Spatial simulations of infectious disease:

environment, behaviour, and their interaction in a primate population

by

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Table of Contents

List of tables

List of figures

Abstract

Recent trends in emerging and re-emerging human infectious disease indicate that zoonotic diseases are on the rise (e.g., SARS, Swine Flu, Bird flu, Ebola, and Lyme disease), creating large economic and social costs. The increasingly dominant role that humans are playing in changing the environment is thought to be a leading cause for this increasing emergence. In this dissertation, I investigated the effects of landscape level changes on a specific host parasite system: red colobus (*Procolobus rufomitratus*) and gastrointestinal nematode parasites within Kibale National Park, Uganda landscape. I first quantified the variation in forest recovery in the region and their effects on the resident primate community. Next, I explored the link between forest structure and red colobus movement patterns by 1) developing a new measure of habitat use (STBBD), quantifying the predilection of an animal to revisit habitat patches, and 2) testing between several hypotheses to explain red colobus movement patterns. Finally, I developed a spatially-explicit epidemiological model using the insights developed in forest structure and red colobus movement patterns. This model was used to assess the disease-related consequences of habitat fragmentation, quantifying the relative effects of the extent of habitat and its spatial configuration. My epidemiological model illustrate that by taking advantage of advances in spatial data analysis it is possible to expand the range of questions that can be addressed, developing a more spatially explicit understanding of infectious disease. I also argue that by including specific landscapes and host behaviours, these approaches increase the relevance of the results for disease management, allowing managers and researches to take a more proactive role and assess the effects of planned or predicted landscape changes on host-parasite dynamics.

Résumé

Les tendances récentes dans les maladies infectieuses humaines émergentes et réémergentes indiquent que les maladies zoonotiques sont à la hausse (par exemple, le SRAS, la grippe porcine, la grippe aviaire, le virus Ebola et la maladie de Lyme), générant d'importants coûts économiques et sociaux. Le rôle de plus en plus dominant que les humains jouent dans la transformation de l'environnement est considéré comme une des principales causes de cette émergence. Dans cette thèse, j'ai étudié les effets des changements au niveau du paysage sur un système hôte-parasite spécifique : le colobe roux (*Procolobus rufomitratus*) et les nématodes gastro-intestinaux dans le parc national de Kibale, en Ouganda. J'ai d'abord quantifié la variation de la reconstitution de la forêt dans la région et leurs effets sur la communauté des primates. Par la suite, j'ai exploré le lien entre la structure de la forêt et les habitudes de déplacement des colobes roux par 1) l'élaboration d'une nouvelle mesure de l' utilisation de l'habitat (ST-BBD), la quantification de la prédilection d'un animal de revisiter des parcelles d'habitat, et 2) des tests avec plusieurs hypothèses afin d'expliquer les habitudes de déplacement des colobes roux. Enfin, j'ai développé un modèle épidémiologique spatialement explicite en utilisant les idées développées dans la structure de la forêt et l'utilisation du territoire des colobes roux. Ce modèle a été utilisé pour évaluer les conséquences des maladies liées à la perte d'habitat, en quantifiant les effets relatifs de la fragmentation et de l'ampleur de la perte. Mes modèles épidémiologiques montrent que, en prenant avantage de l'amélioration des techniques d'analyse spatiale, il est possible d'élargir l'éventail de questions qui peuvent être abordées, en développant une compréhension plus spatialement explicite des maladies infectieuses. Je soutiens également que, en sélectionnant spécifiquement des paysages et des comportements de l'hôte, ces approches augmentent la pertinence des résultats à la gestion de la maladie, permettant aux gestionnaires et aux chercheurs de jouer un rôle plus proactif et d'évaluer les effets des changements prévus ou planifiés du paysage sur la dynamique hôte-parasite.

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Contribution of Authors

The four chapters directly presenting the results of this thesis are written as journal manuscripts that have been published or are in preparation for submission to a journal. The contributions of the co-authors are as follows:

Post-logging recovery time is longer than expected in an East African tropical forest

Published in the journal of Forest Ecology and Management 261 (4), pp. 855-864, 2011.

Author	Contribution
Tyler Bonnell	Performed data analysis, statistical design, and manuscript writing
Colin A. Chapman	Data collection, analysis, and manuscript writing
Rafael Reyna-Hurtado	Analysis and manuscript writing

Analysing small-scale aggregation in animal visits in space and time: the ST-BBD method

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Author	Contribution
Tyler Bonnell	Performed data analysis, statistical design, and manuscript writing
Pierre Dutilleul	Statistical design, analysis, and manuscript writing
Colin A. Chapman	Data collection and manuscript writing
Raja Sengupta	Guided spatial analysis
Rafael Reyna-Hurtado	Data collection and manuscript writing
Raul Uriel Hernández-Sarabia	Data collection

Emergent group level navigation: an agent-based evaluation of movement patterns of a folivorous primate

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Author	Contribution
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Marco Campenni	Model design
Colin A. Chapman	Data collection, model design, and manuscript writing
Jan Gogarten	Statistical design
Rafael Reyna-Hurtado	Idea development and manuscript writing
Julie Teichroeb	Idea development and manuscript writing
Michael Wasserman	Data collection and manuscript writing
Raja Sengupta	Guided spatial analysis and visualization and manuscript writing

How does habitat fragmentation affect an environmentally transmitted parasite in a primate population?

In preparation for submission to the Journal of Ecological Applications

Author	Contribution
Tyler Bonnell	Built and ran the model, statistical design, and manuscript writing
Ria Ghai	Idea development and data collection, manuscript writing
Tony Goldberg	Manuscript writing, idea development
Raja Sengupta	Model development
Colin A. Chapman	Data collection, idea development, and manuscript writing

1. Introduction

1.1. Rise in the emergence of zoonotic diseases

History cautions that infectious disease is an ever present and ever changing problem, requiring constant and sustained efforts to monitoring and control (Cohen 2000). Recent advances in the control of infectious disease in the developed world are unprecedented. From the century spanning from 1900 to 2000 in the United States, the proportions of death associated with infectious disease dropped from approximately 30% to 3%, resulting in a shift to focus on solving chronic diseases, such as cancer and heart disease (Cohen 2000). However, infectious disease still plays a very important role in developing nations and accounts for 25% of deaths worldwide (Morens et al. 2004). It is estimated that there are 300 to 500 million clinical cases of malaria every year (Sachs & Malaney 2002) that cause an estimated 0.7 to 2.7 million deaths per year globally (conservative estimate) (Ito et al. 2002). Converting this to a more comprehensible statistic: every 40 seconds a child dies of malaria (Sachs & Malaney 2002).

Recent trends regarding the emergence of infectious disease point towards the importance of a global control strategy, as local health conditions can create breeding grounds for the emergence of infectious disease that can rapidly spread. This is demonstrated by such diseases as HIV, SARS, Swine flu, H1N1, and West Nile, all of which started as local problems before spreading worldwide. Recent studies tracking emerging or re-emerging infectious diseases in humans suggest that approximately 75% originate from animal populations (i.e., are zoonotic in origin) (Taylor et al. 2001), largely from wildlife populations (Jones et al. 2008). This suggests that a proactive public health strategy must not only focus on human populations, but on wildlife populations as well (Daszak et al. 2000).

Studies examining the rise in zoonotic diseases point to anthropogenic landscape alterations as a primary cause to their emergence (Daszak & Cunningham 2003; Woolhouse & Gowtage-Sequeria 2005). Given the large impact of anthropogenic land use and landscape change globally, ecosystem regulation of infectious disease has been highlighted in the Millennium Ecosystem Assessment as an issue for global human health (Hassan et al. 2005). Where, the specific disease related impacts of anthropogenic changes are thought to depend on the specific ecosystem, the type of land use change, disease-specific transmission dynamics, and the susceptibility of the local human population (Hassan et al. 2005; Ostfeld et al. 2008).

1.2. Thesis objectives

The overall objective of this thesis is to address the question: *how do landscape alterations affect the relationship between hosts and parasites in an infectious disease context*? I approach this question by focusing on a specific study system, and develop new methods to address this question in a wider context.

1.3. Study system

My study system was a population of red colobus monkey (*Procolobus rufomitratus*) and their gastrointestinal parasites, in Kibale National Park, Uganda (Chapman et al. 2005b) (Fig. 1-1). The red colobus monkey is considered as an endangered species, living near to human settlements, and has been the focus of past behavioural and disease ecology research (Struhsaker 1975; Chapman et al. 2005a). The red colobus is an arboreal primate, who's diet is primarily made up of young leaves (Struhsaker 2010). They live in social groups that generally range between 20 to 100 individuals, where females are the typical disperses from their natal group (Struhsaker 2010).

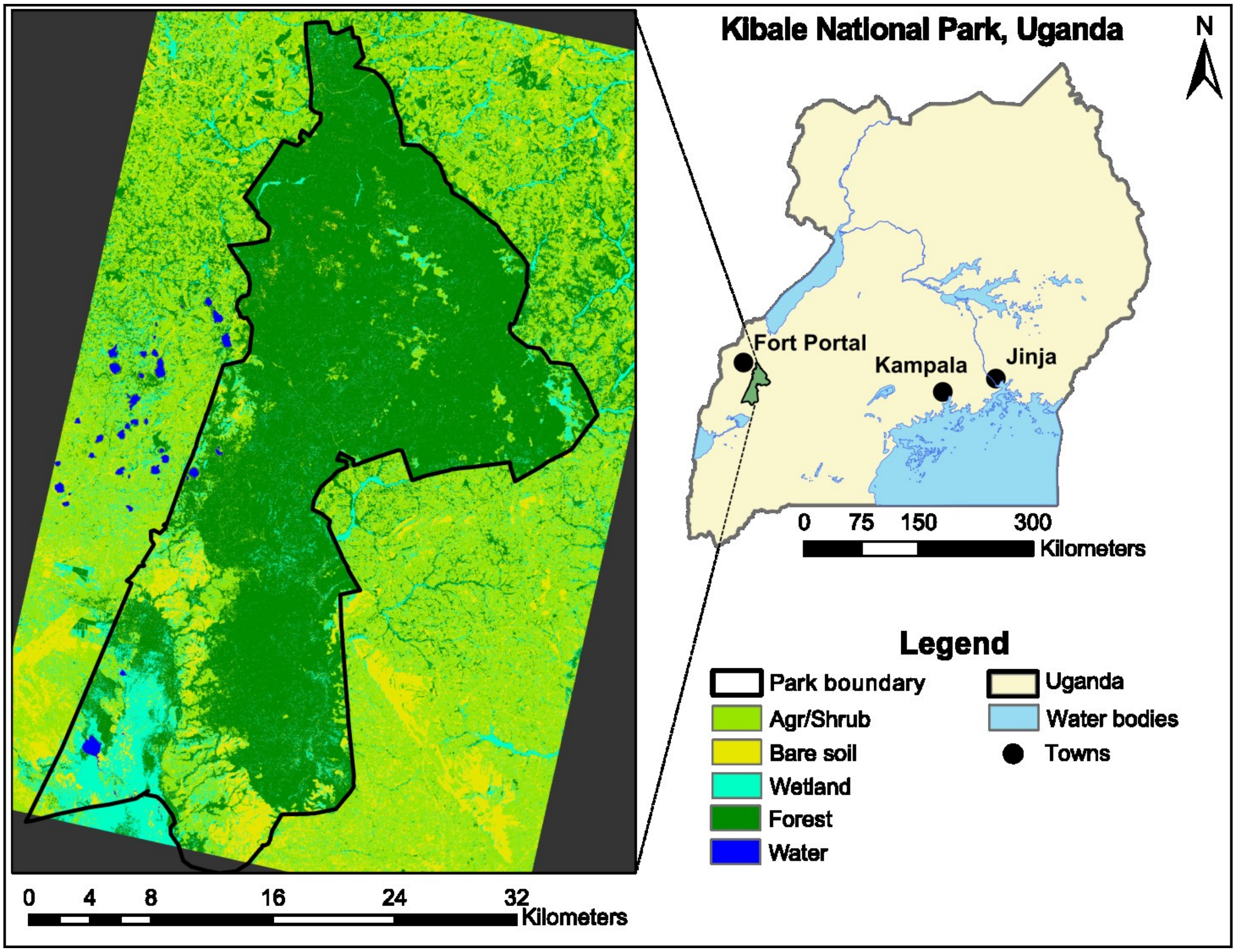

Figure 1-1: Kibale national park, Uganda. Landscape classification was done using a Spot-5 image taken in 2008 using a maximum likelihood classification algorithm (Jacobs et al. Accepted).

The health of nonhuman primates, such as the red colobus, is of specific concern for human public health, due to the high risk that primates pose as reservoirs of zoonotic pathogens (Wolfe et al. 2007; Davies & Pedersen 2008). This is illustrated by such pathogens as the human immunodeficiency virus (HIV; the cause of AIDS) (Hahn et al. 2000) and *Plasmodium falciparum* (the cause of virulent malaria) (Rich et al. 2009), both of which trace their origins to primates. In a recent study on the origins of major human infectious diseases, Wolfe et al. (2007) found that even though non-human primates constitute 0.5% of all vertebrates, their zoonotic transmission has contributed about 20% of the major human infectious diseases.

Gastrointestinal parasites, have been shown to be susceptible to landscape alterations, as well as to be zoonotic (i.e., transmittable from wildlife to humans) (Gillespie & Chapman 2006;

Goldberg et al. 2008). For most of these gastrointestinal parasites an infection is not life threatening to the host; however, they may still affect fitness. In addition, the scale of the infection worldwide, and their synergistic effects with other infections (e.g., HIV) makes them a major human health challenge (Fincham et al. 2003; Bethony et al. 2006). Many of these gastrointestinal parasites have a life stage in which they live outside their host, in the external environment, and have been found to be susceptible to local climatic conditions, influenced by: soil type, vegetation cover, temperature, rainfall, and elevation (Brooker et al. 2004; Bethony et al. 2006; Pullan et al. 2011b). Given that these parasites are also relatively immobile, while in the external environment, they are also reliant on the movement behaviour of their desired hosts. I have chosen to focus on a specific set of gastrointestinal parasites, *Trichuris sp.*, as there has been data collected on these parasites over the past decade in my study area, and data on them can be collected non-invasively and on a regular basis in a non-intrusive manner (i.e., collecting dung and not immobilizing animals). This specific gastrointestinal parasite is also of concern as it has shown to negatively affect red colobus populations (Gillespie & Chapman 2008).

1.4. Approach and methodology

Spatial epidemiology is an emerging field that investigates the interaction between landscape and disease, incorporating landscape scale variables into traditional epidemiology (Ostfeld et al. 2005). In terms of infectious disease, spatial epidemiological studies combine physical environmental variables (e.g., maximum temperature), ecological variables (e.g., host and parasite distributions), and societal variables (e.g., population density and distribution) to develop disease risk maps and spatial models to predict disease emergence or intensity (Thomson et al. 2000; Peterson 2006). Risk maps have been used as tools for public health in the management disease (Suarez 2006; Simoonga 2009; Pullan et al. 2011a); however, there has not been a strong incorporation of host behaviour in spatial epidemiology; a factor which would require spatial-temporal interaction between hosts and the landscape. The effects of landscape variability, such as seasonality, or the behaviour of hosts, such as movement, could greatly add to the understanding of the interaction between the landscape and disease. In this dissertation I explore the possibilities of combining traditional spatial epidemiological approaches with agent-based modeling (ABM), which can combine these spatial and temporal variables in epidemiological research (Auchincloss & Diez Roux 2008).

Agent-based modeling is a modeling approach whereby a system is created from the interactions of its elements (Grimm & Railsback 2005). These elements are given agency, in that they have specific goals and are able to adapt to meet those goals. The application of this modeling technique within epidemiology offers a chance to define the behaviours of hosts and parasites, allowing them to interact together and with the environment, creating system level patterns (e.g., host-parasite dynamics). In the case of a spatially explicit agent-based model, the agents (hosts and parasites) interact on a landscape, which itself can be given characteristics and/or behaviour (Linard et al. 2009; Nunn et al. 2011). This modeling technique develops a virtual laboratory, in which populations can be infected under different landscape characterizations (Bonnell et al. 2010), with different behaviours (Nunn et al. 2008), and with different parasites; offering an exploratory approach to investigate disease dynamics often impossible or undesirable/immoral to perform in the field (Nunn 2009).

1.5. Thesis Outline

Four manuscript-style chapters (chapters 2-5) are presented progressively addressing: landscape changes, their effects on the host, and finally their effects on the relationship between hosts and parasites. In chapter 2 the recovery rate of forest compartments, and their effects on the availability of food for primate populations in our study area, are quantified. Chapter 3 develops a novel metric of habitat use to quantify the predilection of an animal to revisit habitat patches. Chapter 4 tests various movement hypotheses for the red colobus monkey against collected movement data. Chapter 5 combines the landscape data from chapter 2, the methodology and models from chapters 3-4, to develop a spatially explicit epidemiological model. This model is used to explore the disease related impacts of habitat loss on a red colobus population infected with a *Trichuris sp.* like parasite.

2. Post-logging recovery time is longer than expected in an East African tropical forest.

Citation: Bonnell, T.R., R. Reyna-Hurtado, and C.A. Chapman. 2011. Post-logging recovery time is longer than expected in an East African tropical forest. Forest Ecology and Management 261:855-864.

Linking statement: In this chapter I quantify and compare forest heterogeneity between four forestry compartments in Kibale National Park, Uganda. Using this data I estimate the impact and recovery from past land use on primate populations within these compartments. The results from this chapter informed a spatial-temporal understanding of the landscape in which the red colobus forages. This chapter was published in the journal of Forest Ecology and Management in 2011.

Summary: Uncertainty in recovery times of tropical forests can lead to mismanagement, such as in setting inappropriate harvesting rates or failing to achieving conservation targets. We use long-term plot data (17 years) to estimate recovery times of separate forest compartments, which experienced different levels of timber extraction within Kibale National Park, Uganda. We estimate that structural recovery (basal area) of heavily logged and moderately logged compartments will take respectively 112 and 95 years, when compared to adjacent mature forest. Our data suggests that recovery in terms of species composition will take significantly longer. Our estimates of structural recovery are derived from rates of change of diameter at breast height and basal area measurements which have been used traditionally as indicators of forest growth and productivity. Our results suggest that the severity of the logging has an impact on the rate of recovery, with current recovery rates estimated at 0.32 m^2/ha y^{-1} in a moderately logged compartment and 0.25 m^2/ha y^{-1} in heavily logged areas, highlighting the possible benefits of reduced impact harvesting in increasing long-term yields. We investigate how some representatives of the wildlife community were affected by differential recovery times and find that recovery times of frugivorous primate's forest habitats were 2.5 times slower when compared with folivorous primates.

2.1. Introduction

Tropical forests represent important reserves for biodiversity, but they are increasingly under threat from a growing world population and a subsequent increase in land use and resource extraction (Brown & Lugo 1990; Richards 1996). A growing understanding on the effects of resource harvesting on forests is generally leading to the development of more sustainable practices (Lindenmayer et al. 2000). However, these practices are seldom in use in tropical forests (Putz et al. 2000).

There remains much uncertainty on the effects of resource extraction and other natural disturbances on forest dynamics and recovery, especially in tropical forests (Chazdon 2003). Generally, the intensity of the disturbance and local ecological composition of the forest are both thought to be important factors in determining the speed and specific pathway of forest succession following disturbance (Pickett et al. 1987; Chazdon 2003). The ecological make-up of the forest in question plays an important role in its response to disturbance, whereas the intensity of the disturbance (either in magnitude or in repetition) compounds the effects and can drive the system to alternative steady states (Pickett et al. 1987; Chazdon 2003).

Long-term vegetation plots have been employed as an effective tool for monitoring tree population dynamics, allowing researchers to test succession theories and estimate recovery times of forests (Condit 1995; Sheil et al. 2000). A review of previously published studies where long-term vegetation plots were used to compare forest recovery from past logging in East Africa, have shown that the recovery rates of these forests are uncertain (Table 2-1). The longest studies are in the Budongo Forest Reserve (Uganda) and Kakamega Forest Reserve (Kenya) where the authors estimate that a minimum of 60 years is required for recovery to pre-logging conditions (Plumptre 1996; Fashing et al. 2004). In the Kibale and Bwindi Impenetrable National Parks, in Uganda, an unfavorable succession pathway seems to slow down or arrest forest succession (Babaasa et al. 2004; Chapman & Chapman 2004), possibly requiring longer to recover. These studies highlight the uncertainty in the amount of time required to make harvesting sustainable in such forests.

Table 2-1: Studies comparing logged and unlogged forests within 500km of our study site.

Study Site	Authors	Indicators of recovery	Recovery*	Data(years)	Disturbed**
Kibale National Park, Kanyawara	(Chapman & Chapman 1997)	Tree population	>25	0	20
	(Chapman & Chapman 2004)	Tree population	>30	10	30
	(Massimino et al. 2008)	Bird Population	>35	10	33
	(Chapman et al. 2010a)	Tree population	100s-1000s	18	100s-1000s
Mpanga forest, Uganda	(Taylor et al. 1996)	Tree population	>42	25	42
	(Taylor et al. 2008)	Tree population	N/A	38	55 + recent
Kakamega Forest, Kenya	(Fashing et al. 2004)	Tree population	>60	18	59 + recent
Budongo Forest, Uganda	(Plumptre 1996)	Tree population	>55	0	55
	(Owiunji & Plumptre 1998)	Bird Population	>8	0	8
	(Sheil et al. 2000)	Tree Population	100s-1000s	53	100s-1000s
Bwindi Impenetrable National Park, Uganda	(Babaasa et al. 2004)	Gap sizes	>9	0	9

* Recovery time was estimated as years from known disturbance or taken from estimates of authors. In general recovery estimates made by authors refer to a return to the pre-disturbed state.

** conservative estimate: years from disturbance = last year of study data - newest year of disturbance

n/a --- No mention of recovery or the state of the forest system cannot be assessed from the results

As our study site lies within Kibale National Park, Uganda, the unfavorable pathway found there is of specific concern. This pathway is thought to occur where certain ecological factors are present: presence of an elephant population that trample and browse re-growth, aggressive herbaceous undergrowth, and a lack of aggressive colonizing tree species, and is triggered where there is a significant disturbance (Struhsaker et al. 1996; Paul et al. 2004; Lawes & Chapman 2006). A general pattern has emerged in Kibale indicating that large gap sizes in the canopy left leads to arrested succession. Such large gaps have been shown to allow a dense layer of herbaceous plants to develop, slowing seedling recruitment, and increasing seedling mortality (Babaasa et al. 2004; Paul et al. 2004). Furthermore, the presence and density of elephants in the region reinforces the maintenance of this gap, possibly enlarging it, as elephants are found to favor open gaps with herbaceous material as food sites (Struhsaker et al. 1996; Babaasa 2000). Elephant presence in these gaps further increases seedling mortality, as well as the mortality of other younger trees in the surrounding area (Babaasa et al. 2004; Paul et al. 2004; Lawes & Chapman 2006).

The objective of this study is to estimate the recovery time of compartments in the Kibale National Park in western Uganda. This forest was subjected to different intensities of logging in the late 1960s that created a mosaic of conditions from heavily logged to unlogged sites. Our estimates of recovery are derived from long-term plot data (17 years, beginning 20 years after disturbance), from which we are able to compare and evaluate the separate forest compartments through measures of mortality rates, recruitment rates, stem growth rates, stem diameter at breast height (DBH), species composition, and DBH-class distributions. The literature cautions that forests are thought to be in a state of constant flux, and when forest dynamics are observed closely, never really attain a climax state or follow simplistic succession patterns (Whittaker 1972). For this study we focus mainly on structural recovery of the forest, as these estimates are thought to be more predictable over time (Chazdon et al. 2007). We make the assumption that compartments had similar structural composition prior to logging, and will be considered recovered once they are similar in structure to the unlogged plot (following Skorupa 1988). We make this assumption knowing that the study sites are close together (within 1500 m), and have all been classified as Paranari forest (Osmaston 1950). Historical ground surveys suggest that, even though there are major subtypes of Paranari forest, these forests all showed similar cumulative basal area, canopy cover, and stem density measurements (Kingston 1967; Chapman et al. 1997), suggesting a high level of structural similarities between compartments.

We projected the recovery trends for each compartment along the three points in time (1989, 1999, and 2006) which in total represented 37 years after logging. We use basal area and DBH trends to estimate structural recovery. These structural recovery trends are examined for: 1) all tree species, 2) primary food trees of five primate species that are not hunted, the red colobus (*Procolobus rufomitratus*), the black and white colobus (*Colobus guereza*), the grey-cheeked mangabey (*Lophocebus albigena*), the red-tail monkey (*Cercopithecus ascanius*), and the blue monkey (*Cercopithecus mitis*), 3) as well as important timber trees. We estimated recovery time for these tree species using the level of the unlogged forest as the target. Classification of trees into categories based on successional characteristics is used to examine changes over time, to compare within and between compartment population structure. From these estimates we are able to look at recovery from different points of view, allowing us to approximate re-logging times for the area, as well as to ascertain the effects of logging on conservation of primate species.

2.2. Methods

2.2.1. Study site

Kibale National Park is located in western Uganda and is largely composed of moist-evergreen forest (~795 km^2; 0° 13' - 0° 41' N and 30° 19' - 30° 32' E) that receives approximately 1697 mm (1990-2009) of rain each year distributed among two rainy seasons (C.A. Chapman and L.J. Chapman unpublished data). We focus on a subsection of the park (Kanyawara, classified as a *Parinari* forest by foresters) where there has been data collected on forest properties for the past 17 years (Chapman et al. 1997; Struhsaker 1997; Chapman & Chapman 2004; Chapman et al. 2010a). We compare data from four areas within the Kanyawara forest, which have been subjected to different logging histories: K15, K14, K30, and Mikana. Compartment K15, a 360 ha section of the forest, was selectively logged in 1969 (extraction~21 m^3/ha). During the same year compartment K14, a 390 ha section, was slightly and selectively logged (extraction~14 m^3/ha). Due to high heterogeneity in the logging intensity within K14 it was split in two parts: Mikana, which covers a moderately logged section of K14 and the rest of K14, where stump and gap enumeration suggest only light logging had taken place (Kasenene 1987). Compartment K30, approximately 300 ha, has not been commercially logged, having only a few large stems extracted prior to 1970 (0.03-0.04 trees/ha) resulting in little impact on forest structure, and is serving as a control site (Skorupa 1988; Struhsaker 1997). The damage done while harvesting was found to be highest in K15, where it is estimated that 50% of all trees were destroyed by logging and incidental damage (Skorupa 1988; Chapman et al. 1997). Whereas in K14, approximately 25% of all trees in the compartment were destroyed by logging and incidental damage (Skorupa 1988). In K30 there was very little incidental damage, as logging was done by pitsawyers (Skorupa 1988).

We use tree data from three time periods (1989, 1999, and 2006), where 26 plots (200 x 10 m) were used to record identity and diameter at breast height (DBH) values of all trees larger than 10cm DBH. Trees sampled within these plots (> 10 cm DBH) were marked with an aluminum tag for future identification at a height of 1.2 cm on the uphill side. These plots were chosen at random along an existing trail systems (approximately 200km in length), designed in a grid format to give access to the forest. This trail system does to some extent avoid certain areas, such as swampy valley bottoms (Chapman & Chapman 1997). Between plots measurements of slope, the amount of light reaching near to the ground, and the density of ground vegetation was found to be not significantly different among compartments (Chapman & Chapman 1997).

For statistical comparison each 200 m x 10 m plot was considered an independent unit and were grouped into compartments with different logging histories, consisting of heavy logging (K15, n=5), moderate logging (Mikana, n=4), light logging (K14, n=6), and unlogged (K30, n=11); comparisons within and between compartments were then made.

2.2.2. Data Analysis

We tested within compartment variability against between compartment variability to look for significant differences in compartment structure. We also tested within compartment variability through time to look for structural changes in a given compartment. Due to our limited sample size Kruskal-Wallis tests (H statistic) were used to test for the effects between compartments within a year. Differences between two compartments where further tested using a Two-sample Wilcoxon rank-sum (z statistic). To test for differences within compartments between years a Wilcoxon sign rank test (z statistic, paired by plots) was used.

To measure the structural characteristics of the forest plots, we used cumulative DBH (cm/ha) as well as basal area (m^2/ha). Both of these metrics measures the density of timber; cumulative DBH measures the total length of stems accumulated, basal area measures the total area of stems accumulated. Cumulative DBH is then independent of tree size, as it simply adds the DBH of each tree, essentially treating growth on each stem equally. Basal area on the other hand is not independent of tree size; a 2 cm increase on a large stem will have a much greater impact on estimates than on a small stem. This results in basal area estimates to be sensitive to large trees, whereas DBH measures are more sensitive to recruitment and growth in smaller age classes of trees. Since it seems likely that animal populations respond differently to these two different indices, we have reported both.

Tree species found within plots were classified into three categories based on their growth strategies, namely: early, mid, and late successional categories. This classification was based on literature and previous experience of qualified personnel that have lived or worked in the area for more than 20 years (Hamilton 1991; Chapman unpublished data). The composition and proportion of tree succesional categories were then compared between compartments.

