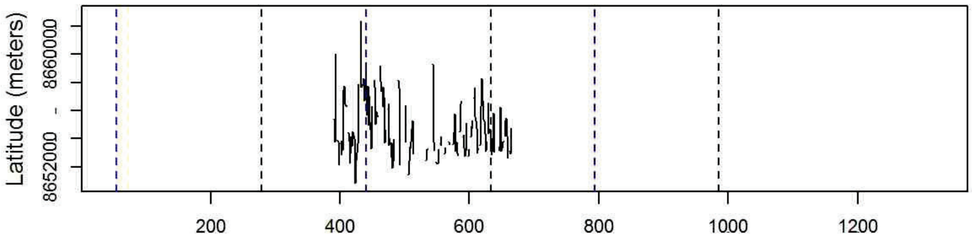




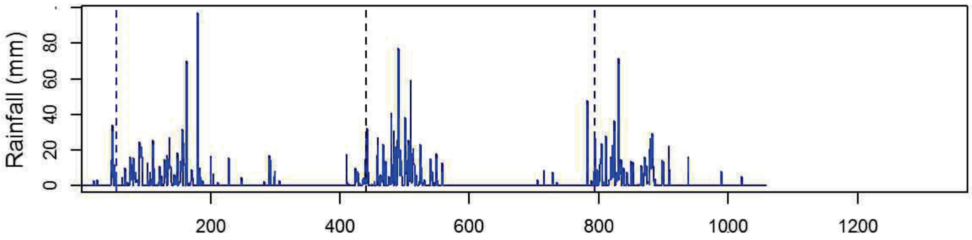
(a) Herd location as a function of time - Longitude



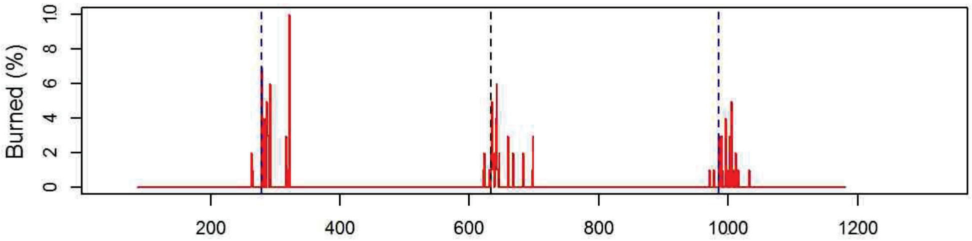
(b) Herd location as a function of time - Latitude



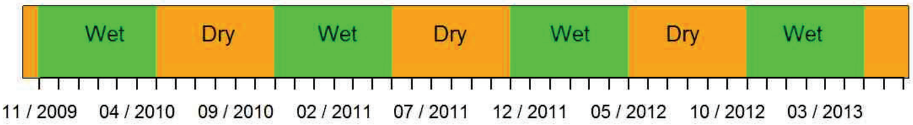
(c) Daily rainfall within annual home range contours (TRMM data)



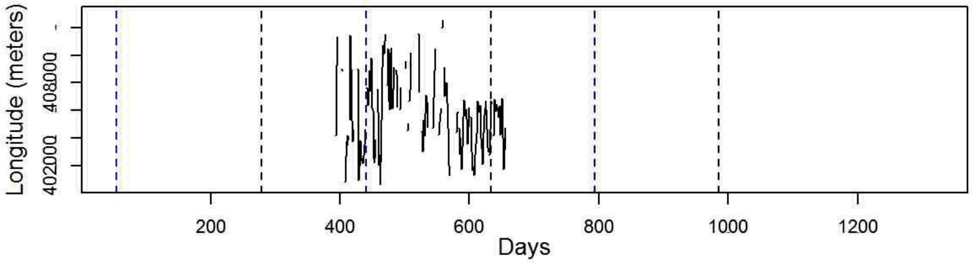
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



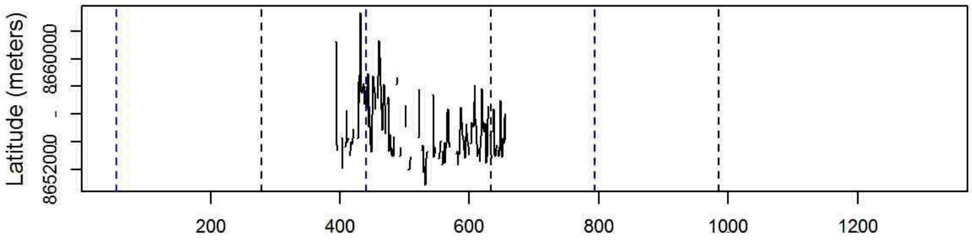
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H10 Collar : Sat21



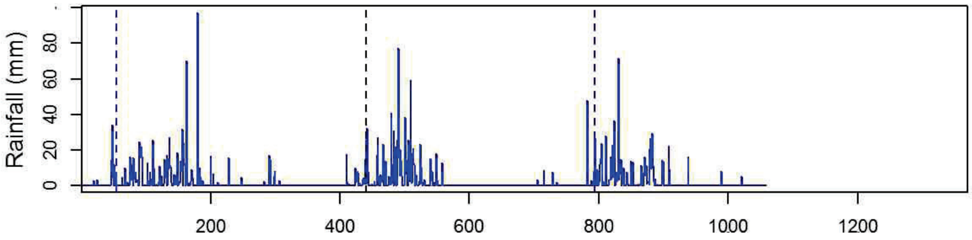
(a) Herd location as a function of time - Longitude



