Disturbance in the Udzungwas: Responses of Monkeys and Trees to Forest Degradation

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Abstract

Tropical forests are one of the world's most threatened biomes. As tropical forests are increasingly destroyed and degraded, there is increasing need for research into the implications for rare species and habitats, and for conservation management. This thesis is a series of four papers investigating species and community responses in the Udzungwa Mountains, an area of international importance for biodiversity. The focus is on both rare species and potential indicators of habitat degradation. The most direct impact of human disturbance is on vegetation structure. However the response of most tropical plant species to disturbance has not been quantified. The Udzungwa area contains many rare and restricted range plant species, and furthermore, is arguably Africa's most important single site for primate conservation. Primates also have high potential as indicators. In particular, diurnal monkeys are easily observed, are mostly dependent on tropical forests, and may show a diverse range of demographic and behavioural responses to disturbance.

Human impacts on the monkeys and trees of the Udzungwas are here assessed at two levels: 1) habitat loss, and 2) habitat degradation. The first analytical chapter (Chapter 2) investigates the relationship between monkey species richness and forest fragment size among 22 sites. Multivariate techniques are used to consider the relationship together with other confounding variables. The results show that there is a log-linear species-area relationship, highlighting the importance of large forests (above 150 km^2) for biodiversity conservation. The results also suggest that hunting and isolation have further influenced the species composition, particularly in the smaller fragments.

The second analytical chapter (Chapter 3) assesses vegetation responses to disturbance using 120 plots, along six transects in the heavily disturbed lowland forest of Matundu. Multivariate analyses are used to assess variation in community composition, species abundance, stem density and diversity in relation to disturbance, environmental and topographic variables. With the exception of diversity, all measures of vegetation structure and composition are shown to have been affected by disturbance. In particular, rare species diversity was negatively related to disturbance, and also the presence of large animal paths. Therefore both humans and elephants seem to have had a large impact on the Matundu ecosystem. Three common tree species, *Funtumia africana*, *Vangueria volkensii* and *Parinari excelsa*, that have significant negative correlation with disturbance, could be used as indicators of forest health. Several environmental and topographical correlates with vegetation structure and composition are also identified.

The third analytical chapter (Chapter 4) is a methodological chapter reviewing techniques for estimating density of clustered animals. This is included in the thesis for use in the monkey-habitat analysis in Chapter 5, and because of the continuing intense debate regarding method selection for primates. The aim of the chapter is to develop a simple guide to method selection. It begins with a

summary of the main debate, and an introduction to four alternative methods that are currently employed for surveying primates. The main controversy in the literature surrounds the debate over prioritising for mathematical framework (perpendicular methods) or for minimising correction factors (animal-observer methods). Three of the four methods have shown reasonable accuracy compared to known primate densities, and the fourth has yet to be tested. Perpendicular methods are the most desirable given appropriate field conditions. However problems arising from the five criteria of visibility, habituation of animals, cluster spread, and available resources, may often preclude their use.

Finally, chapter 5 looks at the relationship between monkey relative abundance, density and social grouping versus habitat. Data are presented on four monkey species (Udzungwa red colobus *Procolobus gordonorum*, Angolan black and white colobus *Colobus angolensis palliatus*, Sykes monkey *Cercopithecus mitis* subsp. and yellow baboon *Papio cynocephalus*) counted along the six line transects used for vegetation survey in Chapter 3. In accordance with ecological theory, the four species respond to habitat disturbance as expected from their dietary specialisation, geographic range, and from previous studies on these and closely related species. The Udzungwa endemic red colobus showed the closest relationship with habitat, and may have the most potential as an indicator of forest habitat quality of all taxa in the Udzungwas. Monkey community composition is also suggested as a good indicator of habitat quality. The results suggest that those areas in the Udzungwa lowlands that contain high densities and large groups of red and black and white colobus monkeys contain the best quality forest in terms of vegetation structure and composition. Those containing mainly Sykes monkeys are the poorest quality.

Overall the thesis shows that monkey and tree communities in the Udzungwa Mountains have been negatively impacted by human activities. However, the results also emphasise the importance of disturbed forests for future conservation of biodiversity. Given that most tropical forests have been disturbed to some extent, management of these areas is of paramount importance, as discussed in Chapter 6. The indicator species and communities identified here may be useful for this, both for identifying priority conservation areas and for monitoring forest recovery.

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Preface

The first major step towards the research presented in this thesis began while investigating environmental enrichment of animals at Paignton Zoo Environmental Park, on the south coast of England. The research was for a sandwich year during my undergraduate studies, and I spent the year giving toys to animals and recording their responses. Keeping animals happy in zoo enclosures, and encouraging them to show wild behaviours, is a major goal of all good zoos. I had an amazing year, partly thanks to the zeal of Dr. Amy Plowman, the zoo’s Scientific Officer, who got me interested in monkeys… and statistical analysis, but I’ll forgive her for that! During the year I also raised funds to go on my first expedition to the forests of Tanzania, thanks to a week spent in cage begging zoo visitors for spare change.

While on my first expedition, I heard about the Udzungwa Mountains, home to the most impressive forests in Tanzania, and two of the world’s rarest monkey species. At the time just the thought of visiting the legendary mountains was exciting enough, so when I was offered the chance to work on an expedition exploring unknown areas of the Udzungwas, I jumped at the chance. I will never forget my first glimpse of Udzungwa endemic and IUCN vulnerable *Procolobus gordonorum*… as they bolted as fast as they could away from me, squealing as they went! So my first encounter with the red colobus wasn’t love at first sight (populations that have been hunted have long memories, and the mere sight of a human is enough to spark alarm calls and flight response). However the illusiveness of red colobus in Ndundulu forest made them yet more intriguing, and I soon learned that in other forests of the Udzungwas, the red colobus were far more tame.

I was eventually put in touch with eminent primatologist Dr. Thomas T. Struhsaker, who was involved in a project elsewhere in the Udzungwas, and later I ended up doing collaborative research under his guidance. His energy and passion for the forest and the monkeys soon rubbed off on me, and most importantly for developing this thesis, the opinion that ecological studies must have relevance for conservation management. I was again woken to this need, by an article in the British Ecological Society bulletin (June 2006 – What is the point of you? Ghazoul, J.), lamenting an apparent lack of interest in “real life” issues among some ecologists. Hence I have resolved to direct my research towards dealing with practical issues in conservation, while also maintaining the ecological components required by some academic journals. I also hope that the research is relevant to researchers and conservation managers outside of primatology and the Udzungwa Mountains.

Acknowledgements

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Thanks to all colleagues for comments on various drafts of the thesis, including co-authors on the four main chapters, and examiners Guy Cowlishaw and Dave Raffaelli. Co-authors appear on the various chapters due to supervisory input and/or contribution of data, as indicated in the text. Most data were collected by myself, between September 2003 and April 2005, unless stated in the text.

Throughout the entire nineteen months of fieldwork, I was assisted by Ruben Mwakisoma, in tree identification and logistics. In addition, various assistants helped to measure trees and arrange field supplies, especially Ally Kuruthumu, Lotti Champuka and Arafat Mtui. Ally Kuruthumu also helped with data entry, as did Rosalind Salter. Fieldwork would also not have been possible without many logistical assistants from villages in Morogoro Region, and rangers from the Udzungwa Mountains National Park. I am extremely thankful to all of these assistants.

I thank several experts for their botanical and statistical input, as indicated separately in the main chapters. These include Drs. Sally Bidgood, Mark Bulling, Calvin Dytham, Roy Gereau, Gurab Murshudov, Kaj Vollesen, and Tom Webb, and all other staff at the Royal Botanical Gardens at Kew. Thanks also to Dave Hay for help with computing and acquiring equipment.

Thanks to the Forestry and Beekeeping Division, Tanzania Commission for Science and Technology (COSTECH), Tanzania Forestry Research Institute (TAFORI), Tanzania National Parks Authority (TANAPA), Tanzania Wildlife Research Institute (TAWIRI) and Wildlife Division, for permission to conduct research. I would especially like to thank TANAPA staff from the Udzungwa Mountains National Park headquarters, for help with arranging fieldwork, and for making me feel welcome during my time in Tanzania. Thanks also to the staff at Twiga guesthouse for their hospitality, and for allowing me to store equipment in Mang’ula, and to Michael Case, Nike Doggart and Andrew Perkin for occasional accommodation in Dar es Salaam.

Thanks to Trevor Jones, Drs. Francesco Rovero and Michele Menegon, and other researchers working in Tanzania, for their help and support, and for sharing the experience. Finally, thanks to my family, friends and colleagues in the Environment Department, for their continued support, love and friendship, despite almost four years that I have spent engrossed in this research.

Author’s Declaration

I declare that this thesis represents my own work, except where due acknowledgement is made, and that it has not been previously included in a thesis, dissertation or report submitted to this university or any other institution for a degree, diploma or other qualification. Colleagues that have contributed data or supervision have been included as co-authors on each chapter, however I have played the dominant role in data analysis and writing.

Signed

Andrew Robert Marshall

“In a moment the ashes are made,
but the forest is a long time growing”

Seneca

Chapter 1 - Introduction to Thesis

Small parts of this chapter published in:

Lovett, J.C., Marchant, R., Marshall, A.R., Barber, J. (2007) Tropical moist forests. In: R. Hesler and Harrison (eds.) Biodiversity Under Threat. Royal Society of Chemistry.

Chapter 1 – Introduction to Thesis

Tropical Forest Disturbance and Loss

Habitat degradation and loss are the greatest threats to terrestrial species (Baillie et al. 2004). Estimates of annual loss of tropical forest range from 8.7 – 12.5 M ha (Chapman & Peres 2001; Mayaux et al. 2005). An area between half and equal size to this is degraded by selective logging each year (Achard et al. 2002; Asner et al. 2005). Loss and degradation of tropical forests are a global concern as more than half of the world's species are found in tropical forests, despite covering only 7 % of the world's surface (WRI 1992). Subsequently, the number of species threatened with extinction in tropical forests is predicted to increase (Whitmore & Sayer 1992). Tropical forest loss and degradation also have implications for climate change, hydrology, nutrient cycling, and natural resource availability (Whitmore 1998). Restoring degraded forests may therefore be one of greatest challenges for ecologists this century (Duncan & Chapman 2003).

Most forms of disturbance are undetectable or only marginally detectable using remote methods (Peres et al. 2006). Assessing the consequences of disturbance by ground surveys, is therefore a major priority for conservation management. Fully quantifying the effects of disturbance would require painstaking work due to the massive number of species involved. However basic criteria for assessing ecosystem health and habitat composition/structure are rarely determined (Balmford et al. 2003). Selection of key species as "indicators", "guilds", or "functional types", can assist in making more rapid assessments (Skorupa 1986 & 1988; Landres et al. 1988; Gondard et al. 2003). Determining the impact of disturbance on rare species is also of importance to determine habitat requirements for management. However testing of species-habitat relationships is often insufficient (Lindenmayer 1999). This is complicated further because disturbance is typically unquantified, and disturbed forests are typically humid, unattractive, and difficult to negotiate (Fig. 1).

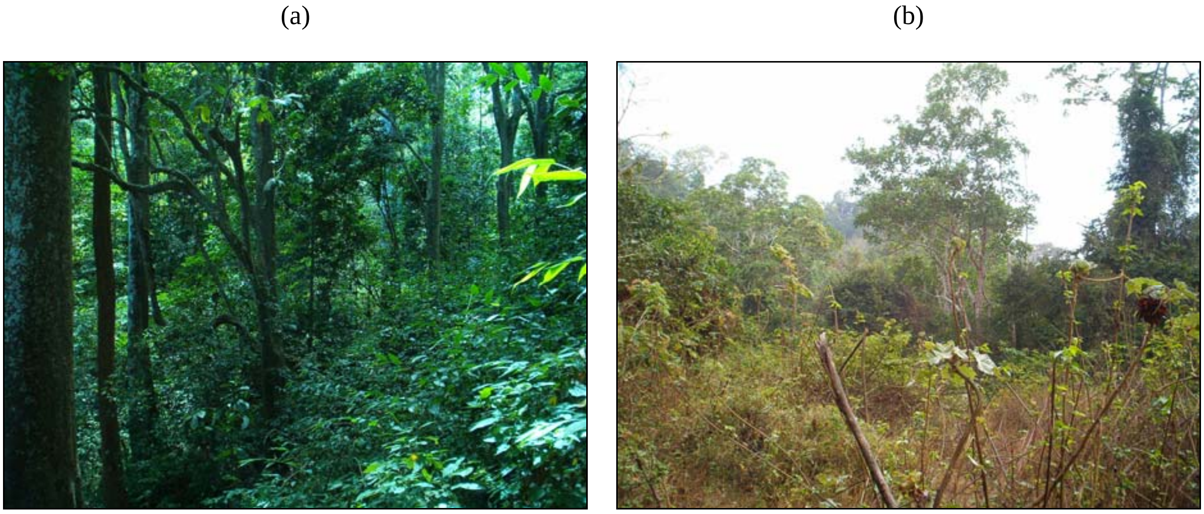

Figure 1. Photographs of (a) closed-canopy forest and (b) heavily disturbed forest in Matundu, Udzungwa mountains, Tanzania.

Selection of Study Site

Eastern Arc Mountains

To investigate the relationships between habitat quality and rare/indicator species, a study site was selected where both anthropogenic disturbance and conservation value were high. The Eastern Arc Mountains, which extend from south-east Kenya to southern Tanzania (Fig. 2), are well known for their conservation value and high human pressure. Global analyses have shown that the Eastern Arc is one of the world's most important areas for the conservation of biodiversity (Burgess et al. 2006). Per unit area, the region also has more endemic species, than all the world's richest biodiversity "hotspots" (Myers et al. 2000), and can least afford further loss of habitat (Brooks et al. 2002). Economic analysis of ecosystem services suggests that the Eastern Arc is worth $620 million to the Tanzanian economy, even without full consideration of the value for water and tourism (Burgess et al. 2006). Most of these forests have legally protected status, however a lack of funds and inadequate management capacity, mean that forests continue to be degraded. Tanzania has one of the most rapidly increasing human populations in the world, making it one of the most susceptible to future species loss (Baillie et al. 2004). It has been reported that human activity has resulted in the loss of 77 % of Eastern Arc forest in the last 2,000 years, most of which occurred within the last 200 years (Schmidt 1989; Newmark 1998). A high proportion of the remaining forest in the Eastern Arc is degraded, however like the majority of tropical forests (Asner et al. 2005), the overall extent of degradation is unknown.

Despite the concerns about disturbance in the Eastern Arc, previous published studies on the impacts of habitat loss and degradation on species composition have been few, and have been biased towards the East Usambara Mountains. The number of understorey bird species in nine forest fragments of the East Usambara Mountains (Fig. 2), was closely related to the size of forest fragments and distance to the nearest source population (Newmark 1991). The absence of seed-dispersing animals in small fragments has been further shown to limit regeneration of some trees (Cordiero & Howe 2001 and 2003). Also in the East Usambaras, vegetation plots showed that stem density and variation in species richness differed between mature and formerly disturbed forests, but not species richness (Huang et al. 2003). A separate study made a similar observation for three sites elsewhere in the East Usambaras, where stem density, invasive species density and ground cover varied with disturbance, but not tree species composition or understorey bird species richness (Newmark 2006). However, 16 yr data revealed that the responses of birds varied between feeding guilds, with terrestrial insectivores most negatively affected (Newmark 2006). Concern about disturbance in Amani forest in the East Usambara Mountains, has led to the establishment of permanent sample plots to monitor forest recovery (Madoffe et al. 2006). Here, species richness has also been negatively affected by disturbance (Schmidt 1989 cited by Madoffe et al. 2006). In the West Usambaras, canopy species composition has been affected by decay of *Newtonia* *buchananii* trees, caused by stem cracks in disturbed areas (Mrema et al. 1998). In the Uluguru Mountains, forest loss has resulted in biodiversity loss and the local disappearance of endemic snakes and near-endemic birds (Burgess et al. 2002).