We included foods (*i.e.*, a specific part from a particular species) that constituted ≥ 4% of the time spent feeding reported by Rudran (1978) and Butynski (1990) for blue monkeys*,* Waser (1975) and Olupot (1994) for mangabeys*,* Harris and Chapman (2007) and Oates (1977) for black-and-white colobus, Rode *et al*. (2006, unpublished data) and Stickler (2004, unpublished data) for redtails, and Chapman and Chapman (2002, unpublished data) and Struhsaker (1975) for red colobus. We chose the 4% cut-off because it included specific food items that were consistently considered important by previous researchers studying these species in this area and our team, while avoiding incorporating large numbers of rarely used species (Chapman et al. 2010b). Using the vegetation plot data, we estimated the cumulative DBH of food trees in each area, for each primate species, at each time period.

Tree species were further classified as timber and non-timber trees based on estimates of extraction within the compartments in the late 1960s. Trees classified as timber trees (n=9) made up more than 90% of extraction (Skorupa 1988) (Table 2-2).

Table 2-2: List of species and their classification into: successional classes (early, mid and late), and primate food trees and value as a timber. The top ten most important species (in terms of percent of total DBH) from each compartment are considered.

Species	Successional characteristics	Primate food tree* (P.r,C.g,L.a,C.m,C.a)	Timber Tree** (T)
Aningeria altissima	Late	P.r	T
Bosqueia phoberos	Late	P.r, C.m	
Celtis africana	Mid	P.r, C.m, C.a	T
Celtis durandii	Mid	P.r, C.g, L.a,C.m,C.a	
Chaetacme aristata	Late	P.r	
Cordia abyssinica	Late		
Diospyros abyssinica	Late	C.m, C.a	
Dombeya mukole	Early	C.m	
Euadenia eminens	Late		
*Fagaropsis angolensi*s	Late		T
Ficus exasperata	Mid	C.g, C.m, C.a	
Funtumia latifolia	Late	C.m	
Leptonychia mildbraedii	Late		
Markhamia platycalyx	Late	P.r,C.g,L.a,C.m,C.a	
Millettia dura	Early	P.r, C.g, L.a, C.a	
Mimusops bagshawei	Late	C.m	
Myrianthus arboreus	Late		
Neoboutania macrocalyx	Early		
Newtonia bucchanani	Late	P.r, C.a	T
Premna angolensis	Late	C.m, C.a	
Pseudospondias microcarpa	Late		
Strombosia scheffleri	Late	P.r	
Teclea nobilis	Late	P.r, C.m	
Trema guineensis	Early		
Uvariopsis congensis	Late	C.m, C.a	

*Primate food trees were taken from the references listed in the methods; *P. rufomitratus* (P.r), *C. guereza* (C.g), *L. albigena* (L.a), *C. mitis* (C.m) and *C. ascanius* (C.a).

**Nine tree species were considered as timber species, and made up >90% of extraction in our study plots (Skorupa 1988). Timber tree species not in the table include: *Chrysophyllum gorungosanum, Fagara angolensis, Olea welwitschii, Parinari excelsa, Prunus africanum.*

2.3. Results

Initial composition, as measured in 1989, of the all the compartments show the dominance of specific species in all compartments; *Celtis durandii, Diospyros abyssinica*, and *Markhamia platycalyx*, which make up the top three species (cumulative DBH) in all the compartments. Considering a larger sub-population of tree species within compartments reveals differing vegetation structures. Using the top ten species within the each compartment, the presence and importance of early succesional classes in the heavily and moderately logged compartments suggest an earlier stage of succession (Fig. 2-1).

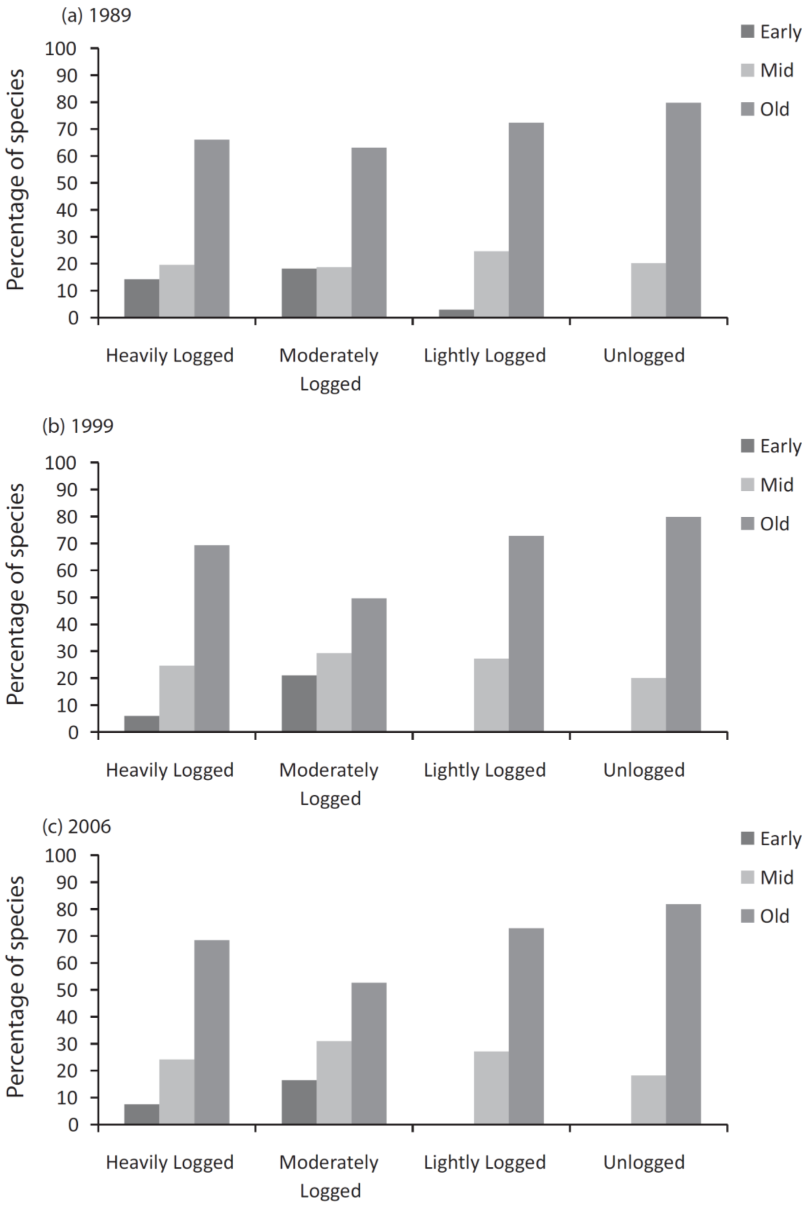

Figure 2-1: Composition of the top ten species within the heavily, moderately, lightly, and unlogged compartments during: a) 1989, b) 1999 and c) 2006. Species where categorized as either early, middle or late successional species based on their life history characteristics.

During the 1989-1999 period recruitment into the heavily logged areas was lower than the unlogged and lightly logged compartments (Wilcoxon two sample test z=2.15 p=0.03, z=2.47 p=0.01; Table 2-3). During this period there was also an effect of compartment logging rate on recruitment (Kruskal-Wallis H=7.98, p=0.046; Table 3). From 1999 to 2006 there was a significant increase in recruitment rates overall (Wilcoxon sign rank test z=-4.28, p<0.01; Table 2-3) with the result that there were no effects of logging on recruitment rates during the 1999-2006 period (Kruskal-Wallis H=4.20, p=0.24; Table 2-3).

Considering individual stems, we find that during the first half of the study (1989-1999) the compartments which underwent heavy and moderate logging show higher mean growth rates than the unlogged or lightly logged compartments (Wilcoxon two sample test: unlogged-heavy z=8.39 , p<0.01; light-heavy z=-5.97 , p<0.01 ; unlogged-moderate z=-3.61 , p<0.01 ; light-moderate z=-2.22 , p=0.03; Table 2-3). Furthermore, the heavily logged compartment was found to have higher growth rates when compared to the moderately logged compartment (Wilcoxon two sample test: heavy-moderate z=2.65, p<0.01; Table 2-3). In the second period, mean growth rates of the stems within the heavily logged compartment was significantly reduced (Wilcoxon two sample test z=3.73, p<0.01) and there was no overall effect of logging history on the average growth rates of stems (Kruskal-Wallis: 1989-1999 H=72.85, df=3, p<0.01; 1999-2006 H=4.35, df=3, p=0.23; Table 2-3). Due to the fact that the data was close to normally distributed, yet failed standard normality tests, a parametric approach was tested revealing only slight changes in the results. The only contradiction was that the moderately and heavily logged areas showed no significant differences in growth rates during the 1989-1999 periods (Scheffe test p=0.367).

Since observations started in 1989 until the last observations in 2006, 470 of the total 2787 trees died; 281 (28.1/y) trees died between 1989 and 1999 and 189 (27/y) trees died between 1999 and 2006. Mortality rates were not significantly different between the two periods and there were no significant differences between compartments (Table 2-3).

Table 2-3: Population dynamics of forest compartments with different logging histories

	Mortality		**Recruitment**		**Stem growth**	
	(stem ha^{-1} y^{-1})		(stem ha^{-1} y^{-1})		(cm DBH y^{-1})	
Logging history	**1999**	**2006**	**1999* a**	**2006 b**	**1999***	**2006**
Unlogged	6.47	6.38	4.73 a	10**	0.22 a	0.25
Light	6.04	6.47	6.83 a	13.33**	0.24 a	0.22
Moderate	8.85	10.22	5.38 a,b	14.64	0.38 b	0.29
Heavy	7.72	8.77	2.6 b	8.57**	0.48 c	0.25**

(*) on the year represents a significant effect of logging history between compartments
(**) on the values represents a significant difference within compartment between years
(a,b,c) depicts differences within a compartment or between study years

The negative effect of logging history on the cumulative DBH of compartments was found to be significant in 1989 and 1999 (Kruskal-Wallis; 1989: H=13.24, df=3, p=0.0041; 1999: H=9.32, df=3, p=0.0254). There was a significant increase overall in cumulative DBH during the 1999-2006 period (Wilcoxon sign rank test: z=3.77, p<0.01), resulting in there being no effect of logging history on DBH in 2006 (Kruskal-Wallis; 2006: H=7.45, df=3, p=0.0589; Fig. 2-2). The rate of change in cumulative DBH was not significantly different between compartments; however, between periods (1989-1999 and 1999-2006) the unlogged compartment showed an increase in growth rates (Wilcoxon sign rank test; z=2.49, p=0.0128). Logging history was also found to have a negative effect on the density of stems (stems ha^{-1}) in 1989 and 1999 (Kruskal-Wallis; 1989: H=10.75, df=3, p=0.0131; 1999: H=8.77, p=0.0325; Fig 2-2); again, in 2006 the effect was found to be non-significant (2006: H=7.206, p=0.0656; Fig. 2-2). In terms of compartment basal area measurements, logging history was a significant factor in all three time periods (Kruskal-Wallis; 1989: X=14.1, df=3, p<0.01; 1999: X=11.2, df=3, p<0.01; 2006: X=10.7, df=3, p<0.01; Fig. 2-2). However, in 2006 the heavily and moderately logged compartments were no longer significantly different than the lightly logged compartment, but remained significantly different than the unlogged (Fig. 2-2).

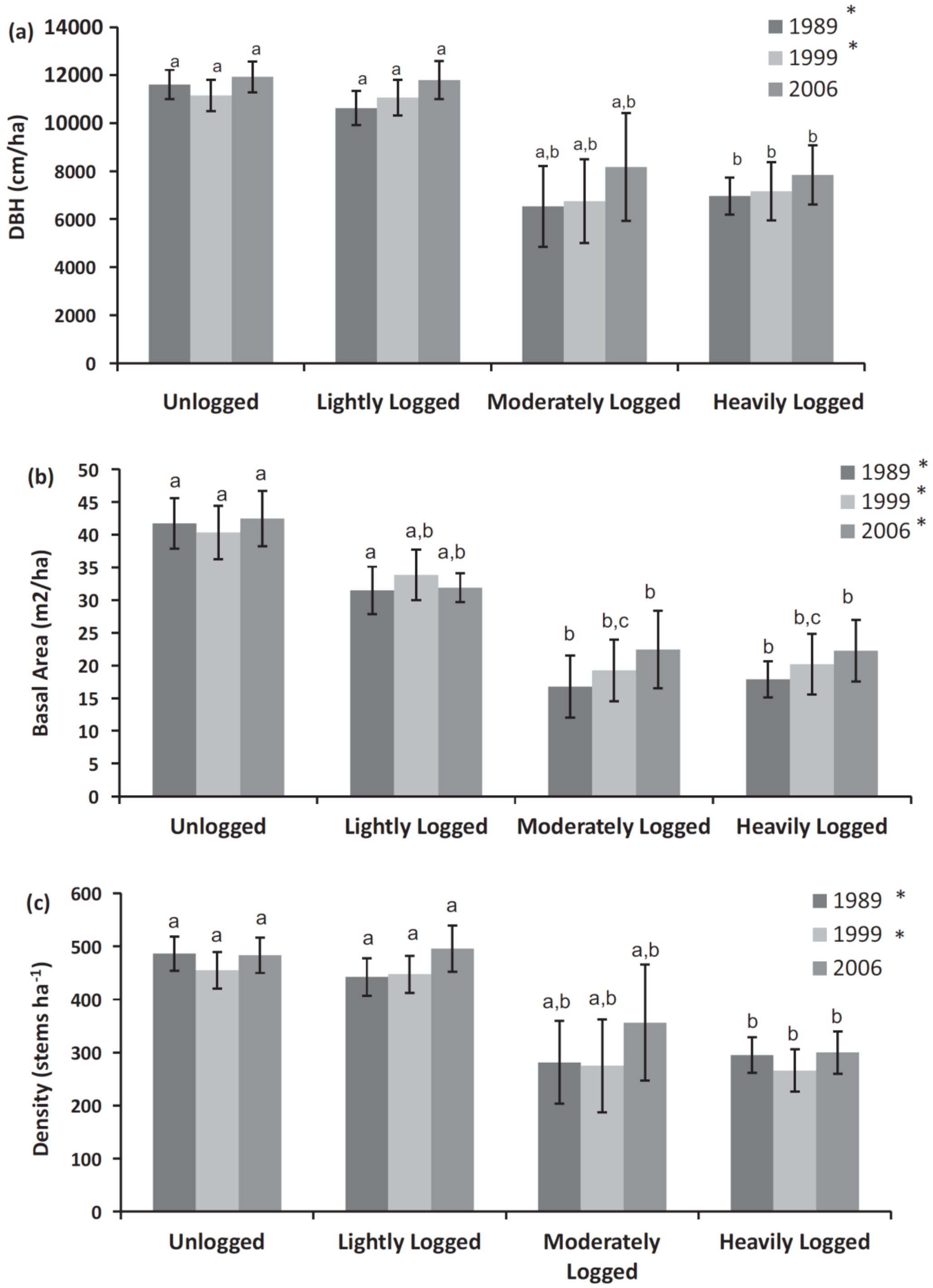

Figure 2-2: Physical properties of compartments: a) average DBH, b) average basal area and c) number of stems per hectare within compartments. Lower case lettering on the bar graphs (a,b,c) represent statistical differences between compartments within years (1989, 1999, 2006).

The DBH class distribution of the tree population within the compartments indicated that in 1989 there was an association between the intensity of logging and a lowered proportion of 10-20 age class and an increase in the proportion of mid-sized trees (Fig. 2-3). As expected, if the logging operation targeted larger trees, there was also trend towards a lower number of large trees and increased intensity of logging (Fig. 2-3). This trend is still apparent from the 2006 data; however, it seems as though the lightly and moderately logged compartments were closer in composition to that of the unlogged compartment, which changed little since 1989. The heavily logged compartment seems to retain similar characteristics as in the 1989 age class distribution (Fig. 2-3).

As would be expected, the composition of the top ten species shows that the heavily and moderately logged compartments have a greater percentage of early- and mid-successional species and a lower percentage of late successional species (Fig. 2-4). But this is not the case for the lightly logged area, where early-successional species have declined (Fig. 2-4). In estimating total species richness in each compartment, only the unlogged compartment shows definite signs that sampling is close to sufficient to estimate true species richness (i.e., the leveling out of species area curve; reduction in the number of singletons and doubletons). However, our current sampling suggest that that logging reduces species richness (Table 2-4).

Table 2-4: Estimates of species richness for forest compartments with different logging histories

Logging History	**S_{obs} (Mau Tao)**	**95% Lower CI**	**95% Upper CI**	**S^{max} (Chao2)**	**# Plots**	**# Stems**
Unlogged	64	53.55	74.45	79.7	11	1079
Lightly Logged	48	38.05	57.95	53.83	6	589
Moderately Logged	46	36.01	55.99	53.65	4	286
Heavily Logged	41	31.26	50.74	46.2	5	303

Sobs = observed species richness; Mau Tao (Colwell 2005)

CI= confidence interval

Chao2 = estimate of total species richness (Colwell 2005)

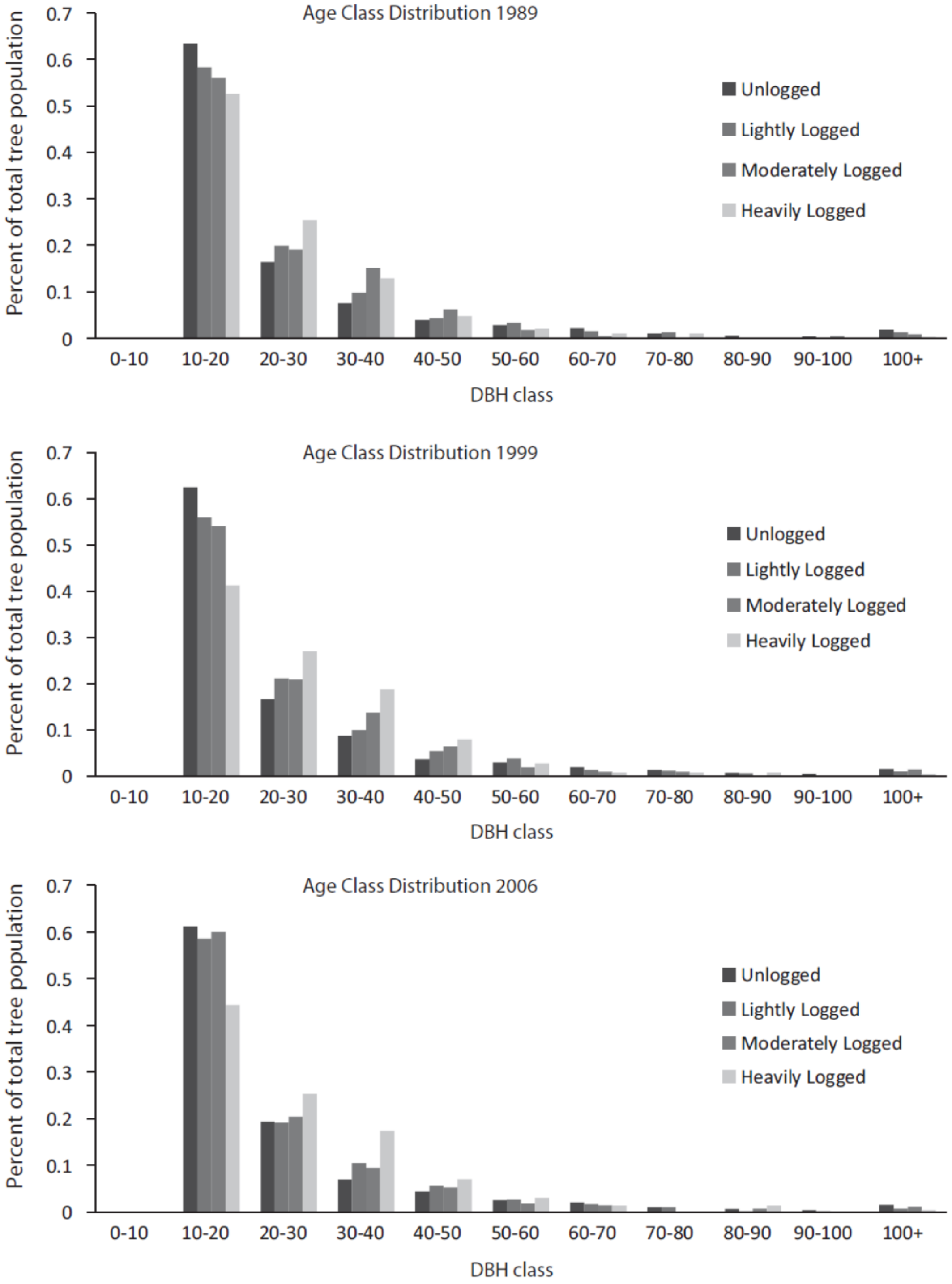

Figure 2-3: Age class distributions of trees within compartments, during the first observations in 1989, second observation in 1999 and last observation in 2006. Each age class is estimated by the DBH (cm) of trees.

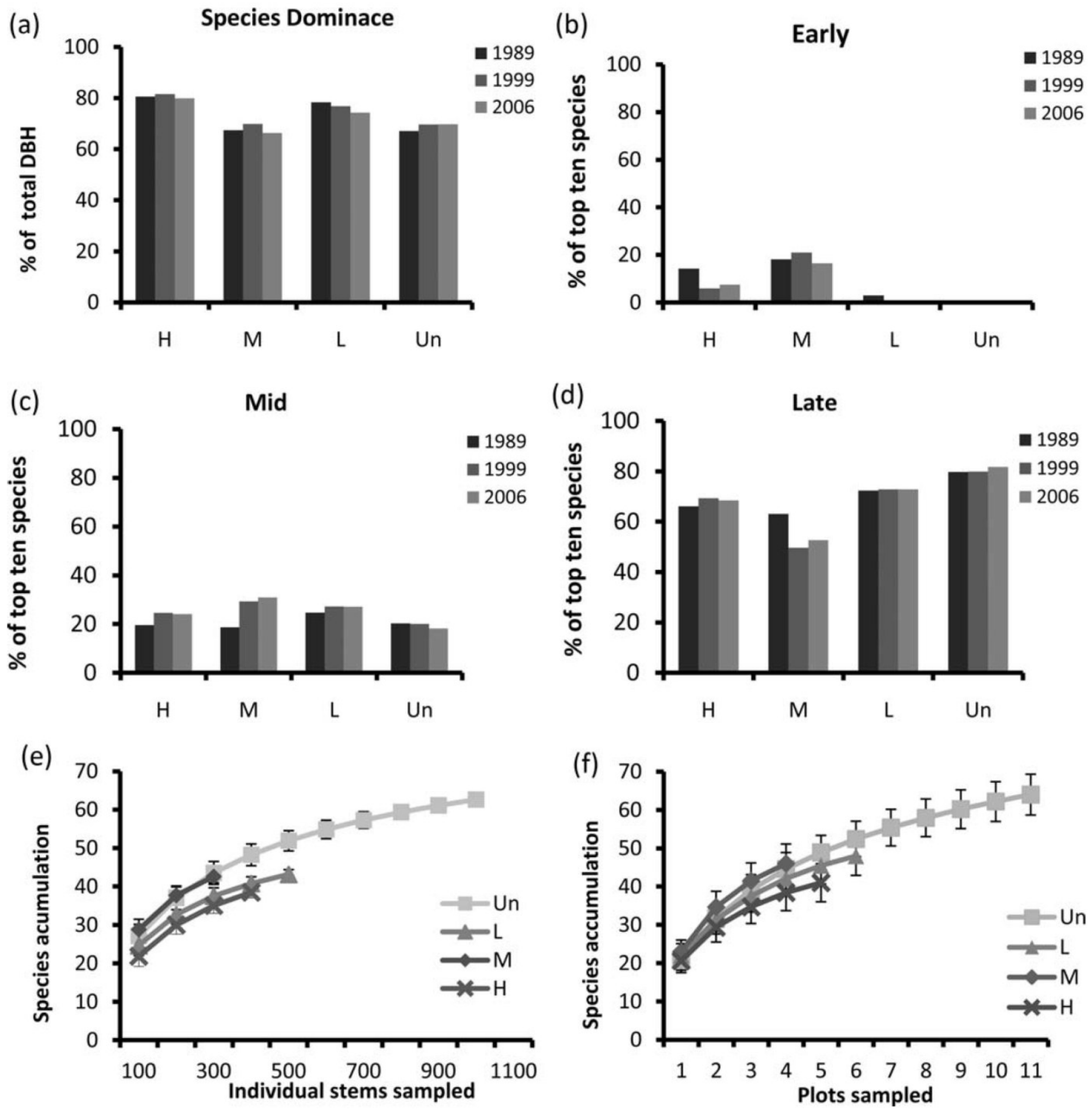

Figure 2-4: Estimates of species composition within compartments: a) dominance of the top ten species within each compartment; species rank was determined by total compartment DBH, and dominance was calculated as total DBH of all ten species divided by total compartment DBH. Estimates of changes in successional classes, measure by DBH, for b) early, c) mid, d) late, and species area curves based on sampling by e) individual stems, and f) sampling by plots.

The logging in the 1960s concentrated on nine timber species (Table 2-2). Estimates of recovery both in terms of cumulative DBH and basal area reveal that the moderately and heavily logged compartments are showing signs of timber species recover; with recovery in the moderately logged being faster than in the heavily logged compartment. Differences between the lightly and unlogged compartments are not great and there are no apparent temporal trends. A large drop in the lightly logged compartment occurred during the 1999-2006 periods as a result of a single very large tree dying. However, due to our limited sample size we cannot make strong inferences from these results.

When closely examining the growth rates of the tree species that serve as food for five primate species that have been studies at Kibale (red colobus, black and white colobus, blue monkey, redtail monkey, and mangabeys), we find that the food tree DBH is lower in the heavily and moderately logged plots than in the unlogged and lightly logged plots for all the species considered, with the exception of black and white colobus (Fig. 2-5e). The lightly logged plots have similar food tree DBH as the unlogged plots, with more food tree DBH for black and white colobus and red colobus monkeys. We find that food tree DBH is increasing in heavily and moderately logged plots, but at different rates. Assuming a linear increase in DBH over time (Chazdon et al. 2007), the rates of increase, measured as DBH/ha y^{-1}, was generally found to be higher in the moderately logged compartment compared to the heavily logged (Fig 2-5g). This was found while considering all trees (light: 67.5, moderate: 101.2, heavy: 50.9), as well as specific food trees of primates (*C. mitis* moderate: 104.0, heavy: 22.4; *L. albigena* moderate: 60.7, heavy: 9.0; *C. ascanius* moderate: 87.2, heavy: 10.6; *C. guereza* moderate: 44.4, heavy: 25.9). However, in the case of the red colobus this trend did not apply (*P. rufomitratus* heavy: 57.1, moderate: 40.7).

From the estimates of DBH change over time (cm/ha y^{-1}), we find that from the initial disturbance in 1969 recovery it will take 34 years at a rate of 66.7 DBH/ha y^{-1} for the lightly logged compartment, 74 years at a rate of 91.2 DBH/ha y^{-1} for the moderately logged compartment, and 111 years at a rate of 50.0 DBH/ha y^{-1} for the heavily logged compartment to reach the cumulative DBH of the unlogged forest. From the estimates of basal area (m^2/ha y^{-1}) we find that recovery will take 95 years at a rate of 0.33 m^2/ha y^{-1} for the moderately logged compartment and 112 years at a rate of 0.26 m^2/ha y^{-1} for the heavily logged compartment to reach the basal area of the unlogged forest. Considering important tree species for given primates (based only on DBH estimates), it will take different times in different compartments for the cumulative DBH of each primates food trees to reach the same as that found in the unlogged forest: *C. mitis* moderate: 53.3y, heavy: 75.9y; *L. albigena* moderate: 53.8y, heavy: 89.4y; *C. ascanius* moderate: 48.4y, heavy: 158.8y; *P. rufomitratus* moderate: 76.0y, heavy: 56.1y; *C. guereza* moderate: 51.2y, heavy: 32.3y) (Fig. 2-5). The cumulative DBH of food trees found in the lightly logged areas are similar (or greater) to the unlogged sites in all estimates except those made with all tree species considered.