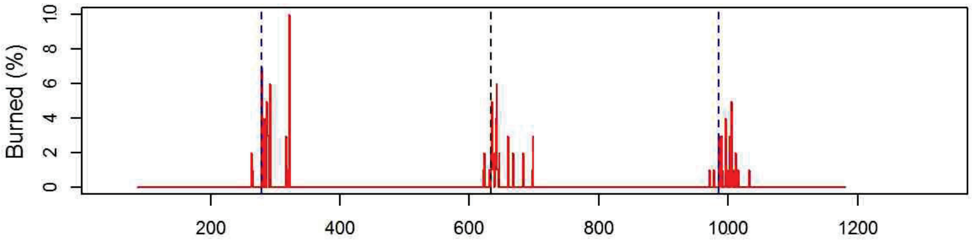
(b) Herd location as a function of time - Latitude



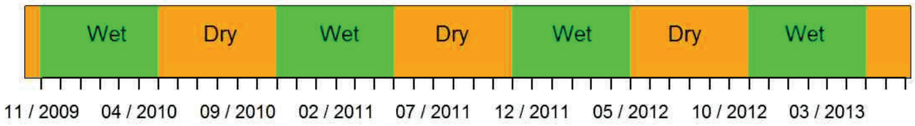
(c) Daily rainfall within annual home range contours (TRMM data)



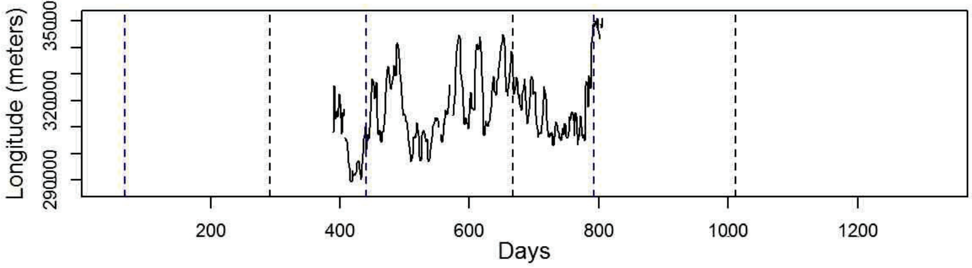
(d) Proportion of home range area burned (%) (Modis MCD 45 data)



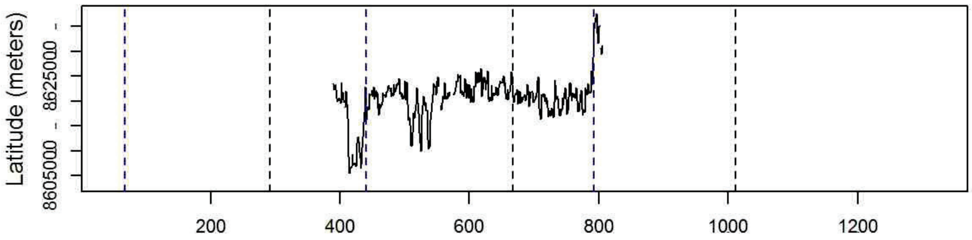
Mozambique - Niassa - Buffalo tracking (2009-2013) Herd : H11 Collar : Sat13



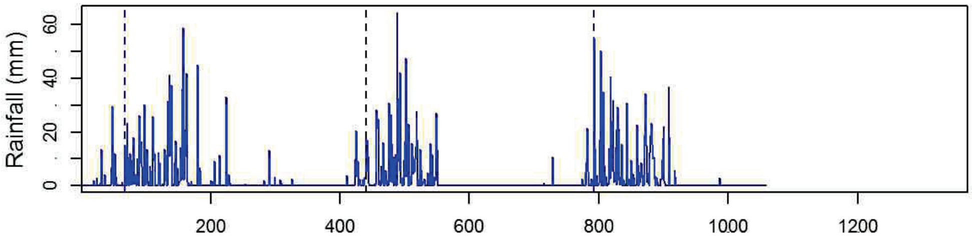
(a) Herd location as a function of time - Longitude



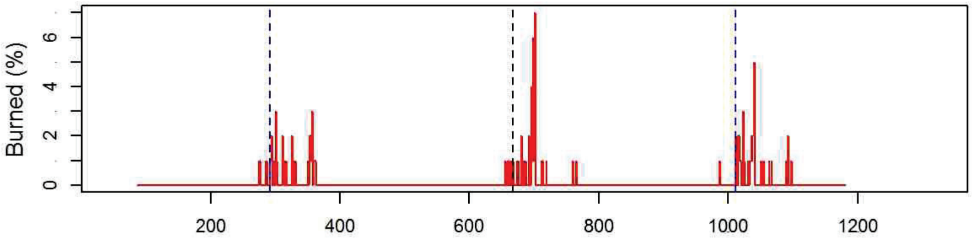
(b) Herd location as a function of time - Latitude

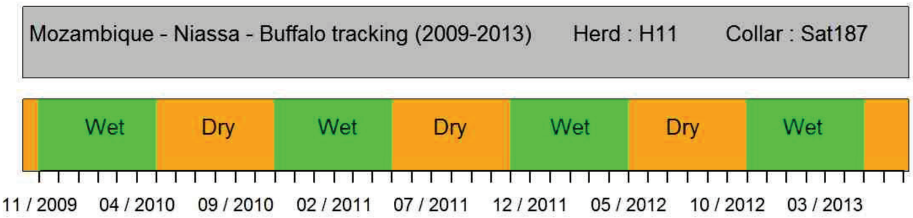


(c) Daily rainfall within annual home range contours (TRMM data)