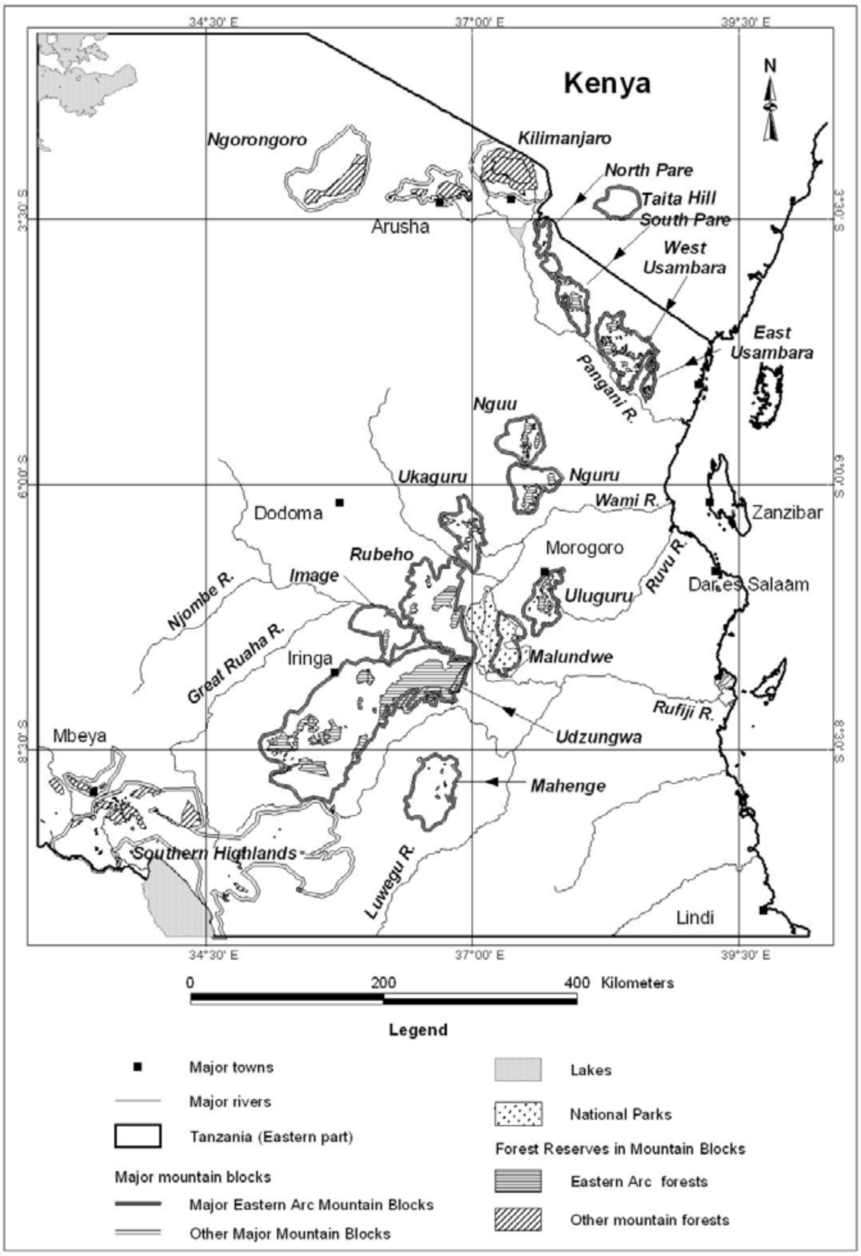

Figure 2. Map of Eastern Arc forests in Tanzania and Kenya.

Udzungwa Mountains

The Udzungwa Mountains (or the "Udzungwas"), are found at the southern end of the Eastern Arc Mountains (Fig. 2). The natural habitat of the 10,000 km^2 area is varied, comprising many fragments of forest surrounded by woodland, bushed grassland and agriculture (Fig. 3). Small human settlements are also prevalent (Fig. 3), and there have been anthropogenic impacts upon most forests. Despite this, more primary, closed-canopy forest is found in the Udzungwas than any other area in the Eastern Arc (Burgess et al. 2006). The area is home to many rare and restricted range species, including 102 vertebrate and 36 tree species, that are endemic or near-endemic to the Eastern Arc. A study of spiders also found that around 80 % of 149 species were previously undescribed, with high species turnover compared to a site only 20 km away (Sorensen 2004). At the time of writing, a Web of Science search revealed that only 36 published studies mention "Udzungwa" or "Uzungwa", compared to 558 mentioning "Serengeti", Tanzania's most famous National Park (http://portal.isiknowledge.com). This shows the imbalance in research among Tanzania's National Parks, and bias towards habitats supporting large numbers of big game, rather than those of importance to biodiversity and endemism.

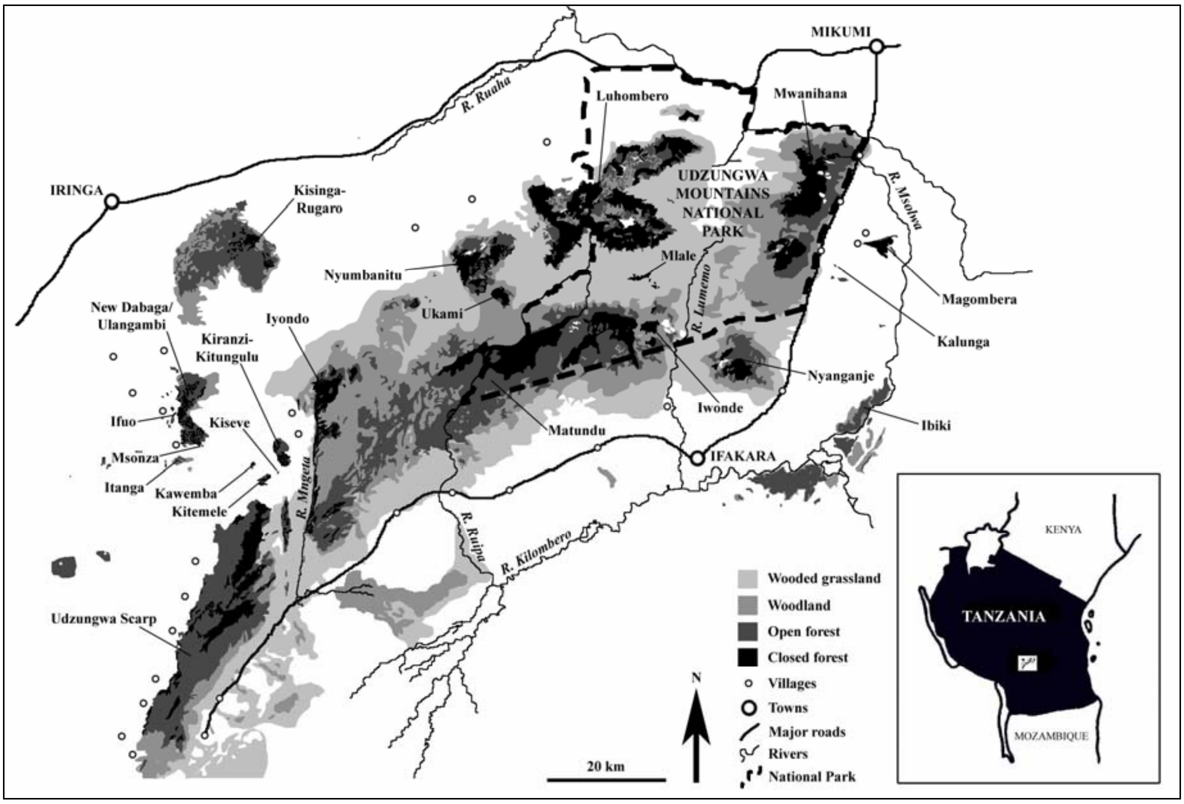

Figure 3. Habitat map of the Udzungwa Mountains (from Chapter 2).

Habitat quality is quite variable between the many forest fragments in the Udzungwas. In the Udzungwa Scarp forest Reserve (Fig. 3), 367 observations of disturbance were observed, and the primary timber species have almost been exhausted (Zilihona et al. 1998). In the same forest, regeneration of timber species *Ocotea usambarensis* was poor, whereas pioneer species were regenerating in gaps (Shangali et al. 1998). Comparisons between disturbed and undisturbed forests, have shown that many rare and restricted-range species have been impacted by forest disturbance in the Udzungwa Mountains (Fjeldså 1999; Frontier Tanzania 2001; Marshall et al. 2005). Ongoing studies of primates, duikers and vegetation in the Udzungwa Mountains (including the results presented in this thesis), are only now beginning to reveal the structural and microhabitat details that contribute to the biodiversity-habitat relations in the Eastern Arc (Struhsaker et al. 2004; Rovero & Struhsaker in press; this study). These studies, together with those from the

Usambaras above, suggest that forest size, connectivity and structure, must be conserved to maintain the high biodiversity value of the region.

Matundu Forest

The majority of this study was conducted in the large (522 km^2) forest of Matundu (Fig. 3). The habitat comprised mostly semi-deciduous forest, with deciduous forests on some of the drier ridgetops and slopes. Matundu was selected for several reasons. The low elevation range (273-800 m) was a primary deciding factor, to minimise confounding variables that may have obscured the effects of disturbance. Furthermore, lowland tropical forests are among the world’s most threatened habitats (Collins 1990; Vieira & Scariot 2006). The high variation in habitat disturbance was also a factor, so that a range of levels of disturbance could be assessed. Logging by various parties up until the 1980s has created large areas of open-canopy forest dominated by tangled climbers, especially *Uncaria africana*. The open-canopy has been further maintained by elephants, which are common in Matundu. The ratio of closed- to open-canopy forest in Matundu is approximately 4:1 (Fig. 3). Logging in Matundu occurred more than 15 years prior to this study, hopefully giving sufficient time for ecological effects to be detected (a concern following previous studies in the Usambara Mountains; Newmark 1998). Finally, Matundu was poorly explored prior to this study. Its proximity and size suggest that it has great potential for conservation of the rare and endemic species of the Udzungwa Mountains. Despite this, previous studies have given Matundu low priority for conservation compared to other Udzungwa forests (Dinesen 1998; Dinesen et al. 2001).

Selection of Study Taxa

Monkeys were selected for this study, as they can be easily observed, are often susceptible to habitat degradtion, and therefore have potential as indicators of ecosystem health. An estimated 90 % of primates live in tropical forests (Rowe, 1996) and are therefore at great risk from the effects of fragmentation and disturbance. An estimated one in four primate taxa are at risk of extinction worldwide, with 30 % of taxa at risk in Africa, primarily due to habitat loss (Mittermeier et al., 2005; Chapman et al., 2006). Primate abundance has also been closely linked to habitat in several species (e.g. Johns & Skorupa 1987; Struhsaker 1997; Cowlishaw & Dunbar 2000). The conspicuous nature of diurnal primates has allowed detailed investigation into behavioural responses to disturbance. Impoverished environments may lead to increased competition and disruption of their complex social organisation. Large social groups may be unsustainable where there is low resource availability, and therefore in some species social group size has been closely related to habitat quality (e.g. Struhsaker 1975 & 1997; Struhsaker & Leland 1979; Dunbar 1988; Janson 1988; Janson & Goldsmith 1995; Struhsaker et al. 2004).

Monkeys were also selected for study because of the unique community resident to the Udzungwa Mountains. With twelve primate species, including three endemic to southern Tanzania, the Udzungwas are arguably Africa's most important area for primate conservation (taxonomy follows Grubb et al. 2003; Jones et al. 2005). The IUCN endangered Sanje crested mangabey (*Cercocebus galeritus sanjei*) discovered in 1979, only occurs in two forests (Udzungwa Scarp and Mwanihana; Fig. 3). The recently discovered kipunji monkey (*Rungwecebus kipunji*), discovered in 2004, only occurs in Luhombero forest (Fig. 3) and on Mount Rungwe in the Southern Highlands (Jones et al. 2005; Davenport et al. 2006). The IUCN vulnerable Udzungwa red colobus (*Procolobus gordonorum*; Figs. 4 and 5) is also endemic to the Udzungwa Mountains, plus a handful of adjacent forests. A third monkey, the Angolan black and white colobus (*Colobus angolensis palliates*; Fig. 4), is limited to the Eastern Arc and coastal forests, and only a few other locations (Rodgers 1981; Dinesen et al. 2001; Anderson et al. in press a). Other monkeys present include Sykes monkey (*Cercopithecus mitis*), yellow baboon (*Papio cynocephalus cynocephalus*) and vervet monkey (*Chlorocebus aethiops*). The remaining primates are galagos (Butynski 1998; A. Perkin pers. comm.), and are not discussed in this thesis.

(a) (b)

Figure 4. Photographs of the two main study species, (a) Angolan black and white colobus (*Colobus angolensis palliatus*) in canopy tree *Antiaris toxicaria*, and (b) Udzungwa red colobus (*Procolobus gordonorum*) in tangled climbers dominated by *Uncaria africana*.

The primary focus of the thesis is on the two colobines (Figs. 4 and 5), and also Sykes monkey. This is because these species are all common to the forests, thus allowing full statistical comparison of variability with habitat. Colobine monkeys are especially conducive to observational studies as they are often easily visible due to their arboreal lifestyle and long periods spent resting, and are easily detected from the loud noises made when jumping. Their relatively cohesive social groups also permit detailed analysis of group sizes (Struhsaker 1975 & 1997; Struhsaker et al. 2004; Marshall et al. 2005). Given the extremely limited numbers, distributions and low level of protection of most other taxa of *Procolobus*, the Udzungwa red colobus also provides a unique opportunity to observe the habitat requirements and ecology of this threatened genus. Across

Africa, monkeys of the genus *Procolobus* are in decline, with nearly 40 % of taxa threatened with extinction (Struhsaker 2005). The more widespread Angolan black and white colobus is also of interest, as there have been very few studies of this species. Prior to this study, even differences in coat colouration of two sexes was undocumented, despite being distinguishable as soon as infants lose their white natal coat (Fig. 6; pers. obs.). Limited available studies suggest that *Colobus angolensis* is more sensitive to forest degradation than congener *Colobus guereza* (Marshall et al. 2005; Anderson et al. in press b), however data are still limited.

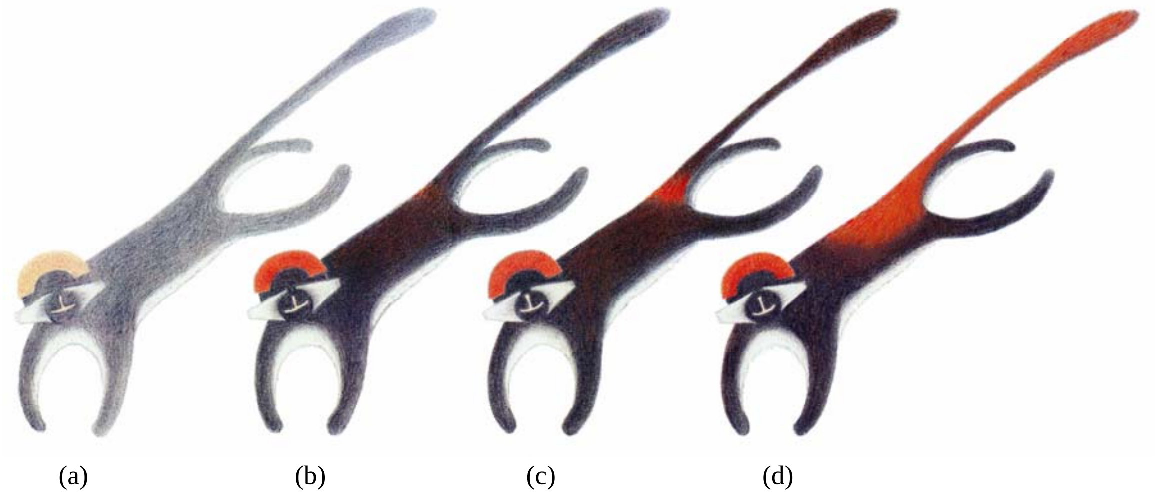

Figure 5. Variation in coat colour of the Udzungwa red colobus (*Procolobus gordonorum*). (b) and (c) show typical colouration, (d) shows red-backed colouration seen occasionally (and perhaps more frequently in the western forests of the Udzunwgas), and (a) shows pale colouration seen only once in Matundu forest.

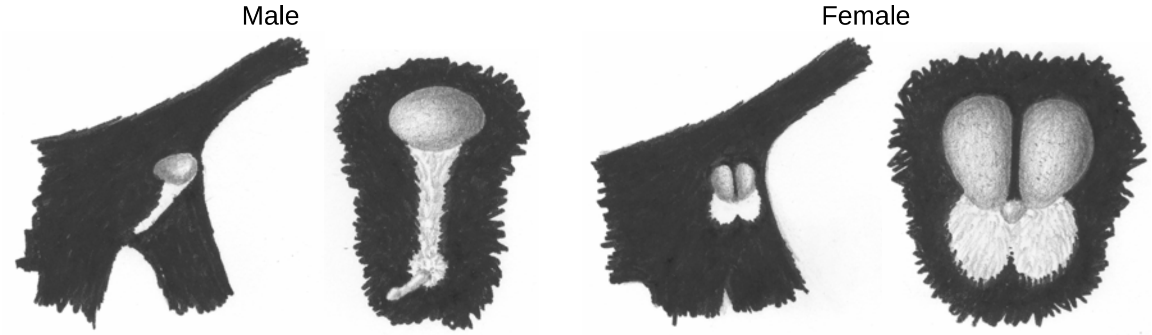

Figure 6. Differentiation between sexes in *Colobus angolensis palliatus*, based on callosities (male joined, female seperate) and white hair around groin and anus (male linear, female two-tufted to rounded).

Thesis Aims

The aims of the thesis are as follows:

1. To determine the impacts of habitat disturbance and loss on rare monkey and tree communities.
2. To investigate the potential of monkeys and trees to act as indicators of habitat quality.
3. To compare and review methods for density estimation and ecological modelling.
4. To update information on the range and density of rare and restricted-range species.
5. To provide new information about a poorly explored area within an international biodiversity hotspot.
6. To help refine the vegetation map of the Udzungwas.
7. To make suggestions for conservation management.

Chapter Outline and Objectives

The research is presented as a series of chapters (2 to 5), in the style of scientific papers. Each chapter can be understood independently from the rest, while contributing to the specified aims of the thesis, as explained in the chapter outlines below. While this means that there is some repetition between chapters, this format has been selected over a more traditional thesis format, to ease subsequent publication of the research. The four main chapters are grouped to deal with the two levels of disturbance, beginning with habitat loss (chapter 2), followed by habitat degradation (chapters 3 and 5), with a methodological review between (chapter 4). After the four main chapters there is a summary discussion (chapter 6), to bring all of the findings together and to present overall conclusions and speculations for future research. To maintain the paper-style format, references cited within each chapter are listed at the end of each chapter.