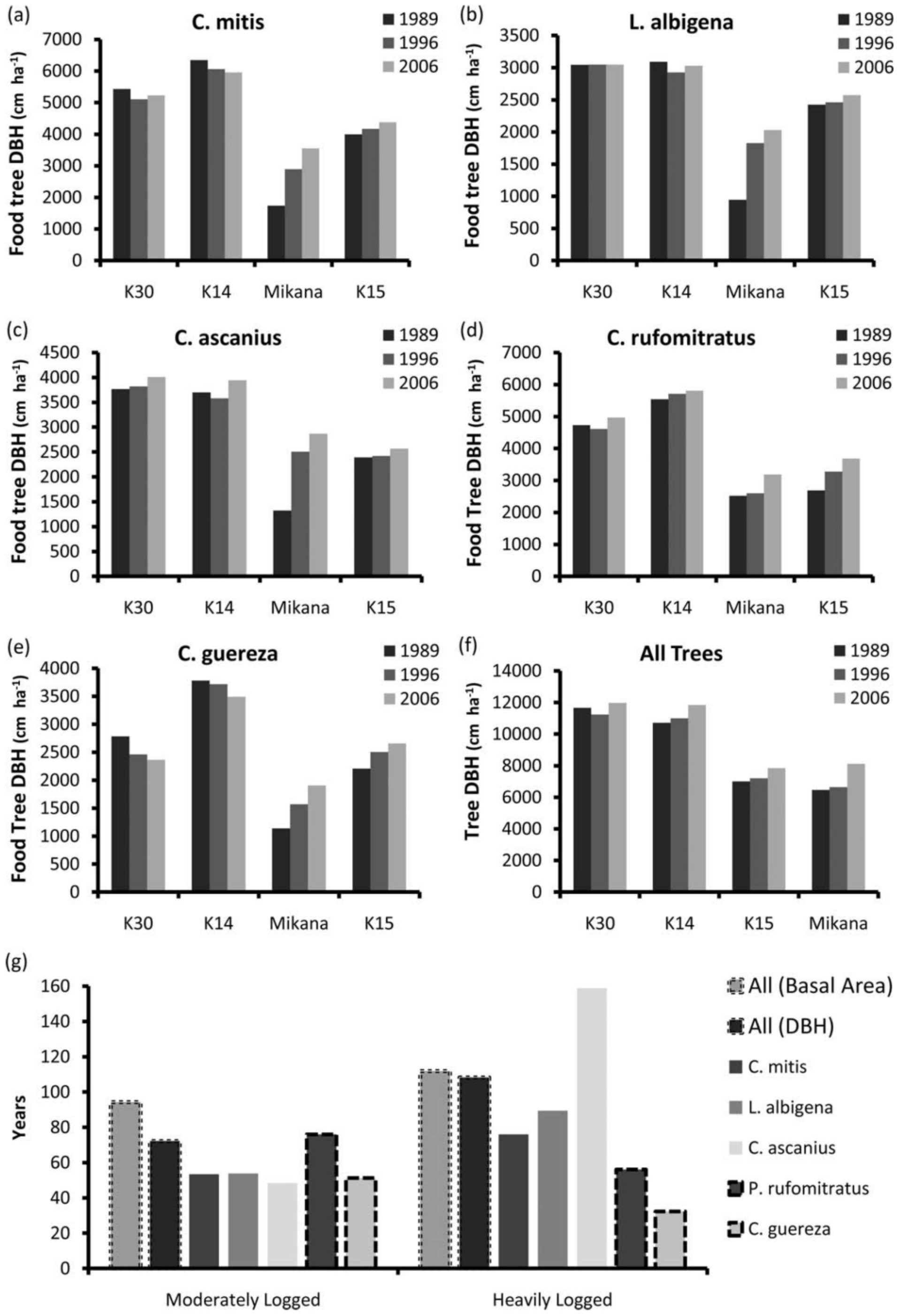

Figure 2-5: Estimates of recovery of primate food trees (DBH): a-e) changes in food-tree for five primate species, f) changes in all trees and g) estimates of recovery time for the heavy and moderately logged compartments. Estimates of recovery in the lightly logged compartment were left out as its DBH/ha values are similar (or greater) to the unlogged sites in all estimates except those made with all tree species considered.

In examining the estimates of recovery for the five Kibale primate species, the frugivorous primate species are more affected than the folivorous species. Folivores (*C. guereza*, *P. rufomitratus* food trees recovered approximately 2.4 times faster in the heavily logged areas, when compared to frugivores (*C. mitis, L. albigena, C. ascanius*) (Fig. 2-6). However caution needs to be taken in interpreting these results, due to the limited number of species considered and since it is possible for populations to rely on less preferred species than those we considered food.

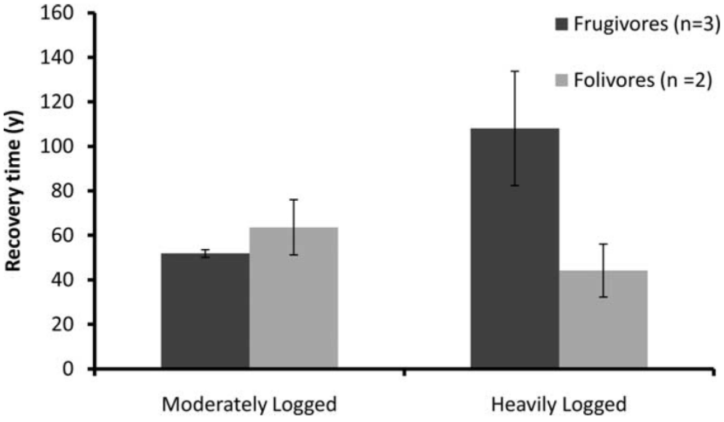

Figure 2-6: Estimates of recovery regarding frugivorous and folivores primate species.

2.4. Discussion

From the first ten years of data collected, the heavily and moderately logged compartments exhibited trends that would be expected from a disturbed forest. They were found to have the lowest cumulative DBH and basal area estimates, individual stem growth rates were higher, there was a lack of large trees, a higher number of medium size trees, and a high percentage of early successional species within the stands. However, some results were counterintuitive, namely that recruitment rates are lowest in the heavily logged compartment and that in the moderately logged compartment species composition suggests a naturally high diversity, when compared to other compartments. The lightly logged compartment on the other hand seems to be moving closer to the composition of the unlogged compartment; cumulative DBH, basal area, and stem growth rates are similar to the unlogged compartment, and there was a reduction in trees classified as early successional species compared to the other logged areas.

In the last seven years of our data we see a change in the heavy and moderately logged compartments: individual growth rates of stems and recruitment rates are now at similar levels as the unlogged and lightly logged areas, and the average cumulative DBH of plots has increased; suggesting some recovery is taking place. However, again there are some unexpected results: the rate of change in total DBH was not significant; composition of early and mid-successional species remains high and in the case of the heavily logged compartment DBH-class distributions show similar patterns as those at the beginning of our study. The lightly logged compartment continued to show signs of recovery: in 2006 the age class distribution was similar to the unlogged compartment, the importance of early successional species was reduced, and the cumulative DBH and basal area estimates has been found to be similar to unlogged areas.

The heavily logged compartment appears to be experiencing recovery at a much slower rate than the lightly or moderately logged compartments. Extrapolation from the last 17 years, using total DBH measurements, predicts that the rate of recovery here is 3.3 and 1.5 times slower than the recovery rates estimated in the moderately and lightly logged compartments. When we consider the recovering compartments we can see that in all cases average DBH per plot has been increasing, suggesting some recovery. However, our density estimates suggest that in the heavily logged compartment this increase in DBH is likely a result of established trees growing larger, whereas the lightly logged and moderately logged compartments show signs of increasing density of stems, suggesting recruitment is a factor in the increase in DBH. This agrees with the results from the age-class distributions as well; lightly logged and moderately logged compartments in 2006 show increases in the proportion of 10-20cm DBH age class trees to similar levels as the unlogged compartment, whereas in the case of the heavily logged compartment this age class is still underrepresented.

The notion of recovery is relative and depends on the ideals and goals of the observer in question. We have estimated recovery times from DBH and basal area estimates of all trees, timber trees, as well as important food trees of certain primate species. By implicitly looking at recovery rates from multiple points of view we hope to gain a better perspective on what recovery times would be optimal for multiple purposes, rather than focus on one particular point of view. For folivorous primate species light logging might prove to be a habitat improvement whereas from the point of view of a frugivorous species it can take as long as 158 years for a heavily logged forest to recover a to pre-logging state. From the point of view of overall DBH measurements our estimates predict that from 74 – 111 years might be needed for recovery to take place (moderately-heavily logged). These estimates are likely to be faster than those of basal area estimates, 95-112 years, due to the fact that cumulative DBH is independent of tree size; whereas basal area estimates take tree size into account. Our results follow other long-term plot studies in our region, Fashing et al. (2004) and Plumptre (1996), which have suggested that 60-80 years might not be sufficient time for forest recovery to take place. In terms of re-logging potential of the compartments estimates of basal area shows that in the lightly logged compartment there remains some large stems. Growth in cumulative DBH shows high levels of recruitment in the moderately logged forest, suggesting recovery. Whereas, in the case of the heavily logged compartment, low levels of basal area and cumulative DBH suggests that a comparatively longer recovery time will be needed.

We considered the rates of recovery we obtained based on DBH and basal area measurements to be relatively optimistic estimates of recovery. The establishment of a community of late successional species is likely to take much longer, perhaps 100s-1000s of years (Finegan 1996; Liebsch et al. 2008; Chapman et al. 2010a). Examining the species composition and change of the top ten species for each compartment over time gives us some indication of how recovery has progressed in the last 17 years, in terms of community composition. However to make specific predictions of recovery times in terms of species compositions has proven difficult (Chazdon et al. 2007), leading to uncertain results. Still, we can see that in the lightly logged compartment early successional species have consistently decreased in importance over time, indicating that it is at a later stage in succession than the heavily or moderately logged compartments.

It is thought that there are numerous ecological factors that become important in determining the speed of recovery of forest stands, and that the severity of the disturbance on the forest plays a major role in determining the magnitude of their effects (Pickett et al. 1987; Chazdon 2003). The specific ecology of this field site and the severity of the disturbance, categorized here, suggests that it is playing a major role in the slow recovery of the heavily logged compartment. This example of recovery in a tropical forest is likely generalizable to other areas with similar ecological compositions within East-Africa: lack of any aggressive colonizing tree species, presence of aggressive shrubs which are a source of food for elephants, and the presence of an elephant population. It is also possible that this cycle, which is triggered above some level of logging and delays recovery of forests, could also be exasperated by other animals which perform a similar role as elephants. Such as bush pigs (*Potomachaerus larvatus*), who are apparently using these cleared areas intensively (C.A. Chapman and R. Reyna-Hurtado unpublished data).

The knowledge of forest recovery time and the factors affecting it can be useful for conservation management in these areas. The example at Kibale, of an unfavorable successional pathway, stresses the importance of knowing the local forest composition, both in terms of its fauna and flora, before deciding on possible harvesting targets or assessing recovery after disturbances; there is clearly no one set rule which can be applied to the rates of regeneration after logging. Here we demonstrate that recovery time can be different depending on the wildlife species or tree species that is considered. In the case of primates it seems that frugivorous species are the most affected when a forest was logged, their food resources showing the slowest rate of recovery. We need to consider this when planning logging activities for an area that may have endangered frugivorous species within its wildlife community. More specific studies are needed to determine the effects on other species, such as pollen and nectar feedings species, as well as granivores.

3. Analysing small scale aggregation in animal visits in space and time: the ST-BBD method

Citation: Tyler R. Bonnell, P. Dutilleul, C.A. Chapman, R. Reyna-Hurtado, R. Sengupta, and U. Sarabia. (2013). "Analyzing small-scale aggregation in animal visits in space and time: the ST-BBD method." Animal Behaviour. 85 (2), pp. 483-492.

Linking statement:

Landscape characteristics influence the movement and grouping patterns of animal populations. In the previous chapter I examined the variability of forest structure (e.g., DBH, basal area, stem density) and food resources (e.g., folivore, frugivore) for primate populations living in Kibale National Park, Uganda. To better understand how these landscape level variables influence movement behaviour of red colobus, I developed a new metric measuring habitat-use from movement data. I was particularly interested in capturing re-use of certain patches of intense use on the landscape (hot spots), which required the method to be spatially-explicit and have a temporal component. The use of hot spots, or intensity to which the habitat patches are visited, is thought to be an important behaviour in the transmission of parasites with an immobile life stage external to the host. We wanted to develop a method to quantify this behaviour from collected movement data, and to be able to compare estimates of habitat use in an objective way, e.g., comparing the intensity of visits on a landscape between different times of year, or between different species, and make inferences about the disease related implications. We were also interested in identifying where on the landscape these areas of high use (or re-use) occur, to gain a better understanding of how the structure and variability of resources on the landscape influence habitat use. In developing a measure to accomplish this, we made use of an existing approach to quantify the level of aggregation in space, and extend it to space and time. In this chapter, I introduce and use our novel spatio-temporal statistical measure (ST-BBD) to quantify the aggregation in site visits across a home range for three primate species. This chapter was published in the journal of Animal Behaviour in 2013.

Summary: Movement behaviour plays an important role in many ecological interactions. As animals move through the environment, they generate movement patterns, which are a combined result of landscape characteristics and species-specific behaviour. Measuring these ranging patterns is being facilitated by technological advances in collection methods, such as GPS collars, that are capturing movement on finer spatial and temporal scales. We propose the use of a novel spatio-temporal analytical framework (ST-BBD), based on the beta-binomial distribution (BBD) model, to measure small-scale aggregation in animal movement datasets, including two simulated and three collected primate datasets. We use this approach to distinguish different habitat uses of 3 primate species and quantify their specific use of the landscape in space and in time, using a parameter of the BBD which measures the variation in sites visited on a landscape. We found that estimates of aggregation in habitat use were higher in the frugivorous spider monkey, compared to the more folivorous howler monkey, and that in the red colobus, aggregation in site visits was dependent on group size and food availability. Applications of this framework to animal movement data could be useful in understanding ecological systems where habitat use is an important factor, such as the relationships between hosts and parasites, or parent plants and seed dispersers.

3.1. Introduction

Movement is a vital process for many animals, affecting a broad spectrum of ecological processes and patterns observed in nature (Nathan et al. 2008). The study of animal movement behaviour has led to much insight into such fields as foraging ecology (Orians & Pearson 1986; Humphries et al. 2010), wildlife management (Chetkiewicz et al. 2006), plant seed dispersal (Vellend et al. 2003), and disease dynamics (Bartel et al. 2011).

With technological advances providing the increasing availability of high-resolution animal movement data, both in time and in space, there is a need to advance methodologies for analysing movement data. Movement is a spatio-temporal process in which an animal moves over a heterogeneous landscape through time. Thus, states and conditions of both the animal in question and the landscape are continuously changing. Different methods have been developed to measure movement characteristics, each capturing some aspect of movement. These different measurements can be separated depending on whether the focus is on space, time, or space and time.

One main branch of spatial approaches focuses on point pattern analysis, where movement data are treated as (x, y) locations measured in a 2-D space (e.g., home range; Millspaugh et al. 2004). These methods search for patterns, or structure, in the distribution of points, which can provide insight into the behavioural ecology of the study species. Another, more complete approach is followed when a temporal component is added to points, tying them together by the sequence in which they were measured. This approach is characterized by the measurement of "between-step characteristics" (e.g., step length or angle) at similar time periods. In analysing between-step measurements, the results are often compared to theoretical distributions as a means of interpretation, such as the Lévy walk, random walk, or correlated-random walk (Viswanathan et al. 1996; Edwards et al. 2007; Humphries et al. 2010). Methods focusing more specifically on the temporal aspects of the data have made use of time series analysis, in which between-step measures (e.g., distance or turning angle) are examined through time to test for autocorrelation in movement behaviour (Dray et al. 2010). Kernel methods have also been applied, classically to (x, y) locations in 2-D space, to derive the probability of occurrence on a landscape, and has recently been extended to estimate probability of occurrence in space and time (Keating & Cherry 2009).

Using animal movement data, we were interested in developing a measure to characterise an animal's use of habitats; specifically, to measure the spatio-temporal variation in use of sites within a habitat. In examining movement data, or following an animal in the field, it is often apparent that some sites are used more intensely, and more often than others. It is possible that there exists a cyclical pattern of site use, one based on seasons or depletion-replenishment of resources, so that the animal in question follows along similar routes on the landscape, or not. The relevant method should allow the estimation of variation in these patterns of habitat use in space and time, and provide a statistically sound way to test for differences, for example, among comparable species. Existing approaches to examine spatio-temporal variation (e.g., Mantel test and correlograms; see Subsection 3.2) do not capture and compare variation between specific areas and periods, and as a whole are more global than local as opposed to the small-scale focus desired here. Therefore, we have evaluated a new approach that uses the beta-binomial distribution (BBD) in a framework where a spatio-temporal grid is created to measure habitat use. Basically, the space and time in which the animal is moving are broken into space-time cubes in which either presence or absence of passage (i.e., Bernoulli trial) is recorded. Space-time cubes have been introduced as sampling units in the field of time-geography, and have been used to map spatio-temporal data for subsequent analysis (Miller 2005). Subdividing the space-time cubes into cells within sampling units following the BBD opens the door to the quantification of spatio-temporal aggregation at smaller scale.

The BBD was applied by Hughes & Madden (Hughes & Madden 1993) in an epidemiological context for investigating the aggregation of diseased plants on agricultural landscapes. These authors showed that when there is uneven chance of finding an infected plant through the landscape (i.e., it is more likely to find an infected plant near another infected plant), the BBD can be useful in quantifying the spatial aggregation of infection occurrences. In a spatio-temporal context, the BBD has been suggested for use with animal movement data (Dutilleul 2011, Chapter 4). In this approach, Dutilleul (2011) proposes an extension on the framework of Madden& Hughes (1995) that consists in measuring the displacement of a spatial unit (i.e., point) through time and quantifying the aggregation of visited areas in space and time.

The objective of our paper is to evaluate the spatio-temporal version of the BBD framework (ST-BBD hereafter), as a tool to estimate the intensity to which an animal uses its home range. We first apply the ST-BBD framework to primate movement data simulated under two behaviour models. We then apply it to movement data collected for three primate species in the field, and quantify the intensity of habitat use within each species and compare it between species. The three species chosen vary in the degrees of frugivory and folivory: spider monkeys rely heavily on fruit resources (frugivorous), whereas howler monkeys and red colobus typically rely on leaves (folivorous). Foraging for fruits in a tropical forest requires finding the few dispersed trees which produce fruit intermittently. By comparison, when foraging for good quality leaves, trees are thought to be less dispersed, offering food more often than fruit trees. Given the varying distribution of resources, both spatially and temporally, we intend to use the ST-BBD framework to quantify spatio-temporal aggregation accordingly and determine differences in habitat use by these two folivorous and one frugivorous primate species.

3.2. Datasets

3.2.1 Simulated data

We first simulated movement data with an agent-based model (ABM) of primate group foraging, which approximates primate group movement behaviour for use in a spatially-explicit epidemiological study (Bonnell et al. 2010). In general, ABMs define characteristics and behaviours of individual agents (e.g., primates, fish, farmers, companies) within a simulation environment, and allow them to interact to create system-level outcomes (see Hemelrijk 2002; Bryson et al. 2007 for use of ABM in behavioural studies). The ABM here was constructed as a general model, made to fit a wide range of primate group foraging behaviours. In this study, we focus on the effect that a foraging trait called ‘weight of remembered sites’ has on overall movement behaviour. This trait is a key model component that affects each primate’s foraging decision making. In the model, the primate agents use a food site index to assess which site, seen or remembered, is the best site to move towards. This food site index is based on the expected amount of food and the distance to such sites, while the parameter ‘weight of remembered sites’ gives extra weight to sites that are familiar (i.e., remembered) to the primate agent (equation 1).

The food site index value at site (x', y') from site (x, y) is given by

$$I(x',y') = \frac{D((x',y'),(x,y))}{F(x',y') * w} \tag{1}$$

where *D*( ) represents the Euclidean distance between two points, *F*( ) is the primate's evaluation of the amount of food at a given site, and *w* is the weight parameter applied to remembered sites.

When preference for remembered sites is increased, simulated primates tend to use selected sites intensively, visiting familiar sites often, and traveling along similar routes connecting these sites. We will thus refer to this behaviour model as the "routing model", because it creates travel routes. On the other hand, with low preference for remembered sites, groups show non-specific ranging behaviours and no heavy use of a specific area. Accordingly, we will refer to that behaviour model as the "non-routing model".

For each type of model, one simulated group of primates (group size = 72) was made to forage on a 1.5 x 1.5 km landscape for six months. Movement data were recorded for five months, after the first month was discounted to sufficiently initialize the memory of individuals in the simulated group. The position of the simulated group was taken every 30 min during the active hours of the day (07:00-20:00), and recorded as a point (x, y) with a time component (t). The 30-min interval was selected because it is very feasible logistically speaking and is therefore often used in field studies (Chapman et al. 2002), and it is a crude time period to avoid autocorrelation given the distances animals can cover in half an hour (Reyna-Hurtado et al. 2009). With the chosen total duration (5 months) and sampling time interval (30 min), the final set of simulated data was composed of two point patterns, each with 3900 point locations in space-time (Fig. 3-1).

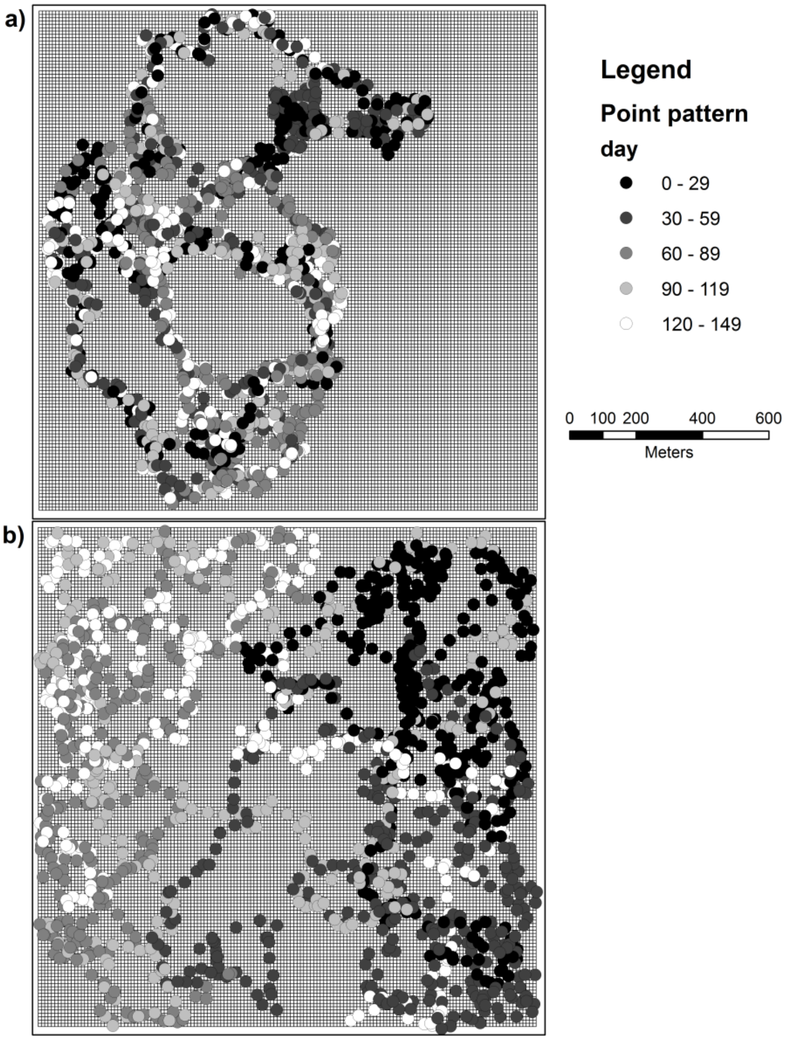

Figure 3-1: Point patterns generated by simulating primate foraging behaviour: a) primate agents with routing behaviour, b) primate agents without routing behaviour. Each simulation, run for 5 months and collecting location every 30 min, created a point pattern of 3900 point locations in space-time.

3.2.2 Collected data

Our second data source consists of GPS points or tracks taken from field measurements of primate group movement. We make use of movement data collected from a highly folivorous primate (red colobus: *Procolobus rufomitratus*), a folivore-frugivore primate (black howler: *Alouatta pigra*), and a highly frugivorous primate (spider monkey: *Ateles geoffroyi*). Red colobus data were collected from August 2006 – June 2010 in Kibale National Park (Uganda), where a group (size 59-104) was followed, and routes were recorded on paper maps showing detailed outlines of a trail system that approximately followed 50 x 50 m squares. There were 363 follows, with an average of 7 h per follow, for 2,564 h of observation in total. A group of black howler monkeys (size 6-8) were followed between January and August 2010 and between May and July 2011 in Calakmul Biosphere Reserve (Mexico), resulting in 214 h of observation with GPS points taken every 15 min. A spider monkey group (size 70-75), which display fusion-fission behaviour and travel almost always in smaller subgroups typically of 2 to 10 individuals, was followed between January and August 2010 and between May and July 2011 in Calakmul, that is, during the same periods as the group of black howler monkeys, resulting in 199 h of follows with GPS points taken every 5 min.

To standardize data collected with different methodologies, each recorded follow was transformed into route data, representing the path the group took. Groups were assumed to travel in a straight line between sampling periods (30 min for simulated primates; 15 min for howler monkey; 5 min for spider monkey; and n/a for red colobus), and re-sampled at 10-meter intervals.

3.3. Methods

3.3.1. The beta-binomial distribution

The BBD is discrete and quantitative in nature, and has been applied to describe spatial, temporal, and spatio-temporal point patterns with a binary mark (Madden & Hughes 1995; Shah et al. 2002; Dutilleul 2011). This distribution applies to counts of ‘successes’ (x) among a number of ‘trials’ (n) per sampling unit. It thus has three parameters: n, the number of trials per sampling unit; p, the expected probability of success in the absence of aggregation; and θ, which measures the variation in the probability of success between sampling units resulting from aggregation and following the beta function (Skellam 1948). Accordingly, θ is the aggregation index parameter (Griffiths 1973; Madden & Hughes 1995). The probability function of the BBD is given by:

$$P(X=x)=\frac{n!}{x!(n-x)!}\frac{\prod_{i=1}^{x}(p+(i-1)\theta)\prod_{i=1}^{n-x}(1-p+(i-1)\theta)}{\prod_{i=1}^{n}(1+(i-1)\theta)}\ \mathit{for}\ x=0,1,2,...,n \qquad (2)$$

where ! denotes the factorial function; Π is the multiplication operator; P($X = x$) is the probability of x successes occurring in n trials. The mean and variance parameters of the BBD are np and $np(1 - p)(1 + n\theta)(1 + \theta)^{-1}$, respectively (Madden & Hughes 1995). In the context of the application of the BBD to analyse movement data, sampling units can be seen as N quadrats of equal area, into which the landscape is first divided and where movement is being observed. Each of the quadrats is then subdivided into n cells of equal area. A cell that has been visited at least once by an animal is considered as "visited", and x represents the number of such cells (x = 0, 1, 2, …, n) (Fig. 3-2). Thus, the landscape is divided into quadrats where the probability of success (i.e., chance of being visited) may be higher or lower depending on the quadrat. The magnitude of this variation in visit frequency is measured by θ, which can also be used as an aggregation index in the analysis of habitat use. This measure of aggregation does not capture the spatial relationships between quadrat counts, but captures the variability in the counts themselves (i.e., how variable are visits on the landscape, and is the variation greater than expected if there were no aggregation?).

The addition of a temporal component to this approach was first suggested by Dutilleul (2011, Chapter 4), and consists in further subdividing the dataset into equal time units (e.g., days, months, years), making each quadrat a space-time cube. It follows that the number of quadrats (N) remains the same, but the total number of cells is equal to the number of cells within a quadrat multiplied by the number of temporal divisions. Accordingly, the point pattern can be analysed temporally, by counting the number of visits per time period (i.e., visits in month 1 are counted on the first layer of cells, visits in month 2 in the second layer, etc.; Fig. 3-2).

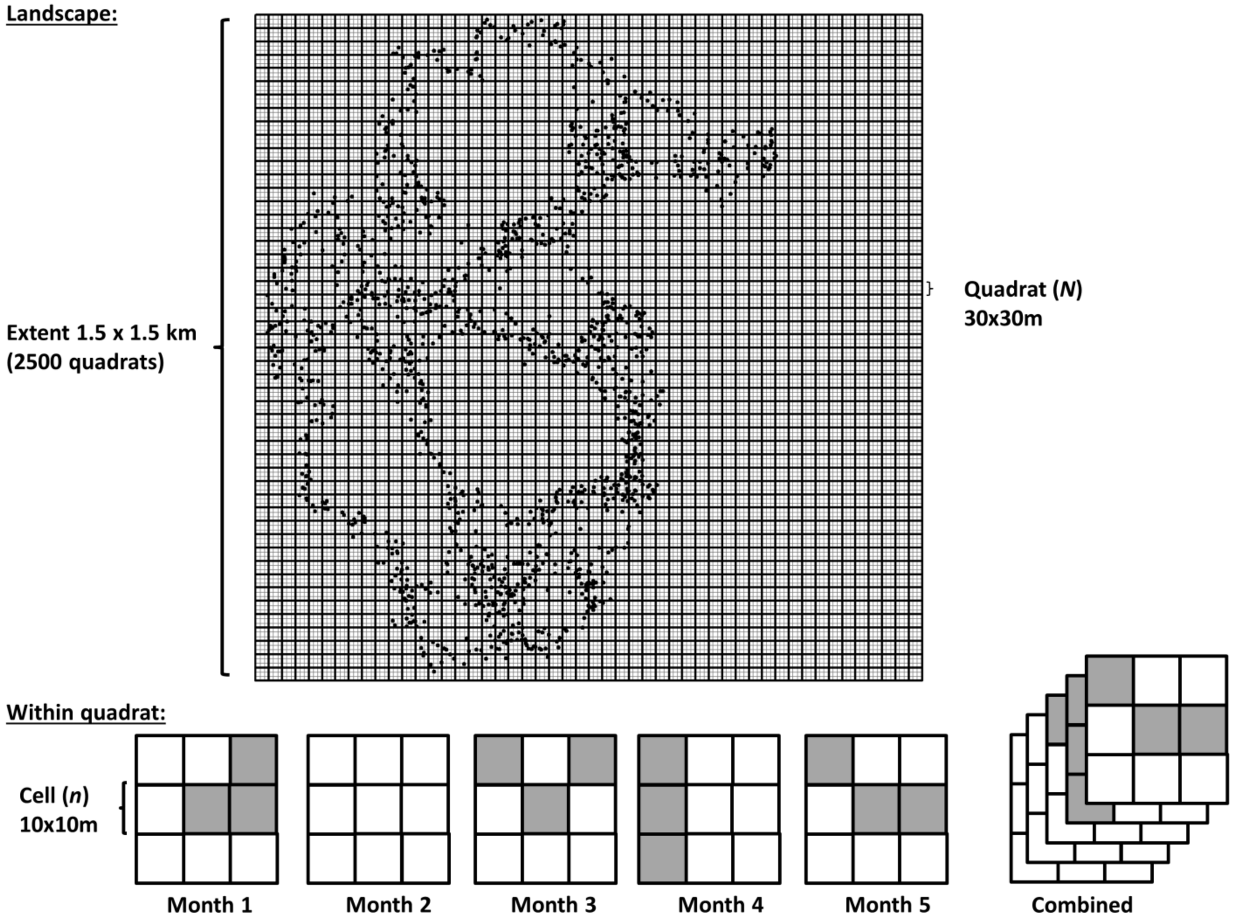

Figure 3.2: Diagram of the ST-BBD framework. In this example, the landscape is first subdivided into equal-sized quadrats ($N = 2500$, 30 x 30 m), quadrats are then subdivided into cells ($n = 9$, 10 x 10 m), and time is divided into equal units (1 month). Within each quadrat, the cells visited during each time period are combined to provide the final visit count per quadrat.