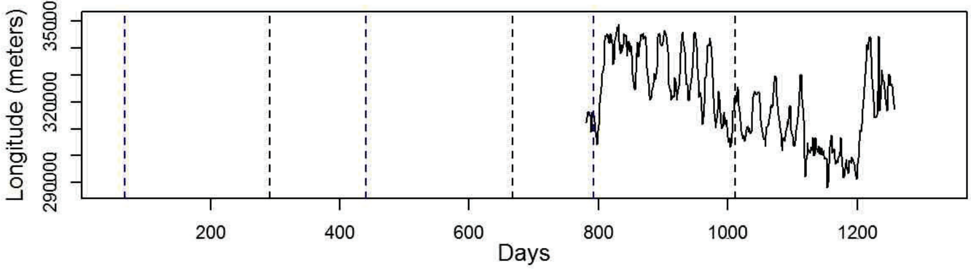


(d) Proportion of home range area burned (%) (Modis MCD 45 data)

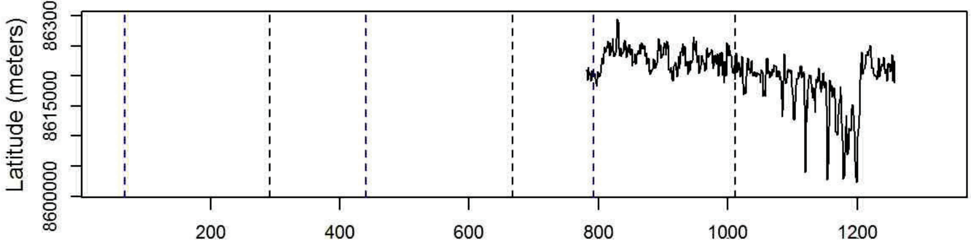




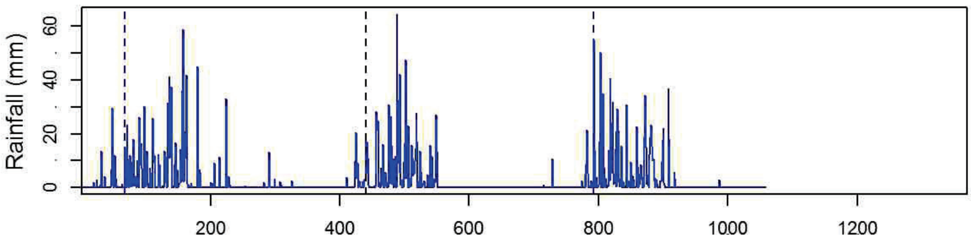
(a) Herd location as a function of time - Longitude



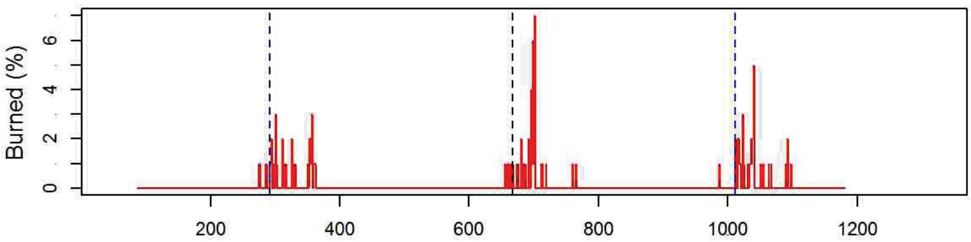
(b) Herd location as a function of time - Latitude