Chapter 2 - The Species-Area Relationship in a Threatened Monkey Community: Controlling for Confounding Variables

The thesis starts at a broad spatial scale, with analysis of trends in monkey communities among all of the main forest fragments of the Udzungwa Mountains. The principal aim of this chapter is to assess the impact of habitat loss, which has divided the Udzungwa landscape into a number of isolated forest fragments. The chapter therefore assesses the relationship between monkey species richness and fragment size, as a test of Island Biogeography Theory (MacArthur & Wilson 1967). The impetus for the chapter comes partly from a recent study suggesting that the species-area relationship does not exist for African primates (Harcourt & Doherty 2005). Unlike this study, a number of covariates are introduced to control for confounding variables. This is because factors such as habitat quality, hunting and elevation are likely to have a major influence on any such trends. Incorporation of multiple variables has been facilitated by recent advances in multivariate techniques (Johnson & Omland 2004; Rushton et al. 2004), and I take advantage of these developments throughout the thesis. This chapter also updates current knowledge of monkey species distributions and habitat in the Udzungwa Mountains.

Chapter 3 - Tree Species and Community Gradients for Assessing Habitat Disturbance

Following the more broad scale approach of chapter 1, this chapter is an analysis of vegetation at the microhabitat level. Plots of large trees are used to assess the impact of forest disturbance on tree communities and species. The impacts of disturbance on forest communities depends on the level of disturbance and the species composition (Horn 1974; Connell 1978; Denslow 1987; Silva et al. 1995; Schnitzer & Carson 2001; Duncan & Chapman 2003; Hitimana et al. 2004; Toniato et al. 2004; Okuda et al. 2004; Villela et al. 2006). Two sets of species are analysed in detail. Firstly, abundant species are assessed for their potential as indicators of habitat quality. Secondly rare and restricted-range species are assessed to determine the cost of disturbance, to assess the importance of Matundu for conservation, and to make suggestions for management. While this chapter is useful for assessment of habitat structure and vegetation composition, it also provides habitat data for correlating with monkey demographic variables in chapter 5.

Chapter 4 - Line-Transect Methods for Estimating Density of Clustered Animals: A Review and Guide with Lessons from the Primates

The fourth chapter tackles the controversial issue of methods for estimating density from line transect counts, and leads into the final chapter which employs some of these methods. There has been extensive debate on the alternative measurements that can be used for estimating density of primates from such data (e.g. Struhsaker 1975 & 1997; National Research Council 1981; Brockelman & Ali 1987; Chapman et al. 1988; Whitesides et al. 1988; Fashing & Cords 2000; Plumptre 2000; Plumptre & Cox 2006). The continuing debate surrounds: a) the use of animal-observer distance versus perpendicular distance to the transect; b) whether to determine individual densities by use of cluster sizes estimated during census walks, independent cluster counts, or counts of only those individuals seen during census walks; and c) whether or not to incorporate information on cluster spread. The chapter aims to bring the many arguments together and to clarify misunderstandings in the literature. The guide is limited to four alternative methods that are likely to be the most applicable given limited time, resources and observers. From this a simple guide to method selection is presented with choices based on the key factors of visibility, level of habituation of animals, cluster spread, study aims, time and resources.

Chapter 5 – Monkeys as Indicators in Lowland Udzungwa

The final analytical chapter assesses monkey-habitat relationships in Matundu forest using four species with differing ecologies. Because of respective decreasing level of dietary specialisation, and geographic range, red colobus are expected to be the most susceptible to habitat degradation, followed by black and white colobus, Sykes monkeys and then yellow baboons. This pattern has been seen in previous studies of these and closely related species (Struhsaker 1975 & 1997; Chapman et al. 2000; Struhsaker et al. 2004; Marshall et al. 2005; Rovero et al. 2006; Rovero & Struhsaker in press). This chapter includes coarse- and fine-scale analyses of the relationship between monkey distribution and social group size, verses topographic and anthropogenic variables, and vegetation variables from chapter 3. Following on from chapter 4, we also estimate population densities, and therefore assess the effect of habitat disturbance on the conservation value of Matundu. This is intended to update published population estimates for red colobus monkeys, which have so far only been based on unsystematic census walks (Dinesen et al. 2001). Like chapter 3, the results are used to determine habitat requirements of rare species, and to determine conservation priorities for management. Beyond the results of this chapter, the discussion puts the findings in context with previous studies in the Udzungwa Mountains and elsewhere, to draw conclusions about the use of primates as an indicator community, and about the ecology and conservation of Udzungwa monkeys.

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Chapter 2 - The Species-Area Relationship in a Threatened Monkey Community: Controlling for Confounding Variables

The Species-Area Relationship in a Threatened Monkey Community: Controlling for Confounding Variables

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Abstract

This study investigates the relationship between species richness and fragment size among monkeys in forests of an area of international importance for biodiversity conservation. There have been many empirical tests of the species-area relationship, however few have dealt with the many confounding variables. Here we update current knowledge of the distribution of seven monkey species found in the Udzungwa Mountains. Using these data from 22 forest fragments, we employ multivariate techniques to determine the species-area relationship, controlling for four variables relating to human pressure and habitat. Unlike a recent meta-analysis for Africa, species richness is shown to have a log-linear relationship with forest area. Correlation between forest area and elevation range suggests that the relationship is largely due to increasing habitat diversity in large forests. Hunting has also had a significant negative effect on species richness in the smallest forests, coupled with the effect of isolation. However hunting may correlate with other unquantified forms of disturbance such as disease. The major conclusion is that large forests support more species, with forests above 150 km^2 being the most important for conservation. The implications for conservation biology and landscape management are discussed.

Key words: Eastern Arc, fragmentation, generalised linear models, primates, tropical forest

Introduction

Tropical forests contain more threatened species than any other terrestrial biome, largely due to habitat destruction (Ricketts et al. 2005). In Africa up to two thirds of the original forest area has now disappeared (Chapman et al. 2006). For species living in fragmented forests, traditional theory predicts an “island effect” whereby species richness declines with increasing isolation and decreasing fragment size (MacArthur & Wilson 1967). There are hundreds, possibly thousands of empirical studies that show species richness declining with fragment size (Lomolino 2000). While the existence of the species-area relationship is widespread, the types of relationship are still under debate (He & Legendre 1996; Lomolino 2000 & 2002; Williamson et al. 2001 and 2002; Tjørve 2003). Determining the shape and rate of decline allows prediction of extinction and extrapolation of species richness (Tjørve 2003), and therefore has major relevance for conservation planning (Lomolino 2000; Desmet & Cowling 2004; McCarthy et al. 2006; Watling & Donnelly 2006).

Despite acceptance of the species-area relationship among ecologists and conservation biologists, there are many confounding factors and we are only beginning to understand the effects of fragmentation on species composition (Williamson 1989; Hanski & Gilpin 1997; Forman 1997; Debinski & Holt 2000; Ross et al. 2002; Marsh 2003). A difficult issue for the species-area relationship is that the impact of disturbance may be greatest in small areas of habitat (McGuinness 1984). Human disturbance in particular can mean that species are exposed to the “double jeopardy” of declining forest area and increasing human pressures (Harcourt et al. 2001). Analysis of species-area curves can be somewhat redundant if there are many confounding variables such as this (McGuinness 1984). However, studies of the species-area relationship that account for the confounding variables are few. Multivariate techniques have obvious potential for dealing with confounding variables, given that the pitfalls are now largely appreciated (Johnson & Omland 2004; Rushton et al. 2004; Whittingham et al. 2006) and that software is now free to download (e.g. http://cran.r-project.org/).

An estimated 90 % of primates live in tropical forests (Rowe 1996) and are therefore at great risk from the effects of fragmentation. One in four primate taxa are at risk of extinction worldwide, with 30 % of taxa at risk in Africa, primarily due to habitat loss (Mittermeier et al. 2005; Chapman et al. 2006). In the neotropics and Asia, the trend in decreasing diurnal primate species richness with fragmentation, supports traditional theory (Harcourt & Doherty 2005; Michalski & Peres 2005). In East Africa, floral diversity, forest size and distance to Pleistocene refugia, are all considered important for primate conservation (Struhsaker 1981). Furthermore, primate species richness per African nation is positively correlated with the area of available habitat (Cowlishaw 1999). However, a recent meta-analysis for Africa failed to find any relationship between diurnal primate species richness and forest fragment size (Harcourt & Doherty 2005). This is surprising given the aforementioned risks of extinction due to habitat loss. Clearly more research is needed to investigate this anomaly.

The Udzungwa Mountains of Tanzania have great potential for investigating the species-area relationship for African primates. With twelve species, the Udzungwa primate community is one of the most species rich in East Africa and one of the most important for conservation in the continent (Butynski et al. 1998; Jones et al. 2005). The Udzungwas are further suited for species-area analysis as they cover a large area (10,000 km^2) with around 1,500 km^2 of forest, including around 570 km^2 of closed canopy forest (excluding the western Udzungwa forests of Mufindi, which are not included in this study). The forest has been divided into many fragments of varying size (Fig.

1). Research into the Udzungwa forests and primates has increased rapidly in recent years. Most research has focused on the endemic Udzungwa red colobus *Procolobus gordonorum*, which has reduced density and group size in degraded and high elevation forests (Struhsaker et al. 2004; Marshall et al. 2005; Rovero et al. 2006; Chapter 5). Dinesen et al. (2001) give the most recent summary of monkey distribution in the area, but only now is the community composition of all of the major forest fragments known. There has been no published research into the specific effects of patch size on Udzungwa primates, however a positive relationship between mammal species richness and fragment size, has been found among six northeastern Udzungwa forests (Jørgensbye 2004).

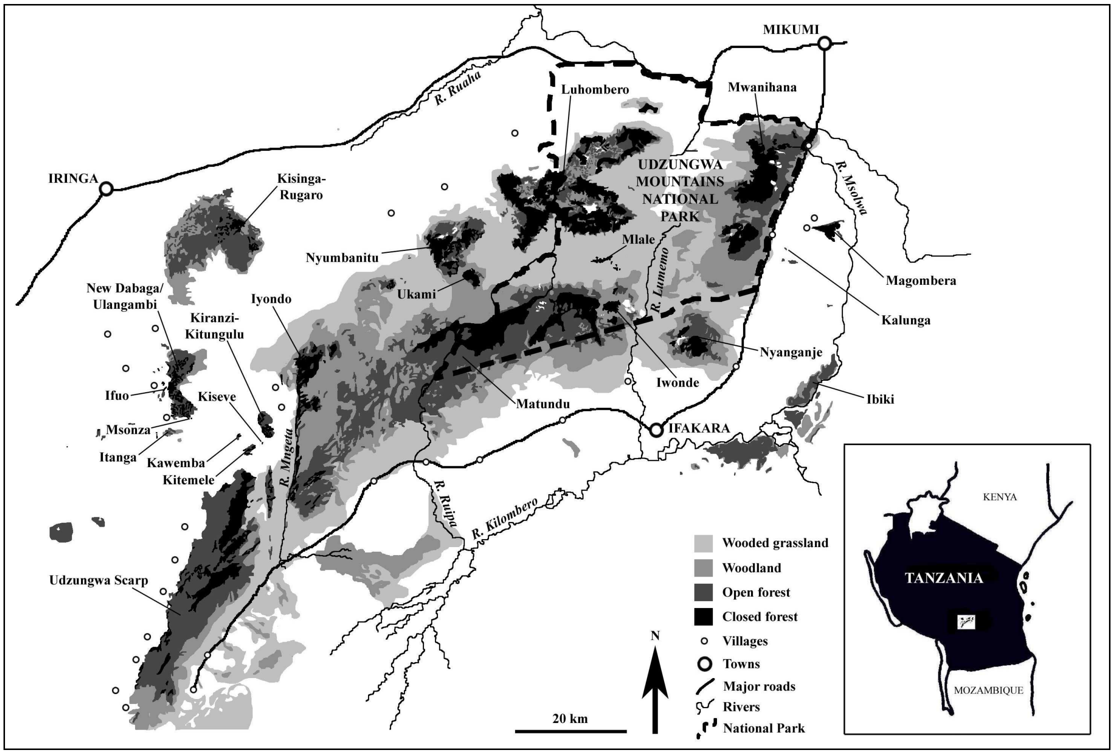

Figure 1. Habitat map of the Udzungwa Mountains based on Landsat imagery and limited ground survey / aerial overflights. Areas of unclassified habitat are mostly agriculture and bushland, with dry *Commiphora* and *Acacia* woodland in the north. This map excludes the forests of Mufindi to the west, which were not included in this study.

Aim and Objectives

Our aim is to test the species-area relationship using monkeys and forest size in the Udzungwa Mountains. In achieving this, our objectives are 1) to explore the potential of linear models for testing the presence and form of the species-area relationship, while controlling for confounding variables, and 2) to determine the major factors influencing species richness. The results are used to test traditional theory, to provide practical information for managing tropical forests and to update the known range of monkeys and forest habitat within this area of international conservation importance.

Methods

Study Areas and Species

Descriptions of the 22 forest fragments covered in this study are presented in Table 1, including size, elevation, levels of monkey hunting, and forest degradation. The fragments range in size from 0.06 to 522 km^2, and in elevation from 300 to 2500 m. Forest sizes were updated from published estimates using Landsat imagery (Landsat ETM+; Global Land Cover Facility/U.S. Geological Survey; Oct 25th and Nov 1st 1999; Paths 167-8; Rows 65-6). Sizes and habitat classifications (Fig. 1 and Table 1), were verified where possible from ground survey and aerial overflights. Some of the forest sizes given in Table 1 are smaller than previous estimates (e.g. Dinesen et al. 2001). In the northeastern forests of Kisinga-Rugaro, Iyondo and New Dabaga/Ulangambi, pitsawing and forest clearance have caused reduction in forest area by around 95 km^2. Forest degradation has occurred within most fragments, and the sites therefore contain varying proportions of open-canopy (heavily disturbed) and closed-canopy forest (Table 1). We also found that 1:50,000 topographical maps used to make previous estimates of forest cover (Government of the United Republic of Tanzania 1983), misclassified some areas of woodland and bamboo as forest. While the habitat classification presented is still a work in progress (e.g. the amount of bamboo in Udzungwa Scarp forest remains unmeasured and topography is not accounted for), we feel that the forest cover estimates presented are sufficient for this study.

The relative level of hunting of monkeys (Fig. 1) was determined from interviews with villagers, personal observations, Nielsen (2006), Pedersen & Topp-Jørgensen (2000) and Nielsen (pers. comm.). Because hunting could not be measured quantitatively, hunting was considered “high” in an area where there were many records of hunting, and “low” if only known from one or two accounts. Most hunting occurred in the northern and eastern forests, in areas dominated by the Hehe tribe. The Hehe people eat monkeys, however among most other tribes in the area, eating of monkeys is a taboo. Despite the taboo, monkeys have been hunted by other tribes in Matundu and Udzungwa Scarp forests, to make shawls used in tribal dancing, and sometimes also for meat. Crop-raiding monkeys including Sykes monkeys, vervet monkeys and yellow baboons are also sometimes killed. The lack of hunting in some fragments (e.g. Magombera and Kalunga), can be seen in the behaviour of colobus monkeys, which do not flee upon sighting humans, unlike populations in the northeastern fragments.

The seven monkeys known within the range are the Udzungwa red colobus (*Procolobus gordonorum*), Angolan black and white colobus (*Colobus angolensis palliatus*), Sykes monkey

(*Cercopithecus mitis*), vervet monkey (*Cercopithecus aethiops*), yellow baboon (*Papio cynocephalus*), Sanje mangabey (*Cercocebus galeritus sanjei*), and the recently discovered kipunji monkey (*Rungwecebus kipunji*). Three of these species are endemic to southern Tanzania and are of international importance for conservation as defined by IUCN red-list criteria (*R. kipunji* – Critically Endangered; *C. sanjei* – Endangered; *P. gordonorum* – Vulnerable; Baillie 2004; Jones et al. 2005).

Table 1. Description of forest fragments used for investigating the species-area relationship in the Udzungwa Mountains. Forest size and elevation was taken from Dinesen et al. (2001), Struhsaker et al. (2004) and 1:50,000 maps. Landsat imagery and limited ground survey were used to estimate the sizes of forests that deviated markedly from published estimates, unpublished forest sizes, and coverage of closed canopy forest. Isolation is defined as the distance to the central block of wooded/forested habitats in Fig. 1.

Forest	Size (km^2)	Closed canopy (km^2)	Isolation (km)	Elevation (m)	Hunting of monkeys
Matundu	522.0	104.4	0.0	273-800	low
Udzungwa Scarp	230.0	100.0	0.0	300-2050	high
Luhombero	221.0	147.3	0.0	1350-2500	low
Mwanihana	177.0	106.2	0.0	300-2300	none
Kisinga-Rugaro	99.0	6.19	17.5	1600-2300	high
Nyumbanitu	49.0	24.5	0.0	1350-2350	low
Nyanganje	42.0	21.0	0.0	300-950	none
Iyondo	36.0	21.6	0.0	1000-1850	low
New Dabaga/Ulangambi	32.0	12.8	11.5	1740-2100	high
Ibiki	19.5	0.0	16.0	250	none
Kiranzi-Kitungulu	11.0	4.4	4.0	1520-1934	low
Magombera	10.2	8.5	9.5	286	none
Ukami	6.0	4.8	0.0	1100-1600	none
Iwonde	5.0	5.0	0.0	1050-1500	none
Kitemele	2.99	1.2	3.5	1440-1820	high
Kalunga 1998 *	2.65	0.0	3.5	280	none
Mlale	2.0	2.0	0.0	1040-1180	none
Kawemba	0.57	0.23	7.5	1520-1700	high
Ifuo	0.57	0.11	27.0	1940-2000	high
Itanga	0.42	0.0	17.0	1860-2020	high
Kiseve	0.22	0.22	5.5	1540-1730	high
Kalunga 2005 *	0.1	0.0	3.5	280	none
Msonza	0.06	0.06	1.8	1780-1880	high

* Data for Kalunga forest were obtained before and after clearance for agriculture.