3.3.2. Variability and autocorrelation in animal visits of a landscape

The variance parameter of a beta-binomial distribution is calculated differently than for a binomial distribution because the calculation of the former does not assume that the 'trials' are independent (i.e., an animal's visits of cells within a quadrat can be correlated). If Y_i denotes the Bernoulli distribution (visit/no visit) for cell $i = 1, \ldots, n$ in a given quadrat, X denotes the number of cells visited within the quadrat and X follows a BBD, then

$$Var(X) = Var(\sum_{i=1}^{n} Y_i) + 2\sum_{i=1}^{n}\sum_{j=i+1}^{n} Cov(Y_i, Y_j) = np(1-p)\frac{(1+n\theta)}{(1+\theta)} \quad (3)$$

After isolating the covariances and standardizing them into correlations, it becomes clear that the autocorrelation within a quadrat, through the correlations between visits and no-visits of cells, is a function of n and θ:

$$2\sum_{i=1}^{n}\sum_{j=i+1}^{n} Corr(Y_i, Y_j) = \frac{(1+\theta)}{(1+n\theta)} - 1 \quad (4)$$

Accordingly, θ can be said to be a measure of the autocorrelation of animal movement within quadrats, and as the variability in quadrat counts grows, so too will the autocorrelation between cell visits within quadrats. If n remains constant in the proposed spatio-temporal framework, the parameter θ can thus be used to answer the question: If a primate has visited a quadrat before, is it more likely to visit it again?

Another approach, based on the so-called "Mantel correlograms", has been proposed to characterise autocorrelation in animal movement datasets (Cushman et al. 2005); the Mantel correlogram was originally derived by Oden & Sokal (1986) and Sokal (1986) from Mantel's (1967) test statistic. Whereas the Mantel test statistic essentially is a correlation coefficient between spatial distances and corresponding temporal distances (e.g., times taken during travels), the hypotheses tested in the analysis of Mantel correlograms concern differences in mean time traveled among a certain number of spatial distance classes (Dutilleul et al. 2000). This approach has been used to assess how reliant the current movement is on past movements (Cushman et al. 2005). The ST-BBD method proposed here and the Mantel correlograms measure autocorrelation in two different aspects of the same phenomenon: habitat use (ST-BBD) vs. movement patterns (Mantel correlograms). Given the application or question of interest, it would be important to know which type of autocorrelation it would be better to measure. To highlight the differences in the two approaches, consider an example in which the results would be drastically different. If animals traveled in paths that are similar to previous paths, but are shifted in space, this would result in a significant result in the Mantel test (relationship between distances in space and time), whereas in the ST-BBD approach, since paths do not pass over the same area, it would measure no small-scale aggregation (habitat use).

Variograms and spatial correlograms based on Moran's *I* and Geary's *c* statistics (instead of Mantel's test statistic) can be used to analyse and quantify autocorrelation among quadrats, using the number of cells per quadrat visited by animals as raw data or quadrat counts (Madden &

Hughes 1995; Dutilleul 2011, chapter 5). This is likely to be an important factor to consider when addressing questions related to the definition of quadrat size and how the probability of quadrat visit varies with landscape properties; see below.

3.3.3. Implementation of the spatio-temporal BBD framework

To create the ST-BBD framework, a program was written in the Java programing language with GeoTools (geotools.org), in which the movement data (e.g., route data) and grid characteristics (i.e., number of quadrats, quadrat and cell sizes, temporal division) are the inputs. The program uses the scale inputs provided by the user to generate a spatio-temporal sampling framework, and outputs the number of cells visited in each quadrat. The analysis of the quadrat counts was then performed with the SAS Version 9.2 software, using a code graciously provided by Dr. L. V. Madden, as well as in the R programing language. The SAS code calls the procedure NLMIXED to fit the BBD to the count data of visits per quadrat, where the estimation of p and θ is performed by maximum likelihood. The Bayesian Information Criterion (BIC), a measure of the goodness-of-fit of a model that incorporates a relevant penalty for the number of parameters (Schwarz 1978), was used to determine if the BBD was more appropriate than the binomial distribution. When this was found to be the case, it meant there was sufficient aggregation in the movement data to warrant the use of the BBD.

3.3.4. Analyses

We first evaluated the ST-BBD framework by applying it to the simulated data, using a time scale of 30 days and a spatial grid of 50 x 50 quadrats (30 x 30 m each), with 3 x 3 cells (10 x 10 m each). The simulated data are controlled in terms of sampling regimes, and include very different movement behaviours, offering ideal datasets to explore the use of the new framework.

We then applied the ST-BBD framework to estimate the levels of aggregation in monthly movement data from the three primate species individually, to analyse within-species variation. To control for differences in sampling effort between months, monthly movement patterns were first produced from 5 follows within each month. Movement patterns were then sampled using a minimum bounding grid, with 30 x 30 m quadrats subdivided into nine 10 x 10 m cells, to obtain visit counts per quadrat for the red colobus and the howler monkey (ranges of spatial autocorrelation in counts: RC, 51 m; HM, 47 m); the spider monkey was sampled with 60 x 60 m quadrats subdivided into 36 10 x 10 m cells (range of spatial autocorrelation in counts: SM, 80 m). For the red colobus, we estimated monthly aggregation within 3-month periods. For the howler and spider monkeys, monthly aggregation was estimated within 2-month periods due to smaller samples sizes.

To compare levels of habitat use between species, sampling effort was controlled by re-sampling species data to equal observation times. Given the limited data available for the spider and howler monkeys (February – April, June and July), a time span covering 5 months was chosen. A sub-sample was taken from each primate species, resulting in an average of 176 h of follows for each primate (howler monkey: 174 h, spider monkey: 177 h, red colobus: 178 h). A minimum bounding grid of 25 x 25 quadrats (60 x 60 m), with 6 x 6 cells (10 x 10 m), was used to obtain spatial and temporal counts for each species (Fig. 3-2).

Comparisons between θ estimates, obtained by maximum likelihood, are based on 95% confidence intervals, assuming estimates are normally distributed (i.e., an asymptotic property of maximum likelihood estimators).

3.4. Results

3.4.1. Simulated data

Movement data generated with the routing model produced quadrat counts in which a few quadrats had a high number of visits and many quadrats had zero visits (Fig. 3-3). Comparatively, movement data generated with the non-routing model produced more quadrats with low numbers of visits and less quadrats with high numbers of visits, but fewer quadrats with no visits (Fig. 3-3).

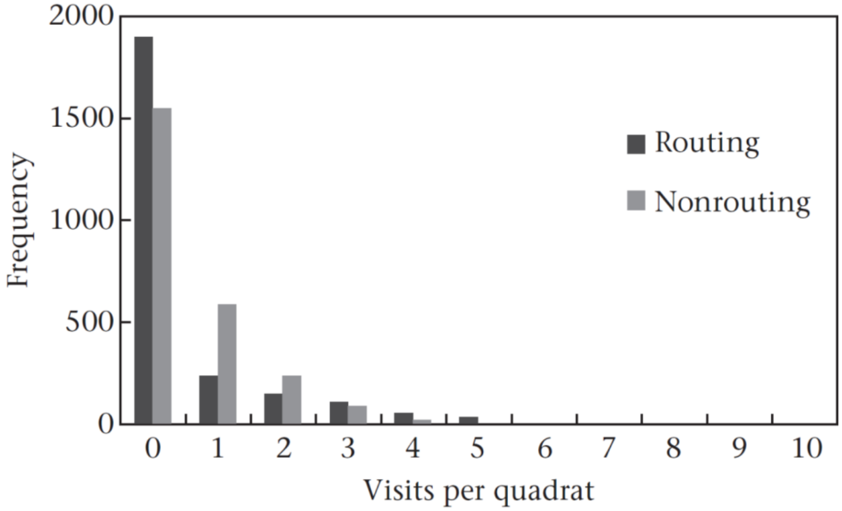

Figure 3-3: Histograms of the number of visits within quadrats for the simulated data, obtained with the routing vs. non-routing model. A count of visits for each quadrat was done each month (*n* = 9 cells), then all 5 months were combined for the final quadrat count presented in this figure (*n* = 45 cells).

When fitting the BBD to quadrat counts, we found that the BBD consistently fitted better than the binomial distribution, indicating aggregation in the data (i.e., the probability of visit was uneven throughout the landscape; Table 3-1). This difference was less striking, though, in the data simulated with the non-routing model (Table 3-1). At the scale of one month, when considering movement patterns for each month separately (purely spatial analysis), there was no consistent trend in the aggregation index estimates from the two simulated movement datasets (Fig. 3-4). When considering all five months together (spatio-temporal analysis), the difference between the two estimated measures of aggregation was statistically significant (Fig. 3-4), the estimate dropping in the case of the non-routing model (88% lower) compared to the routing model (10% lower); this results clearly reflects the amount of overlap between months in the latter case.

Table 3-1**:** Estimates of the index of aggregation parameter (θ) for the data simulated using two different behaviour models: considering individual months and combined months (All). The Bayesian information criterion (BIC) is presented for the fitted beta-binomial and binomial distributions; lower scores imply a better fit.

a) Non-routing behaviour model

Month	Binomial	Beta-binomial	Theta	Lower	Upper	Mean
	BIC	BIC	θ	95% CI	95% CI	n*p
1st	2224.3	2043.9	0.085	0.058	0.111	0.137
2nd	2081.4	2014.6	0.042	0.026	0.059	0.130
3rd	1858.8	1750.4	0.063	0.040	0.086	0.108
4th	1798.7	1764.5	0.031	0.016	0.046	0.107
5th	2001.7	1911.8	0.052	0.032	0.071	0.121
All	5524.2	5321.7	0.012	0.010	0.015	0.603

b) Routing behaviour model

Month	Binomial	Beta-binomial	Theta	Lower	Upper	Mean
	BIC	BIC	θ	95% CI	95% CI	$n*p$
1st	1891.9	1786.2	0.061	0.038	0.083	0.111
2nd	2066.6	1934	0.067	0.044	0.090	0.125
3rd	1912.6	1734.4	0.092	0.062	0.123	0.110
4th	1819.2	1750.8	0.046	0.027	0.065	0.107
5th	1780.5	1729.7	0.039	0.022	0.056	0.104
All	6080.2	4737.9	0.055	0.046	0.064	0.554

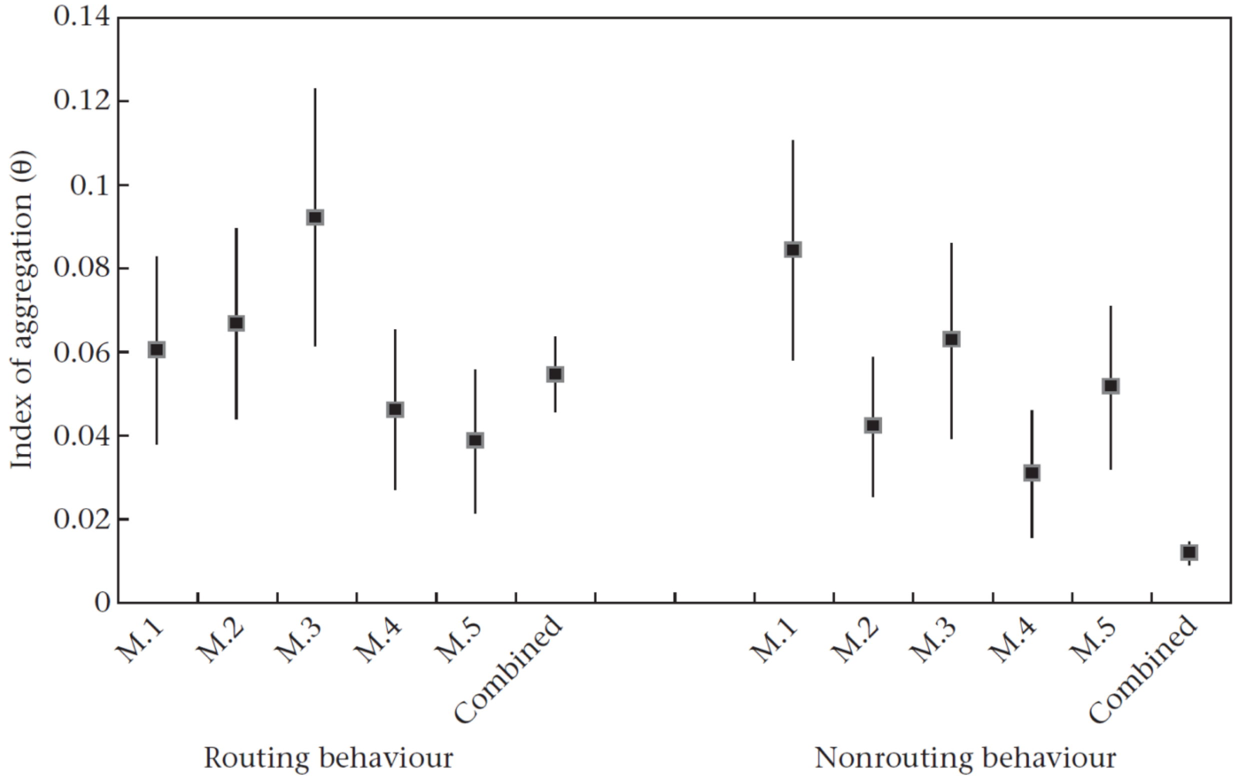

Figure 3-4: Aggregation index estimates for each month ($n = 9$, $N = 2500$) and for all 5 months combined ($n = 45$, $N = 2500$), for both types of simulated movement behaviour. The bars represent 95% confidence intervals.

3.4.2. Collected data

To obtain visit counts per quadrat, the movement patterns of the three primate species were sampled for an appropriate quadrat size taking into account differences in spatial autocorrelation and field extent (Fig. 3-5).

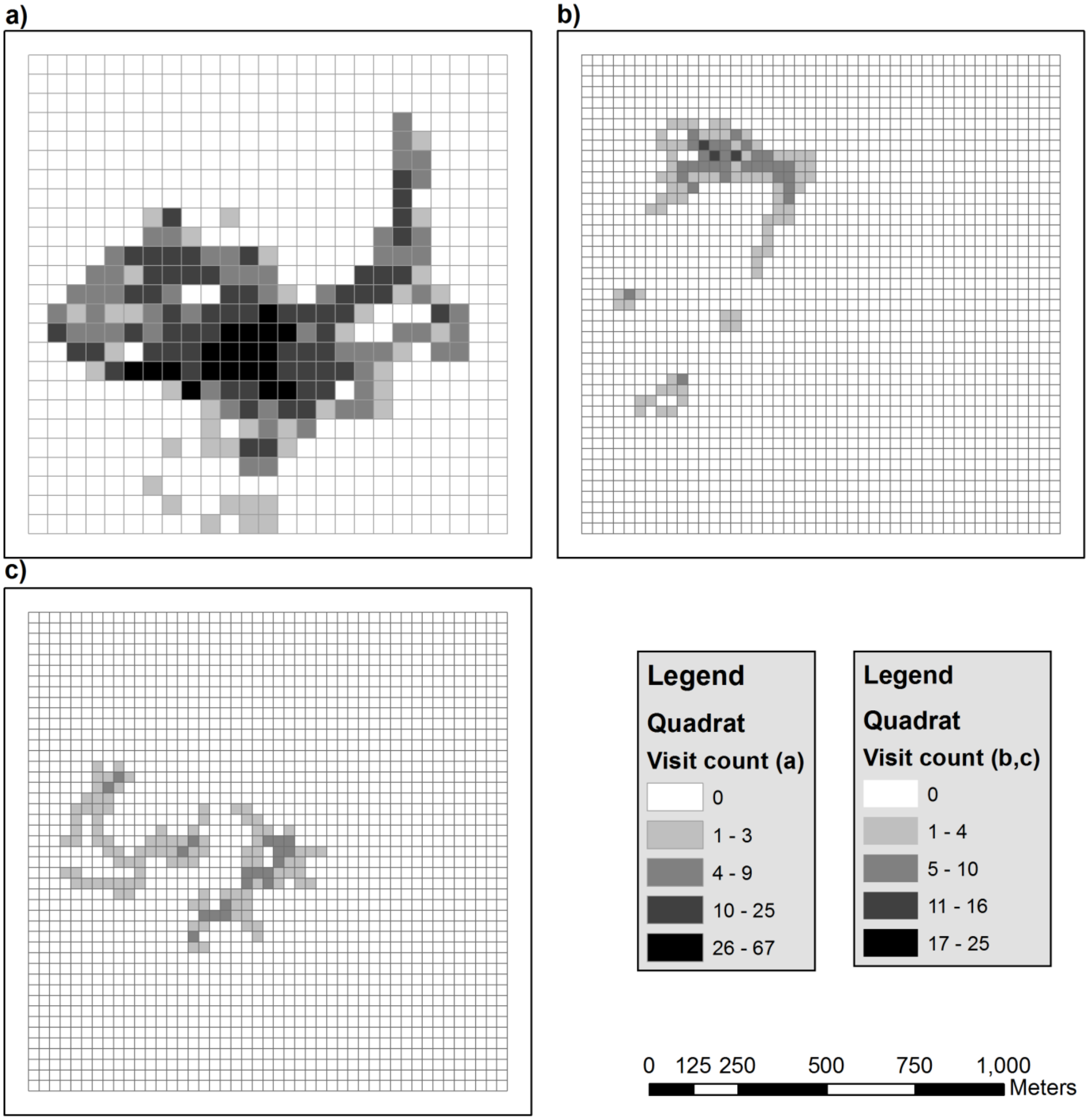

Figure 3-5: Movement patterns of three primate species: a) spider monkey, b) red colobus, and c) howler monkey. The spider monkey sample grid is composed of 25 x 25 quadrats (N=625, 60 x 60m). The red colobus and howler monkeys sample grid is composed of 45 x 45 quadrats (*N*=2500, 30 x 30 m). Quadrats are shaded based on the number of visited 10 x 10 m cells (a: n = 1296; b & c: *n* = 45); quadrats were resampled every month during a 5-month period.

Monthly estimates of the visit aggregation index for the red colobus were made for all the months with more than 5 follows per month (35 months in total; Fig. 3-6a). Estimates were then computed over 3-month periods, capturing habitat re-use by the red colobus between months (Fig. 3-6b). This revealed large fluctuations in aggregation over time, with a peak of index estimates in August – February 2008 (Fig. 3-6b). The estimated aggregation index for all months combined, capturing habitat re-use over the 35 months, was 0.076, that is, 63% lower than the mean (0.204) of estimates over 3-month periods. Sampling effort was not found to be significantly correlated with movement aggregation index estimates (Spearman's rank-based coefficient = 0.32, $P = 0.07$).

Spider monkey movement data showed significantly higher levels of aggregation during the dry season (March – April) than during the wet season (July - Aug) (95% CI for the difference between 2-month means: March – April and July - Aug [0.058, 0.358]). The aggregation index estimated by using all months was 0.12, that is, 543% lower than the mean (0.27) of 2-month estimates (Fig. 3-6c). Sampling effort was not found to correlate with movement aggregation index estimates (Spearman's rank-based coefficient = 0.50, $P = 0.45$).

Howler monkey movement data showed no significant difference in aggregation between months, February vs. March and March vs. April (Fig. 3-6d). The month of April had a total of 36 h, compared to 37 h in March and 40 h in February. The overall estimate of aggregation was 0.23, that is, 22% lower than the mean (0.29) of 2-month estimates.

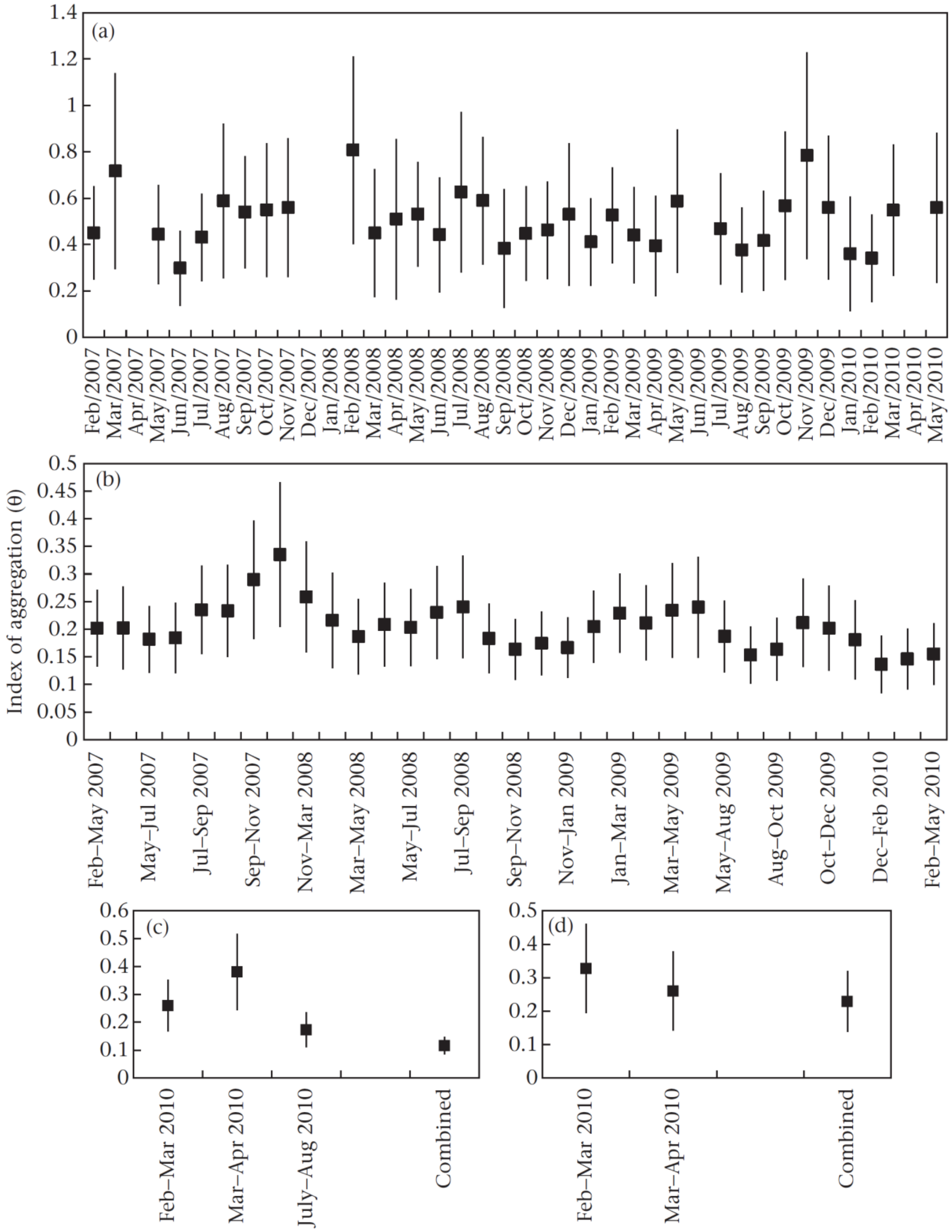

Figure 3-6: Index of aggregation for monthly movement patterns of the red colobus, spider, and howler monkeys. Aggregation index estimates for the red colobus are presented: (a) for each month (purely spatial approach), and (b) for 3-month periods (spatio-temporal approach). Aggregation of movement (c) for the spider monkey and (d) for the howler monkey are estimated over 2-month periods (spatio-temporal approach). The ‘combined’ value is an estimate over all months. The bars represent 95 % confidence intervals for the true but unknown aggregation index values.

In between-species comparisons, movement aggregation of the spider monkey (mean index value: 0.192) differed from that of the howler monkey (mean: 0.107) (Table 3-2). The red colobus falls in-between, with a mean aggregation index value of 0.157) (Table 3-2). Again, raising the temporal scale to 5 months (as with the simulated data, see Fig. 3-4), the aggregation index estimates dropped compared to the average of individual monthly estimates for all three species (red colobus 45%, spider monkey 38%, and howler monkey 33%).

Table 3-2: Estimates of the index of aggregation (θ) for the three primate species. Theta estimates based on 5-month movement patterns are given, together with their 95% confidence intervals. In all cases, the beta-binomial distribution provided a better fit than the binomial distribution based on BIC.

Time scale	Primate	θ Estimate	Lower CI	Upper CI	Mean or difference of means
5 months					
	Spider Monkey	0.192	0.137	0.246	0.018
	Howler Monkey	0.107	0.049	0.166	0.003
	Red Colobus	0.157	0.063	0.252	0.003
Differences					
	Spider - Howler	0.085	0.005	0.164	0.015
	Spider - Red colobus	0.035	-0.075	0.143	0.015
	Red colobus - Howler	0.050	-0.061	0.161	<0.000

3.5. Discussion

Within the ST-BBD framework, movement behaviour which frequently re-uses specific areas results in higher variation in the probability of visits on the landscape. Movement behaviour which does not re-use the same areas results in lower values and variability of the probability of visits on the landscape. Using the BBD parameter θ, alias 'aggregation index', as a measure of this variability, we were able to quantify differences in habitat use and assess their significance.

The differences in movement behaviour between the routing and non-routing models were successfully distinguished as a result of the spatio-temporal nature of the ST-BBD. By breaking up space into space-time cubes, movement patterns which overlapped in the same quadrat at different times were captured. In contrast, the purely spatial approach, in which no temporal component was considered, did not reveal important differences between models. This was shown with simulated data, by comparing monthly estimates of θ with 'combined' estimates obtained over 5 months (Fig. 3-4).

The spatio-temporal approach, which incorporates an overlap of months, was useful in distinguishing movement behaviours within each primate species (Fig. 3-5). In the case of the red colobus, it allowed the detection of significant fluctuations through time, a peak in aggregation centered on August 2007 – February 2008, and a slight decrease overall in the aggregation of movement patterns on a monthly basis, suggesting a decrease in revisits to similar sites between months over a long period (Fig. 3-6b). Spider monkeys showed a significantly higher level of aggregation during the dry season. This could be a consequence of the high use of a single tree species (*Ficus spp*) during the dry season, whereas fruit resources in the wet season are generally highly available due to the mast fructification of another highly preferred species (*Brosimum alicastrum*; Sarabia-Hernandez unpublished data). Similar significant variation was not found within the howler monkey movement patterns (Fig. 3-6d).

Comparisons between the three species showed that spider monkeys had the highest movement aggregation (Table 3-2). Overall, the distance traveled was larger for the spider monkey, with ~34.8 km during the 177-h sub-sample, compared to ~5.3 km for the howler monkey and ~4.5 km for the red colobus. Such inter-specific differences are likely partially induced by the more dispersed food sources for frugivorous primates. The spider monkey movement patterns suggest the heavy use of a central area (sleeping sites), with forays to the periphery, suggesting a central foraging strategy (Chapman 1988). The fact that spider monkeys started at, and often returned to, a few main sleeping areas each night resulted in a few quadrats with higher numbers of visits. Routing behaviour is evident in the movement from and to these central areas (Fig. 3-5). Also, fruits are distributed in a patchier way than leaves, and visits of fruit patches could influence the level of aggregation in spider monkey movement data, compared to the other two species which are more folivorous. Howler monkeys moved more slowly through the landscape and revisited sites less often. Aggregation index estimates for the red colobus showed higher variability within a month and through the standard error of the combined estimate, with no significant difference with the spider and howler monkeys, though.

The amount of data that we have collected for the red colobus allowed the exploration of habitat use over a longer temporal extent than for the howler and spider monkeys, in search of possible explanations for the observed variability in movement aggregation. The observed red colobus group has gone through substantial size changes, from an initial group of ~59 in July 2006 to ~104 in September 2011. Along with this increase in group size over time, we observed a global decreasing trend in the aggregation index estimates (Fig. 3-6b). Using a simple linear regression, predicting θ by time since data collection started (31 months) revealed a significant decrease (intercept = 0.248, slope = -0.002, $F = 5.48$, error df = 29, $R^2 = 0.16$, $P = 0.03$). The increasing group size could play a role in this decrease by depleting food sources to a greater spatial extent (i.e., increasing revisit times), or by traveling further due to increased intra-group feeding competition (i.e., selecting new areas). Large oscillations in the estimates of θ are also seen at smaller time scales (Fig. 3-6b), suggesting other influencing factors. The inclusion in the regression of an estimate of food availability, derived from phenology data of tree species in the study area (Chapman et al. 2005a), provides gains in predictive power ($F = 7.3$, error df = 28, adj $R^2 = 0.30$, $P = 0.003$). This measure of food availability was also found to be significantly correlated with estimates of θ once the global decreasing trend was removed (Pearson's sample simple linear correlation coefficient = 0.41, $t = 2.44$, df = 29, $P = 0.02$). This suggests that both group size and food availability could be affecting the re-use of habitat by the group between months, and fits with current theory regarding the group foraging behaviour of the red colobus (Snaith & Chapman 2008).