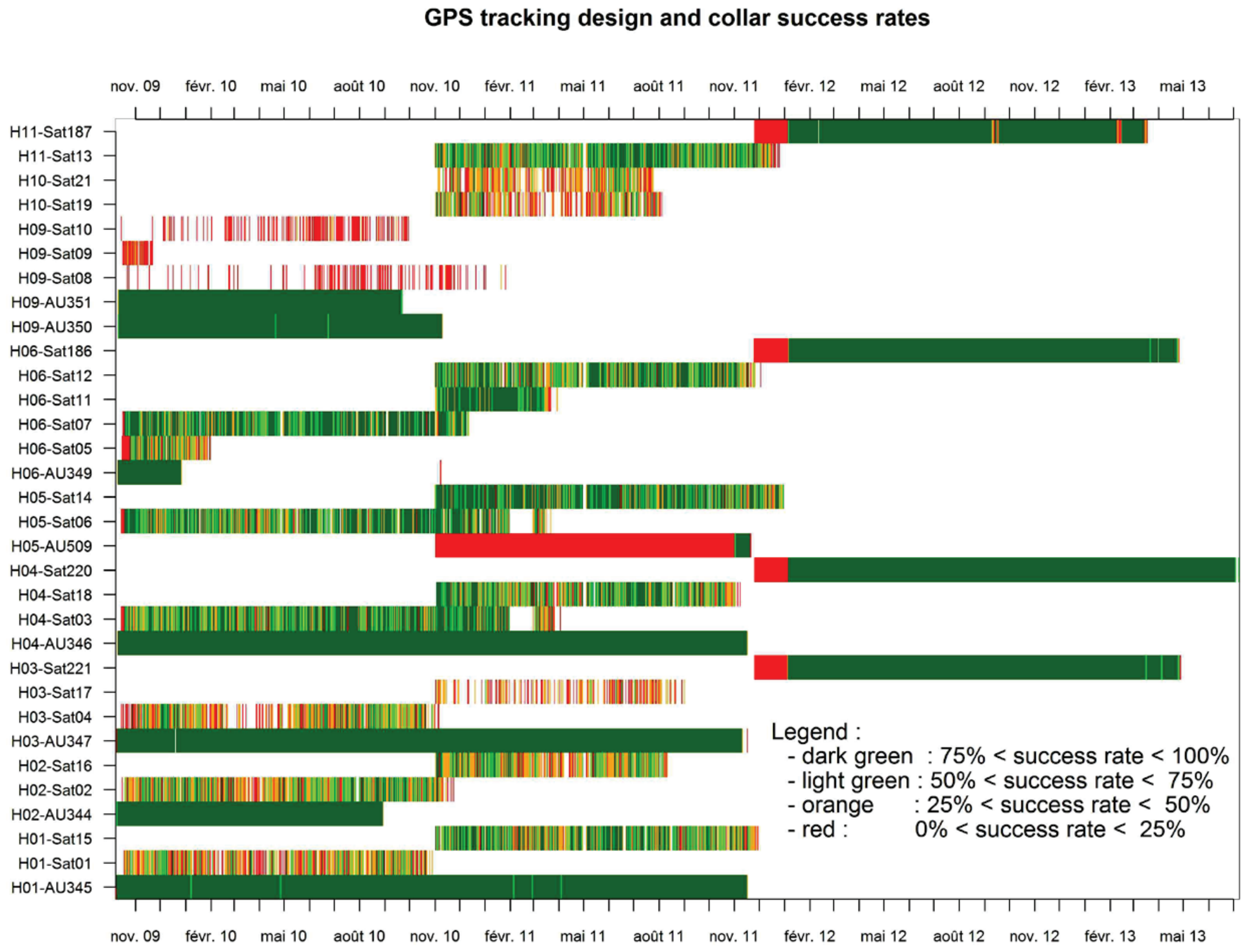


(c) Daily rainfall within annual home range contours (TRMM data)



(d) Proportion of home range area burned (%) (Modis MCD 45 data)





GPS tracking design and collar success rates

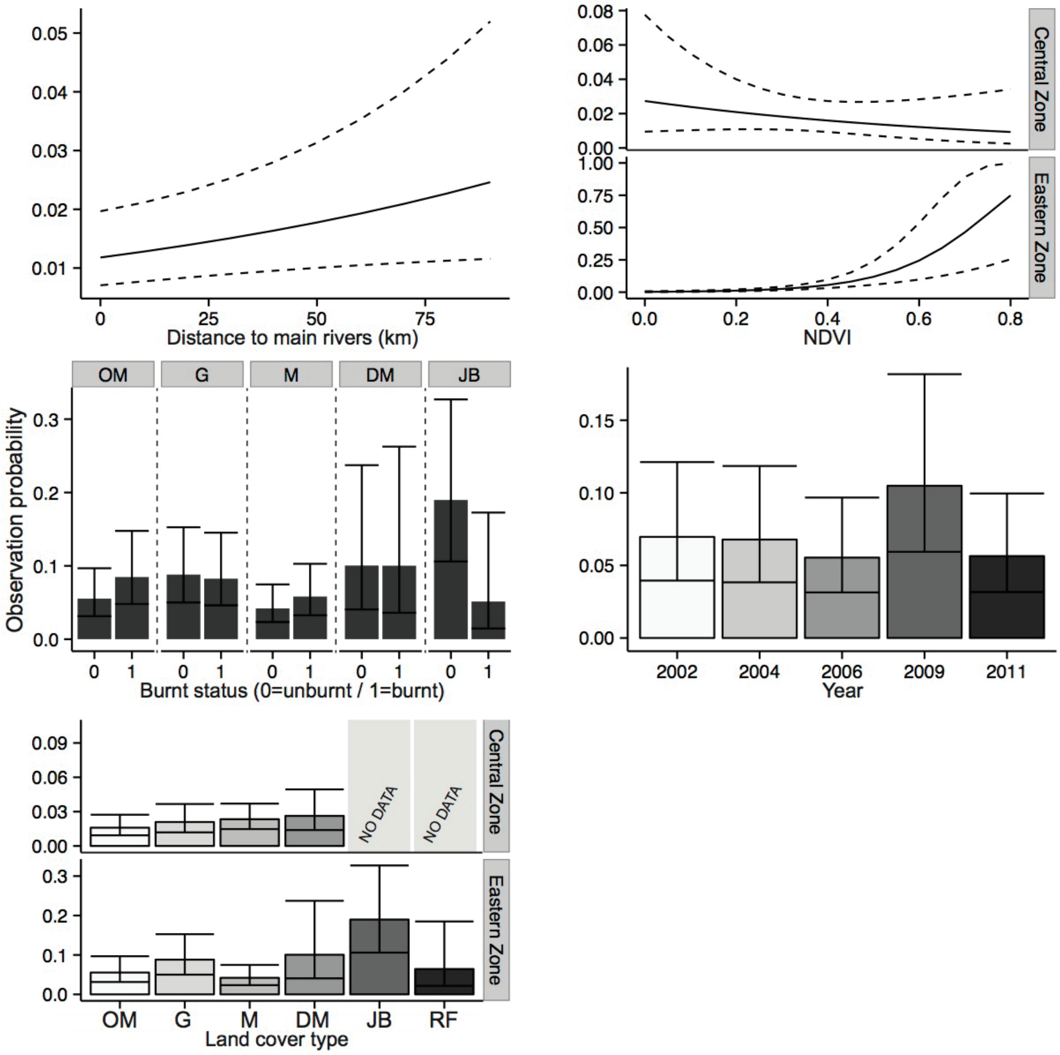
ANNEXE V - APPENDIX V

APPENDICES CHAPTER 4

Predicting spatial distribution of wildlife in relation to environmental covariates: an application to aerial surveys in Niassa National Reserve, Mozambique

FIGURES V.7 TO V.10

Submitted to Landscape Ecology


0.05
0.04
0.03
0.02
0.01
0
25
50
75
Distance to main rivers (km)
0.08
0.06
0.04
0.02
0.00
Central Zone
1.00
0.75
0.50
0.25
0.00
Eastern Zone
0.0
0.2
0.4
0.6
0.8
NDVI
Observation probability
OM
G
M
DM
JB
0.3
0.2
0.1
0.0
0
1
Burnt status (0=unburnt / 1=burnt)
0.15
0.10
0.05
0.00
2002
2004
2006
2009
2011
Year
0.09
0.06
0.03
0.00
NO DATA
NO DATA
Central Zone
0.3
0.2
0.1
0.0
Eastern Zone
OM
G
M
DM
JB
RF
Land cover type