Data Collection

The data presented here are for diurnal primates (i.e. monkeys). The nocturnal primate community (galagos or bush babies) could not be determined with certainty due to cryptic behaviour. The monkey species composition of most fragments was determined from field visits between 1999 and 2005 by Marshall (Matundu, Luhombero, Mwanihana, Nyumbanitu, Iyondo, New Dabaga/Ulangambi, Magombera, Kalunga and Msonza), Jørgensbye (Kiranzi-Kitungulu, Kitemele, Kawemba, Ifuo, Itanga, Kiseve and Msonza) and Rovero (Udzungwa Scarp, Luhombero and Mwanihana) lasting a minimum of 16 days each. The forests of Ukami and Iwonde were visited by Marshall for only five and two days respectively. Due to their small size, we felt that this was adequate to determine the resident species composition. Presence of species in other forests and from Kalunga forest before clearance for agriculture, were determined from the literature and personal communications (Ehardt et al. 1999; Dinesen et al. 2001; Dinesen pers. comm.). The forest of Ibiki was visited for only one day by Marshall and for one day by Thomas Struhsaker. Information for Nyanganje was obtained following conversation with Udzungwa National Park ecologist Abel Mtui, after only a three-day trip. Ibiki and Nyanganje were not included in the statistical analyses, because the resident status of baboons could not be determined from these short trips. However the species composition data are presented for the purpose of updating range information.

For all forests, monkey species were considered "resident" in a fragment if at least one social group was seen. Species were not considered resident if only individuals or bachelor groups were seen. Furthermore, monkeys were considered "transitory" rather than resident, if only seen at the forest edge, or not continually present. This mostly applied to baboons and vervet monkeys because these species are typically savanna-dwelling, and were assumed to utilise adjacent non-forest habitats. In one forest (Kalunga 2005), the last remaining black and white colobus group was also transitory, as they spent large amounts of time feeding in an adjacent rubber (*Hevea* sp.) plantation.

Statistical Analyses

A generalised linear model (GLM) using poisson error and log link functions (Maindonald & Braun 2003), was used to model the relationship between species richness and independent variables as listed above, using the computer program *R* (version 2.2.1; http://cran.r-project.org/). Quantitative independent variables included forest area (Table 1), habitat disturbance (the proportion of closed canopy forest; Table 1) and isolation. For the purpose of this study, isolation was defined as the distance to the central block of wooded/forested habitats in Fig. 1. This was preferred over other measures of isolation as the non-forested habitats within this block were considered less of a barrier to dispersal than the human-dominated landscape outside of this block. Mean elevation was not included as an independent variable because this would be a poor descriptor for the larger forests. Instead we included elevation range (maximum minus minimum elevation). Given that this is the main determinant of vegetation community composition in the Udzungwa Mountains (Lovett et al. 2006), this can be considered an approximate measure of habitat diversity. Finally we included two qualitative (dummy) independent variables, deciduousness (mostly semi-deciduous or mostly evergreen) and hunting (zero, low or high; Fig. 1). The reason for including deciduousness as a variable was to control for variation in habitat type between fragments. While habitat variation is far more complex than this dichotomy, vegetation data are not available to improve on this.

Spearman's rank correlation was first used to check for autocorrelation between independent variables. Elevation range showed significant positive correlation with forest area ($r_s = 0.805$, $p < 0.001$, $n = 21$). Elevation range also showed less correlation to species richness ($r_s = 0.589$) than forest area versus species richness ($r_s = 0.813$) and was therefore dropped from the analyses (following Schadt et al. 2002). To reduce skewness, $\log_{10}$ and square-root transformations (shortened to "log" and "√" in the text), were then applied to the variables forest area and isolation respectively. Because of recent concerns raised over automated model selection (Whittingham et al. 2006), we employed two methods for GLM model selection, including a full (global) model, and backward stepwise regression using the Akaike Information Criterion (AIC). The influence of potential outliers in the GLM model was determined by calculating Cook's Distance values. Outliers were considered to have serious influence if near to or greater than one (Maindonald & Braun 2003). We also employ univariate tests of Spearman's rank correlation, using Hochberg corrections to adjust for repetitive testing (Hochberg 1988). The Hochberg method was preferred over other multiple endpoint adjustments (e.g. Bonferroni and Holm correction), due its increased power (Hochberg 1988; Wright 1992). All analyses are repeated for both resident species and total species seen in each fragment (however vervet monkeys were excluded from all analyses as they were never seen in the forest interior).

Results

From our exploration of the forests and literature, the locations of monkeys found in Udzungwa are given in Table 2. Despite past documentation of their presence (Lovett & Pocs 1993), red colobus were not confirmed in the forests of Kiranzi-Kitungulu and Kisinga-Rugaro, by either field visits or the recent literature. So for the purpose of this analysis, they are treated as absent. However, given that some areas were not searched, they may still contain very small numbers of this species. Also, one villager reported that red colobus are very rare in Kiranzi-Kitungulu.

All analyses of resident species suggest that the number of species per forest fragment was best modelled using the variable log forest area (Table 3). These analyses also find weak evidence for a negative relationship between species richness and both hunting and isolation (Table 3). Repeating the analysis including resident species as well as transitory species, bachelor groups and solitary individuals (Table 2) produced similar conclusions, although the full model was narrowly not significant, hunting became a strong predictor for the AIC stepwise model and Spearman correlation (Table 3). There was also near-significant negative relationship between species richness and deciduousness (Table 3).

Table 2. Monkey species present (x = resident, o = transitory, - = absent, 1 = solitary individuals only) in the study forests. Forests are ordered by decreasing fragment size. Only resident species are used in the analyses.

Forest name	***R. k.***	***C.s.***	***P.g.***	***C.ang.***	***C.m.***	***P.c.***	***C.aeth.***
Matundu (east)	-	-	x	x	x	x	-
Udzungwa Scarp	-	x	x	x	x	o	o
Luhombero	x	-	x	x	x	-	-
Mwanihana	-	x	x	x	x	x	-
Kisinga-Rugaro	-	-	-	x	x	-	-
Nyumbanitu	-	-	x	x	x	-	-
Nyanganje*	-	-	x	x	x	o/-	o/-
Iyondo	-	-	x	x	x	-	-
New Dabaga/Ulangambi	-	-	x	x	x	-	o
Ibiki*	-	-	x	x	x	x/o	-
Kiranzi-Kitungulu	-	-	-	x	x	-	-
Magombera	-	-	x	x	x	-	o
Ukami	-	-	x	x	x	-	-
Iwonde	-	-	x	x	x	-	-
Kitemele	-	-	-	-	x	-	-
Kalunga 1998	-	-	x	x	x	-	-
Mlale	-	-	x	x	x	-	-
Kawemba	-	-	-	-	x	-	-
Ifuo	-	-	-	x	x	-	-
Itanga	-	-	-	-	-	-	o
Kiseve	-	-	-	-	x	-	-
Kalunga 2005	-	-	x	o	1	o	-
Msonza	-	-	-	x	-	-	-

*Not included in the statistical analyses due to insufficient survey

Table 3. GLM analyses and Spearman correlation of species richness versus log forest area, square root isolation, habitat degradation, deciduousness, and hunting. Tests are repeated for resident species and total species (including resident species, transitory species, bachelor groups and solitary individuals). Significant variables are shown (GLM $p < 0.05$; Spearman correlation $p < 0.05$ adjusted by Hochberg correction), with near significant variables in parentheses. All GLM models were significantly or near significantly better than a null model (ANOVA resident species: full model $F = 2.46$, $p = 0.031$; AIC model $F = 5.98$, $p = 0.003$; total species: full model $F = 2.19$, $p = 0.052$; AIC model $F = 5.24$, $p = 0.005$). Square brackets show GLM model statistics including Akaike Information Criterion (AIC) and percentage of deviance explained (%D; 100 × [1 – Residual Deviance/Null Deviance]). Variables are listed in order of relationship strength. "+" = positive trend, "–" = negative trend, "√" = square root. Bold text indicates variables that are "strong predictors", i.e. significant in at least two models.

	Resident species		Total species	
Test	Significant variables	*p*	Significant variables	*p*
GLM (Full)	**Log forest area** $^{+}$	**0.015**	(Log forest area $^{+}$)	(0.083)
	[AIC 70.89, %D 76.22]		[AIC 78.06, %D 63.62]	
GLM (AIC stepwise)	**Log forest area** $^{+}$	**0.004**	**Log forest area** $^{+}$	**0.021**
	(Hunting $^{-}$)	(0.097)	**Hunting** $^{-}$	**0.040**
	[AIC 65.27, %D 74.23]		[AIC 72.53, %D 60.91]	
Spearman correlation	**Log forest area** $^{+}$	**< 0.001**	**Log forest area** $^{+}$	**0.001**
	√ Isolation $^{-}$	0.002	**Hunting** $^{-}$	**0.002**
	(Hunting $^{-}$)	* (0.0210)	√ Isolation $^{-}$	0.013
			(Deciduousness $^{+}$)	(0.061)

* Narrowly not significant due to Hochberg adjusted alpha 0.0167

No monkeys were resident in the small forest of Itanga. The occurrence of a forest altogether without monkeys is surprising given that monkeys were found in three smaller fragments. This further highlights the high level of hunting in the northeastern forests of Udzungwa, which almost certainly explains the reduced species richness of the smallest of these fragments. Isolation by agriculture and settlements is likely to further impede recolonisation of these forests. The effect is that the seven small forests (< 11 km^2) that are both isolated and where monkeys are hunted, have a lower species complement than the six other small forests (Mann-Whitney U-test: $n = 13$, $U = 4.0$, $p = 0.014$; Fig. 2). The species most affected by this is the red colobus, which is absent from the all of the small forests that are both isolated and hunted, yet present in all of the remaining six small forests.

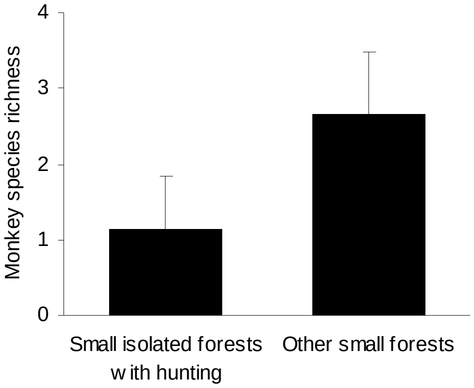

Figure 2. Mean and standard deviation monkey species richness in isolated small forests (< 11 km^2) where monkeys are hunted, versus other small forests.

Determining the shape of the species-area relationship requires further investigation. Repeating the GLM analyses using area data without the log transformation produced a much weaker model (AIC stepwise model: AIC 70.07, % deviance explained 44.08; Full model: not significantly different from a null model $F = 1.73$, $p = 0.124$), showing that a log-linear relationship is more suitable than a linear relationship. Figure 3 shows the log-linear trend suggested by the analyses above. When the x-axis is viewed on a logarithmic scale, the trend is very convincing (Fig. 3a), however using an untransformed x-axis suggests that one data point may be having high influence (Fig. 3b). This data point is from Matundu forest, and given its large area, it is surprising that it does not contain more monkey species. This may be because the habitat in Matundu is unlike other large forests. Because of its low elevation range it is dominated by semi-deciduous lowland forest with few evergreen tree species. It has also been very heavily disturbed by logging. Cook’s Distance values were therefore calculated to determine the influence of all points. These were well below 1.0 (all <0.5), suggesting that no points have had serious influence over the observed trend.

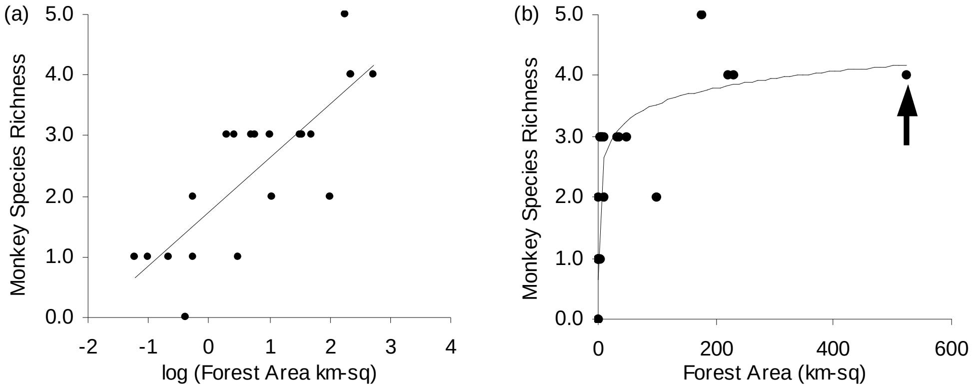

Figure 3. Scatterplots showing the significant logarithmic relationship between forest area and monkey species richness, using (a) logarithmic *x*-axis, and (b) untransformed *x*-axis. The arrow indicates Matundu forest, which has more deciduous habitat than the other large forest fragments.

Discussion

Confounding Variables for the Species-Area Relationship

Contrary to the recent meta-analysis of primate species-area trends (Harcourt & Doherty 2005), the results show that in some African forests, there is a clear relationship between area of forest and the number of primate species. Forest area is the best predictor of monkey species richness in forest fragments of the Udzungwa Mountains (Table 3). Only the four largest fragments sustain resident populations of large papionins (baboons and mangabeys; Table 2). The species-area relationship is not however sufficient to explain the species composition of some northeastern forests. Here, high human populations have influenced species richness, largely through hunting and isolation.

The recent meta-analysis of diurnal primate species-area trends excluded fragments above 100 km^2 (Harcourt & Doherty 2005). This may explain why their results did not show a species-area trend for Africa. Excluding fragments above 100 km^2 from the Udzungwa data, also removes the observed trends. Two other issues might also be considered to investigate the unusual result of Harcourt & Doherty (2005). Firstly, the ecology of the species involved is likely to be important. Species that occur inside small forests but rely on external resources such as crops have an "effective patch size" that is far greater than the area of the forest alone (Andrén 1994). This is why we have been cautious when treating the two savanna species (yellow baboons and vervet monkeys) as "resident". Sykes monkeys could arguably be treated with the same caution, as they occasionally raids crops, however it is still a predominantly forest species (Chapter 5).

A second issue is that univariate analysis does not allow consideration of external influences. We have seen that hunting and isolation influence the species richness of a forest fragment. Furthermore, simply referring to all fragments as "forest" implies consistency in habitat type.

Matundu forest is the largest fragment in our data, yet it contains neither the Sanje mangabey or kipunji. Based on the species-area relationship alone, this is unexpected. However, the Matundu habitat may simply not be suitable for these two rare papionins. Unlike the other three large fragments, Matundu consists of low elevation semi-deciduous forest with very few montane or submontane tree species. The Udzungwa red colobus also declines in abundance with elevation (Marshall et al. 2005). This may explain why it is missing from all of the small high elevation forests (≤ 11 km^2, >1600m). However, given that we found no negative relationship with deciduousness, and that red colobus persist in the small, unhunted evergreen forests of Mlale, Iwonde and Ukami, hunting is the more likely cause. There may also be some unmeasured disturbance variables that correlate with hunting. For example the prevalence of pathogenic gastrointestinal parasites has been shown to increase with fragmentation and human disturbance (Gillespie et al. 2005; Gillespie & Chapman 2006). We also did not consider forest shape (e.g. edge:volume ratio) as there was little variation among fragments.

This leads to the important question of why the species-area relationship exists in natural populations. Island biogeography theory suggests that the underlying relationship occurs because large population sizes are less susceptible to random extinctions (Macarthur & Wilson 1967). However, it is doubtful that island biogeography theory has much biological meaning given the complexity of natural systems (McGuinness 1984; Williamson 1989), and there are many interpretations as to why the species-area relationship exists (Hill et al. 1994). Our observed positive relationship between fragment size and elevation range, like many previous studies (Hill et al. 1994), suggests that habitat diversity is a major factor. Fragments of small size are likely to have small elevation range, low habitat diversity, and are therefore less likely to have suitable habitats for all primate species. The case of the large forest of Matundu already discussed, serves to emphasise this further, as the low primate species richness can be explained by the unexpectedly low habitat diversity for a forest of its size.

For the purpose of this analysis, the monkey populations in the fragments have been treated as isolated from one another. While this is reasonable given the rate of fragmentation, there may be potential for gene flow between some fragments, as even the forest-dependent species in this study have been observed occasionally in non-forest habitats. In landscape functioning the matrix plays a major role, as it is the most connected habitat (Forman 1997). *Colobus angolensis* in the coastal forests of Kenya frequently use matrix habitats, particularly where there is tall vegetation or *C. angolensis* food (Anderson et al. 2007). In our study, none of the patches are connected by forest, however four pairs of forests may be divided only by woodland or wooded-grassland: Iyondo-Matundu, Mwanihana-Nyanganje, Nyumbanitu-Ukami, and Ndundulu-Nyumbanitu. Two pairs of forests also have less than one kilometre gap separating them: New Dabaga/Ulangambi-Itanga and New Dabaga/Ulangambi-Msonza. Combining pairs of forests would not however have had a marked effect on the observed species-area relationship, as most of the small fragments that are driving the relationship are clearly separated by agricultural land and human settlements. Also given that most of the matrix of the Udzungwa Mountains is dominated by short and dry bushed- or sparsely wooded grassland, it is generally a poor conduit for dispersal. Because of this, the lack of data on dispersal, and the low number of completely isolated fragments, we did not take a metapopulation approach to our analysis (e.g. Anderson et al. 2007). However this could be an interesting avenue for future studies.