The temporal and spatial scales chosen to be used in applications of the ST-BBD method have an effect on the aggregation measured. In our study, the analyses of movement data at the spatial scale of 60 x 60 m quadrats and on the time scale of one month revealed higher levels of spatio-temporal aggregation for the spider monkey. However, the categorisation of landscape as visited or non-visited during a month does not permit to determine the type of use of the visited area. An animal simply passing by an area and an animal spending much of the day within a given area would both be considered visiting the site at the time of observation. To capture residency time within patches for primates, temporal scales shorter than a month should be considered, thereby measuring a different type of aggregation and habitat use.

Looking further at effects of spatial and temporal sampling and subsampling units on estimates of θ, we varied quadrat and cell size choices using simulated data (routing and non-routing behaviours) and estimated θ each time. We found that increasing cell size and the total number of quadrats separately produced increased θ estimates; conversely, increasing quadrat size spatially and temporal division separately resulted in decreased θ estimates. These trends make sense when thinking about what θ measures, variability of the probability of visit among quadrats and autocorrelation among cells within a quadrat, and how this variability relates to the within-quadrat spatial-temporal resolution defined by the number of cells within a quadrat for a given quadrat size. If cells are made successively smaller, resulting in more and more cells per quadrat, more detail will be captured in space and time within a quadrat (increased spatial-temporal resolution). Conversely, if spatial-temporal resolution is lowered, there will be less detail in space and time within a quadrat. At the extremes, quadrats would simply be either visited or not visited (lowest spatial-temporal resolution), or there would be an over-detailed gradient in quadrat visits (very high spatial-temporal resolution). Direct comparisons between estimates of θ should therefore be limited to those obtained with the same or similar scale choices (e.g., Table 3-2).

For between-species comparisons of the level of aggregation in visits, the sampling effort would also need to be controlled as much as possible, for example by re-sampling to equal observation times. Within the red colobus species, a minimum of ~60 h of follow time per month was found to be enough to obtain significant aggregation index estimates; this number of hours might be used as a basis for minimum sampling regime in future studies (Fig. 3-7).

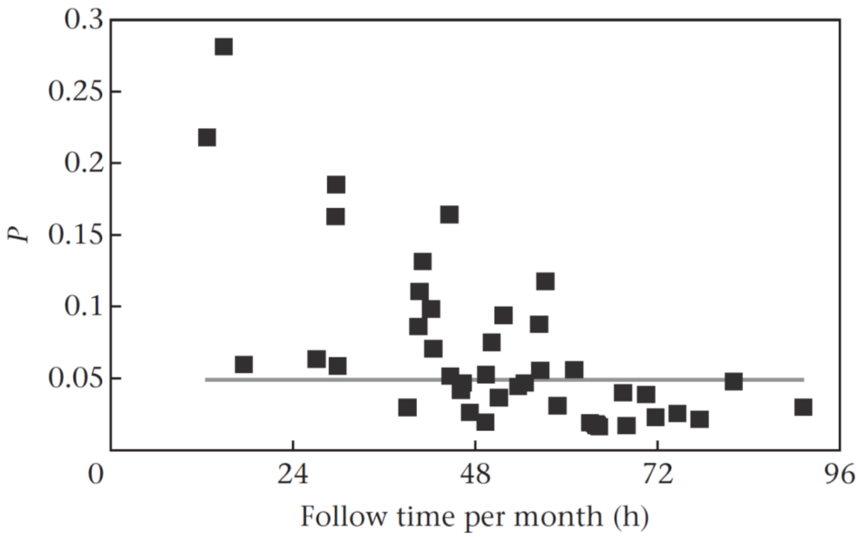

Figure 3-7: Effect of sampling effort (number of hours of follows per month) on the probability of significance of monthly aggregation index estimates. The effect was tested on the red colobus data (total of 46 months). The gray line represents the significance level of 0.05.

Sampling rates of movement could also affect the estimated mean visit count of the BBD, as a group would likely visit more novel areas over time. Madden et al. (1995) have shown that, although there is no mathematical relationship between the estimated mean of the BBD and the θ estimate, they are often related. From the plant disease literature, we would expect that as the mean number of animal visits (or disease incidents in the plant disease literature) increases, estimates of θ would be increasing first and then decreasing, following an upside-down u-shaped relationship. In our sampling conducted in space and time (i.e., using space-time cubes), the number of cells per quadrat (*n*) increases with increasing sampling in time, resulting in shifting values of the mean ($n*p$). The resulting trend in θ estimates obtained from 1, 3 or 6 months of collected data is a decreasing parabolic one, as more sampling time is added. Madden et al. (1995) suggest the use of the Binary Power Law to examine the relationship between the expected mean and the observed variance.

The results of our evaluation of the ST-BBD method clearly support that it can help develop insight into a species' use of its habitats by the estimation of spatial and temporal aggregation in movement data. Furthermore, the corresponding approach could be useful in estimating the effects of varying resource distributions (e.g., seasonal) or landscape structures (e.g., corridors, fragmentation) on habitat use. In the near future, especially relevant applications could examine the landscape effects on host-parasite interactions when movement behaviour and habitat use are important factors, e.g., with gastro-intestinal parasites with a free living stage in the external environment or with tick-borne diseases such as the Lyme disease).

4. Emergent group level navigation: an agent-based evaluation of movement patterns in a folivorous primate

Citation: Bonnell T.R., Campennì M., Chapman C.A., Gogarten J.F., Reyna-Hurtado R.A., Teichroeb J.A., Wasserman M.D., Sengupta R. (2013) Emergent Group Level Navigation: An Agent-Based Evaluation of Movement Patterns in a Folivorous Primate. PLoS ONE 8(10): e78264.

Linking statement:

Observational studies of red colobus, and other herbivorous species, have generated varied hypotheses on how individuals meet energetic and safety requirements, while living in social groups. Individuals in social groups often have to meet these requirements when resources are distributed unevenly in time and space. In this chapter I use a simulation approach to test between various behavioural hypotheses of how individual red colobus accomplish these requirements. In a simulated environment, I reproduce a landscape representative of one confronted by our study group, and introduce red colobus agents with varying sensory capabilities and behavioural responses. By comparing the resulting group level movement patterns of the constructed red colobus agents, it is possible to make inferences about which behavioural assumptions best compare against observed movement (Grimm et al. 2005). Of particular interest was how different assumptions about spatial memory effected foraging patterns of the simulated groups. This chapter examines the movement of one red colobus group in detail, and focuses on developing a behavioural understanding of movement patterns. If the behavioural responses of individual red colobus are better understood, resulting changes in movement from social or ecological alterations can be better estimated. The result of this chapter, a movement model for red colobus groups, was a requirement for the spatially-explicit epidemiological model considered in the last chapter in this dissertation. This chapter provides a crucial link between landscape characteristics and the movement and grouping patterns of the red colobus hosts. Furthermore, the methodology developed in this chapter, combining cognitive, biological, and ecological interactions, provides advancement of a more behavioural understanding of movement patterns in the movement ecology literature. This chapter was published in the Public Library of Science ONE in 2013.

Summary: The foraging activity of many organisms reveal strategic movement patterns, showing efficient use of spatially distributed resources. The underlying mechanisms behind these movement patterns, such as the use of spatial memory, are topics of considerable debate. To augment existing evidence of spatial memory use in primates, we generated movement patterns from simulated primate agents with simple sensory and behavioral capabilities. We developed agents representing various hypotheses of memory use, and compared the movement patterns of simulated groups to those of an observed group of red colobus monkeys (*Procolobus rufomitratus*), testing for: the effects of memory type (Euclidian or landmark based), amount of memory retention, and the effects of social rules in making foraging choices at the scale of the group (independent or leader led). Our results indicate that red colobus movement patterns fit best with simulated groups that have landmark based memory and a follow the leader foraging strategy. Comparisons between simulated agents revealed that social rules had the greatest impact on a group's step length, whereas the type of memory had the highest impact on a group's path tortuosity and cohesion. Using simulation studies as experimental trials to test theories of spatial memory use allows the development of insight into the behavioral mechanisms behind animal movement, developing case-specific results, as well as general results informing how changes to perception and behavior influence movement patterns.

4.1. Introduction

Many species face the need to find resources that vary both spatially and temporally, and observed patterns of movement often suggest complex behavior to face these challenges. The mechanisms and processes driving these movement patterns have been a topic of considerable debate, suggesting mechanisms such as spatial memory, internal time measures, communication, and reliance on conspecifics (Heinrich 1988; Boinski & Garber 2000; Janmaat et al. 2006). These types of questions can, and are being, examined with many different approaches, and largely focus on defining how, why, and where individuals move (Nathan et al. 2008). Simulation models, which attempt to represent individuals, show a promising multidisciplinary approach which can incorporate developments in biology, cognitive science, and ecology in testing movement hypotheses. In representing individuals, biological understanding can inform what sensory and movement capabilities individuals are capable of, whereas developments in cognitive science inform how individuals process this incoming information, and how they choose actions in response to this information (e.g., rule-of-thumb, re-enforced learning) (Prete 2005; Prescott et al. 2007). The inclusion of an ecological understanding further recreates the conditions under which individual movement and foraging occurs (e.g., social hierarchies, predation risk). Agent-based modeling has been used to model movement patterns (Bennett & Tang 2006; Tang & Bennett 2010), and facilitates multi-disciplinary approaches (Axelrod 2006). The agent-based modeling approach has shown success as an experimental tactic, in which competing models of micro-level description are compared against emergent macro-level patterns (Bankes 2002; Bryson et al. 2007). Using this experimental approach and focusing on defining individual perceptions and behaviors, it is possible to effectively test various individual movement hypotheses against real-world observed group movement data.

Primates are good candidates to explore this approach, and test how it can be used in developing and refining behavioral theories of movement. Primates have been the target of numerous field studies, which have convincingly demonstrated that they are capable of remembering food locations (Garber 1989; Byrne 2000; Janson 2007; Janson & Byrne 2007). Various hypotheses have been proposed regarding how primates retain and use information about their landscapes, including the use of Euclidean, landmark, or route based cognitive maps (Byrne 2000; Janson & Byrne 2007). The Euclidean memory hypothesis involves organisms retaining/memorizing the locations of resources so they can calculate distances and angles irrespective of their current surroundings (Poucet 1993; Normand & Boesch 2009), whereas both route and landmark based mechanisms are topological, relying on site association. In this case individuals calculate distance and angles to a subset of remembered sites associated with a familiar site on the landscape (i.e., I am at site A and I know site B is nearby). Both hypotheses have received support (Poucet 1993; Milton 2000; Di Fiore & Suarez 2007); however, testing between them and determining what an animal remembers or how it uses this memory has proven extremely difficult in a field setting (Janson & Byrne 2007). The difficulty of testing such hypotheses in the field has encouraged the development of computer generated models of foraging behavior (Garber & Hannon 1993; Te Boekhorst & Hogeweg 1994; Boyer et al. 2006; Ramos-Fernandez et al. 2006; Sellers et al. 2007; Boyer & Walsh 2010).

To add to existing experimental data, we built simulated primates that are able to perform some actions of a real primate (e.g., move, eat, digest) and sense important characteristics of their surroundings (e.g., food, predation risk, landscape structure, group mates, non-group mates). Once we had defined a primate's capabilities and sensory inputs, we then explored decisions at the individual level. By defining individual level behavior and examining group level movement we were able to validate and compare between behavior models using different assumptions.

We apply this approach to the red colobus monkey (*Procolobus rufomitratus*) where we examined simulated agents (12 types), representing alternative hypotheses, each with varying social interactions, abilities to retain spatial information, and different methods of using this spatial memory (Fig. 4-1). We ran simulated foraging trials of these different primate agents, and described the resulting group level foraging patterns. Comparing the simulated group level patterns to movement field data, we made inferences about what abilities or attributes are most important in reproducing the observed movement patterns.

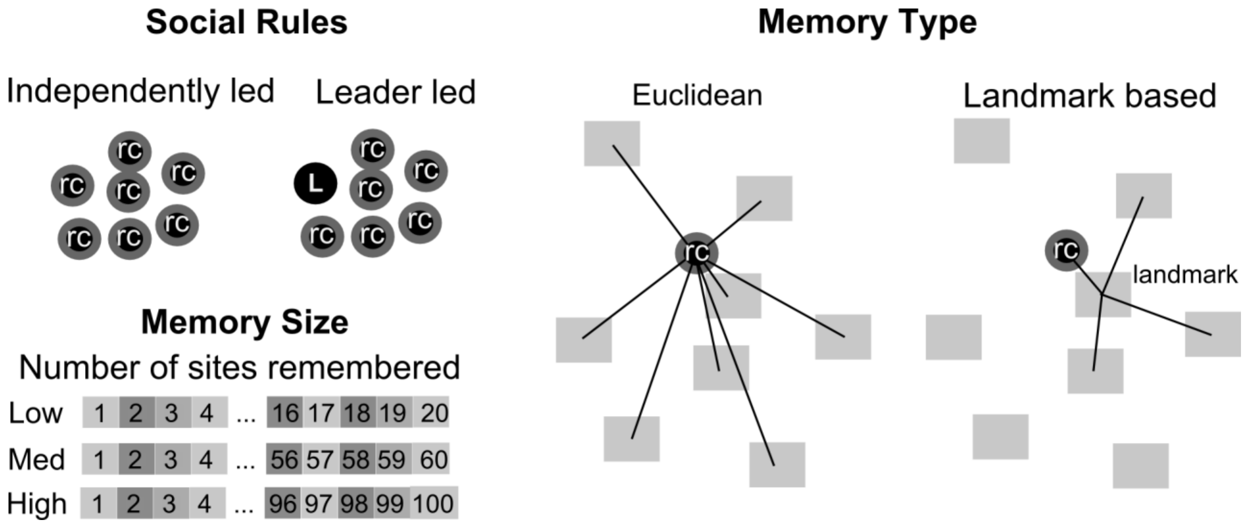

Figure 4-1: Simulated primate agents (dots), each representing a foraging hypothesis examining the effects of group social rules, memory type, and amount of memory on foraging behavior.

4.2. Methods

Movement Data

Long-term data on red colobus movement were collected from August 2006 to June 2010 in Kibale National Park (Uganda). A single study group, that grew from 59 to104 animals, was followed, and movements recorded on detailed (50 * 50 m grid) trail maps. The data set included 363 follows, with an average length of 7 h per follow, for 2,564 h of observation. Between August 2007 to June 2008, GPS points of the center of the group were recorded in addition to map locations and the group was generally followed from 8:00 until 13:00, five days per week, for 1,388 h of observation. Permission to conduct the research in Uganda was given by the National Council for Science and Technology, the Uganda Wildlife Authority, and McGill University Animal Care.

Movement model

Model description follows the ODD (overview, design, details) protocol (Grimm et al. 2010), designed to standardize descriptions of individual- or agent-based models. The model was constructed in Java using Repast Simphony, and is available from: (code.google.com/p/emergent-group-navigation/).

4.2.1. Overview

Purpose

The purpose of the model was to simulate group movement patterns based on various hypotheses of perception and behavioral responses of individual red colobus monkeys.

Entities, state variables, and scales

The model was composed of two types of agents: resources and primates. The model's base was a landscape where resource polygons made up a gridded surface covering an area of 108ha. A scale of 30×30 m was chosen for each cell, as this roughly estimates the average canopy size of the major trees in which a large proportion of primate social groups would feed (Tombak et al. 2012), thus we assume foraging decisions were made at this scale. Each polygon contained state variables, current amount of resources and maximum resource levels. A resource polygon, if reduced by foraging, was able to re-grow at a constant rate ("grow back rate"), until it reached its maximum resource level.

The primate agents foraging on the resource surface are represented as a point in a continuous space, moving among resource polygons. Agents had two state variables; energy level and the desired number of near-by group mates to be considered safe from predation. Each agent also retained a list of remembered sites (i.e., polygons), containing location, and food estimates.

Foraging simulations were run for 6 months, where one time step in the model represented one half-hour and each day was considered to be 13 h (the active period is from 07:00 to 20:00 (Struhsaker 1975)). A time step of 30 minutes was chosen because it was the unit of measurement used in our long-term field observations (Snaith & Chapman 2008).

Process overview and scheduling

Within a time step, each primate agent, the order of which was randomly chosen, responded to internal and external stimulus using a simple behavioral algorithm. The primate agent first made a movement decision: to move towards group mates, a food site, or to simply rest. This movement decision was based on external factors: near-by group mates, visible food sites, as well as internal factors: energy level, desired number of nearby group mates, and remembered food sites (see Submodels: movement-choice, and choose-food-site). Following this movement choice the agent decided whether to try and feed at its given location based on its current energy levels (see Submodels: energetics). Once all primate agents had been processed, the resource polygons performed a re-grow step based on a uniform regrowth parameter, simulating regeneration of food resources (Fig. 4-2).

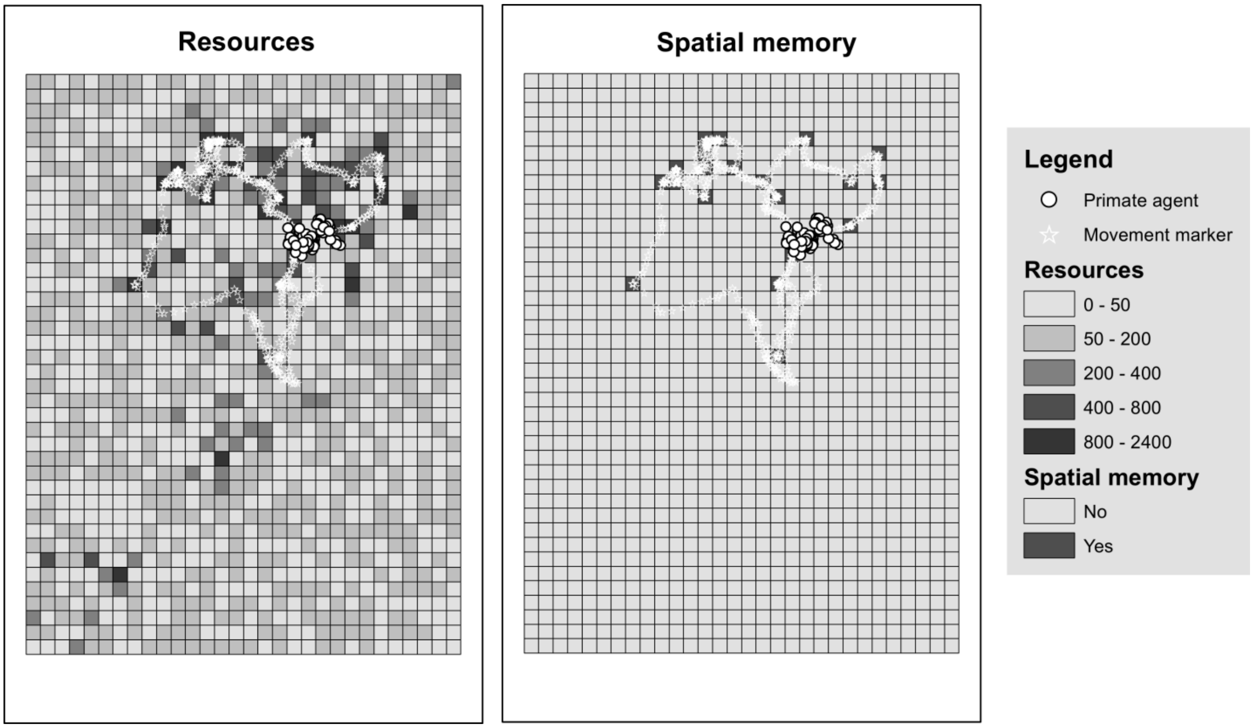

Figure 4-2: Simulation environment representing: primates (dots), recorded group position (stars), resource and memory landscapes (girds).

4.2.2. Design Concepts

Basic principles

Movement patterns were driven by the interaction between the distribution of resources on a landscape and the primate agent's capabilities and behaviors. Agents were made to retain varying numbers of resource sites in memory (low-20, medium-60, high-100), and could recall the distance and direction to all these sites (Euclidean) or a subset of these sites based on a nearby landmark (landmark based). Agents also either considered all their neighbours equally (independently led) or depended on a leader (leader led) when considering their safety. This resulted in 12 different types of agents (e.g., an individual with Euclidean memory and low retention, within a group containing a leader) representing different hypotheses. By comparing the movement patterns of groups, each made up of a single type of the 12 possible agents, insight could be gained as to the individual behavioral processes behind observed group level movement patterns for red colobus monkeys.

Emergence

Group moment patterns emerge from individual primate agents balancing their respective safety and feeding requirements. Given different perceptions and behavioral responses, individual agents made different foraging and safety choices altering the movement patterns of the group (Fig. 4-3).

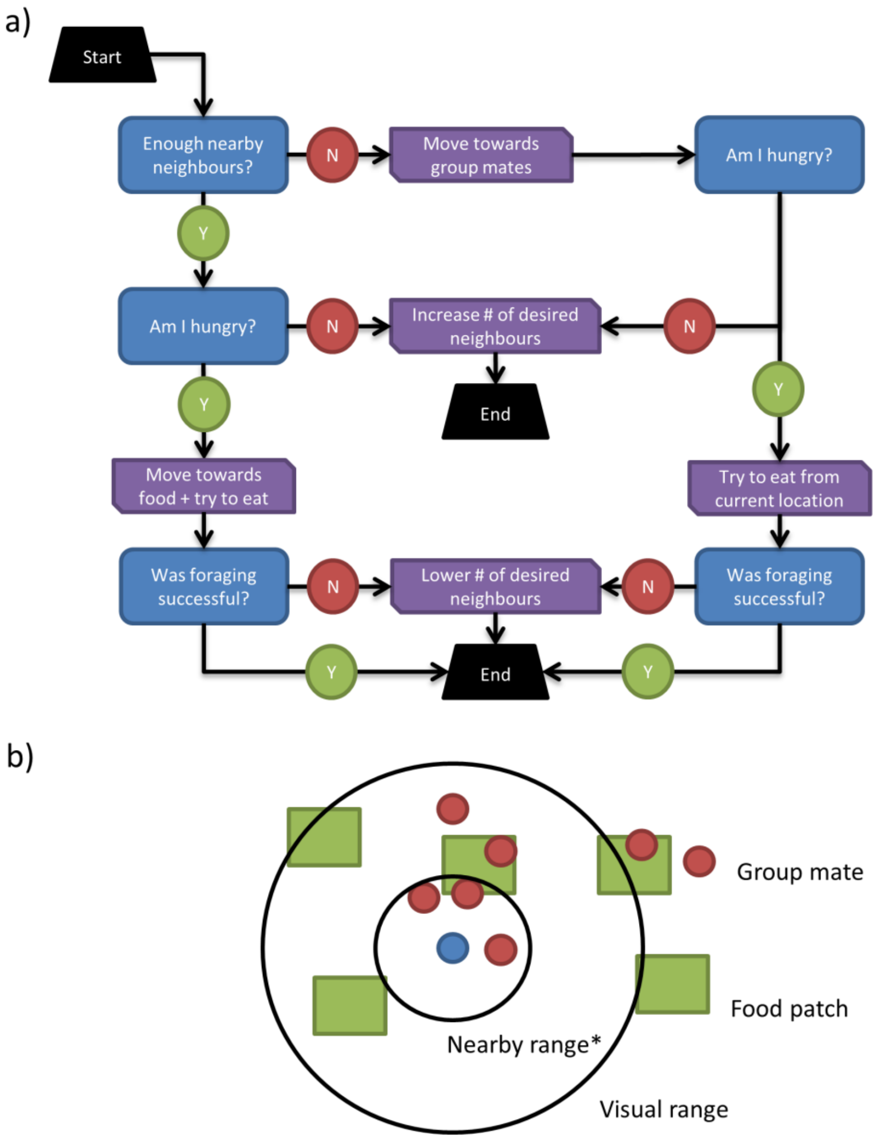

Figure 4-3: Group movement model. a) Algorithm for basic individual movement behaviour, modeling the trade-off between safety benefits of group living against foraging completion costs

(see Bonnell et al 2010). The algorithm is run for every individual each time step (start to end blocks). Varying the type and amount of spatial memory affects foraging choices available, whereas social structure affects individual safety requirements. b) Diagram depicting sensory inputs for an individual primate agent (blue circle). Nearby range, defines the area in which group mates add to an individual's safety, and visual range defines the area in which food sites are visible. Outside of the visible range individuals can remember sites based on the type and amount of spatial memory they possess.

Adaptation

To meet both feeding and safety requirements agents were able to vary the desired number of nearby group mates, allowing them to adjust the level of safety they desired. This allowed the agent, in times of high food stress, to be less attached to the group, prioritizing feeding; whereas, in times of food security the agent could prioritize safety, and reduce predation threats through dilution, although no predation occurred in the model.

Objectives

Primate agents attempted to satisfy, to the best of their ability, their safety and feeding requirements. There was no one optimal solution to this balance, as the optimal solution varied based on the individual, the availability of resources, and the position of group mates at any given time.

Sensing

Agents were able to see all resources within visual range (50 m), and detect primate agents within a secondary larger range (200 m). Primate agents were also able to sense their internal energy levels, and to recall sites based on their respective mental representations of the landscape (see Submodels: spatial-memory).

Interaction

Primate agents interacted with each other in the model by adjusting their spatial location. By moving towards a desired site, they affected the safety of others within the group. The primate agents also depleted the levels of the resources on the landscape, creating food competition.

Stochasticity

At each time step the order that primate agents were processed was randomly chosen. When a primate agent moved to a chosen resource polygon, it was located randomly within its boundaries. Movement at this scale was subject to processes not included in this model (e.g., within group social structure / demographics), and was therefore included as a random factor in the model.

Collectives

Primate agents formed a group, where individual interactions affected other group mates foraging decisions. To model within group decision making we included two extreme cases: independently led, where all agents were considered equal, and leader led, where all other agents attempted to stay near a leader for safety (see Submodels: group-foraging).

Observations

At the end of every time step during simulation, the center of the simulated primate group was marked, capturing the position (x,y) and time (step). As groups occasionally performed fission and fusion in the model, a recursive algorithm was implemented to estimate the center of the group. A center point, based on the location of all individuals within the group, was tested to see if a buffer of 100m contained 80% of the group or more. If it did not, the furthest individual from the point was removed and the center was re-calculated on this sub group. This was repeated until the center point passed the 80% rule to ensure that the center point represents that of the majority of the group, and resulted in a center point for each time step.

4.2.3. Details

Input data

To model foraging patterns mimicking observed patterns we developed an estimate of the resource environment in which the observed data was collected. We estimated a resource landscape based on the collected GPS movement data from the red colobus focal group. By overlaying a grid of 30x30 m, covering the home range of the observed group, we counted the number of consecutive hours spent in each grid. Grids with a zero count were weighted by sampling from a uniform random distribution varying from 0 to ¼ h. Each grid (n = 1,200) was thus assigned a relative weight to distribute resources in the simulation. This represents our assumptions of a resource landscape with widely available low quality foods, with specific areas representing high value food sites. This landscape was used in all foraging trails.

Initialization

Initialization of the model focused on defining the total amount and the grow-back rate of resources on the simulated landscape. Movement patterns of the simulated group were sensitive to these parameters, and their final values were chosen by fitting simulated group foraging behavior to observed group foraging behavior, specifically, average daily step length, home range size, and group spread. By fitting the model to these movement patterns we, 1) estimated long-term food availability (monthly home range size), 2) estimated short-term food availability (average daily step length), and 3) ensured that individuals were able to meet their energetic and social requirements without breaking group cohesion. Systematic variation of the total amount of resources and grow-back rate was used to select final parameter values (Table 4-1), which resulted in: an average home range size of all 12 agent types of 20.5 ha (observed: 10-50ha), an average daily step length of 171 m/7h follow (observed: 213 m/7h follow), and an average group spread of 5043 m^2 (observed: 1878m^2). The observation data on red colobus was taken from our observed group, as well as published data on neighboring groups (Snaith & Chapman 2008). The fit suggested that under the current assumptions, our group model, based solely on the trade-off between safety and food competition, underestimated group movement per day, and overestimated group spread.

Table 4-1: Model parameters describing landscape and primate agents.

Categories	**Parameter Name**	**Value**	**Units**
Environment	Resource re-grow rate	8	energy units/step
	Total amount of resources	168000	energy units
Group behavior	Group size	70	individuals
	Safe radius	50	meters
Primate capabilities	Distance to sense food	50	meters
	Distance to sense group mates	200	meters
	Time spent feeding	43	% of day
	Max travel distance (one step)	100	meters
	Defined by agent type		
	Foraging decision making	Independent/Leader	social rules
	Memory retention	20,60,100	remembered sites
	Memory Type	Euclidean/Landmark	cognitive map
	Distance of landmark memory	100	meters

As our simulated foraging trials lasted only 6 months we assumed a relatively static memory model, where individuals were assigned memory at the start of the simulation. Each individual was given memory of the location of top resource sites on the landscape, the number of which was represented by their memory retention abilities. Their memory of how much food at each site was initialized at the start of the simulation, but thereafter was reliant on the last time they were in visual range of the site.