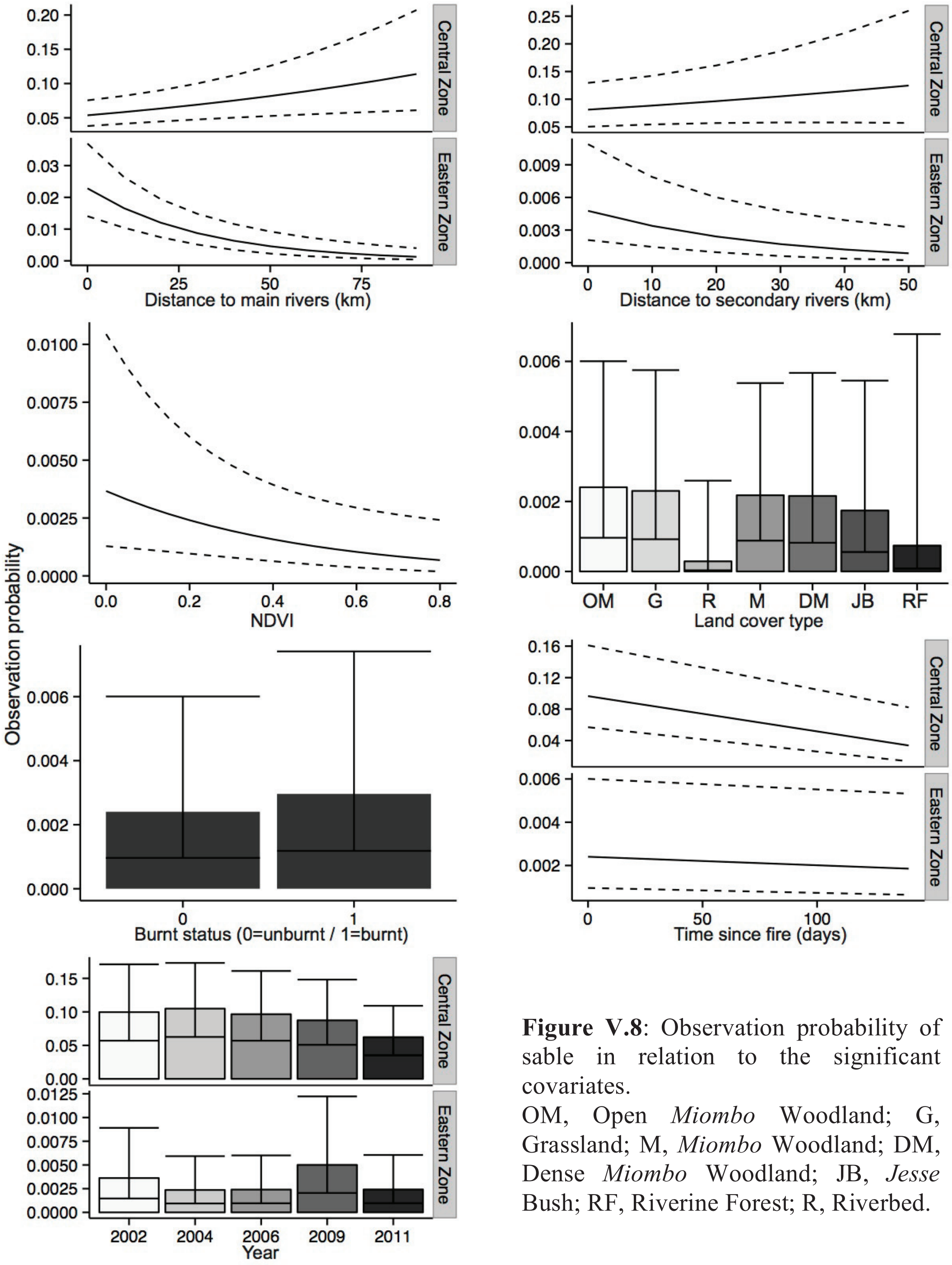


Figure V.8: Observation probability of sable in relation to the significant covariates.

OM, Open *Miombo* Woodland; G, Grassland; M, *Miombo* Woodland; DM, Dense *Miombo* Woodland; JB, *Jesse* Bush; RF, Riverine Forest; R, Riverbed.