Status of Rare Monkeys in the Udzungwas

Of interest to conservation is that the two rarest monkeys (Sanje mangabey and kipunji) are only resident in evergreen/semi-evergreen forest fragments above 177 km^2 in size, but their ranges do not overlap. The Sanje mangabey also makes use of woodland and gallery forest, but only in areas continuous with these fragments (NORPLAN 1999; Ehardt et al. 1999; Rovero et al. 2006). Yellow baboons are sympatric with the Sanje mangabey, however they distribute themselves differently within the forest (Ehardt et al. 1999; Rovero et al. 2006). This may indicate that competitive exclusion has played a part in shaping their distribution, given that all are large, omnivorous monkeys. Conservation of the largest forest fragments is therefore paramount to the survival of Udzungwa's two rarest monkeys. Presently, only one of these fragments (Mwanihana forest) has maximum level protection under Tanzanian law, within the Udzungwa Mountains National Park. The entire known Udzungwa population of the highland mangabey and approximately half the population of the Sanje mangabey, occur outside of the Udzungwa National Park (Jones et al. 2005; Rovero unpublished data). Both of these large forests have been proposed for future inclusion in the National Park.

Hunting has influenced the status of Udzungwa monkeys, especially the endemic red colobus. This species is especially vulnerable to hunting because of conspicuous behaviour, including extended squealing calls and loud jumping through the forest canopy. In Kibale forest (Uganda), this behaviour has been suggested as a major cause of red colobus (*P. badius tephrosceles*) population decline, due to their vulnerability to hunting by chimps (Struhsaker 1999; Mitani et al. 2000; Struhsaker pers. comm.). Furthermore, Miss Waldron's red colobus (*P. badius waldronii*), formerly resident in Ghana and the Ivory Coast, has been hunted to near extinction (Oates et al. 2000; McGraw 2005). Other taxa of red colobus are also seriously threatened by hunting pressure (Struhsaker 1999 and 2005). The behaviour of other common monkeys in the Udzungwas makes them less vulnerable to hunting. Sykes monkeys for example flee low in response to humans, making only quiet "chirp" alarm calls, and are thus hard to hunt. Black and white colobus are also less conspicuous than the red colobus, as they live in smaller groups and are able to hide very effectively, often making only a low "ogh" call before hiding from humans (this call has probably not been described previously, Struhsaker pers. comm.).

Despite the apparent effects of hunting, the widespread occurrence of the Udzungwa red colobus is encouraging given that it is not known outside of this range. The persistence of red colobus in Kalunga forest after reduction to only 0.1 km^2 is particularly interesting. However, in cases of rapid destruction such as this, a lag in response is common (Cowlishaw 1999; Debinski & Holt 2000; Dunn 2004; Chapman et al. 2006). In addition to the forests above, the species occurs in small forest patches between Mwanihana and Matundu (Fig. 1; pers. obs.). It also makes seasonal use of woodland areas, and occurs in gallery forest along most rivers, including the Kihansi, Lumemo, Msolwa, Ruaha, Ruipa and Udagaje (Fig. 1; Decker 1994; NORPLAN 1999; pers. obs.; Jones and Moyer pers. comm.). Rare sightings to the south and east of the known range, have not been confirmed (pers. obs.; Ehardt, Frontier Tanzania and Jones pers. comm.). If the species is present in these areas it is likely to be in very low numbers. From this, we estimate that the red colobus range extends over a land area of around 1,400 km^2, i.e. 14 % of the Udzungwa Mountains. The area of Udzungwa red colobus range consisting of high quality (closed canopy) forest habitat is only around 558 km^2 (Table 1), i.e. 39.9 % of its range and 5.6 % of the Udzungwa Mountains. This suggests that the classification of the species as vulnerable on the IUCN red list (Baillie 2004) is appropriate.

The Species-Area Relationship and Landscape Management

The shape of the species-area relationship is commonly used for predicting extinctions and designing nature reserves (Lomolino 2000). Gradients (e.g. *z*-scores) can be used to determine the rate of decline in species with area, and therefore to determine the management effort required to reach a predefined conservation target (Desmet & Cowling 2004; Watling & Donnelly 2006). Given our low sample size we did not want to make these kind of extrapolations for the Udzungwa Mountains. Instead the log-linear relationship between species-area and fragment size suggests that species richness increases to a fragment size of around 150 km^2 (Fig. 3b). Therefore conservation management to assist growth of forests above this size, would be expected to encourage a species-rich primate community. Management of forests based on species richness may be sufficient to conserve biodiversity, as areas with high species richness have been shown to coincide with presence of taxonomically important species (Hacker et al. 1998). However, it should be noted that species richness is the least informative measure of biodiversity. Also, the presence of a species in a fragment gives no indication of population health, or habitat quality for that species. Furthermore, reserve design requires consideration of several factors, and species richness alone is insufficient for conservation (Struhsaker 1981; Harcourt et al. 2002; Orme et al. 2005; McCarthy et al. 2006; Chapter 3).

Regardless of the shape of the species-area relationship, or the absence of indicators beyond species richness, the importance of large closed canopy forest is clear without the need for procrastination. This and previous studies (Chapter 5) show that monkeys are useful as indicators of habitat quality, and in the Udzungwa Mountains, they are also a major draw for tourists and researchers. So management based around primate community composition and population health, makes sense for both conservation and income generation. In Udzungwa, conservation of large forests is especially important given that the two rarest species are only associated with large fragments. Annual fires set deliberately in the Udzungwa grasslands are threatening biodiversity. Current management activities are insufficient for preventing these fires, which if stopped would encourage corridor formation between some of the smaller fragments (Marshall et al. 2001), and would therefore increase the mean fragment size. Furthermore, community-based management in the northeastern forests and Kalunga, has been ineffective in preventing hunting and forest loss (Nielsen 2006), and at the time of writing the Kalunga forest had been completely converted to agriculture. Also despite the limited evidence for the importance of isolation, this should not be ruled out as a key factor for species conservation. More data are needed to investigate this.

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Chapter 3 - Tree Species and Community Gradients for Assessing Habitat Disturbance

Tree Species and Community Gradients for Assessing Habitat Disturbance

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Abstract

With the continuing disturbance of tropical forests, comes increasing pressure for managers to quantify and mitigate the effects. However basic information on the ecology and habitat requirements of rare species and communities is lacking. Basic indicators of habitat quality and conservation success are also lacking. Here we present data for trees ≥ 20 cm dbh surveyed in 120 0.2 ha plots, along a gradient of disturbance in a tropical lowland forest of the Udzungwa Mountains in Tanzania. We describe the community composition and use generalised linear models (GLMs) and canonical correspondence analysis to determine the community, species, diversity and structural responses to forest degradation, in relation to environmental variables. The distribution and diversity of 17 rare species are also analysed using GLMs. In the absence of direct measures of human disturbance we use cover and damage of climbers as an approximate index of disturbance, aswell as the presence of large animal paths and the distance from human settlements. The results highlight that heavy forest disturbance has negative implications for forest health beyond simple structural deterioration. Overall species diversity was not related to disturbance, however community composition, stem density and rare species diversity were all closely related to disturbance, as well as several environmental variables. Seven rare species were absent from the most disturbed areas. Rare tree species diversity was also negatively related to the presence of large animal paths, suggesting that elephant activity is not conducive to their conservation. Three locally common species, *Funtumia africana*, *Vangueria volkensii*, and *Parinari excelsa* are further identified as potential indicators of forest health. The implications for management are discussed.

Key words: *deforestation, detrended correspondence analysis, Eastern Arc, liana, logging*

Introduction

Lowland tropical forests are among the world’s most threatened habitats (Collins 1990; Vieira & Scariot 2006). As human activities continue to degrade areas of old growth forests, the conservation importance of degraded forests is increasing (van Gemerden et al. 2003a). Research into the effects of degradation on forest structure and composition is therefore paramount for conservation planning. Despite this, knowledge about the response to forest degradation of plant species and communities is poor. Such information is particularly important for the conservation of rare species and establishing IUCN Red List criteria (IUCN 2001). Assignment of indicators or "functional types" according to species responses to disturbance has also emerged as a promising management tool for diagnosing the disturbance process, assessing long-term changes, and for making conservation management decisions (Gondard et al. 2003).

Forest degradation has been shown to negatively affect water retention (Bruijnzeel 2004), natural resource availability, (McDonald et al. 2003; Shanley & Luz 2003), nutrient cycling (Vitousek & Sanford 1986; Villela et al. 2006) and genetic diversity (Lowe et al. 2005; Jennings et al. 2001), contribute to global warming (Reddy & Price 1999), and increase invasability by non-native species (Brown & Gurevitch 2004). The response of forest tree species to disturbance is largely species-specific (e.g. Duncan & Chapman 2003) and dependent on the scale of disturbance. Forest that has had low-to-moderate intensity disturbance generally has higher plant diversity than mature forest due to the presence of both early and late successional species (Horn 1974; Connell 1978; Toniato et al. 2004). Low intensity disturbance therefore helps to maintain forest diversity and community structure (Denslow 1987; Schnitzer & Carson 2001). Conversely high intensity disturbance can cause significant changes in species composition, structure and diversity (Connell 1978; Silva et al. 1995; Hitimana et al. 2004; Toniato et al. 2004; Okuda et al. 2003; McLaren et al. 2005; Villela et al. 2006).

Opening of the forest canopy caused by logging stimulates rapid growth of pioneer vegetation. Even selective logging for one species can lead to widespread damage. An average of ten trees were severed or crushed per treefall in one study (Feldpausch et al. 2005). Logging at medium-to-high rates also increases the density of woody climbers (lianas), which has been shown to negatively affect tree growth, stature, fecundity and regeneration (references in Gerwing 2006). Forest regeneration may be hindered and can take many decades to regenerate. In central Amazonia the recovery of forest biomass following slash-and-burn agriculture has been estimated at 175 years (Gehring et al. 2005). From the supposed link between geographic range and extinction risk (e.g. IUCN 2001), we would expect rare species to be the most susceptible to habitat degradation. While this may be true in most cases, rarity does not necessarily infer extinction risk (i.e. population decline or expected decline; Mace & Kunin 1994). Instead species have varying responses to extinction risks such as habitat disturbance, as determined by a complex interplay of biological and anthropogenic factors (Purvis et al. 2000; Isaac & Cowlishaw 2004; Cardillo et al. 2005). However species and community responses to logging have been poorly studied, and the susceptibility of many rare forest plants to disturbance is unknown. Improved accessibility of statistical tools provide the opportunity to test the impacts of disturbance while also allowing for other influences. In particular, multivariate techniques allow exploration of gradients in community and species data, simultaneously accounting for several variables (ter Braak 1986; Johnson & Omland 2004).

The Eastern Arc and Coastal Forests of Tanzania and Kenya contain the richest forests for biodiversity in mainland Africa (Rodgers 1998). Per unit area, the region has more endemic plants than all the world's richest biodiversity "hotspots" (Myers et al. 2000). Most of these forests are protected under Tanzanian law, however ineffective management means that forests continue to be degraded. Human activity has resulted in the loss of 77 % of Eastern Arc forest in the last 2,000 years, most of which occurred within the last 200 years (Newmark 1998). A high proportion of the remaining forest in the Eastern Arc is degraded, however like the majority of tropical forests (Asner et al. 2005), the overall extent of degradation is unknown.

The Udzungwa Mountains in the south of Tanzania contain the largest forest area in the Eastern Arc, however around 897 km^2 of the 1,500 km^2 of forest (61 %) is degraded (Marshall et al. submitted). Negative effects of forest degradation in Udzungwa have been noted for several animal taxa (Fjeldså 1999; Frontier Tanzania 2001; Struhsaker et al. 2004; Marshall et al. 2005; Rovero et al. 2006), however the consequences for plants have not yet been determined. The vegetation community of the Udzungwa Mountains is shaped by several environmental factors (Hall 1986; Lovett 1996, 1998 & 1999; Marshall et al. 2001a and 2001b, Lovett et al. 2006a), however the human impacts have not been adequately assessed. Comparisons between the flora of two high elevation forest reserves note fewer species and community types in the more disturbed of the two forests, however this may have been an area effect (Marshall et al. 2001a and 2001b). There has been no published data on the vegetation of the lowland forests of the Udzungwa Mountains.

Aim and Objectives

The aim of this paper is to determine the impact of disturbance on vegetation composition and structure in an area of international conservation importance. In achieving this our objectives are to determine: 1) the degree to which community composition, stem density and diversity are related to disturbance variables relative to environmental and topographic variables; 2) key species that are closely related to the variables, and hence may have potential as indicators; 3) responses of rare species and rare species diversity to disturbance. Using the results, we discuss the implications of disturbance for vegetation ecology, and for the conservation of biodiversity and rare species. We also discuss how the results have practical use for conservation management.

Methods

Study Area

The survey was carried out in a large (522 km^2) fragment of lowland forest in the Udzungwa Mountains (Fig. 1). The forest, known in the literature as Matundu, is mostly semi-deciduous with deciduous forests on some of the drier ridgetops and slopes. Approximately 104 km^2 of the area comprises closed canopy forest (Chapter 2). Matundu was chosen for this survey due to its limited elevation range (273-800 m) and for the high level of human impact. The habitat has been heavily degraded by extraction of timber, both for commercial and local use. Consequently the majority of Matundu comprises short trees, often covered by a dense matt of climbers dominated by *Uncaria africana*, and with tall trees up to 50 m occasionally emergent. The Food and Agriculture Organisation defines forest as, "Land spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10 percent, or trees able to reach these thresholds in situ." (FAO 2004). Although trees are short in much of Matundu (often below 5 m in height), their coverage exceeds 10 %, and most have the potential of exceeding 5 m in height where not restricted by climbers. We therefore define all areas of Matundu without continuous canopy as "open forest", regardless of tree height.

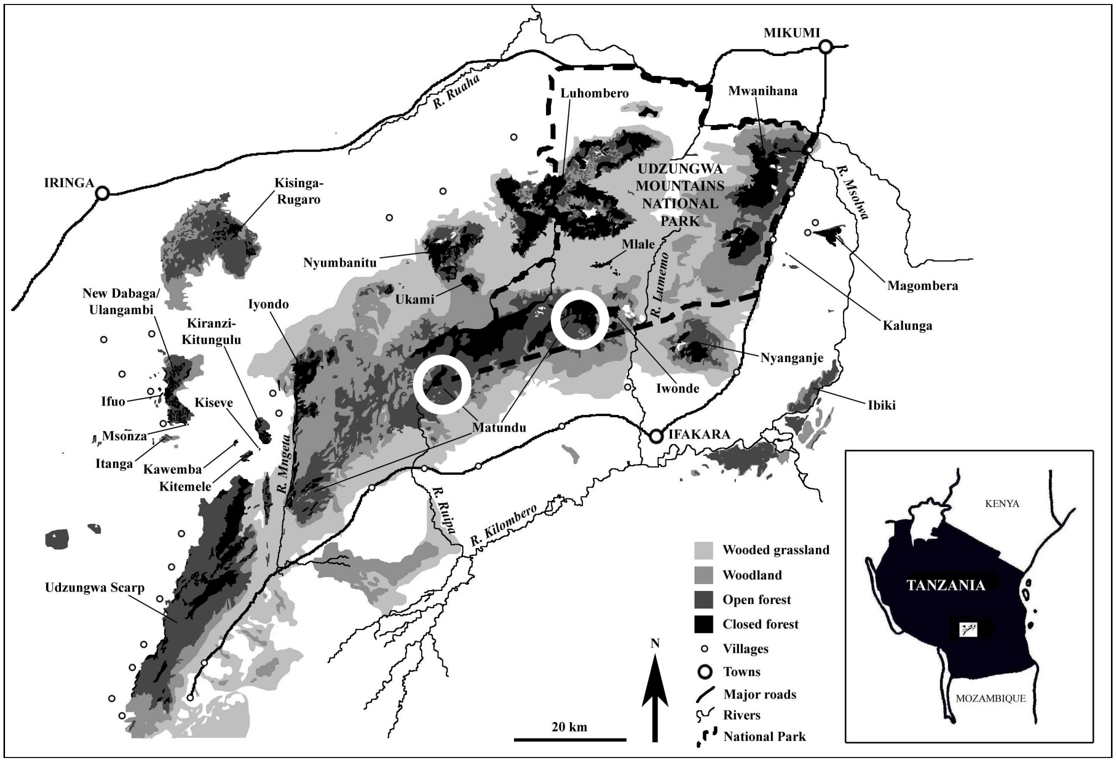

Figure 1. Habitat map of the Udzungwa mountains showing location of study sites (white circles) for vegetation survey in Matundu forest (from Chapter 2).

Vegetation Data

Fieldwork was conducted by ARM between September 2003 and April 2005. Vegetation was sampled using “gradsects”, i.e. transects positioned to maximise sampling of a particular gradient, in this case disturbance (Austin & Heyligers 1989). Transects may be preferred where vegetation types are not practical for other plot-based methods (Sutherland 1996). In Matundu forest the densely tangled understorey restricts movement, so moving between individually placed plots would be difficult and would substantially damage the habitat. Transects also allowed the vegetation data to be suitable for comparison with concurrent wildlife surveys in the same areas. Transects 4 km in length were positioned to capture the main habitat variations within Matundu. Three were placed in moderate-to-heavily logged forest in the vicinity of the Ruipa river in central Matundu (Mkungusi, Lusolwa and Machumbo; Fig. 1), at elevations 290 to 385 m. Three more transects were placed in the east of Matundu (Bwawani, Itula and Isaula; Fig. 1), comprising heavily logged to unlogged forest, at elevations of 355 m to 700 m. Transects were cut as straight as possible, however difficult terrain and irregularly-shaped habitat meant that transects contained many turns.