Submodels

Group-foraging: For a social species like the red colobus, group dynamics are important when considering foraging and movement (Cunningham & Janson 2007; L. Conradt et al. 2009). Group-mate choices can influence the behavior of others within the group. Grouping in primates is thought to increase the safety of individuals, by mitigating predation (Van Schaik & Van Hooff 1983), but can have negative effects by increasing food competition (Snaith & Chapman 2008). To take this into account we allowed the simulated primate to adapt and balance its needs to gain safety within a group against the increased food competition experienced by being with other foraging conspecifics (Chapman & Chapman 2000; Snaith & Chapman 2008). The animal accomplished this, within our model, by measuring its food intake and in cases where feeding targets were not met, it could lower the number of group-mates needed to meet its safety requirements, thereby prioritizing foraging behavior. In cases where feeding targets were met, it could increase the number of group-mates desired, thereby prioritizing safety. Specifically, at the beginning of its step if the agent had its target energy level it would increase its desired number of nearby neighbours by one, if however the agent was below its target level, and failed to get food during its step, then the agent decreased its desired nearby neighbours by one. This approach mirrored that of (Getz & Saltz 2008) and (Bonnell et al. 2010) where, allowing individuals to vary their goals between safety and feeding, a group's behavior showed complex fission-fusion dynamics, such as those seen in the wild. This produced a group that was highly democratic (i.e., independently led), where each individual weighed his/her foraging decisions based on their location, influencing other agents foraging decisions. As an alternative social rule in making group foraging decisions, we added the presence of a leader, where in considering safety all other agents attempt to keep this leader nearby. The leader then played a larger role in making foraging decisions, as its movements influenced others to a greater degree (i.e., leader led).

Energetics: Primate agents were driven to forage based on internal energy requirements. Each primate agent aimed to maintain 100 energy units and was considered to be hungry when energy levels fell below this level. The amount eaten per feeding event, was assumed to be constant, and was defined by observed feeding time (red colobus spend 43% of the day feeding (Struhsaker 1975; Snaith & Chapman 2008)). Given that the model is divided into 26 half-hour steps, 11 steps (i.e., 43% of their day) should be sufficient to meet their energy requirements. Energy loss per step was constant, and was set as a ratio of target energy divided by the number of steps per day.

Movement-choice: Movement choices were made by agents by first comparing their desired level of group safety. If the level of safety was acceptable, agents then made the decision to move towards a desirable food site or to rest based on if they were hungry. If the level of safety was not met, then agents moved towards the average location of the nearest set of group mates, the number of which was defined by the desired number of group mates to be considered safe.

Chose-food-site: Food sites, either within visual range or remembered, were compared by ranking them based on the distance and the amount of food expected (Boyer et al. 2006; Ramos-Fernandez et al. 2006), $I_{(x',y')} = d\big((x,y),(x',y')\big) \, / \, r(x',y')$ where the food site index, I( ), was calculated for a resource at point (x',y') from the primates current location (x,y), using the Euclidean distance, $d(\,)$, and the primates estimate of resources $r(\,)$. Once a food site was chosen, the primate agent would then move towards it. If the food site was contained within the agent's visual radius and was considered safe, the agent was assumed to move directly to the site. The agent decided if the move was safe based on whether there were enough neighbours nearby at the new site. If the desired food source was beyond this threshold (e.g., from a remembered site) or was not considered safe, then the agent would move to a safe alternative in the direction of the chosen site, moving the agent as far as possible towards their desired site while still remaining safe. By again comparing food sites with the food site index, using the distance to the chosen site as the distance factor, the agent could then choose the best site leading to the desired site.

Spatial-memory: Spatial memory was defined in our model as either "Euclidean" or "landmark based." In the Euclidean framework we assumed agents had a global picture of remembered sites. Under this assumption, primate agents developed a list of all remembered sites, from which they could determine the distance, direction and expected amount of resources.

In contrast, using the landmark based memory framework, we assumed agents had knowledge of remembered sites associated with a given landmark. Under this assumption primates could only recall a list of remembered sites associated with the last landmark seen. Landmarks were set as any remembered site, and were associated with any other remembered site within 100m. A primate agent then recalled a list of all sites associated with its current landmark, and could determine the direction, distance and expected amount of resources at these sites.

As our foraging trials are short (6 months) we assume a static number of remembered sites, which are not forgotten over time. The amount of resources remembered at these sites however is dynamic. Once the agent had gone out of visual range of a remembered site, it assumed that the resource would grow back at a constant rate each time step, equal to the global environmental "grow back rate." This assumes that the primate agents within our model have a good idea of the grow-back rate of their resources. When a remembered site comes within visual range again, the agent can update its memory of resource amount.

4.3. Analysis

The resulting group movement patterns from each agent type were compared against the observed movement patterns (Grimm et al. 2005). Foraging patterns compared were: monthly spatio-temporal aggregation; daily step-length distribution, and daily path-tortuosity. The distribution of daily step lengths (sum of all group movement in one day), after removing the mean (as this was used in calibrating the model), and the distribution of daily path tortuosity were compared to the observed distribution by using a Kolmogorov-Smirnov test, with the null hypothesis that the observed distribution came from the same distribution as the simulated distribution. The D statistic, measured by the Kolmogorov-Smirnov test, was used as a measure of similarity to the observed distribution and was used to compare between simulation fits to the observed data (e.g., agent type 2 vs. 3). Daily step tortuosity was calculated as a ratio between the total distance traveled and the net distance traveled, $\log(D_{total} / D_{net}^{2})$. A log transformation was used to normalize the data, whereas the net distance was squared as it commonly increases linearly with step length (Whittington et al. 2004). Additionally, a measure of skewness for the step length distribution and a t-test for comparing mean path tortuosity were used to compare between observed and predicted movement patterns.

Estimates of monthly habitat use were made using a spatial-temporal beta-binomial framework (ST-BBD) (Bonnell et al. 2013b), where time and space in which the animal is moving is subdivided based on a beta-binomial distribution. This approach captures variation in the probability of visiting areas on the landscape; high variability when select few sites are visited often, and low variability when many areas are visited equally. This variation is quantified in this framework by the index of aggregation parameter, θ. A spatial-temporal beta-binomial grid consisting of 30x30 m quadrats, each made up of nine 10x10 m cells recording visits/non-visits during 30 day periods, was overlaid on the simulated and observed movement data. Simulated data was subsampled to meet the collection intensity of the observed data (i.e., 5 days per month and 7 hours per day).

To test for the combined effects of group social rules, memory type, and memory retention, a regression tree approach was used. We used the 'ctree' function from the 'party' package in R (R core development team 2012), a regression tree approach using conditional inference to subdivide the data using a minimum criterion of $p<0.05$. Step length, tortuosity, and group spread were used as dependant variables in separate regression trees, with group social rule, memory type, and memory retention as explanatory variables.

4.4. Results

Observed data: red colobus

The red colobus group in Kibale National Park, Uganda had a mean daily step length of 213 m (max 645 m), mean path tortuosity of -1.69, and a mean monthly index of aggregation 0.15 (mean 95% confidence interval: 0.11,0.19). Daily step length showed a positive skew (0.79), indicating the presence of infrequent long distance travel events.

Simulated data compared to observed data

Compared to the observed group, none of the simulated groups were found to have similarly distributed daily step lengths (Table 4-2). However, an effect of social rule on group movement was apparent, as overall, groups governed by a leader had lower D statistics compared to the independently led groups (Table 4-2). Leader led groups were also found to have higher positive skew in their distributions, fitting better to the observed positive skew in the observed distribution (Table 4-2).

Comparing simulated and observed distributions of daily path tortuosity suggested that leader led groups with landmark based memory (low-mid memory retention), and leader led groups with Euclidean (mid-memory retention) and landmark based memory (low memory retention) did not differ from the observed distribution (Table 4-3). Comparing mean levels of daily path tortuosity, groups with landmark based memory and low memory retention in both the leader and independently led groups were not found to differ from the observed mean (Table 4-3).

Table 4-2: Comparison of daily step length between simulated and observed primate groups; all comparisons with the K-S test were found to be significantly different ($p<0.05$).

Kolmogorov-Smirnov - D statistic				
Social group	**Memory**	**20**	**60**	**100**
Democratic	**Euclidean**	0.32	0.29	0.27
	Topological	0.30	0.27	0.30
Leader	**Euclidean**	0.25	0.29	0.27
	Topological	0.29	0.22	0.18
Distribution skew				
Social group	**Memory**	**20**	**60**	**100**
Democratic	**Euclidean**	-0.08	-0.01	0.04
	Topological	-0.10	<-0.01	0.50
Leader	**Euclidean**	0.39	0.32	0.32
	Topological	0.94	0.85	0.66

Table 4-3: Comparisons of daily step tortuosity between simulated and observed primate groups (mean observed group tortuosity = -1.7); '*' indicates no significant difference at the $p=0.05$ threshold.

Kolmogorov-Smirnov test - D statistic				
Social group	**Memory**	**20**	**60**	**100**
Democratic	**Euclidean**	0.16	0.17	0.19
	Topological	0.10*	0.09*	0.15
Leader	**Euclidean**	0.14	0.10*	0.17
	Topological	0.10*	0.15	0.13
Welch's two-sample t-test				
Social group	**Memory**	**20**	**60**	**100**
Democratic	**Euclidean**	-3.72	-3.63	-5.05
	Topological	-1.90*	-2.48	-3.01
Leader	**Euclidean**	-3.08	-2.03	-4.62
	Topological	0.75*	-2.40	-2.67

Comparing spatial-temporal range use with the observed data revealed that all groups did not differ significantly from the observed red colobus group (95% confidence interval for the difference between the simulation and observed mean). However, there was significant variation between agent types (Fig. 4-3). Groups governed by a leader, with landmark based memory and high memory retention were found to have significantly lower spatio-temporal aggregation than groups governed by a leader and with Euclidean memory type (low, med, and high).

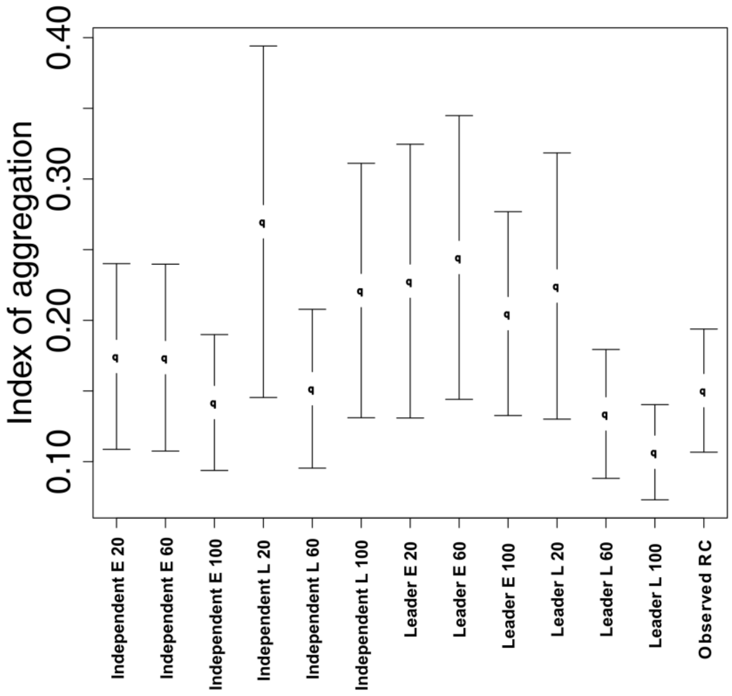

Figure 4-4: Index of aggregation for the observed and simulated red colobus groups. Error bars on the graph represent 95% confidence intervals.

Effects of social rule, memory type and memory retention

Regression tree results revealed a significant effect of social rules, memory type, and memory retention on daily step length (Fig. 4-4). Social rules explained most of the variance in daily step length, splitting the data into leader and independently led group categories.

Considering daily path tortuosity, the regression tree approach found significant effects of memory type and memory retention, but none for group social rules (Fig. 4-4). Memory type explained the most variance, subdividing groups into Euclidean and landmark based memory types.

Analyses of group spread found that memory type explained most of the variation in group spread (Fig. 4-4). Significantly more heterogeneity in the landmark based memory type was found compared to the Euclidean memory type. In the case of groups with Euclidean memory, significant differentiation was only found with social rules, with no effect of memory retention. The smallest mean group spread was seen in leader led groups with Euclidean memory (3863m^2), whereas the largest mean group spread was found in the independently led groups with a landmark based memory and high to mid-memory retention (60 sites: 6960m^2, 100 sites: 6350m^2).

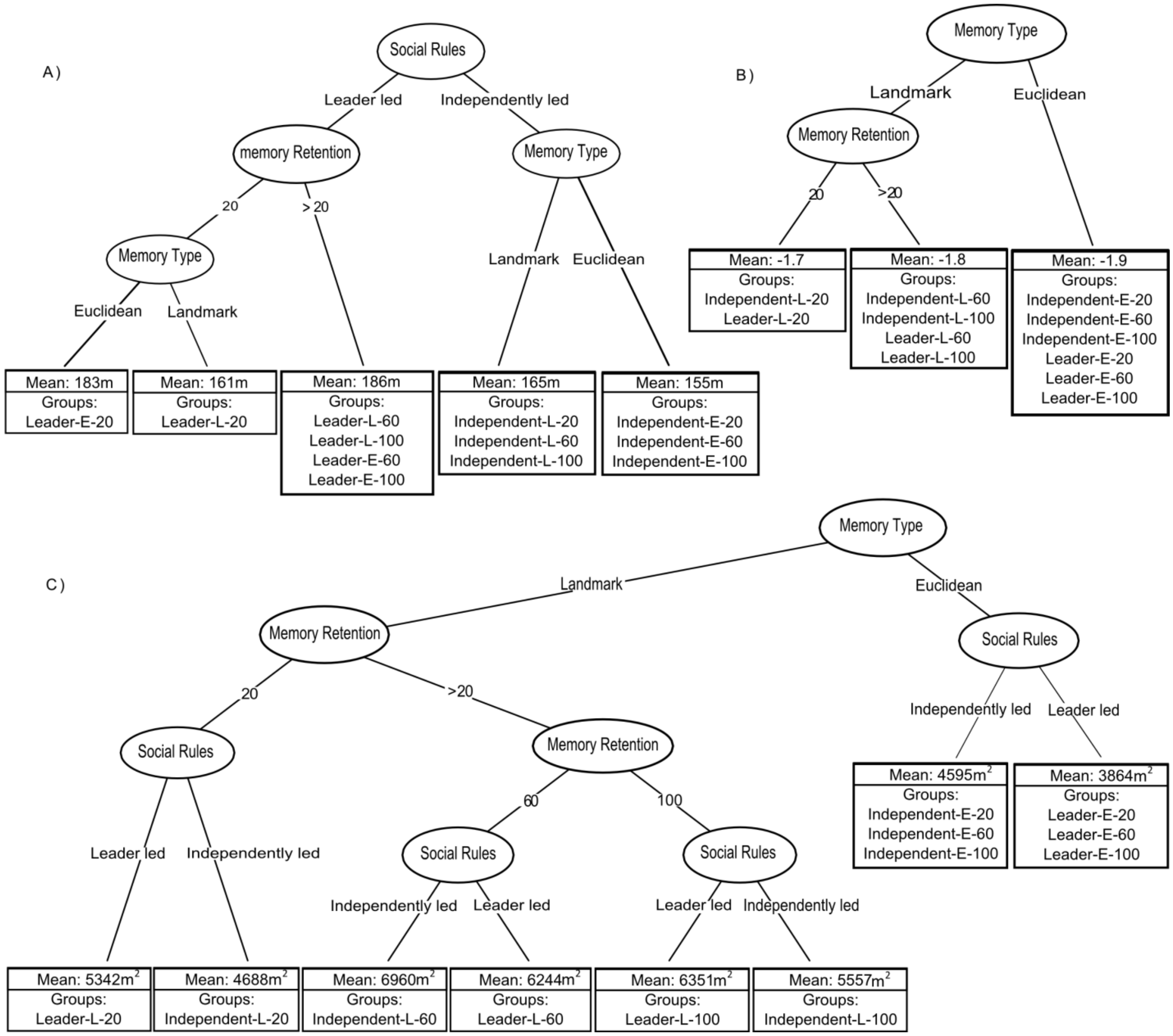

Figure 4-5: Conditional regression trees of a) daily step length, b) path tortuosity, and c) group spread, using group social rules, memory type, and memory retention as explanatory variables.

4.5. Discussion

Using simulated primates, with sensory abilities and simple behavioral responses to these stimuli, we compared simulated movement patterns with the observed movement patterns of a red colobus group. By defining various types of simulated primates, we were also able to test for the general effects of social rules, memory type, and memory retention, giving insight into the processes behind primate movement patterns.

Social rules were found to be the most important factor affecting the step length of simulated groups (Fig. 4-4). Leader led groups showed an ability to make longer moves compared to independently led groups which often lacked a clear consensus as to the direction of movement. Furthermore higher levels of discord in the independently led groups masked the effects of individual agent memory retention; whereas, in the case of the leader led groups, memory type and memory retention were found to be significant factors in daily step length (Fig. 4-4). This suggests that social rules governing groups are important factors to consider when elucidating individual foraging strategies/abilities from group level movement patterns. In the case of the leader led groups, when memory retention was high, there was no effect of memory type. This suggests that at high memory retentions the effects of memory type on step length should be small, and that daily step length might not be effective in distinguishing memory use in animals that are thought to have high memory retention.

In the case of path tortuosity, memory type was the most important factor distinguishing simulated groups. Higher homogeny in groups with Euclidean memory suggests that social rules and memory retention did not affect path tortuosity. In contrast, groups with landmark based memory were found to be significantly affected by memory retention (Fig. 4-4). This is likely due to the fact that as memory retention increased, more nearby food sites were included in memory, allowing high-value sites to be more connected to other high-value sites, creating a network-like structure consisting of high-value sites connected by low-value sites. Group foraging patterns were often found to follow along similar paths or routes, visiting high-value sites and displaying cyclical patterns. This route following behavior was seen in groups with landmark based memory types, as well as groups with Euclidean memory types (similar to Boyer & Walsh 2010), and resulted in similar measures of home range use between simulated and observed movement patterns (Fig. 4-3).

Group foraging, as described in our model, resulted in groups that would contract in times of resource abundance and would expand in times of food stress, allowing us to use the measure of group spread as a means of comparing group level foraging competition/success. We found that memory type was the most important factor, followed by memory retention, then finally group social rules in determining group spread. The relative homogeny in the groups with the Euclidean memory type (Fig. 4-4), suggested that group foraging success was not strongly affected by memory retention; that groups with 20 remembered sites did as well as those with 100. In the case of groups with landmark based memory, we saw a division based on memory retention, but not necessarily indicating more foraging success with higher memory retention. We observed that the least successful groups in our model, in terms of group cohesion, were those with landmark based memory and mid/high memory retention. This was partially explained in the model by the fact that as memory retention went up, less valuable sites at the periphery of the home range were included, which, once depleted by a group, were left without a good option to move towards (no, or limited, site specific memories nearby). This resulted in the group relying on visual cues alone to forage, until they found a familiar site. These exploratory events resulted in times of high food competition within the simulated group, resulting in increased group spread.

Increasing memory retention also had the generally weak effect of lowering the levels of movement aggregation, average θ values being lower for groups with 100 sites compared to 20 sites (comparing groups with similar social rules and memory types), and was most apparent in the leader led group with landmark based memory (Fig. 4-3). These groups likely benefited the most from increases in memory retention as they have limited site specific memories, reducing movement possibilities, and have less group discord compared to the independently led groups. This would allow them to take advantage of the increases in memory retention and use more of the landscape, thereby reducing aggregation in their movement patterns.

Comparing the 12 types of agents, or hypotheses, to the observed red colobus data, we found that leader led groups fit step length distributions best; whereas, groups with landmark based memory fit distribution of daily path tortuosity best, specifically those with low memory retention (20 sites). Comparing the three groups, which have leader led social rules and landmark based memory with observed movement aggregation revealed that all three are not significantly different than the observed levels. Given these results, the group with leader led social rules regarding foraging choices, and landmark based memory with low (20 sites) memory retention fit best to the observed red colobus data. The suggestion of lower memory retention (i.e., 20 instead of 60, or 100 sites), could possibly indicate that the group is heavily reliant on a smaller subset of food trees, rather than a smaller memory size. As well, when memory was increased in the model, lower resource sites are added resulting in a saturation of benefits from increases in memory retention. With a more detailed description of the dietary requirements of red colobus and a more detailed picture of their resource landscape, the point at which this threshold occurs would likely increase. The selection of the leader led group model was largely due to the lack of a clear consensus as to the direction of movement in the independently led groups. Future work could test the effects of varying within-group decision-making while foraging (e.g., communication, group demographics) to examine its effects on group movement patterns.

4.6. Conclusion

The approach taken here is based on strong inference, comparing and contrasting which individual level assumptions best fit with observed group level data in an experimental manner. The complex task of representing behavioral responses to stimuli, in a way which represents the behavior of a particular animal, is challenging. Focusing on reproducing group movement patterns, as opposed to those by a single individual, offers a higher level of predictability and is more feasible for collective behavior, rather than individual behavior (Goldstone & Janssen 2005). As well, work in the field of action selection shows promise in linking developments in cognitive science and behavior (Prescott et al. 2007), and presents a means to expand from the simple behavioral algorithm used in our example, to allow for more individual level behavioral flexibility and complexity seen in many different species (Prete 2005).

In a more general context, landscape structure and animal movement patterns can be better mapped due to advances in geographical information systems, remote sensing, and animal tracking (e.g., GPS) technology. This type of approach will be useful to examine such animal movement datasets, and the refinement of such datasets would allow for higher power of falsifiability of various hypotheses, leading to a better behavioral understanding of animal movement.

5. How does habitat fragmentation affect an environmentally transmitted parasite in a primate population?

Linking statement:

For directly transmitted parasites a population of hosts can be thought of as discreet habitat patches. The location of these hosts, in space and in time, represents habitat connectivity, and determines the contact structure on which the parasite population is constrained. Typically, this contact structure has been defined by mathematical models. In these models it is difficult, or infeasible, to include a detailed description of space, reducing the ability to explore how spatial structure affects infectious disease. In this chapter I made use of the results and methods of the previous three chapters to develop a host contact structure that is dependent on landscape characteristics. I used the red colobus movement model developed in chapter 4 and incorporated multiple groups within a landscape, defining forest structure and resource distribution using satellite remote sensing. As red colobus movement is based on behavioural responses of individual red colobus to social and ecological conditions, any change in the forest landscape directly affects movement patterns. Changes to forest structure then has direct influence on the contact structure of the hosts on which the parasite population spreads. I use this method to simulate the spread of *Trichuris* parasites through a red colobus population. *Trichuris* is an intestinal helminth that is found within the primate population of Kibale. This parasite spreads by fecal-oral transmission, passing eggs in the stool of the host, which mature in the environment and infect other potential hosts when ingested. In this chapter I aim to add to the literature on the spatial influence on infectious disease following fecal-oral transmission routes. To do this I focus on a specific study site (red colobus – *Trichuris* in Kibale National Park, Uganda) to parameterize the epidemiological model, and systematically alter the landscape to tests for more general effects of landscape changes. By altering the landscape in a systematic way the relative effects of both the extent of habitat and its spatial configuration can be quantified, allowing for comparisons with other disease systems. This chapter is in preparation for submission to the journal Ecological Applications.

Summary: Landscape changes are important modifiers of disease transmission. To investigate the role of habitat fragmentation, we model a host-parasite system in Kibale National Park, Uganda, consisting of red colobus monkeys (*Procolobus rufomitratus*) and an environmentally transmitted helminth (*Trichuris* sp.). A spatially-explicit epidemiological model was created were landscape structure influenced parasite transmission by altering red colobus behaviour and subsequent transmission opportunities. Comparing *Trichuris* egg output from simulated hosts to collected data, we define a best fit model parameterization. We use this best fit model to explore disease-related consequences of landscape changes, quantifying the relative effects of habitat loss and spatial configuration. Our results identify an interaction between habitat loss and configuration, where the spatial configuration of remaining habitat becomes increasingly important as habitat is removed. Specific spatial configurations of habitat were found to reduce the functional connectivity of the landscape for red colobus groups, resulting in lower prevalence of infection at the population level. However, overall the model predicts that the magnitude of habitat loss will have a greater effect on parasite transmission than the spatial configuration of habitat. Thus, in designing conservation strategies, our results suggest that conservation of habitat extent will be the most effective approach at decreasing transmission opportunities for environmentally transmitted parasites.

5.1. Introduction

Landscape level changes have significant impacts on parasitism in wildlife populations (Patz et al. 2004; Ostfeld et al. 2005), with landscape composition and configuration being influential in many host-parasite systems, including Lyme disease (Allan et al. 2003; Brownstein et al. 2005), chronic wasting disease (Farnsworth et al. 2005), and hanta virus (Langlois et al. 2001). Landscape composition refers to the extents and types of land covers, whereas configuration refers to their spatial arrangement (Turner 1989; Ritchie et al. 2009). Given that 75% of the world's ice free land has been anthropogenically modified (Ellis & Ramankutty 2008), a better understanding of how landscape change affects parasitism is warranted (Foley et al. 2005) and needed to construct informed conservation plans.

Habitat fragmentation is a common anthropogenic landscape alterations, where the ecological implications have been the subject of much research (Ewers & Didham 2006). Fragmentation of habitat at a landscape level can be considered as a result of two factors: a reduction in habitat extent and a spatial configuration leading to isolated habitat patches. Habitat fragmentation can reduce host contact rates within a population by isolating sub-populations depending on the scale and the movement behaviour of the host species (McCallum & Dobson 2002). However, fragmentation may also increase the intensity with which subpopulations use isolated habitat patches, e.g., due to reduced foraging opportunities (Irwin 2008). The resulting disease related consequences of habitat fragmentation will then largely depend on the transmission mode of the parasite in question (e.g., directly or environmentally transmitted). In the case of environmentally transmitted parasites, transmission opportunities may be increased when the spatial configuration of habitat results in isolated patches, where intensity of habitat use by host is elevated (Nunn & Dokey 2006). However, considering the effects of a reduction in habitat extent, transmission opportunities may similarly increase due to increased shared habitat use (e.g., due to increased host ranging behaviour to meet nutritional demands and reduced foraging options) (Nunn & Dokey 2006). The importance and interaction of habitat extent and its configuration on transmission of environmentally transmitted parasites are not well known.

Epidemiological modeling has been a useful tool for understanding the spread of infectious diseases. Traditionally, disease spread through a host population is modeled using differential equations within susceptible-infected-recovered (SIR) models (Anderson & May

1992). However, a limitation of this approach is the assumption that all individuals are equally likely to contact each other. This assumption is likely to be invalid in heterogeneous landscapes, or in highly social hosts. To understand how disease spreads in populations where there is significant heterogeneity in host contact, network modeling has been successfully used (Eubank et al. 2004; Keeling & Eames 2005). However, a limitation of network modeling is that the network structure is generally static (but see Gross et al. 2006; Vernon & Keeling 2009) and does not directly incorporate complex landscapes or host behaviours. Thus, it is of limited value where landscapes and host contact structures are dynamic. Spatially-explicit agent-based models have been proposed as a means to represent both host behaviour and landscape structure (Auchincloss & Diez Roux 2008; Linard et al. 2009; Nunn 2009; Bonnell et al. 2010; Roche et al. 2011; Lane-deGraaf et al. 2013). This approach focuses on individual hosts whose behaviours can be represented by algorithms. The host population contact structure on which the parasite spreads emerges from the interactions between hosts and their environment, as well as interactions among hosts.

In this study we develop a spatially-explicit agent-based model to investigate the role of habitat fragmentation on the spread of an environmentally transmitted helminth (*i.e.*, parasitic worm) in a red colobus (*Procolobus rufomitratus*) population within Kibale National Park (hereafter Kibale), Uganda. We make use of extensive long-term data collected from our study population to model: 1) the strength of association between parasite transmission parameters and the distribution of parasites across the host population and 2) the transmission-related consequences of landscape changes, quantifying the relative impacts of habitat extent and spatial configuration.

5.2. Methods

5.2.1. Overview

We use a spatially explicit agent-based modeling approach to define: 1) the landscape, 2) host behaviour, and 3) the parasite (Fig. 5-1). Our model used remotely sensed data to represent a landscape on which simulated red colobus hosts forage. Long-term behavioural data (Snaith & Chapman 2008; Chapman et al. 2010b, Chapman unpublished data) were used to develop a red colobus movement model, simulating habitat use and host behaviour. A parasitic agent was then introduced into the simulated population and it was parameterized to spread following a life history representative of the parasite *Trichuris* sp. This parasite genus is a soil transmitted whipworm with a global distribution that is common in primates (Stephenson et al. 2000; Gillespie et al. 2005). Our model description follows the ODD protocol: Objectives, Design concepts, and Details section (Grimm et al. 2010). This protocol uses a standard structure, consisting of specific sections and subsection, designed to facilitate communication and comparison of agent-based models. Model code is available at code.google.com/p/lhp-model/.