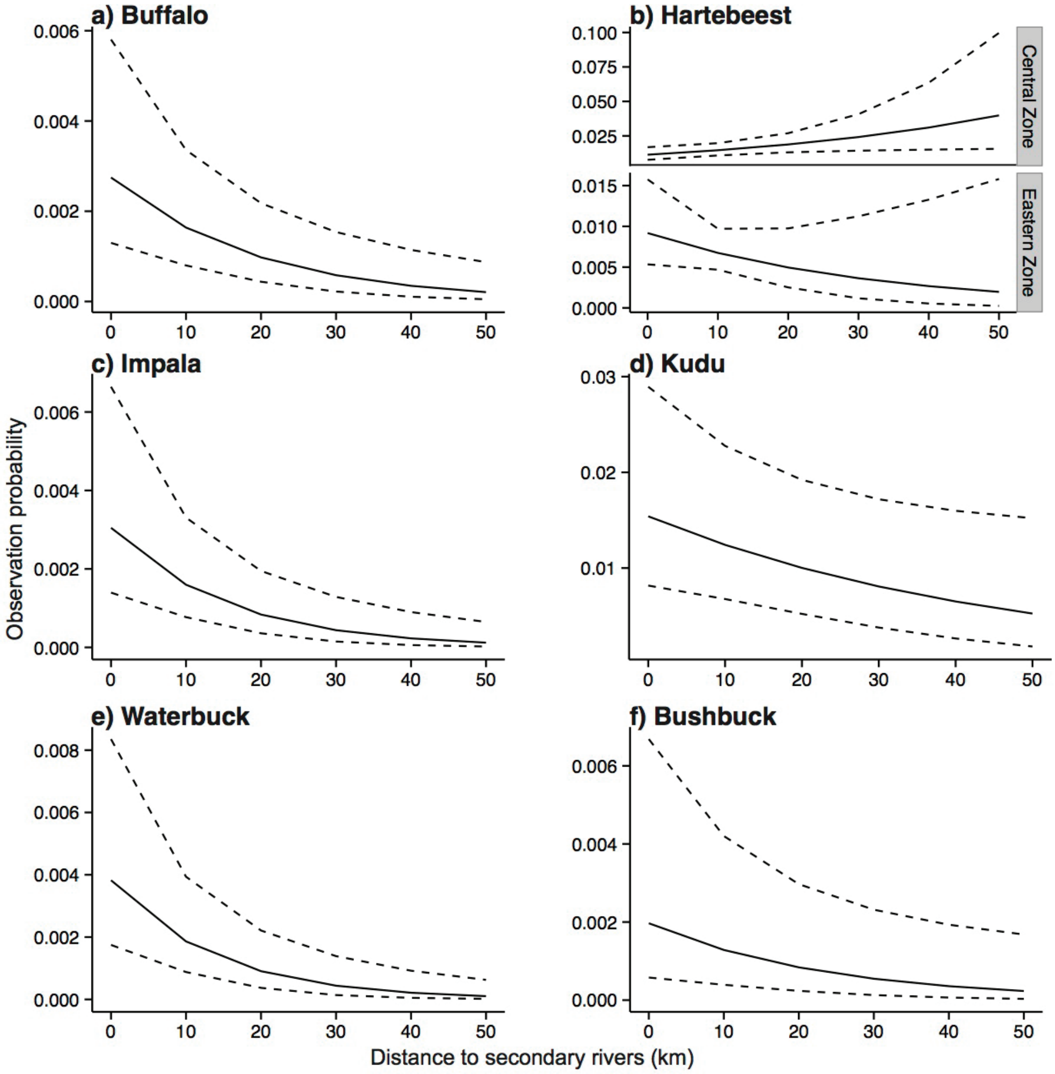


Figure V.9: Observation probability of 6 species in relation to the distance to secondary rivers