Trees with bole centre within 5 m either side of transects and at least 20 cm diameter at breast height (dbh; 1.30 m) were measured and identified. Smaller trees of dbh 10 to <20 cm were measured and identified within 2.5 m either side of transects. The dbh of the largest stem of all trees was measured using a dbh-calibrated tape measure, and height measured using a laser rangefinder (Bushnell Yardage Pro 500DX). For the purpose of analysis, transects were divided into 200 m plots, giving 120 plots of 0.2 ha for “large” trees (≥ 20 cm dbh), and 0.1 ha for “small” trees (10 to <20 cm dbh). This plot size was chosen as a compromise between gaining a sufficient number of stems per plot for analysis and minimising plot length. Samples for all species, and for any tree of uncertain identification were collected, pressed and dried. All specimens were taken to the Royal Botanic Gardens at Kew and were identified by Dr. Kaj Vollesen, together with ARM.

Predictor Variables

To determine the influence of human disturbance on the forest relative to environmental influences, ten variables were recorded for each 200 m plot. Slope and aspect were measured at 50 m intervals. The presence of swamps and rivers/streams was recorded if present within 50 m of each plot. The presence of ridgetops, valley floors and large animal paths, was recorded if extending at least 50 m through any plot. Elevation was taken from 1:50,000 topographic maps (Government of the United Republic of Tanzania 1983).

The level of disturbance by humans was not directly measurable in the area as there are no quantified records of logging rates. Furthermore, cut tree stumps could also not be quantified as many were too decayed to determine whether they had been cut or had decayed naturally. Instead, given the relationship between disturbance and woody climber density (references in Gerwing 2006), we used the proportion of small trees (10 to ≤ 20 dbh) smothered by woody climbers (≥ 50 % of canopy surface of each tree) as an approximate index of disturbance. We only include small trees to remove the influence of tall emergents that may be climber free even in the most heavily disturbed habitats. We also included trees that were broken, bent or deformed. Climber cover/damage is not a direct measure of human disturbance, as it incorporates disturbance by elephants, storms and other natural causes of treefall (e.g. Rice et al. 2004; Lawes & Chapman 2006). However given the extensive logging that has occurred in Matundu forest, the disturbance is thought to have been largely due to logging. Trees with < 50 % climber cover/damage were not included in the index as a low density of climbers may be beneficial for species diversity, ecosystem diversity and biomass (references in Gerwing 2006). As an additional estimate of human presence we measured the distance to the nearest settlements using a Garmin Geko 201 global positioning system. For this, the position of settlements that existed at the time of logging was used (based on conversations with village elders), rather than current settlements, which are much further from the forest.

A predictor variable to represent transect identity was not included, due to confounding associations with other predictor variables including elevation and climber coverage. This was not considered to be a serious omission, as there was high overlap in vegetation community types between different transects.

Statistical Analyses

Community analyses for large trees were carried out using ordination methods. Divisive methods such as TWINSPAN were not used because they have proven unreliable without subsequent testing using other multivariate procedures (Oksanen 2006; J. Birks pers. comm.). Although ordination methods may be susceptible to the influence of outliers, they are more powerful than classification methods and can better detect gradients and the nature of clusters (Belbin & McDonald 1993). From the various ordination methods, we selected Detrended Correspondence Analysis (DCA) over Correspondence Analysis to avoid curvature, and over Principal Component Analysis (PCA), due to the DCA axis 1 length exceeding two standard deviations (J. Birks pers. comm.). DCA was carried out with species that were rare in each plot downweighted, to minimise the influence of outliers and to focus the analysis on broad community trends.

Canonical Correspondence Analysis (CCA; ter Braak 1986 and 1995; Legendre & Legendre 1998) was used to analyse the environmental and human influences on community types. Species that were rare in each plot were downweighted as for DCA, and predictor variables were used as detailed above. Aspect data were converted from circular compass bearing data, to “northness” and “eastness” by taking the cosine and sine of each angle converted to radians (following Clark et al. 1999). These and the slope data were averaged for each 50 m interval. Before running the analysis, all predictor variables were tested for autocorrelation using Spearman’s rank correlation and variance inflation factors (VIF). Autocorrelation was considered serious for Spearman’s $r \geq 0.7$ (following Schadt et al. 2002) and for VIF ≥ 10 (following Groß 2003). From this, correlation coefficients were below 0.7 and VIF scores were ≤ 2.24, for all predictors.

Automated forward selection and backwards elimination was used to produce a parsimonious CCA model. However, because of the errors associated with automated model selection (Whittingham et al. 2006), we also highlight all predictor variables with biplot scores ≥ 0.4, to avoid Type II errors. Model significance was determined using ANOVA permutation tests with 200 permutations (ter Braak 1995). The key species associated with the observed gradients were determined using simple statistical tests. Only species that were common among plots were tested to determine broad trends rather than trends resulting from spatial clustering. For this, the number of large stems (≥20 cm dbh) of trees occurring in at least 10 % of plots (12 plots) was tested against all variables found to be of importance from the CCA model, using Spearman’s Rank correlation. To account for these repetitive tests, significance level alpha was adjusted by dividing alpha (0.05) by the number of tests (Bonferroni correction; Bland & Altmann, 1995). This conservative form of endpoint adjustment was preferred over the many alternatives because false identification of indicator species would be costly for conservation management.

The relationships between predictor variables and the number and diversity of large trees, were analysed using generalised linear models (GLM; McCullagh & Nelder 1989). Due to normally distributed dependent variables, a Gaussian error function was used. Most predictor variables were also normally distributed, however square root transformation was required to normalise village distance. Model refinement was carried out using a backward elimination process, removing the variable with least predictive power by hand at each step, until only variables contributing significantly to the model remained. Additional methods for GLM model selection (backward selection by AIC, and an unreduced model; Chapters 2 and 3) were also tested but had no effect on the principle variables, and so are not presented. The measure of diversity used was the inverse Simpson index $1/D = \Sigma(p_i^2)$, where p_i is the proportional abundance of species i. The inverse form was used so that high values correspond to high diversity.

"Rare species" were classed as those included or proposed for inclusion on the IUCN Red List, or known only from the Eastern Arc and Coastal Forests of Tanzania, Kenya and Mozambique (Gereau & Luke 2003; Baillie et al. 2004; Lovett et al. 2006b; Gereau pers. comm.). The relationship between predictor variables and inverse Simpson index of rare species, was analysed using GLM as for the density and diversity analyses above. Inverse Simpson indices were calculated using all stems ≥ 10 cm dbh in 0.1 ha plots. In addition to the predictor variables listed above, the density and diversity of these stems were also included in this analysis. The response of each rare species to disturbance was assessed using Mann-Whitney *U*-tests on the number of stems per plot in areas with < 50 % (60 plots), versus ≥ 50 % (60 plots) climber cover/damage. Mann-Whitney *U*-tests were preferred over Spearman's Rank correlation as rare species tended to be few in number and therefore absent from most plots.

Calculation of inverse Simpson index, VIF scores, DCA, CCA and GLM model development and testing were carried out using the computer package *R* version 2.1.0 (http://cran.r-project.org/). All other tests were performed using *SPSS* version 11.0.1 (www.spss.com).

Results

Habitat Description

A total of 5,509 stems were measured and identified from 138 species. The top ten species for small trees (10 to ≤ 20 cm dbh) accounted for 64.2 % of stems and for large trees (≥ 20 cm dbh) 55.6 % (Table 1). A full species list including authorities is presented in Appendix 1. The 3,346 large trees comprised 109 species, dominated by *Lettowianthus stellatus* (12.9 % of stems) and *Funtumia africana* (16.7 %). The 2,163 small trees comprised 113 species, dominated by *Funtumia africana* (26.6 %). The 120 plots sampled a broad range of habitat degradation, with the proportion of small trees covered/damaged by climbers ranging from 0 to 1. Climber cover/damage was also evenly distributed among plots, with 60 plots having < 50 % of small trees smothered or damaged, and 60 having ≥ 50 %.

Of the four axes produced by DCA analysis, community composition of trees ≥ 20 cm dbh was described sufficiently by DCA axis 1 alone (eigenvalue 0.501 versus only 0.289 for DCA axis 2). DCA axis 1 largely described the community gradient from disturbed semi-deciduous lowland habitats in the western plots, to less disturbed semi-deciduous/evergreen habitats in the eastern plots (Appendix 1; Fig. 2). Western sites had significantly higher DCA axis 1 scores than eastern plots (*t*-test: $t = 5.483$, $p < 0.001$), however community gradation along axis 1 was however continuous, with no divisions (Fig. 2). The community composition was broadly related to disturbance as shown by significant relationship between DCA axis 1 scores and climber cover/damage (Spearman Rank Correlation: $r_s = -0.446$, $p < 0.001$; Figs. 2 and 3). However high residual variance ($r_s^2 = 0.199$; Fig. 3), suggests that additional factors are involved in shaping the community, as tested below using CCA.

Table 1. The ten most common species among trees in 0.2 ha plots (large trees ≥ 20 cm dbh) and 0.1 ha plots (small trees 10 to < 20 cm dbh) in Matundu forest. Data presented include frequency of trees per plot, percentage of trees out of the total sampled (3,346 large and 2,163 small), and the number of plots in which each species was found.

Large trees				*Small trees*			
	Freq	**%**	**Plots**		**Freq**	**%**	**Plots**
Funtumia africana	558	16.7	57	*Funtumia africana*	569	26.6	57
Lettowianthus stellatus	430	12.9	87	*Sorindeia madagascariensis*	119	5.6	38
Shirakiopsis elliptica	260	7.8	66	*Lettowianthus stellatus*	87	4.1	43
Xylopia parviflora	252	7.5	78	*Tabernaemontana pachysiphon*	84	3.9	6
Erythrophleum suaveolens	181	5.4	57	*Tarenna pavettoides*	67	3.1	28
Anthocleista grandiflora	113	3.4	41	*Diospyros zombensis*	62	2.9	24
Sorindeia madagascariensis	101	3.0	39	*Bersama abyssinica*	60	2.8	35
Milicia excelsa	93	2.8	46	*Voacanga africana*	51	2.4	34
Bersama abyssinica	87	2.6	51	*Blighia unijugata*	51	2.4	13
Tabernaemontana pachysiphon	72	2.2	5	*Cordia peteri*	38	1.8	30

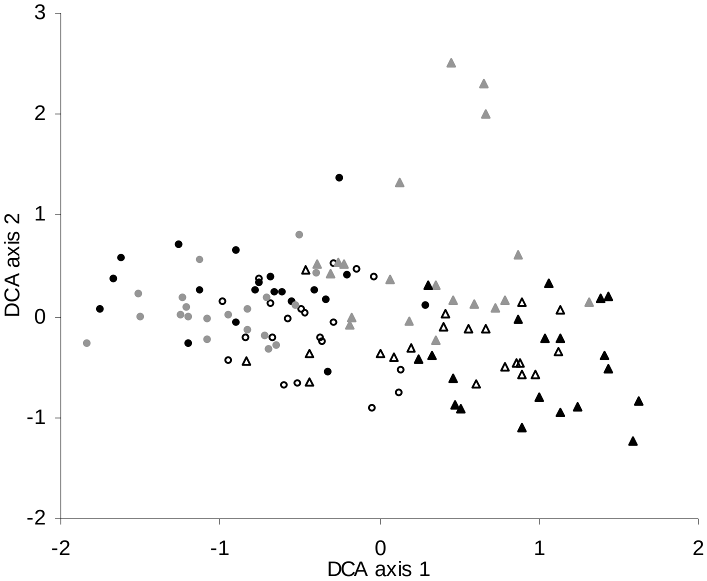

Figure 2. DCA biplot for large trees (≥20 cm dbh) for western sites (circles) and eastern sites (triangles). Points are labelled by transect (● Mkungusi, ● Machumbo, ○ Lusolwa, △ Bwawani ▲ Itula, ▲ Isaula).

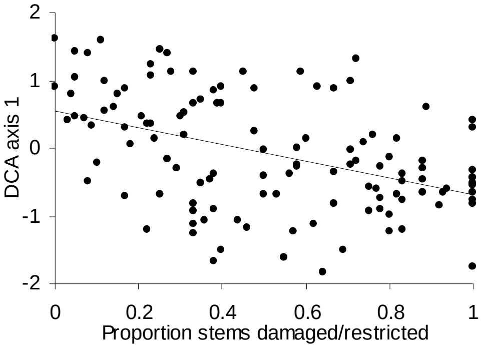

Figure 3. Relationship between disturbance (climber cover/damage) and DCA axis 1 scores for stems ≥20 cm dbh.

Community Composition

Canonical Correspondence Analysis revealed eight predictor variables with biplot scores >0.4 for CCA axes 1 to 4 for trees ≥ 20 cm dbh (Table 2; Fig. 4). The predictor with the highest mean biplot score for axes 1 to 4 was climber cover/damage (shorthand notation “climbers”; mean biplot score 0.43), followed by the angle of the slope (“slope”; 0.41), presence of large animal paths (“path”; 0.39), distance to nearest village (“village”; 0.36), elevation (“elevation”; 0.34), presence of rivers or streams (“stream”; 0.30), presence of swamp (“swamp”; 0.29) and presence of valley (0.27). These eight variables modelled community composition with high significance (permutation test: $F = 2.81$, $p < 0.005$, $n = 120$). Model selection by automated forward selection and backwards elimination however found that only the variables slope, elevation, village, climbers, swamp, and stream made significant contribution (permutation test: $F = 3.27$, $p < 0.005$, $n = 120$).

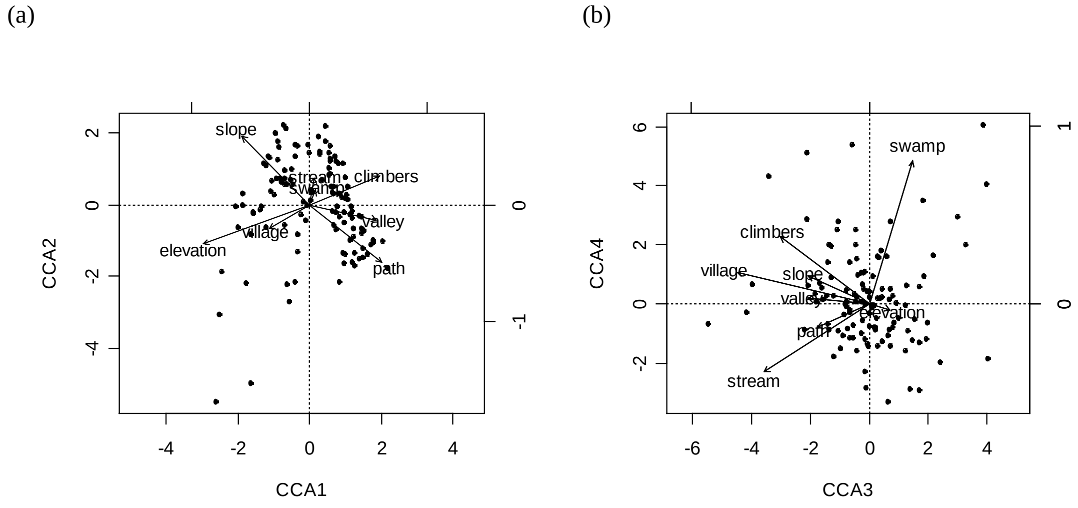

Figure 4. CCA biplots for large trees (≥20 cm dbh), including (a) axis 1 vs axis 2, and (b) axis 3 vs axis 4. Biplot arrows are shown for all predictor variables with biplot scores >0.4 for at least one of the four axes (Table 2). See text for definition of variables.

Table 2. Biplot scores for predictor variables from a CCA model of large tree (≥ 20 cm dbh) community composition. Percentage variance explained for CCA axes 1 to 4 are given in parentheses. See text for definition of variables.

Variable	Axis 1 (39.0)	Axis 2 (15.9)	Axis 3 (13.1)	Axis 4 (10.3)
Slope*	-0.575	0.575	-0.299	0.187
Northness	0.151	0.241	-0.224	-0.339
Eastness	-0.056	0.042	0.356	0.297
Elevation*	-0.900	-0.342	0.098	-0.011
Village*	-0.342	-0.189	-0.732	0.164
Climbers*	0.588	0.257	-0.482	0.400
Path	0.613	-0.467	-0.314	-0.155
Swamp*	0.054	0.096	0.270	0.741
Stream*	0.038	0.257	-0.586	-0.329
Valley	0.564	-0.111	-0.355	0.039
Ridge	-0.398	-0.142	0.303	-0.145

* Variables selected for model using automated forward selection and backwards elimination (permutation test: $F = 3.2662$, $p < 0.005$).

Several of the common species showed significant relationships with the predictor variables (Table 3). The canopy trees *Funtumia africana* and *Shirakiopsis elliptica* were closely related to all four of the main predictors from CCA analysis and can therefore be considered good indicators of community composition. The two species however behave in contrasting ways. *F. africana* is typical of undisturbed, high elevation forests on steep slopes away from large animal paths. From field observations, this species is typical of regenerating forest and is frequently monodominant until old growth forest species take over. Conversely, *S. elliptica* is typical of disturbed, low elevation forest on flat ground with high presence of large animal paths. This species showed extreme adaptation to smothering by climbers, with 82.5 % of stems (241 out of 292) of all sizes, covered by climbers. Table 3 also highlights that *Funtumia africana*, *Parinari excelsa* and *Vangueria volkensii* can be considered representative of undisturbed forest.

Density and Diversity

The density of large stems (≥ 20 cm dbh) was not related to diversity measured using inverse Simpson index (Pearson correlation: $p = 0.762$, $r = -0.028$, $n = 120$). GLM analysis also showed that these two descriptors are under different influences from the predictor variables (Table 4). Both stem density and diversity increase with slope and decrease with elevation, however only diversity decreases with distance from settlements, and only density increases with northness, presence of ridgetops and presence of rivers or streams.