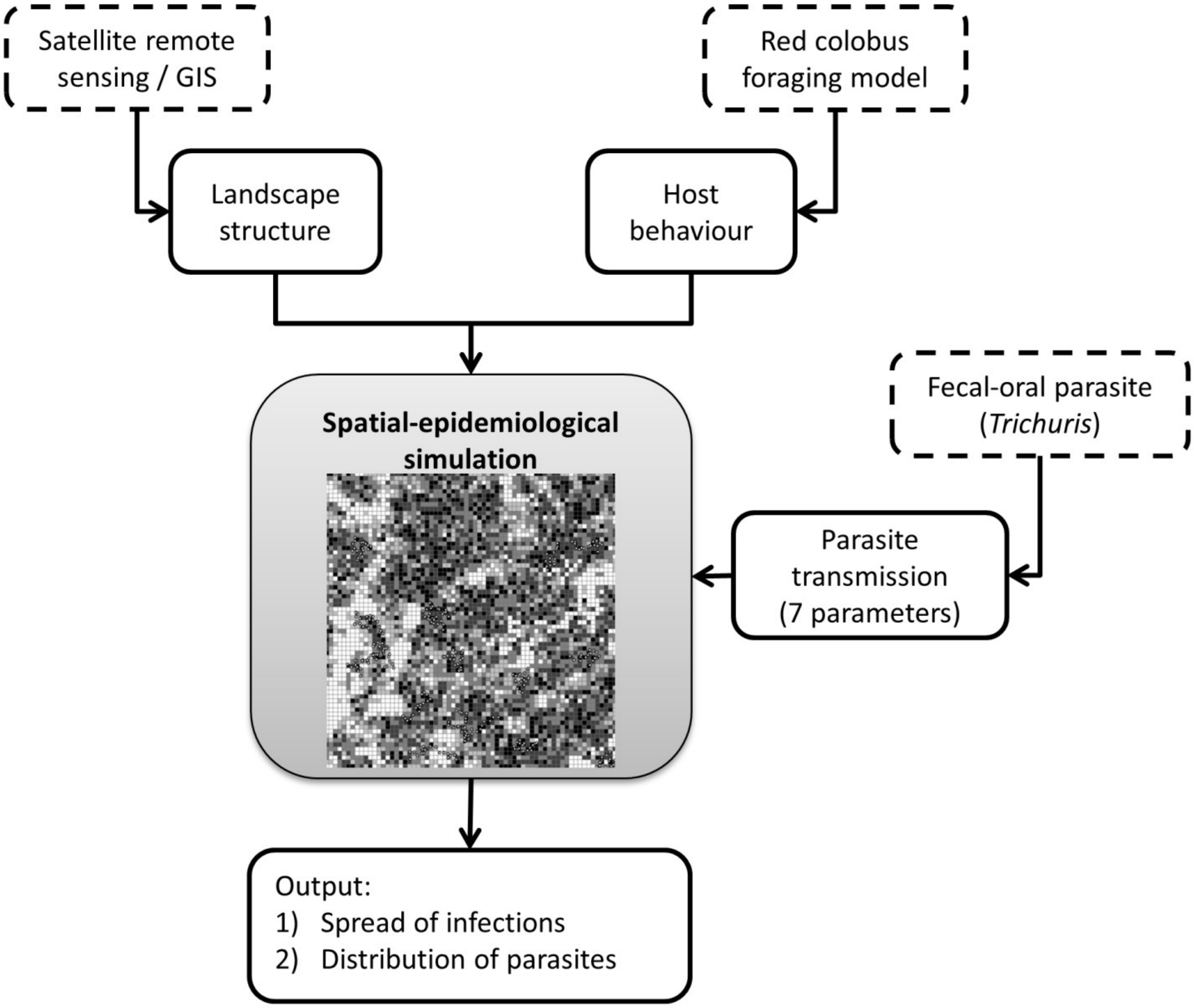

Figure 5-1: Overview of model construction: incorporating remote sensing, host behavioural, and parasitological data.

5.2.2. Study site / Disease system

Kibale is composed of moist-evergreen forest (74%), grasses/shrubs (22%), and wetland areas (4%) (Jacob et al. accepted) and harbours 13 primate species. The region around Kibale has undergone drastic changes in land cover. It is estimated that within a 5km buffer zone around the park there has been a 47% reduction in forest cover between 1984 and 2008, the majority of which has been caused by forest conversion to farmland (Hartter & Southworth 2009; Jacob et al. accepted). Wildlife are becoming isolated in a progressively degraded and fragmented habitats (Chapman et al. 2013). Groups of red colobus in fragments have higher prevalence of gastrointestinal parasites than those living within the protected, continuous, national park, including nematodes (Salzer et al. 2007; Gillespie & Chapman 2008; Salyer et al. 2012). In fact, previous research has shown the degree of human disturbance of fragments affects parasite richness (Gillespie & Chapman 2006) and rates of bacterial transmission (Goldberg et al. 2008).

We focus our study on whipworm, parasites of the genus *Trichuris*. *Trichuris* follows a general transmission cycle of soil-transmitted helminths (STH) (Brooker et al. 2006; Adam & Mutanga 2009) and commonly infects this red colobus population (Gillespie et al. 2005; Gillespie & Chapman 2008; Goldberg et al. 2012). *Trichuris*. reproduces sexually within the large intestine of its host, subsequently passing eggs that are deposited in the feces of infected hosts. The eggs embryonate and develop to infective stage within the environment, where they persist in soil and surrounding vegetation (Bowman et al. 2003). Infection of a susceptible red colobus host occurs through the ingestion of an infective stage egg. Since red colobus are arboreal, it is thought that most *Trichuris* infections occur through the ingestion of contaminated leaves or the use of contaminated branches and subsequent hand-to-mouth transmission. Alternatively, red colobus often come to the ground, and they do so especially frequently in forest fragments, where the canopy is discontinuous (Goldberg et al. 2008; Goldberg et al. 2012).

5.2.3. Parasitology

To parameterize our model we collected data on actual *Trichuris* infections in red colobus. While observing groups we opportunistically collected fecal samples deposited by focal animals. We endeavored to ensure that fecal samples were independent (*i.e.*, an individual was sampled only once per month or per group observed). Fecal samples were collected in sterile tubes, and the date, time of collection, species, sex, location, and habitat were recorded. At the end of each day, 1 g of feces was mixed with 2 ml of 10 % formalin. Samples were shipped to McGill University for analysis. We used a modified formalin-ethyl acetate concentration method, as recommended by the Clinical and Laboratory Standards Institute for the recovery of intestinal parasites (Young et al. 1979; Garcia et al. 2005). The entire sediment, typically 5-15 slides, was examined under 10X objective magnification to determine parasite infection status (Gillespie et al. 2005; Greiner & McIntosh 2009). Eggs per gram of feces (EPG) was used as a proxy of infection intensity (*i.e.*, the relative severity of infection within the individual). Prevalence of infection (*i.e.,* number of individuals identified as positive divided by the total number of individuals, converted into a percentage) was also calculated.

5.2.4. The model

Objectives

Purpose: The model was designed to determine the consequences of habitat fragmentation on transmission of *Trichuris* in a population of red colobus.

Entities, state variables, and scales: The model was composed of red colobus agents that foraged on a gridded resource landscape as points in continuous space. *Trichuris* was modeled as discreet populations representing the 4 stages of the species lifecycle: 1) non-infective eggs, 2) infective eggs in the environment, 3) larvae developing in the red colobus host intestine, and 4) adults in the large intestine of red colobus agents. Red colobus agents had state variables: desired number of nearby group mates, group identity, energy level, and the number of larvae and adult stage parasites in their gut. Landscape cells had state variables: energy level, number of immature eggs, and number of infectious eggs. *Trichuris* populations have state variables: age, stage, and number of individuals.

The model covers a 2 x 2 km area, encompassing 17 groups of red colobus. The model was run simulating 5 years, where each day was represented by 26 half-hour steps. Half-hour steps were chosen as this is the time period in which behaviour data was recorded (Snaith & Chapman 2008) and red colobus are generally active from 07:00-20:00 (Struhsaker 2010), resulting in 26 half-hour steps per day (Fig. 5-2).

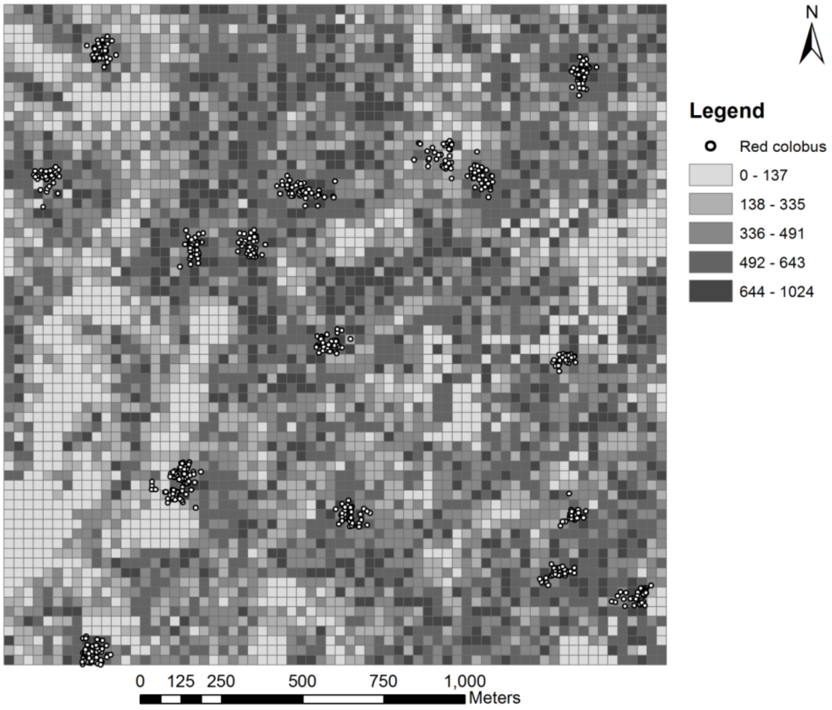

Figure 5-2: Model environment for simulating the spread of a fecal-oral parasite.

Process overview and scheduling: In each time step all primate agents updated their knowledge of their external environment. Parasite populations within the gut of the host were then updated. Each primate agent then went through its own behavioural algorithm, responding to their particular surroundings and internal states. At the end of each step all cells in the landscape performed a regrow step and parasite populations within cells were updated.

Design Concepts

Basic principles: The model was composed of three main parts: landscape, host, and parasite. The goal of our host model was to reproduce the contact structure of the host population. To do so, we simulated the movement and grouping behaviour of red colobus (see submodel: *Red-colobus-movement*) on a spatially-explicit environment derived from satellite remote sensing data (see Details section: input data). Transmission of parasites through this simulated population was then dependent on seven parameters following a fecal-oral life-cycle: maturation time in the environment, life expectancy in the environment, probability of host ingesting a parasite, maturation time in the host, life expectancy in the host, rate of reproduction, and maximum burden (Fig. 3, see submodel: *parasite-transmission*).

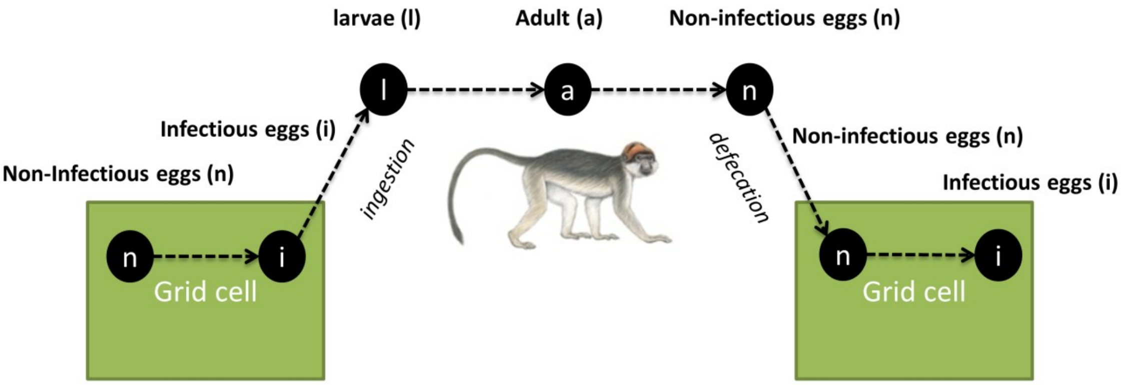

Figure 5-3: Transmission model for a fecal-oral parasite. The progression of one nematode group is presented, maturing from an initial group of non-infectious eggs in the environment, to a reproduction stage within a host, and defecation of a new nematode group. Illustration by Stephen D. Nash/CI/IUCN/SSC Primate Specialist group. Used with permission.

Host contact structure: Red colobus were organized into distinct groups. Individuals within the group were able to see food sites within a 50 m food-search-radius, as well as other red colobus within a second larger radius of 200 m. When a red colobus moved it affected the safety and foraging choices of others in its group. Changes to environmental conditions then had a direct impact on the movement and grouping patterns of red colobus. As transmission of the parasite is reliant on the movement and grouping patterns of the host, landscape changes impact the spread of the parasite through the host population.

Model Output: We recorded the spread of parasites through the host populations and the distribution of parasites within the host population at the end of the simulation. To monitor spread, we recorded the number of infected individuals at each time step, as well as the number of cells contaminated with parasite eggs at the end of the simulation. To monitor distribution we recorded the number of eggs in the last defecation of all hosts at the end of the simulation.

Model Details

Input data: Input data were used to develop landscape characteristics and host density. Remote sensing data from the SPOT-5 sensor (November 2008) were used to develop a resource landscape for the red colobus. The image was georeferenced and unscaled to radiance values in

Envi 4.8, and no atmospheric correction was done. Radiance measures in the remote sensing data were compared with forest data comprised of 26 vegetation plots (10 x 200 m) containing measures of total DBH of red colobus food trees (Chapman et al. 2010a). Linear models comparing the total amount of red colobus food to average pixel values within these transects were created. Using the "leaps" package in the R programming environment (Lumley 2009; R Core Team 2013) and comparing models using Bayesian Information Criterion (BIC), a final model was selected. BIC is a model selection criterion to choose among a set of models, based in part, on a likelihood function. It is closely related to Akaike information criterion (AIC). The final model used the green band and the variance in the NIR band (9 x 9 window) and showed an adjusted r-squared value of 0.41 ($p<0.001$).

$$DBH = -5.6(Var_{nir}) - 76.3(Green) + 4440.6 + \epsilon\big(N(0{,}248)\big) \qquad \text{Eq1.}$$

The residuals of this model were normally distributed (Shapiro-Wilk, W=0.97, p=0.63), and not heteroskedastic (Studentized Breusch-Pagan test, BP = 3.94, df=2, p=0.14). The predictor variables were also not significantly intercorrelated (Pearson's product-moment correlation: r=0.33, t=1.7, df=24, p=0.10). The use of the green band and the variance in the NIR band is consistent with other linear models using the SPOT sensor to quantify forest biophysical characteristics, such as above ground biomass and basal area (Castillo-Santiago et al. 2010).

To extrapolate this linear model to areas surrounding vegetation plots, the Spot 5 image was used to classify land cover in our study area. An unsupervised classification algorithm was used to identify 5-10 spectrally similar land covers (ISODATA, ENVI 4.8). Seven land covers were identified by the unsupervised classification algorithm. The best classification, testing against ground-truthed data augmented by points taken from Google Earth imagery (Geo-eye 2010), resulted when these spectrally similar land covers were re-grouped into 4 types: forest, agriculture/shrub, bare soil, and water. Finally, swamp land cover was separated from land cover classified as forest using a decision tree approach, classifying forest pixels as swamp if: $EVI<0.26$, $NIR<100$, and topography was classified as a plane, channel, or pit. Our chosen values produced a land cover classification with an overall fit of 84% (Table 5-1).

Table 5-1: Confusion matrix of land cover classification

	Ground reference data						
Class	forest	swamp	shrub	bare	water	Row total	User accuracy %
Forest	71	7	2	0	0	80	89
Swamp	0	27	0	0	0	27	100
Agr/Shrub	20	0	100	5	0	125	80
Bare soil	0	0	18	44	0	62	71
Water	0	0	0	0	25	25	100
Column total	91	34	120	49	25	319	
Producer accuracy %	78	79	83	90	100		84

An estimate of the total DBH of red colobus food trees per forest pixel was calculated using the linear model Eq.1, other land cover classes were assigned a value of zero as these habitats were either not used by red colobus groups (i.e., swamp, bare land, water) or very rarely used (*i.e.,* agriculture/shrub – CAC unpublished data).

The DBH surface derived from the remote sensing data was then used in the simulation model to estimate food availability for red colobus. To convert DBH values to food availability and to select food regrowth rates, we compared movements of simulated groups to observed groups. We found that a conversion of 0.46 food/DBH and a regrowth rate of 1.25 food/step reproduced observed home range sizes: 4 groups (size: 25, 40, 45 and 52) in the study area showed an average home range of 35.5 ha (Snaith et al. 2008) compared to 34.6 ha (standard deviation of 10.3 ha) from the simulated groups (17 groups, size: mean 40, standard deviation 4.5). The regrowth rate of 1.25 food/step resulted in a recovery time of an average site to be approximately 12 days. This fits well with what is known of the regrowth of young leaves (the primary red colobus food source) in tropical forests, which are generally in expansion (from bud to mature leaf) for only 1-3 weeks (Coley & Barone 1996).

Population density was defined as the number of groups within the 4 km^2 area. Line transect data estimate a density of groups in the study area of 4.2 groups per km^2 (Chapman et al. 2010b). To match these data we populated the simulation with 17 groups (4.2 groups/km^2 * 4 km^2 = 16.8), where each group size was selected from a probability distribution based on group size counts of known groups in the region (~N (mean=43, sd=4)). This resulted on average of 183 individuals/km^2 (43 individuals/group * 17 groups / 4 km^2), which compares well with empirical estimates of individuals/km^2 showing approximately 176-219 individuals/km^2 (Struhsaker 2010 pp.76, Chapman unpublished data).

Submodels:

Red-colobus-movement and intergroup dispersal: We used a movement model developed in Bonnell et al. (2013a), where various individual-based movement models were tested against observed red colobus group movement patterns. We select the movement model that was most successful for representing observed movement patterns: leader led groups, where individuals have a landmark-based memory and can remember up to 20 food sites. We initialized the memory of individuals within groups at the start of each simulation by giving them knowledge of the highest value food sites within an expected home range (35.5 ha). Individuals chose to move by balancing competing goals of safety and foraging. Agents attempt to limit feeding competition by lowering the number of group mates nearby, and try to maximize safety by being near as many group mates as possible. Priority between these competing goals shift based on individual foraging success, maximizing safety when feeding is good and lowering safety when feeding is low. By balancing these competing interests, the group movement produced mimics observed red colobus movement. By using this movement model, we incorporate important parasitic disease related behaviours, such as moving along similar routes and visiting familiar sites. To this model we add two additional behaviours that may be important for parasite transmission: the use of sleeping sites and dispersal of individuals between groups.

Choice of returning to the same sleeping sites is a potential factor influencing the exposure to a parasite with an immobile life-stage in the external environment (Gilbert 1997). To incorporate this behaviour we add the requirement each night that the group seek out a sleeping site. Two hours before the end of the day (18:00) the leaders' safety was made dependant on being in a sleeping site, where any remembered site on the landscape could act as a potential sleeping site. The static nature of memory in Bonnell et al. (2013a) did not allow groups to adjust to habitat removal, often resulting in groups remaining in areas no longer able to support them. To enable groups to adjust to the changes in the environment we allowed groups to update their memory of food sites, where every month individuals would re-initialize their memory based on the 20 highest value sites within 35.5ha.

Dispersal of individuals between groups can play an important role in parasite spread (Nunn & Dokey 2006). We include dispersal within the model by introducing a probability that an individual will disperse from a group ($P_{dispersal}$). If dispersal occurs the individual will no longer consider group mates while foraging and will forage on its own until it sees another non-native group, which it will join. Detailed follows have identified ~3 immigrations per year (Struhsaker 2010). By varying the probability of dispersal in our model and monitoring the average number of immigration events into each group per year, we select a dispersal probability which gave us an average of 2.7 immigration per group.

Parasite Transmission: The basic unit in the parasite model was a group of *Trichuris* parasites. Within a group, age, time to maturation, and life stage is assumed to be homogeneous. Each fecal deposition of eggs into the environment created a new parasite group. Subsequent transmission, survival, and reproduction were modeled at the level of these groups. Each group contained a number of *Trichuris*, their age, and their current life stage: non-infectious egg (n), infectious egg (i), developing larvae (l), and adult (a) (Fig. 5-3).

A newly deposited group of non-infectious eggs in the environment passes through a latent period ($M_{n,i}$), before eggs are considered infectious. Groups in the environment have a life expectancy of D_{env}, where eggs are considered to have died or to have become unavailable to red colobus hosts (e.g., washed away by rainfall). Ingestion by a local host is a function of the number of infectious fecal deposits within the current area (cell) times the probability of ingestion occurring ($P_{i,d}$). If transmission occurs, a random portion of eggs from one fecal deposit in the cell is successfully ingested. Once ingested, the eggs are considered to be a new group consisting of developing larvae within the host. This group passes through a latent period ($M_{d,l}$) and, if there is room in the host gut (B_{max}), matures to the adult stage. Adults in the host intestine then reproduce at the rate of $R_{L,N}$ and have a life expectancy of D_{host}. As the adults reproduce the newly created non-infectious eggs are added in the host gut, where a random portion of eggs are passed when defecation occurs ($P_{defecation}$), creating a new nematode group in the environment.

5.3. Analyses

We set ranges of parasite parameters based on observable transmission dynamics of *Trichuris* in other host systems (Roepstorff & Murrell 1997; Acha & Szyfres 2003; Petkevicius et al. 2007) (Table 5-2) and used a Latin Hypercube Sampling (LHS) regime to select 200 points from the parameter space. LHS is a statistical method of choosing stratified-random parameter values from a range of possible values. The model was then run for each parameter set.

Table 5-2: Parameters used to describe transmission of parasite groups, and the range of values tested.

Location	**Parameter**	**(min, max)**	**Units**	**Description (reference)**
Environment	$M_{n,i}$	(14,28)	Days	Maturation time (Acha & Szyfres 2003)
	D_{env}	(30,90)	Days	Life expectancy (Acha & Szyfres 2003)
	$P_{i,l}$	(0.000001, 0.0001)	%	Probability of being ingested
Host gut	$M_{l,a}$	(60,90)	Days	Maturation time (Acha & Szyfres 2003)
	D_{host}	(1,2)	Years	Life expectancy (Anderson et al. 2013)
	$R_{a,n}$	(0.0026, 2.6)	Eggs per day / (adult female)	Rate of reproduction
	B_{max}	(1000,10000)	Adult larvae	Gut size

First, we quantified the strength of association between the seven transmission parameters of the parasite and measures of spread within the host population using general linear models (GLM). To compare the magnitude of effects between parameters we standardized each, subtracting by its mean and dividing by its standard deviation. To quantify the growth rate of infections (r_0) within the host population we fit a logistic curve, using the gcFitSpline function in the grofit package of R (Kahm et al. 2010), using the maximum growth rate of the logistic model as an estimate r_0. This estimate allowed us to compare the spread of infections between simulations. The total area contaminated was calculated as the number of cells containing eggs at the end of the simulation.

Second, we selected the parameterization that best fit the observed data by comparing simulated and empirical parasite distributions within hosts. To compare observed data with the simulated results we randomly selected 98 fecal samples at the end of each of simulation run, matching the sampling intensity of the field data (n=98). We then used a Kolmogorov-Smirnov test to determine how well the distribution of simulated egg counts fit the observed egg counts, using the D statistic as a measure of this distance. We repeated this procedure 100 times for each simulation run, summing the calculated D statistic, resulting in a distance measure for each parameterization.

Finally, with the best fit parameterization, we then tested the effects of changing landscape variables. To examine the effect of habitat loss we removed a percentage of habitat (DBH) from the landscape (Fig. 5-4). We chose a maximum habitat reduction of 30%, as groups were not able to adjust their foraging behaviour to meet energetic demands above this value. As we do not include nutritional effects, such as increased susceptibility, we limit the maximum habitat removal to constrain our experiments to where energetic demands are met. By varying the total amount of DBH removed from the landscape (low = 10%, medium = 20%, and high = 30%) and the size of patches removed (small = 0.8 ha, intermediate = 10.9 ha, and large = 32.5 ha) we generated landscapes varying in habitat extent and spatial configuration, along a gradient from many small patches removed to few large ones. We ran the model 30 times for each combination of landscape alterations (n=270) and quantified the impacts of magnitude of loss and spatial configuration using two-way analysis of variance.

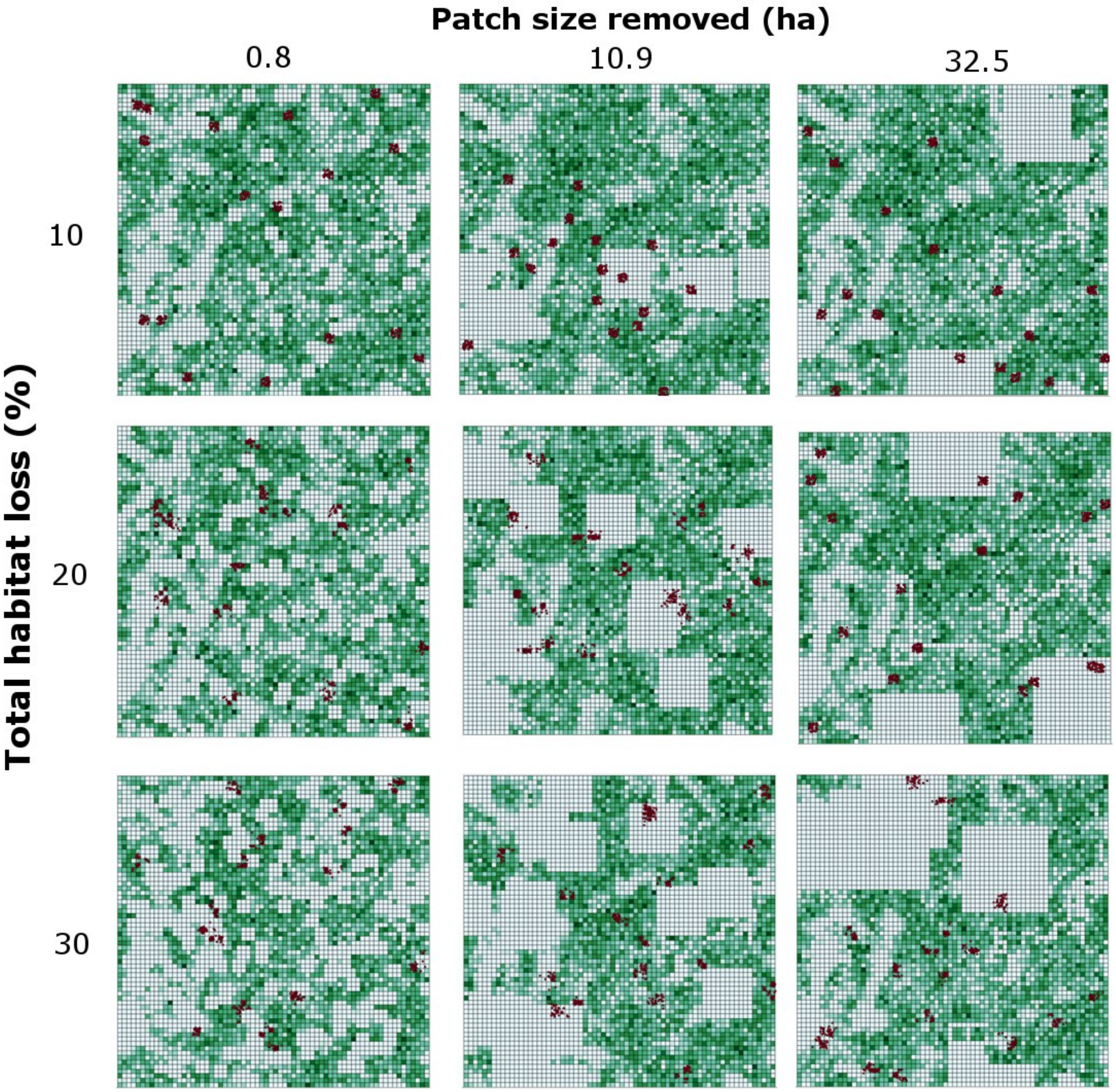

Figure 5-4: Modeling habitat loss by altering the magnitude of the loss (DBH removed / total DBH) as well as the size of individual patches removed (ha).

5.4. Results

Observed parasite patterns in red colobus

From empirical data (n=98 individuals), prevalence of infection was 43.7%, and average egg burden was 6.7 eggs/g of feces. The distribution of eggs counts best fit a negative binomial model: *k*=0.22, mean = 2.94 (comparing against geometric and Poisson distributions), where the k parameter is a shape parameter used as an index of aggregation (lower *k* values indicate higher aggregation). The best fit distribution then suggests aggregated counts of eggs in the red colobus population.

Strength of association between parasite parameters and disease outcomes

Fecundity, transmission probability, and life expectancy in the environment had the strongest association with both the rate of increase in infections (**r_0**) and total area contaminated at the end of the 5 year simulations (Table 5-3).

Table 5-3: Strength of association between parasite parameters and disease outcomes: rate of increase in infections (r_0), and total area contaminated. Parameterization which fit best to observed data is presented.