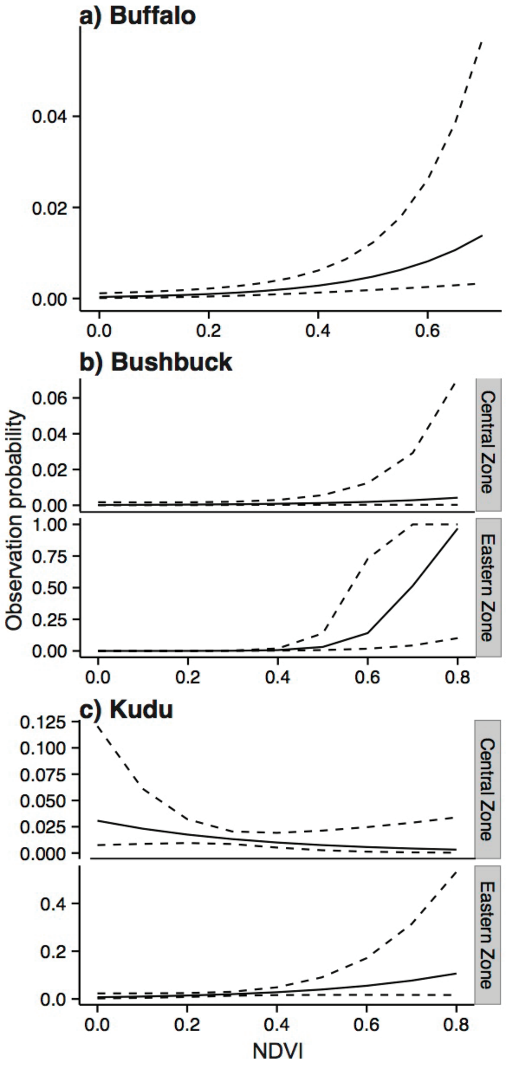


Figure V.10: Observation probability of 3 species in relation to NDVI

ANNEXE VI - APPENDIX VI

FEUILLES DE TERRAIN / FIELD FORM

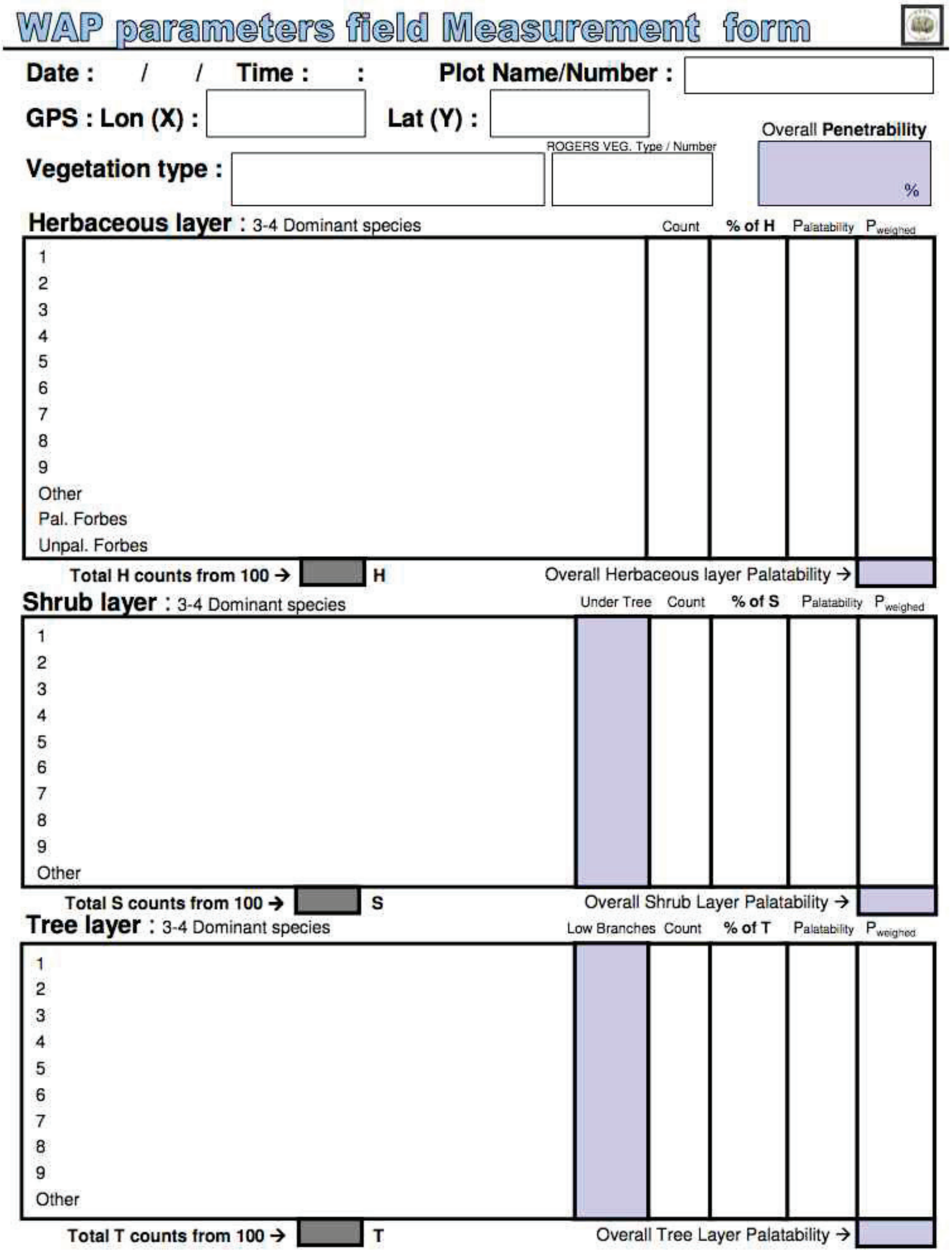
A - CARTE DE LA VEGETATION

VEGETATION SURVEY

(CHAPITRE 2)

B - QUESTIONNAIRES

(CHAPITRE 6)



WAP parameters field Measurement form

Date : / / **Time :** : **Plot Name/Number :**

GPS : Lon (X) : **Lat (Y) :**

ROGERS VEG. Type / Number

Overall **Penetrability**

Vegetation type :

%

Herbaceous layer : 3-4 Dominant species

	Count	% of H	Palatability	$P_{weighed}$
1				
2				
3				
4				
5				
6				
7				
8				
9				
Other				
Pal. Forbes				
Unpal. Forbes				

Total H counts from 100 → ▨ **H** Overall Herbaceous layer Palatability →

Shrub layer : 3-4 Dominant species

	Under Tree	Count	% of S	Palatability	$P_{weighed}$
1					
2					
3					
4					
5					
6					
7					
8					
9					
Other					

Total S counts from 100 → ▨ **S** Overall Shrub Layer Palatability →

Tree layer : 3-4 Dominant species

	Low Branches	Count	% of T	Palatability	$P_{weighed}$
1					
2					
3					
4					
5					
6					
7					
8					
9					
Other					

Total T counts from 100 → ▨ **T** Overall Tree Layer Palatability →

INQUERITO DE SEGURANCA ALIMENTAR

SECCAO 1: Introducao

Data:	Entrevistador:	Aldeia:	
Nome do Entrevistado (Opcional):		Sexo: **M / F**	Idade:
Nivel de educacao:	Tribo:	Entrevistado é Chefe de família/esposa/outro:	

SECCAO 2: Socio-Economia Domestica

2.1 Numero & Composicao

N. ind. nesta casa: 0-6: 6-12: 12-18: M>18: F>18: Old Age:

Quantos homens adultos: Quantas mulheres adultas:

Numero total de pessoas:

A quanto tempo vivem nesta casa?

2.2 Economia

Tem machamba? **S/N**

Vende seus produtos? **S/N**

Produz suficiente para si e a familia? **S/N**

Produz a mais? **S/N**

Vende o que produz a mais? **S/N**

Tem estes artigos? **S/N** (+ numero)	1. Galinhas	2. Galinha do mato	3. Pato	4. Coelho	5. Cabrito	6. Cao

Compra o que nao tem? **S/N**

Se sim, aonde compra?

Se nao, onde arranja o que precisa?

Alguem trabalha ou ganha salario?

Tem outros meios de fazer dinheiro (marque na lista)?

1. Faz cestos	2. Corta bamboo	3. Transporte	4. Arranja radios	5. Caça	6. Trabalho oficial	7. Tabaco
8. Vende comida	9. Ganyo	10. Mel	11. Pesca	12. Outros?		

2.3 Area de cultivo

Tamanho da area cultivada?

No. de machambas?

Como arranja sementes? E' facil?

Pratica a rotacao de campos? **S/N**

Qual o tipo de terra?

Que ferramentas usa na machamba?