Table 3. Relationship of common species (present in ≥ 10 % of plots) with key predictor variables from CCA modelling (biplot score ≥ 0.4). The number of large stems (≥ 20 cm dbh) of all species listed had significant relationships with the given variables (Spearman rank correlation with Bonferroni adjusted alpha 0.05 / 8 = 0.00625). Predictor variables are ordered by their relative contribution to the first four CCA axes. See text for definition of variables.

Predictor variable	Species with positive relationship to predictor	Species with negative relationship to predictor
Climbers	*Shirakiopsis elliptica* *Voacanga africana*	*Funtumia africana* *Vangueria volkensii* *Parinari excelsa*
Slope	*Funtumia africana* *Pachystela brevipes* *Blighia unijugata* *Zanha golungensis* *Rothmannia manganjae*	*Erythrophleum suaveolens* *Anthocleista grandiflora* *Shirakiopsis elliptica* *Margaritaria discoidea* *Diospyros zombensis*
Path	*Shirakiopsis elliptica* *Anthocleista grandiflora* *Erythrophleum suaveolens* *Margaritaria discoidea*	*Funtumia africana* *Pachystela brevipes*
Village distance	None significant	*Vitex doniana* *Margaritaria discoidea* *Pteleopsis myrtifolia* *Diospyros zombensis* *Lettowianthus stellatus*
Elevation	*Funtumia africana* *Parinari excelsa* *Vangueria volkensii*	*Shirakiopsis elliptica* *Anthocleista grandiflora* *Bersama abyssinica* *Ochna holstii* *Margaritaria discoidea* *Lettowianthus stellatus* *Sorindeia madagascariensis*
Streams/rivers	*Afrosersalisia cerasifera* *Treculia africana* *Bersama abyssinica*	*Combretum molle*
Swamp	*Bridelia micrantha*	*Erythrophleum suaveolens*
Valley	*Anthocleista grandiflora* *Bersama abyssinica* *Shirakiopsis elliptica*	*Funtumia africana* *Vangueria volkensii* *Parinari excelsa*

The most significant relationship for large stem density is a negative relationship with climber cover/damage (Table 4). Because it would be expected that disturbed areas have few large trees, this supports our assertion that climber cover/damage is an appropriate index of disturbance. Given the already noted relationship between climber cover/damage and community composition, this also suggests that stem density and community composition are positively related. This is confirmed from testing stem density versus DCA axis 1 (Pearson correlation: $r = 0.371$, $p < 0.001$, *n* = 120), however there remains a high level of unexplained variance ($r^2 = 0.138$). There is no significant relationship between stem diversity and DCA axis 1 (Pearson correlation: *r* = -0.141, *p* = 0.126, *n* = 120). Finally, a biplot of diversity versus climber cover/damage also shows no evidence of a peak in diversity at intermediate levels of disturbance (Fig. 5).

Table 4. Significant predictor variables for GLM analysis of density (number of stems ≥ 20 cm dbh per plot; Null Deviance=541.94, Residual Deviance=366.87; 37.84 % variance explained) and diversity (inverse Simpson index; ND=664.10, RD=559.36; 15.78 % variance explained), including test statistics and level of significance. See text for definition of variables.

	t	***p***
Density		
Climbers	-10.326	2×10^{-16}
Northness	3.728	0.000193
Elevation	-3.588	0.000333
Slope	3.491	0.000481
Ridge	3.287	0.001014
Rivers/streams	3.244	0.001179
Diversity	***t***	***p***
Slope	3.690	0.000343
Village distance	-2.728	0.007362
Elevation	-2.668	0.008733

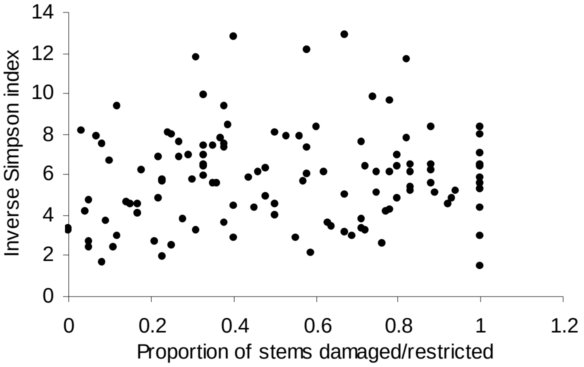

Figure 5. Biplot of disturbance (as measured by climber cover/damage) versus diversity. Note there is no evidence for a peak in diversity at intermediate levels of disturbance.

Rare Species

Seventeen rare species were found, of which seven were only found in the 60 least disturbed plots (≥50 % climber cover/damage; Table 5). Only two rare species were not found in the 60 least disturbed plots (*Gomphia sacleuxii* and *Shirakiopsis trilocularis*; Table 5). Mann-Whitney *U*-tests show that disturbance has a significant negative relationship with *Leptonychia usambarensis*, *Millettia semseii*, *Khaya anthotheca* and *Drypetes usambarica* and a near-significant negative relationship with *Grewia goetzeana* (Table 5). Only one of the rare species was positively related to disturbance (*Cordia peteri*). GLM analysis showed that disturbance (climber cover/damage) is also negatively related to overall rare species diversity (Table 6). However, the strongest predictor was the negative effect of paths, followed by a positive relationship with northness and negative relationship with ridgetops (Table 6).

Table 5. Rare species and number of stems ≥ 10 cm dbh in 0.1 ha plots. Figures are presented for stems in low and high disturbance areas compared using Mann-Whitney *U*-tests (<50 % and ≥50 % climber cover/damage). Superscript letters indicate plots found to have statistically greater number of stems (*a*) $p < 0.05$ and (*b*) $p = 0.052$. IUCN Red list criteria are from Baillie et al. (2004), Gereau & Luke (2003) and Gereau pers. comm. (CR = Critically endangered, VU = Vulnerable, PT = Proposed threatened, NT = Near threatened). Range information is taken from Lovett et al. (2006b) (EA = Eastern Arc Mountains of Tanzania and Kenya, CF = Coastal Forests of Tanzania, Kenya and Mozambique, T = One location in Tanzania outside EA/CF, M = Mozambique not CF, Z = Zanzibar).

					Stems per plot (mean ± sd)	
	IUCN	Known range	Stems	Plots	Low disturbance	High disturbance
Lettowianthus stellatus	NT*	EA/CF	301	84	2.73 ± 2.90	2.28 ± 2.89
Cordia peteri	PT	EA/CF	54	37	0.32 ± 0.70	0.58 ± 0.85^a
Millettia semseii	VU	EA	34	12	0.53 ± 1.44^a	0.03 ± 1.18
Oxyanthus pyriformis$^+$	PT	EA	19	14	0.18 ± 0.54	0.13 ± 0.47
Khaya anthotheca	VU	Tropical Africa	16	14	0.22 ± 0.49^a	0.05 ± 0.22
Aoranthe penduliflora	VU	EA/CF	10	3	0.17 ± 0.87	0.00 ± 0.00
Grewia goetzeana	DD	EA/CF	8	7	0.17 ± 0.37^b	0.02 ± 0.13
Dialium holtzii	VU	EA/CF/M	7	6	0.08 ± 0.33	0.03 ± 0.18
Drypetes usambarica	PT	EA/CF	7	4	0.12 ± 0.56^a	0.00 ± 0.00
Leptonychia usambarensis	-	EA/CF/T	7	6	0.17 ± 0.37^a	0.00 ± 0.00
Vismia orientalis	PT	EA/CF/T	5	2	0.03 ± 0.26	0.05 ± 0.39
Premna schliebenii	VU	EA/CF/E.Africa	3	2	0.05 ± 0.29	0.00 ± 0.00
Shirakiopsis trilocularis	VU	EA/CF	2	2	0.00 ± 0.00	0.03 ± 0.18
Gomphia sacleuxii	PT	EA	1	1	0.00 ± 0.00	0.02 ± 0.13
Isoberlinia scheffleri	VU	EA	1	1	0.02 ± 0.13	0.00 ± 0.00
Polyalthia verdcourtii	CR*	EA/CF	1	1	0.02 ± 0.13	0.00 ± 0.00
Vitex mossambicensis	PT	CF/Z	1	1	0.07 ± 0.13	0.00 ± 0.00

* Proposed status $^+$ Subspecies *tanganyikensis*

Table 6. Significant predictor variables for GLM models of rare species diversity (inverse Simpson index; ND=91.17, RD=72.75; 20.20 % variance explained). See text for definition of variables.

	t	***p***
Path	-3.823	0.00021
Northness	2.986	0.00345
Ridge	-2.630	0.00972
Climbers	-2.461	0.01534

Discussion

Disturbance and Gradients

Heavy forest disturbance has implications for forest biology beyond simple structural deterioration. Although some species persist in disturbed areas, the overall community composition is altered (Table 2; Figs. 3 and 4). Community responses assumed to result from the accumulation of individual responses by different species (Whittaker 1956; Vazquez & Givnish 1998). High level disturbance results in short stature forest with few trees (Table 4) and is characterised by species that are able to resist the heavy weight of smothering climbers (Table 3). Rare species in Matundu are particularly threatened by disturbance (Tables 5 and 6), thus supporting the theory that species with small geographic range are the most susceptible to becoming rare (e.g. IUCN 2001). However, the positive effect of low-to-moderate disturbance on species diversity is well known (Horn 1974; Connell 1978; Toniato et al. 2004). Conversely, the results show there is no relationship between climber cover/damage and overall species diversity (Table 4; Fig. 5). This suggests that disturbance in Matundu has exceeded the level of disturbance that is beneficial for biodiversity. The increased diversity in areas near to former settlements (Table 4), suggests that regeneration in formerly disturbed areas may be restoring some of the biodiversity value. However this observation is hard to substantiate without further investigation.

It is not only the rare species that are important for conservation management. In this study, three species can be considered “disturbance sensitive”, as they are characteristic of areas without the tangled layer of climbers indicative of disturbance (*Funtumia africana*, *Vangueria volkensii* and *Parinari excelsa*; Table 3). Conversely, *Shirakiopsis elliptica* and *Voacanga africana* can be considered “disturbance adapted” (Table 3). Such assignment of plants into functional types can be useful for monitoring or predicting impacts of disturbance (Gondard et al. 2003). The identification of *P. excelsa* as representative of undisturbed forest is particularly useful. This large tree is easily identifiable both on the ground and from the air, and could be used as a target species in rapid assessments of habitat quality. The geographic range of *P. excelsa* is however one of the most extensive of all trees in our sample, widespread in tropical Africa and Central and South America (Solomon 2006). That a widespread species should be indicative of the best quality forests emphasises the importance for habitat conservation over conservation based on single species. Conservation efforts based on the distribution of one rare species may not conserve the important habitats or overall biodiversity, unlike conservation based on disturbance sensitive functional types.

Logging in the tropics is often unquantified because it is illegal and/or occurs in areas without sufficient resources to complete and store documentation. Without quantification of logging (and other disturbance), ecological models cannot fully assess species or community distributions.

Given the importance of species distributions and habitat threats for conservation management (e.g. IUCN red list criteria; IUCN 2001), it is essential to develop methods for estimating disturbance. In the absence of written records, logging levels have been estimated from the number of standing stems remaining or the number of cut stumps (e.g. Skorupa 1986; Gillespie & Chapman 2006). However cut stumps may be decayed or hidden, and stem density is under other influences such as slope or elevation. Our use of climber cover/damage provides a simple alternative, that is closely related to the density of stems (Table 4). However as stated, climber cover/damage will include other forms of disturbance. By including only trees with >50 % coverage of climbers, we have minimised the inclusion of low-level disturbance such as tree falls. We assume that the canopy was originally opened by logging, but the tangled secondary habitat has probably been perpetuated by elephants, as seen elsewhere in Africa (Lawes & Chapman 2006).

Like many tropical forests, logging in Matundu forest has been greatest in areas with high accessibility. These tend to be areas that are flat, low elevation and close to human settlements. This explains some of the observed correlations between environmental variables and climber cover/damage. Furthermore, transects were positioned to maximise sampling of the disturbance gradient rather than environmental gradients, so there is bias towards variation in disturbance. Despite this, some interesting environmental gradients have emerged (Fig. 4; Tables 2, 3 & 5). The importance of elevation for vegetation community composition in the Udzungwa Mountains has been highlighted in earlier studies (reviewed by Lovett et al. 2006a). Despite the low elevation range of this study (290 to 700 m), elevation is by far the best predictor of community composition along CCA axis 1 (Table 2). Community and species distribution is also related to slope, village distance, large animal paths, streams/rivers, swamps and valleys (Fig. 4; Table 3). The diversity of rare species increases with slope, yet decreases on ridgetops (Table 6). Stem density is also mostly related to topographic features (besides cover/damage as discussed above; Table 4).

Rare species diversity, aswell as the density of *Funtumia africana* and *Pachystela brevipes*, were also negatively related to large animal paths (Table 6), while four other species were positively associated with large animal paths (Table 3). Overall community composition also showed some relationship to large animal paths, however this was not identified by the stepwise model (Table 4). The large animal paths in Matundu forest were created and are used regularly by large animals including elephants, buffalos and hippopotami. Elephants are the most likely influence on vegetation as they are browsers rather than grazers, and are well known for their destructive behaviour (Lawes & Chapman 2006). Elephants may trample or tear up regenerating trees, providing habitat favourable only to climber-tolerant trees (e.g. *Shirakiopsis elliptica*; Table 3), while propagating the seeds of those trees and climbers that they eat. This has importance for analysing results of line transect studies. This study did not selectively use large animal paths, but passed along them whenever they coincided with the randomly chosen routes. The use of paths for ecological surveys is not recommended (Sutherland 1996; Buckland et al. 2001). However, cutting a transect through tropical forest can be destructive and time consuming and using large animal paths may therefore be more practical. In such cases, this study suggests that the presence of paths should be accounted for in the analysis, for example by inclusion as a covariate. This will be most important for ground-dwelling animals, which may rely on paths to move around. However this study shows that canopy trees (and therefore presumably arboreal animals) are also affected by the presence of paths.

Conservation of Matundu Forest

Recent assessment of the conservation priorities in the Udzungwa Mountains did not recognise the importance of Matundu forest for conservation (Dinesen et al. 2001). Conversely, we see Matundu forest as being pivotal for the long-term conservation of the Udzungwa ecosystem. The results show that the forest contains several rare and forest-dependent species. Matundu is also the largest forest fragment in the area, and largely protected from future disturbance under National Park legislation. In addition, its position between other major forest fragments (Fig. 1) means it is a key corridor for wildlife dispersal. Conservation of Matundu forest is therefore vital and the results lead to two main practical implications for this. Firstly, the study has updated knowledge of the range and abundance of species in an area of high conservation value. For instance *Polyalthia verdcourtii* was previously only known from the small forest of Magombera in the Kilombero valley to the east of the Udzungwa Mountains (R. Gereau pers. comm.).

Secondly, the results can be used to make future management decisions. This study has shown that previous management (primarily selective logging) has led to structural habitat degradation and community reorganisation. Because of the extent of degraded forest in the tropics, Duncan & Chapman (2003) state that, “One of the greatest challenges for ecologists this century will be restoring forests on degraded tropical lands”. Forest regeneration may be hindered in parts of Matundu where elephant densities are high. For the time being, active management (e.g. cutting of restricting climbers) may not be necessary, due to the high number of regenerating *Funtumia africana* stems. Instead, one priority now should be to monitor regeneration in areas of degraded forest to determine whether the recovery will continue. To aid this, plots were marked with metal tags at 50 m intervals. A second priority is to ensure that the area of Matundu forest to the west of the Udzungwa Mountains National Park is not overexploited. Management of this area is currently limited and the forest continues to be degraded by illegal activities.

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Appendix

Appendix 1. Species list including number of stems in each size class, and presence/absence in eastern and western plots. Hehe names were mostly provided by Ruben Mwakisoma of Katarukila village and were mostly consistent with latin names. Additional names were provided by Daniel Miyayambe (Kisegese village) and Leonardi Mweinoma (Lumemo village).