<table>
<tr><th colspan="3">Parameter</th><th colspan="2">t-value (r_0)</th><th colspan="2">t-value (area)</th></tr>
<tr><td colspan="3">Intercept</td><td colspan="2">18.00</td><td colspan="2">51.30</td></tr>
<tr><td colspan="3">Fecundity ($R_{a,n}$)</td><td colspan="2">14.87</td><td colspan="2">21.81</td></tr>
<tr><td colspan="3">Life expectancy in environment (D_{env})</td><td colspan="2">8.07</td><td colspan="2">16.83</td></tr>
<tr><td colspan="3">Transmission Probability ($P_{i,l}$)</td><td colspan="2">7.99</td><td colspan="2">8.22</td></tr>
<tr><td colspan="3">Maturation in environment ($M_{n,i}$)</td><td colspan="2">-2.14</td><td colspan="2">-3.05</td></tr>
<tr><td colspan="3">Life expectancy in host (D_{host})</td><td colspan="2">-1.99</td><td colspan="2">0.159</td></tr>
<tr><td colspan="3">Size of host gut (B_{max})</td><td colspan="2">-0.957</td><td colspan="2">-1.56</td></tr>
<tr><td colspan="3">Maturation in host ($M_{l,a}$)</td><td colspan="2">-0.42</td><td colspan="2">-0.537</td></tr>
<tr><th colspan="7">Best fit model</th></tr>
<tr><td>Fecundity ($R_{a,n}$)</td><td>Transmission ($P_{i,l}$)</td><td>Maturation Env ($M_{n,i}$)</td><td>Maturation host ($M_{l,a}$)</td><td>Life expectancy env (D_{env})</td><td>Life expectancy host (D_{host})</td><td>Gut size (B_{max})</td></tr>
<tr><td>2.10</td><td>3.70e-5</td><td>23</td><td>70</td><td>67</td><td>551</td><td>2140</td></tr>
</table>

A linear model describing the rate of increase in infections (r_0) explained 75% of the variance when taking into account the fecundity, transmission probability, and life expectancy of eggs in the environment ($F = 204.7$, $p<0.001$, adj $r^2 = 0.75$):

$$r_0 \wedge 0.1 = 1.28 * R_{L,n} + 0.38 * P_{i,D} + 0.52 * D_{env} + \text{error} \sim N(0,0.33) \qquad \text{Eq1}$$

A comparisons of the log-likelihoods for the Box-Cox power transformation (MASS package, R-programming environment), suggested the use of 0.1 as a transformation factor, which resulted in the residuals of the model being normally distributed (Shapiro-Wilks: W=0.98, p=0.06). The untransformed model showed equivalent results, but the residuals fail the Shapiro-Wilks test.

Best fit model parameterization

The parameterization resulting in the least deviation from the observed distribution of fecal egg counts showed a combined d-statistic of 9.58, a prevalence of 41.9%, and an intensity of 5.4 eggs/gram (Table 5-3). Most of the population had relatively minor infections, with only a few individuals (n=3) shedding more than 50 eggs/gram of feces. A negative binomial distribution was the best fit for the simulated data (comparing against geometric and Poisson distributions), showing a k value of 0.21. Running the best fit parameterization 30 times resulted in a mean prevalence of 42.10% (sd = 13.30) and an average egg burden of 3.89 (sd = 1.68) eggs/fecal deposit.

Landscape changes

Using a two-way analysis of variance to analyse the effects of landscape change on prevalence, the interaction between habitat loss and spatial configuration was significant ($F_{4,261}$=4.83, p-value<0.001). We therefore separated our analyses of spatial configuration and habitat loss. Considering the effects of spatial configuration on prevalence within low (10%), medium (20%), and high (30%) habitat loss scenarios, it was found that the effects of spatial configuration was significant in scenarios with high (30%) reductions in habitat, and marginally significant with medium (20%) reduction in habitat, and not significant with low (10%) habitat reductions (low: $F_{2,87}$=0.54, p-value=0.58; medium: $F_{2,87}$=3.06, p-value=0.052; high: $F_{2,87}$=10.24, p-value<0.001). Changes in spatial configuration during high habitat loss scenarios resulted in significantly lower prevalence when intermediate patch sizes were removed (prevalence = 52%), compared to small (prevalence = 70%) and large (prevalence = 61%) patch sizes (Tukey test, p<0.05). Similarly, considering the effects of habitat loss while holding spatial configuration constant, habitat loss had a significant effect on prevalence when low ($F_{2,87}$=16.24, p<0.001) and high ($F_{2,87}$=11.80, p<0.001) patch sizes were removed, but not when medium sized patches were removed ($F_{2,87}$=0.49, p=0.61) (Fig. 5-5). Post-hoc Tukey tests showed that increases in habitat loss led to increases in prevalence when small patches (diff=0.21, p<0.001) were removed as well as large patches (diff=0.16, p<0.001), but not when intermediately sized patches were removed (diff=0.02, p-value=0.78).

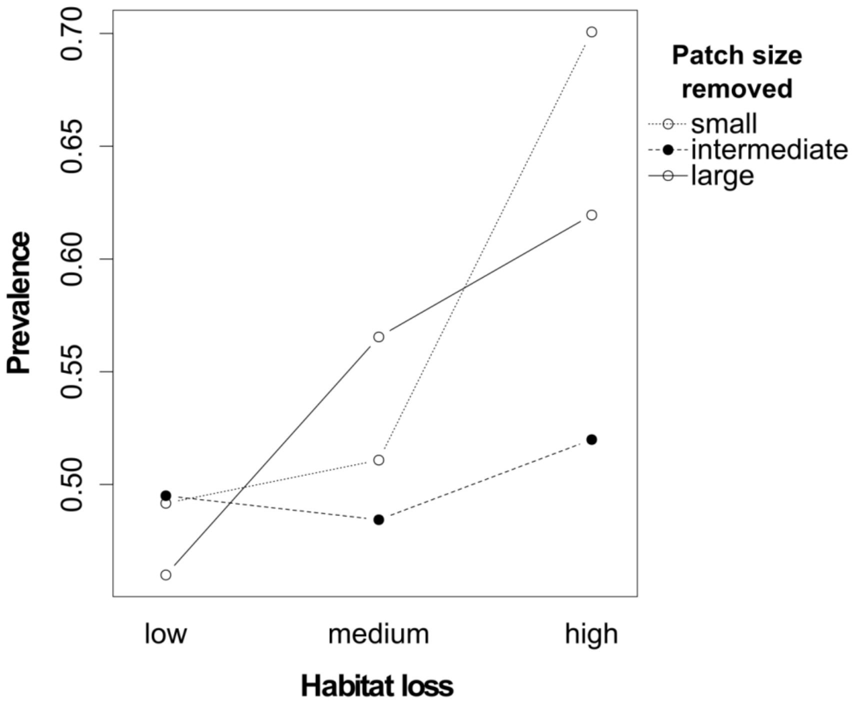

Figure 5-5: Plot of the interaction between the extent of habitat and the size of patches removed on infection prevalence.

Egg burden measures were transformed (1/egg burden), resulting in groups having similar variances (Levene test: $F_{8,261}$=1.77, p-value=0.08), with residuals normally distributed (Shapiro-Wilk: W=0.99, p-value=0.66). Egg burden was affected by the magnitude of the habitat loss ($F_{2,261}$=41.87, p-value<0.01), whereas the effect of patch size removed was marginally non-significant ($F_{2,261}$=2.95, p-value=0.054) (Fig. 5-6). The interaction between total habitat loss and spatial configuration was marginally non-significant ($F_{4,261}$= 2.33, p-value=0.056). A post-hoc Tukey test showed that increasing habitat removal overall led to increases in egg burdens: low=3.96, medium=4.53, high=6.78 (p-values<0.01; values are back-transformed into egg/gram).

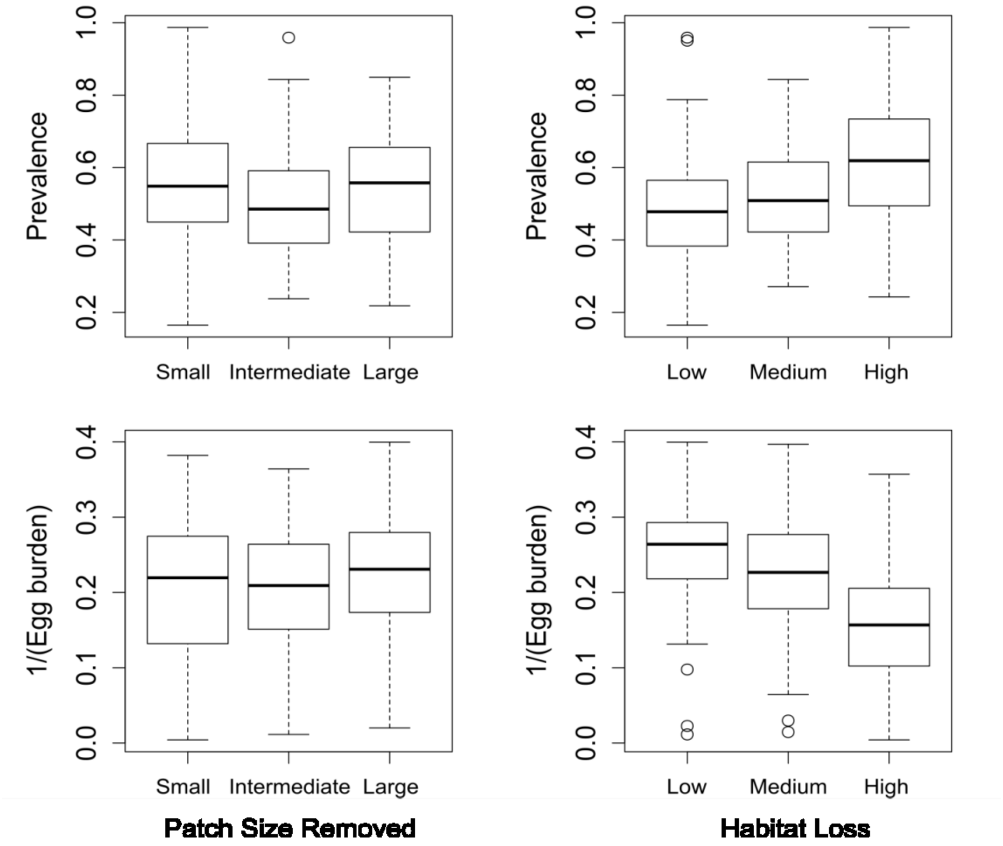

Figure 5-6: Boxplots of egg burden and prevalence of infections under simulated habitat loss and fragmentation scenarios.

5.5. Discussion

Using our spatially-explicit agent-based model we investigated the relationships between habitat extent and spatial configuration on the spread of an environmentally transmitted parasite in a red colobus population and found a significant interaction between the two on final parasite prevalence. Specifically, spatial configuration of the habitat was most important in conjunction with high habitat loss scenarios. In these scenarios prevalence decreased by 16-21% when intermediate patch sizes were removed, suggests that this spatial configuration led to reduced functional habitat connectivity as experienced by red colobus groups. When many small patch sizes (*i.e.*, 0.8 ha) were cut away many connections between areas remained on the landscape. Similarly, when small numbers of large patches were cut away (*i.e.*, 32.5 ha) few large connections remained. However, when medium-sized patches were removed (*i.e.* 10.9 ha), this landscape configuration increased isolation, resulting in reduced contact between groups and therefore fewer intergroup transmission events.

The extent of habitat loss was found to increase prevalence when small and large patch sizes were removed (i.e., when the spatial configuration did not significantly affect functional connectivity, Fig. 5-5). However, prevalence increased in the population due to different mechanisms. When many small patches were removed transmission increased due to individuals experiencing more feeding competition, resulting in increased group movement (e.g., larger home range sizes) (Fig. 5-7). When few large patches were removed transmission increased due to groups congregating within the remaining high value patches, resulting in higher local host densities (Fig. 5-7). In both cases the amount of habitat shared between host groups increased.

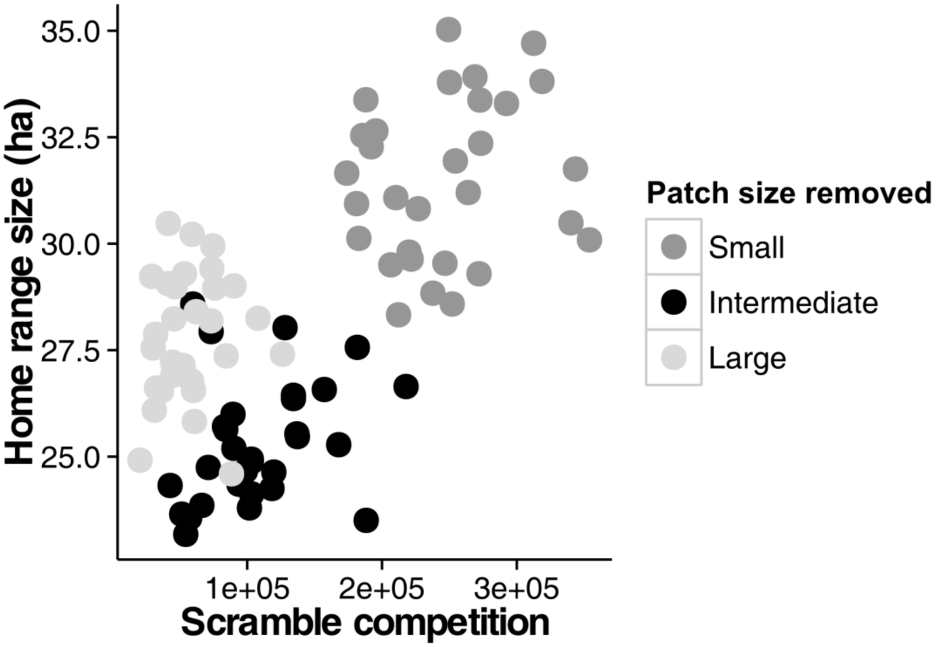

Figure 5-7: Comparing the effects of patch size removed in high (30%) habitat loss scenarios. Scramble competition was counted when an individual was not successful in a feeding attempt. Both home range and scramble competition were calculated for each size of patch removed from 30 simulation runs of 3 months.

Habitat loss was also found to increase intensity of infections (i.e., egg output of simulated hosts). The effects of spatial configuration and the interactions between habitat loss and configuration were marginally non-significant. The model suggests that the role of habitat loss on egg output was due to reduced foraging options, resulting in higher intensity of habitat use (e.g., mean cell visits per habitat loss scenario: low=184 visits/cell, mid=188 visits/cell, high=194 visits/cell; $F_{1,78}$=36.77, p-value<0.01). In a similar model of environmentally transmitted parasites, Nunn et al. (2011) showed that parasite spread was strongly influenced by the intensity of habitat use by a host. Our results show similar effects with regards to intensity of infections.

Sensitivity analysis suggests that transmission probability, egg longevity in the environment, and reproductive potential of the parasite were the most influential parameters in determining spread. In the case of transmission probability, areas of constrained travel (e.g., corridors), use of defecation sites (e.g., latrine behaviour), and areas where ground travel occurs have all been suggested as possible areas influencing the probability of transmission occurring (Freeland 1976; Stoner 1996; Gilbert 1997; Gillespie & Chapman 2006; Chapman et al. 2013). Similarly, the nutritional status of hosts has been shown to have a significant influence on the reproduction potential of helminth parasites (Gulland 1992; Chapman et al. 2006). The significant role that longevity of infectious eggs in the environment played in our model also suggests that a better understanding of the factors relating to egg survival and infectivity outside the host could be important. Development and survival of *Trichuris* in the environment has been shown to be influenced by climatic factors, such as temperature (max survival at 37-40 C) and high relative humidity (Weaver et al. 2010; Pullan & Brooker 2012). Climatological data from our study site suggests there has been a long term trend towards increasing rainfall (Chapman et al. 2005a), with increasing variability in seasonal rainfall patterns (i.e., longer dry periods within the rainy season) (Hartter et al. 2012), potentially affecting survival of *Trichuris* eggs in the external environment.

5.6. Conclusion

A better understanding of the disease-related consequences of landscape changes can result from integrated models, combining landscape composition and configuration, host behaviour, and parasite life-cycle. We have presented a simulation model, employing spatial data (satellite remote sensing), behavioural (animal movement data), and parasitological data (fecal samples) to make quantitative predictions about the relative effects of changes to the extent of habitat and its spatial configuration on an environmentally transmitted parasite. The model was able to identify important parameters (variability in transmission, longevity in the environment, and reproduction of the parasite), and mechanisms (e.g., functional connectivity, intensity of habitat use, and shared use of habitat) of how fragmentation influences parasite transmission. Our results suggest that landscape management strategies (e.g., designing corridors or spatial distribution of habitat patches) which balance a trade-off between reducing both the intensity to which groups utilize habitat and the extent to which habitat is shared between groups would lead to reduced transmission of environmentally transmitted diseases. Our model also predicts that as habitats become more fragmented, the amount of habitat will play a more prominent role than its spatial configuration in influencing transmission, suggesting that conservation of habitat extent is the most important factor reducing transmission opportunities.

6. Final Summary

Accelerating trends for the emergence or re-emergence of infectious diseases in humans and wildlife and the large economic and social costs they carry have resulted in increased interest in this field. I propose that the use of a novel spatio-temporal analytical frameworks and the use of agent-based models that are spatially explicit can create novel insights to the field of disease ecology. My dissertation expanded and contributed to the following four major topics.

First, using forest transect data, I estimated the recovery time of tropical forest in Kibale National Park, Uganda. I found that recovery time was slowest in the heavily logged sections. The implication for red colobus, as well as for other primates (particularly frugivorous primates) was a reduced quality of environment in those locations (Bonnell et al. 2011).

Second, to understand interactions between animal movement and disease dynamics I needed better ways to measure the habitat use from movement data, thus, I developed a novel spatio-temporal method. This method aimed at quantifying the variation in visits to habitat patches, a behaviour that is often of importance in directly transmitted diseases. Using this method, I compared the movement patterns between and within three primate species. I found that food availability and group size correlated with variation in this measure in the red colobus monkey (Bonnell et al. 2013b).

Third, to gain a better behavioural understanding of movement patterns in the red colobus, I tested various hypotheses against observed movement in a spatially-explicit simulation environment. These experiments suggested that groups led by a leader, and where individuals in the group use landmark based memory, were the best behavioural models of group movement (Bonnell et al. 2013a).

Fourth, using the results from preceding chapters, I developed a spatially-explicit epidemiological model to quantify the effects of habitat fragmentation on the spread of an environmentally transmitted parasite. By altering the landscape and infecting a population of red colobus with a parasite following the life-cycle of *Trichuris* I was able to quantify the relative effects of habitat loss and habitat spatial configuration. The results suggest that the magnitude of habitat loss will have the largest impacts on transmission opportunities, and that the effects of habitat spatial configuration will have greater impacts as habitat loss increases.

6.1. Spatial and temporal interactions in complex systems

This dissertation's overall aim was to develop a better understanding of how landscape structure, host behaviour and parasite characteristics interact. This required studying elements separately (Ch. 1-2), as well as combinations of these elements (Ch. 3-4). Ultimately, to study the properties of these interacting elements, agent-based modeling techniques integrated within a GIS framework was used. This approach allowed for flexibility and detailed descriptions of the interacting elements: GIS to describe the landscape, and agent representations for hosts and parasites.

To analyse these systems, the idea of emergence has been a useful concept, allowing for inferences to be made about the behaviours of elements in the system. For example, in chapters 4 and 5, observed data were used to build models of interactions that best reproduced emergent system-level behaviours. In chapter 4, I described individual-level behaviours of red colobus and examined the resulting patterns of their interactions at a group level. I then populated a landscape with multiple groups in chapter 5, and used this simulated population as the structure on which disease spread could be simulated. The use of observed field-data was key in identifying the important processes and interactions that reproduced the emergent phenomena of interest: red colobus group movement. At the population level, when multiple groups were considered, many of the emerging patterns were not implicitly characterized, nor initially appreciated. For example, groups often repelled each other by reducing foraging quality around the areas of the home range they were using at the time, and avoided each other by having a different set of spatially remembered sites. However, the rate and extent to which groups repelled or avoided each other was not implicitly tested in the model, and only emerged at the level of the population not at the level of the group where the model of group movement was calibrated. The use of emergent models are likely to force wider and wider set of unexpected outcomes as models move up in scale (e.g., individual –> group –> population). Methodologies to test for and accommodate these secondary results both in choosing the most representative models and in interpreting the model outcomes need to be defined. For example, when testing group level outcomes of different individual-level traits, should the effects on the population level outcomes be counted, should they weigh more or less than the group level? How can these secondary emergent phenomena be identified or measured?

After completion of the chapters of this dissertation, it has become apparent that a useful method of dealing with some of these issues would be to consider a hierarchical approach, in which the process of interest is considered at different scales, e.g., hierarchical reductionism (Anderson 1972; Bedau & Humphreys 2008). In this way one can examine one scale above and below the process of interest to look for upwards and downward causation in trying to explain the observed processes (Fig. 6-1).

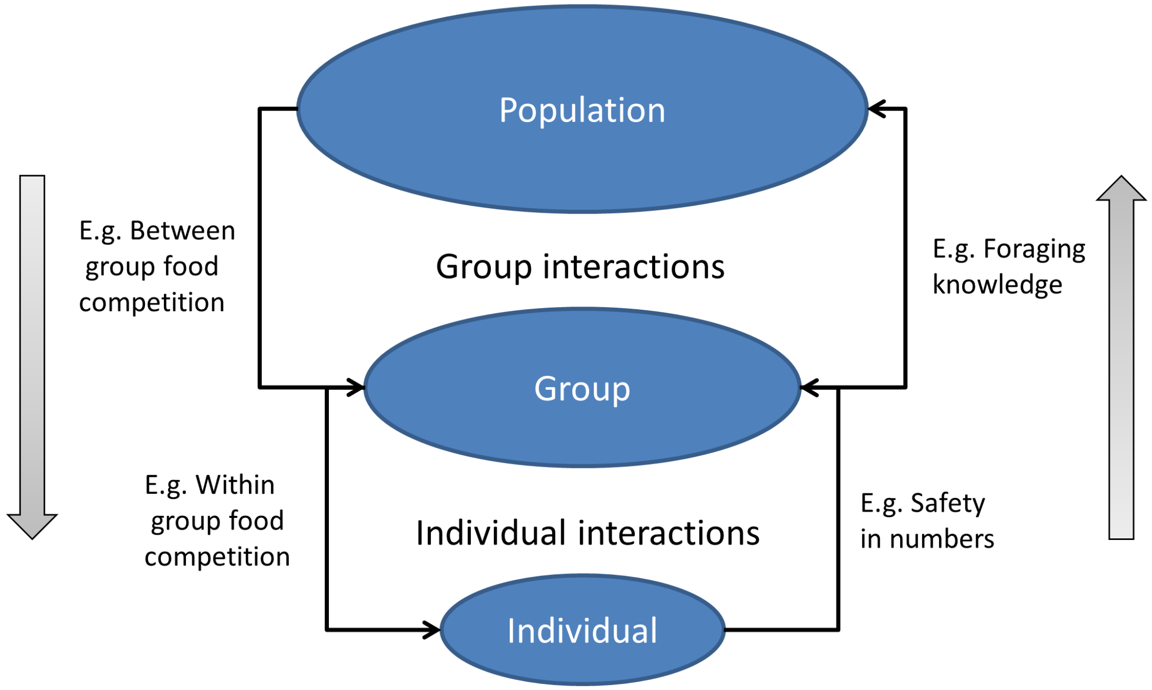

Figure 6-1: Hierarchical model determining the distribution of red colobus groups in space and time: up-ward causation is a property of the lower scale influencing the higher scale, and down-ward causation is a property of the higher scale influencing the lower scale.

6.2. Concluding remarks

This dissertation explores two main foci where a multidisciplinary team was assembled to address a question of interest: a) movement ecology, and b) spatial epidemiology (Fig. 6-1). The first multidisciplinary team focused on developing models to better understand of the proximate behaviours behind observed movement patterns (Fig. 6-1a). The second multidisciplinary team focused on addressing how landscape changes alter disease spread though a red colobus population, incorporating details on the disease ecology and the biology of our specific study system (Fig. 6-1b).

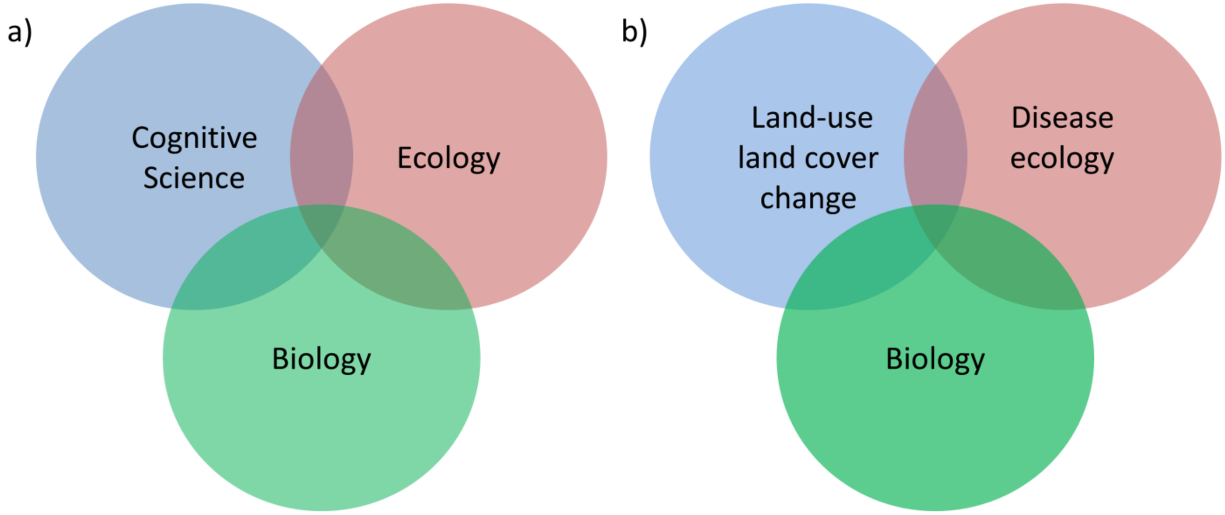

Figure 6-2: Multidisciplinary approach looking at questions in a) movement ecology and b) spatial epidemiology.

The development of a structured environment containing our team's collective assumptions about the system of interest allowed for the inclusion of a wider set of determining variables (e.g., landscape, movement patterns, animal cognition and perception). An advantage of this integration was that it generated many secondary questions. For example, if foraging patterns are, at least in part, driven by spatial memory, could risk of disease transmission influence the evolution of spatial memory and foraging patterns? In what cases would selection pressures be expected to favour less memory capacity, or less shared memory between groups? How would the distribution of resources and virulence of the parasite change these pressures?

The ability to share and communicate the developed models though the interdisciplinary teams, however, was found to be limited due to the level of final model complexity. The use of standardized methods of describing the agent-based models, such as the Objectives-Design-Details approach (Grimm et al. 2006), was useful in some cases, but the detailed and rigid nature was sometimes a hindrance in publication (i.e., reviewers did not appreciate its value) and in communication to non-modeling audiences. Conversely, the visualization of a dynamic GIS showing group movement behaviour was found to be very useful in communicating the behaviours and assumptions of the model, allowing individuals not intimately involved with the research to develop a better understanding of the model. This was increased further when individuals were able to easily alter parameters and immediately see the resulting changes. Furthermore, breaking the model into (simple) component parts, where complexity of the model could be gradually increased, was also found to increase the understanding of the interworking of the model (e.g., red colobus movement model with no spatial memory → with spatial memory → multiple groups → with parasites). Model complexity was also found to reduce the ability to explore model behaviour. This resulted in reduction in the range of sensitivity analysis performed during chapters 4-5: limiting the number of remembered sites (20, 60, 100), and landscape alterations (loss: 10%, 20%, 30%; patch size removed: 0.8 ha, 10.9 ha, 32.5 ha) that were explored. The range tested during the sensitivity analysis could have missed interesting behaviour (e.g., Ch.4: memory size effects from 0-20 sites) that could be further explored using more advanced computing hardware or code implementations (e.g., parallelization of model processes).

In the field of spatial epidemiology, current advances in GIS and spatial analysis have already led to significant developments, increasing our understanding of the disease-related consequences of landscape changes. However, host-parasite-landscape systems are complex, in that they are a result of the interaction of many different processes. To better understand these complex systems, it is often necessary to develop multidisciplinary teams with expertise in many research areas. To incorporate developments and facilitate communication between distinct research fields, GIS and ABM has proven useful in this dissertation, but much work is needed to increase communication and objective analysis of these models. The further integration of process models within GIS offers one opportunity to incorporate multiple processes in a structured simulation environment (Brown et al. 2005). Standardized of such computational environments could allow for the exploration of the interactions between many processes thought to influence transmission of parasites (e.g., forest structure, host foraging, and parasites life-cycle and transmission dynamics), leading to a more comprehensive view of the disease related impacts of environmental change. The ability of such systems to incorporate detailed descriptions of landscapes would be of great value, as disease related impacts of landscape changes are thought to be largely site specific (Ostfeld et al. 2008), and could lead to better disease management planning. It would allow managers and researchers to take a more proactive role by developing simulating models aimed at predicting/understanding the behaviour of specific host-parasite-landscape systems facing environmental changes, such as climate or landscape changes.

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