O que planta?	1.	2.	3.	4.	5.
Quanto produz? (kg por ano)	1.	2.	3.	4.	5.

As machambas sao individuais para a casa? **S/N**

Se nao, com quem partilha?

Como decide onde cultivar?

Por quantos meses consegue guardar sua producao?

Razao principal na falta de colheita?

Tem algum comentario sobre a dinamica socio-economica do seu lar?

SECCAO 3: Percepcao e atitude sobre a dieta e seguranca alimentar

3.1 Abastecimento alimentar

Tem problemas de abastecimento alimentar? **S/N**

Tem comida suficiente? **S/N**

Tem comida suficiente para todos na sua casa? **S/N**

Tem comida durante epoca chuvosa? **S/N**

Tem comida durante a epoca seca? **S/N**

Em que parte do ano e' mais importante ter comida?

Teve comida suficiente ano passado? **S/N**

O ano anterior? **S/N**

Dois anos atras? **S/N**

Maior razao pela mudanca?

Fala por si ou pela aldeia toda quanto a situacao do ano anterior?

Tem outros problemas em relacao a abastecimento alimentar?

3.2 Composicao da dieta	Tem todos os artigos alimentares que precisa? **S/N**

Artigos em falta? **S/N**	Possiveis detalhes dos artigos em falta:	
Itens alimentares	Disponiveis? **S/N**	Accessiveis? **S/N**
1.		
2.		
3.		
4.		
5.		
6.		

Costuma trocar pelo que falta? **S/N**	De exemplos das coisas que troca?
Itens alimentares	Troca
1.	
2.	
3.	
4.	
Tem mais algum problema quanto a dieta alimentar?	

3.3 Prospecto	E' possivel resolver os teus problemas alimentares? **S/N**
Na sua opiniao, como pode resolver?	
Quem pode resolver os teus problemas? Tu/SGDRN/Autoridades/Outros	
Tem mais comentarios de como pode resolver os seus problemas alimentares?	

SECCAO 4: A Dieta

4.1 Disponibilidade	**Favor completar a lista no appendix I**
Qual a sua dieta principal? Arroz/Farinha/Mandioca	
Para a sua casa, Quanto deste artigo precisa por semana/mes?	
Como mede por refeicao?	
Qual o principal "caril"?	Como mede o "caril" por refeicao?

Quais sao os caris mais comuns todos os meses? (escolhe 3)						
1. Galinha	2. Cabrito	3. Galinha do mato selvagem	4.Galinha do mato domestica	5. Carne fresca	6. Carne seca	7. Pato
8. Coelho domestico	9. Feijao	10. Ovos	11. Peixe fresco	12. Peixe seco	13. Outros	
Quantas vezes por semana tem uma refeicao com estes caries?(Ou por mes)						
1. Galinha	2. Cabrito	3. Galinha do mato selvagem	4.Galinha do mato domestica	5. Carne fresca	6. Carne seca	7. Pato
8. Coelho domestico	9. Feijao	10. Ovos	11. Peixe fresco	12. Peixe seco	13. Outros	
Quais sao os caries mais comuns na carne do mato? (5 escolhas)				1. Peixe	2. Crocodilo	3. Hipopotamo
4. Ngolombwé	5. Ndinu	6. Gungusi	7. Soala	8. Txivalama	9. Bufalo	10. Ndopé
11. Mbavala	12. Ndogolo	13. Sindi	14. Mbunda	15. Ndandala	16. Mbundju	17. Ngosé
18. Pala pala	19. Elefante	20. Outro				

Em que epocas e mais facil encontrar peixe? **Seca/Chuvosa**	Quais os meses com mais facilidade de encontrar peixe?
Em que epocas e mais facil encontrar carne? **Seca/Chuvosa**	Quais os meses com mais facilidade de encontrar carne?
Como prefere o peixe? **Fresco/Seco**	
Se tivese dinheiro, quantas vezes compraria peixe? **Todos os dias/semana/mes**	
Como prefere a carne? **Fresca/Seca**	
Se tivesse dinheiro, quantas vezes compraria carne? **Todos os dias/semana/mes**	

Tem mais comentarios sobre a disponibilidade de artigos comestiveis?						
4.2 Custo		**Favor completar a lista no appendix I**				
O que compraria se tivesse 100MT?			1. Galinha	2. Galinha do mato	3. Peixe	4. Carne fresca
5. Carne seca						
Tem mais comentarios sobre o custo de comida?						
4.3 Preferencia		Se tivesse quantidades iguais dos seguintes produtos, quais irias escolher (Sem custo)?				
1. Galinha	2. Cabrito	3. Galinha do mato selvagem	4.Galinha do mato domestica	5. Carne fresca	6. Carne seca	7. Pato
8. Coelho domestico	9. Feijao	10. Ovos	11. Peixe fresco	12. Peixe seco		
Prefere comprar carne fresca ou seca? **F/S**			Prefere comprar peixe fresco ou seco? **F/S**			
Prefere comprar galinha ou galinha do mato? **G/GM**			Prefere carne domestica ou do mato? **D/M**			
Prefere peixe ou carne? **P/C**						
Tem mais algum comentario em termos de preferencias?						

SECCAO 5: Conclusao

Reconhece algum beneficio em viver na Reserva?

O que acha da Reserva do Niassa? **MB B M MM Sem comentario** Outro:

Qual e' o objectivo da Reserva do Niassa?

Acha que as pessoas e os animais podem viver juntos? **S/N** Porque?

Acha importante proteger a vida selvagem? **S/N** Porque?

Acha dificil o acesso a produtos alimentares na Reserva do Niassa? **S/N**

Porque?

Esta feliz a viver na Reserva do Niassa?


PROJETO
BÚFALO