Species (authorities from Solomon 2006)	Hehe name (Swahili in parentheses where known)	Stems dbh 10-20	Stems dbh > 20	West transects			East transects		
				1	2	3	4	5	6
Chionanthus mildbraedii (Gilg & Schellenb.) Stearn	Mnocha/Mnosa	35	30	x	x	x	.	.	.
Erythroxylum fischeri Engl.	Kitsege Kiang'uku (Mfupa Wa Kuku)	29	.	x	x	x	.	.	.
Psychotria capensis (Eckl.) Schönland	Memenang'olo Majani Makubwa	10	.	x	x	x	.	.	.
Oncoba spinosa Forssk.	Msasi	4	.	x	x	x	.	.	.
Diospyros zombensis (B.L. Burtt) F. White	Nyakatitu	62	31	x	x	x	.	x	.
Annona senegalensis Pers.	Mundope	10	25	x	x	x	x	.	.
Combretum zeyheri Sond.	Mtaagata/Kitaagata	.	5	x	x	x	x	.	.
Oxyanthus pyriformis (Hochst.) Skeels subsp. tanganyikensis Bridson	Mkolongo	19	.	x	x	x	.	.	x
Vitex doniana Sweet	Mkoga (Mfulu)	21	57	x	x	x	x	x	.
Margaritaria discoidea (Baill.) G.L. Webster	Mpalang'anga	18	54	x	x	x	x	x	.
Celtis gomphophylla Baker	Mbefu	36	53	x	x	x	x	.	x
Treculia africana Decne.	Msaya	3	17	x	x	x	x	x	.
Afzelia quanzensis Welw.	Mbalikila	5	5	x	x	x	x	.	x
Markhamia lutea (Benth.) K. Schum.	Mtalawanda	16	3	x	x	x	x	x	.
Diospyros mespiliformis Hochst. ex A. DC.	Mnyalati/Mnyalapi	14	.	x	x	x	x	x	.
Harrisonia abyssinica Oliv.	Msangalasi	8	.	x	x	x	x	x	.
Lettowianthus stellatus Diels	Mswehile	87	430	x	x	x	x	x	x
Shirakiopsis elliptica (Hochst.) Esser	Ngulukanziwa	32	260	x	x	x	x	x	x
Xylopia parviflora Spruce	Mpoloto	30	252	x	x	x	x	x	x
Anthocleista grandiflora Gilg	Mbala	10	113	x	x	x	x	x	x
Sorindeia madagascariensis Thouars ex DC.	Mpilipili	119	101	x	x	x	x	x	x

Milicia excelsa (Welw.) C.C. Berg	Miangi (Mvule)	27	93	x	x	x	x	x	x
Bersama abyssinica Fresen.	Mbasamono	60	87	x	x	x	x	x	x
Pachystela brevipes (Baker) Baill. ex Engl.	Msambisa	22	54	x	x	x	x	x	x
Pteleopsis myrtifolia (M.A. Lawson) Engl. & Diels	Mnepa	7	50	x	x	x	x	x	x
Combretum molle R. Br. ex G. Don	Mlama	12	36	x	x	x	x	x	x
Voacanga africana Stapf	Mkongosa 2	51	31	x	x	x	x	x	x
Khaya anthotheca (Welw.) C. DC.	Mkangazi	2	25	x	x	x	x	x	x
Holarrhena pubescens Wall. ex G. Don	Mtomvutomvu Dume	25	3	x	x	x	x	x	x
Tricalysia pallens Hiern	Memenang'olo Matunda Madogo	14	.	x	x	x	x	x	x
Ochna holstii Engl.	Mkwaliti Jike	29	29	.	x	x	.	.	.
Vepris simplicifolia (Engl.) Mziray	Mkomangufi	17	6	x	.	x	.	.	.
Xeroderris stuhlmannii (Taub.) Mendonça & E.C. Sousa	Mkrismasi 2	.	4	x	.	x	.	.	.
Schrebera trichoclada Welw.	Mung'ulung'ulu Dume 2	11	3	x	.	x	.	.	.
Ehretia cymosa Thonn.	Mgongolakatchuka	9	1	x	x	.	.	.	.
Terminalia stenostachya Engl. & Diels	Mlembelembe	1	1	x	.	x	.	.	.
Ximenia americana L.	Mtundwa	3	.	.	x	x	.	.	.
Vangueria apiculata K. Schum.	Muhomang'ambako	2	.	x	.	x	.	.	.
Bombax rhodognaphalon K. Schum.	Mwali (Msufi Pori)	1	14	.	x	x	.	x	.
Pericopsis angolensis (Baker) Meeuwen	Muvanga	1	4	x	.	x	x	.	.
Catunaregam pentandra (Gürke) Bridson	Mtutumo	12	.	x	.	x	x	.	.
Antiaris toxicaria Lesch.	Msenda	5	26	x	x	.	x	x	.
Dialium holtzii Harms	Mpande	1	11	x	.	x	x	.	x
Trilepisium madagascariense Thouars ex DC.	Mfilafila 2	8	10	x	x	.	x	x	.
Casearia gladiiformis Mast.	Mbasuka 1	20	6	x	.	x	x	x	.
Pseudolachnostylis maprouneifolia Pax	Msolo	3	6	x	.	x	x	x	.
Stereospermum kunthianum Cham.	Mtalandi	7	6	x	.	x	x	x	.
?*Cassia* sp. 1	Mlingalinga	3	5	x	x	.	x	x	.
Markhamia obtusifolia (Baker) Sprague	Mputi	8	1	.	x	x	x	x	.
Funtumia africana (Benth.) Stapf	Mtomvutomvu	569	558	x	x	.	x	x	x
Erythrophleum suaveolens (Guill. & Perr.) Brenan	Mwahe	26	181	.	x	x	x	x	x
Zanha golungensis Hiern	Mkalanga	7	40	x	x	.	x	x	x

Cordia peteri Verdc.	Mufwele	38	35	x	x	.	x	x	x
Afrosersalisia cerasifera (Welw.) Aubrév.	Mkumbulu	7	31	.	x	x	x	x	x
Bridelia micrantha (Hochst.) Baill.	Mwisa	21	28	x	.	x	x	x	x
Terminalia sambesiaca Engl. & Diels	Mpululu	4	21	x	.	x	x	x	x
Pterocarpus tinctorius Welw.	Mninga Maji	4	18	x	x	.	x	x	x
Blighia unijugata Baker	Msebele/Mchebele	51	15	x	.	x	x	x	x
Antidesma vogelianum Müll. Arg.	Mkandekande	21	13	.	x	x	x	x	x
Trichilia dregeana Sond.	Muhubasi 1	3	7	x	.	x	x	x	x
Tarenna pavettoides (Harv.) Sim	Mkumbangubi	67	1	x	x	.	x	x	x
Leptactina platyphylla (Hiern) Wernham	Mtombakotombako Matunda Mwishoni	30	.	x	x	.	x	x	x
Pouteria alnifolia (Baker) Roberty	Mtombakotombako 4	.	4	.	x	.	.	.	.
Diospyros squarrosa Klotzsch	Mkoko	.	1	.	x	.	.	.	.
Tamarindus indica L.	Mkwaju	.	1	.	.	x	.	.	.
Lannea ?humilis/schimperi	Mlangali	1	1	.	.	x	.	.	.
Ekebergia capensis Sparrm.	Mulimuli/Limulimuli	.	1	x	.	.	.	.	.
Croton ?*sylvaticus* Hochst. ex Krauss	Mwisukulu	.	1	.	x	.	.	.	.
Mallotus oppositifolius (Geiseler) Müll. Arg.	Sunguluti 2	2	1	x	.	.	.	.	.
?*Milletia* sp. 1	Mfungulu	1	.	.	.	x	.	.	.
Shirakiopsis trilocularis (Pax & K. Hoffm.) Esser	Mpalang'anga Dume	2	.	x	.	.	.	.	.
Gomphia sacleuxii (Tiegh.) Verdc.	Mtonanambi	1	.	.	x	.	.	.	.
Allophylus africanus P. Beauv.	Uhehefu	2	.	x	.	.	.	.	.
Diplorhynchus condylocarpon (Müll. Arg.) Pichon	Mtogo	5	7	.	.	x	x	.	.
Millettia usaramensis Taub.	Muhafu Dume	10	2	x	.	.	.	x	.
?*Milletia* sp. 2	Muvanga 2	5	2	.	x	.	x	.	.
Dombeya sp.	Mtowo	3	1	.	.	x	.	x	.
Millettia semseii J.B. Gillett	Muhafu Jike	21	31	.	x	.	.	x	x
Ficus sycomorus L.	Mkuyu	4	14	.	x	.	x	x	.
Dracaena mannii Baker	Mdetema	21	7	x	.	.	x	.	x
Dichapetalum stuhlmannii Engl.	Mtuguto	5	4	x	.	.	x	.	x
Flacourtia indica (Burm. f.) Merr.	Mgogola	9	1	x	.	.	x	x	.
Ochna macrocalyx Oliv.	Mkwaliti Dume	6	.	x	.	.	x	x	.

Parinari excelsa Sabine	Msaula	25	57	.	x	.	x	x	x
Rothmannia manganjae (Hiern) Keay	Msebesebe/Mchebechebe	29	34	.	x	.	x	x	x
Parkia filicoidea Welw. ex Oliv.	Mnyasa	1	8	x	.	.	x	x	x
Tabernaemontana pachysiphon Stapf	Mlowulowu	84	72	.	.	.	.	.	x
Unknown 3	Mufwele 2	2	9	.	.	.	x	.	.
Aoranthe penduliflora (K. Schum.) Somers	Mtombakotombako Matunda Pembeni	5	8	.	.	.	.	.	x
Myrianthus holstii Engl.	Mfutsa	.	5	.	.	.	.	.	x
Burkea africana Hook.	Mkalati	.	5	.	.	.	x	.	.
Strombosia scheffleri Engl.	Mobangwi	2	3	.	.	.	.	.	x
Ficus exasperata Vahl	Msafya	.	3	.	.	.	.	x	.
Mimusops aedificatoria Mildbr.	Mfilafila 1	1	2	.	.	.	.	x	.
Unknown 1	Mkrismasi	.	2	.	.	.	x	.	.
Isoberlinia scheffleri (Harms ex Engl.) Greenway	Mgumegume	.	1	.	.	.	.	x	.
Ficus vallis-choudae Delile	Mkuyu 2	.	1	.	.	.	.	x	.
Lannea ?*schweinfurthii* (Engl.) Engl.	Mlangali 2	1	1	.	.	.	x	.	.
Faurea saligna Harv.	Mlembelembe 2	.	1	.	.	.	x	.	.
Cussonia zimmermannii Harms	Mnyongamembe	.	1	.	.	.	.	x	.
Elaeis guineensis Jacq.	Msalisi	.	1	.	.	.	x	.	.
Ficus ?ovata Vahl	Msosa (Mdamba)	.	1	.	.	.	.	x	.
?*Newtonia* sp.	Mtalula	.	1	.	.	.	x	.	.
Sterculia quinqueloba (Garcke) K. Schum.	Mtelelanyabo 2 (Muhembeti)	.	1	.	.	.	x	.	.
Unknown 2	Mtowo 3?	.	1	.	.	.	.	x	.
Premna schliebenii Werderm.	Mtugutu (Mtiki Pori)	3	1	.	.	.	.	x	.
Maytenus undata (Thunb.) Blakelock	Mvalambi	.	1	.	.	.	x	.	.
Unknown 4	Mwembeng'ongo ya Pori	.	1	.	.	.	x	.	.
Garcinia buchananii Baker	Mduidui	1	.	.	.	.	.	x	.
Polyalthia verdcourtii Vollesen	Mkovati	1	.	.	.	.	.	.	x
Vitex mossambicensis Gurke	Mnunganunga	1	.	.	.	.	.	x	.
Hymenocardia acida Tul.	Mpeme	1	.	.	.	.	x	.	.
Vangueria infausta Burch.	Msada	1	.	.	.	.	x	.	.
Tetrapleura tetraptera (Schumach. & Thonn.) Taub.	Msonobali Pori 2	1	.	.	.	.	.	.	x

Combretum adenogonium Steud.	Mtaagata/Kitaagata 2	1	.	.	.	.	x	.	.
Turraea robusta Gürke	Mtombakotombako 1	1	.	.	.	.	.	x	.
Premna senensis Klotzsch	Mung'ulung'ulu	1	.	.	.	.	x	.	.
Vismia orientalis Engl.	Mvavata 2	5	.	.	.	.	x	.	.
Rinorea arborea (Thouars) Baill.	Sunguluti 1	3	.	.	.	.	.	x	.
Lannea antiscorbutica (Hiern) Engl.	Mnyonzi	9	20	.	.	.	x	x	.
Monodora grandidieri Baill.	Mgecha	10	17	.	.	.	.	x	x
Ficus sur Forssk.	Msombe	13	15	.	.	.	x	x	.
Grewia goetzeana K. Schum.	Mkole Dume	3	10	.	.	.	x	x	.
Quassia undulata (Guill. & Perr.) D. Dietr.	Muhubasi 2	3	10	.	.	.	.	x	x
Brachystegia spiciformis Benth.	Muhani	.	9	.	.	.	.	x	x
Ricinodendron heudelotii (Baill.) Heckel	Muwonowono	.	9	.	.	.	x	.	x
Syzygium cumini (L.) Skeels	Muvenge 2	2	3	.	.	.	x	x	.
Tabernaemontana odoratissima (Stapf) Leeuwenb.	Mlowulowu 2	10	2	.	.	.	x	.	x
Piliostigma thonningii (Schumach. & Thonn.) Milne-Redh.	Msegese	2	2	.	.	.	x	x	.
Sterculia appendiculata K. Schum.	Mtelelanyabo (Mgude)	.	2	.	.	.	x	x	.
Majidea zanguebarica Kirk ex Oliv.	Mulimuli 2	2	2	.	.	.	x	.	x
Harungana madagascariensis Lam. ex Poir.	Mvavata	1	1	.	.	.	x	x	.
Vangueria volkensii K. Schum.	Msadasada	37	19	.	.	.	x	x	x
Morus mesozygia Stapf	Msisina	5	15	.	.	.	x	x	x
Albizia gummifera (J.F. Gmel.) C.A. Sm.	Mtanga	3	11	.	.	.	x	x	x
Drypetes usambarica (Pax) Hutch.	Mwelesi	6	3	.	.	.	x	x	x
Leptonychia usambarensis K. Schum.	Mlinditi Mti	7	.	.	.	.	x	x	x
Didymosalpinx norae (Swynn.) Keay	Mwata	5	.	.	.	.	x	x	x

Chapter 4 - Line-Transect Methods for Estimating Density of Clustered Animals: A Review and Guide with Lessons from the Primates

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Line-Transect Methods for Estimating Density of Clustered Animals: A Review and Guide with Lessons from the Primates

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Abstract

Considerable debate has surrounded the selection of methods for estimating density from line-transect distance sampling (LTDS) in clustered populations. Here we review the four contemporary methods (perpendicular modelling of cluster centres, perpendicular modelling of centre of measurable individuals, strip transects, and animal-observer distance), for collecting and analysing such data, resulting in a guide to method selection. For selecting methods we use the six selection criteria of visibility, level of habituation of animals, cluster spread, study aims, time and resources. We use the literature, illustrative diagrams and field data from the Udzungwa Mountains in Tanzania, to clarify and synthesise the debate. The paper has relevance for all clustered animals in poor visibility habitats, however examples are drawn primarily from the order primates, because of the high number of studies and intense debate. We first consider the many assumptions and requirements of LTDS, then highlight the problem of adjusting for cluster size and spread, followed by description and discussion of the applicability of the four methods. The methods with the best theoretical framework are not always the most applicable, so the assumptions and correction factors must be considered carefully. Perpendicular methods have better mathematical justification than non-perpendicular methods. However the assumptions of perpendicular methods are frequently broken in poor visibility habitats or with unhabituated animals. Despite lack of mathematical backing, the simplest method based on animal-observer distances is the most practical to employ. We do not reject any of the four methods outright as all have proved accurate (except for one method that remains to be tested) and empirical tests are required to improve our understanding of all methods. We also emphasise that a key part of determining the most appropriate method, is to determine where the errors lie and to minimise bias.

Key words: abundance, census, detectability, forest, monitoring

Introduction

Despite several publications on methods for estimating density of clustered animals, contrasting studies among the order primates show that opinions remain deeply polarised. Although no method is without bias, the most accurate density estimates are obtained from complete counts (e.g.

McNeilage et al. 2001), or focal group studies of home range size and overlap (National Research Council 1981; Chapman et al. 2000; Fashing & Cords 2000). However, these methods require sampling effort beyond the capabilities of most studies and are only feasible over a relatively small area. In most cases, line-transect distance sampling (LTDS) is the most practical method for estimating primate population densities (Struhsaker 1997; Plumptre 2000). Making direct counts along line-transects is complicated where visibility is poor (e.g. degraded forests). This presents many difficulties for density estimation, and there has been extensive debate on how best to obtain accurate estimates (e.g. Struhsaker 1975 & 1997; National Research Council 1981; Brockelman & Ali 1987; Chapman et al. 1988; Whitesides et al. 1988; Fashing & Cords 2000; Plumptre 2000; Plumptre & Cox 2006).

Rationale for Line-Transect Distance Sampling

The basic output from counts along line-transects is the encounter rate, i.e. the number of observations per distance walked. While this can be useful as a measure of relative density, for monitoring change over time, or for dealing with interobserver bias (Seber 1982; Butynski & Koster 1994; Mitani et al. 2000; Rovero et al. 2006), it does not account for variation in visibility or detectability. Data on how far an observer can see through vegetation, from 8 transects in the Udzungwa Mountains in Tanzania, are presented in Fig. 1. The significant differences between transects show how visibility can vary between sites, in this case largely in relation to habitat disturbance. In addition, animals in disturbed or hunted forests may have more cryptic behaviour, which can exacerbate the problem (Johns 1985). Testing for difference in mean sighting distance between sites (Lopes & Ferrari 2000), is not sufficient, as Fig. 1 also shows a difference not just in mean visibility, but also in the distribution of data points. Nor can this be dealt with by using simple correction factors. Furthermore, models accounting for visibility using inanimate objects, cannot simulate the behaviour and detectability of wild animals.

The problem of visibility and detectability along line-transects can be dealt with by measuring the distance from the transect or observer, to each observation (distance sampling). The sample area is then estimated from the decline in observations with increasing distance. This can involve modelling the decline and estimating the number of observations missed (Fig. 2), or estimating a reliable sighting distance, to give a strip within which all individuals or clusters of individuals have been seen with certainty (Burnham et al. 1980; National Research Council 1981; Brockelman & Ali 1987; Whitesides et al. 1988; Buckland et al. 1993 & 2001). Note that we are using the term “cluster”, after Buckland et al. (1993 & 2001), rather than “group”. The term “group”, to some, may infer a complete aggregation of all individuals that usually associate together. During a census walk, the actual point of measurement could be a complete group, but could also be a temporary foraging party or subgroup. This information can be hard to determine in the limited time during a census walk (National Research Council 1981; Plumptre 2000).

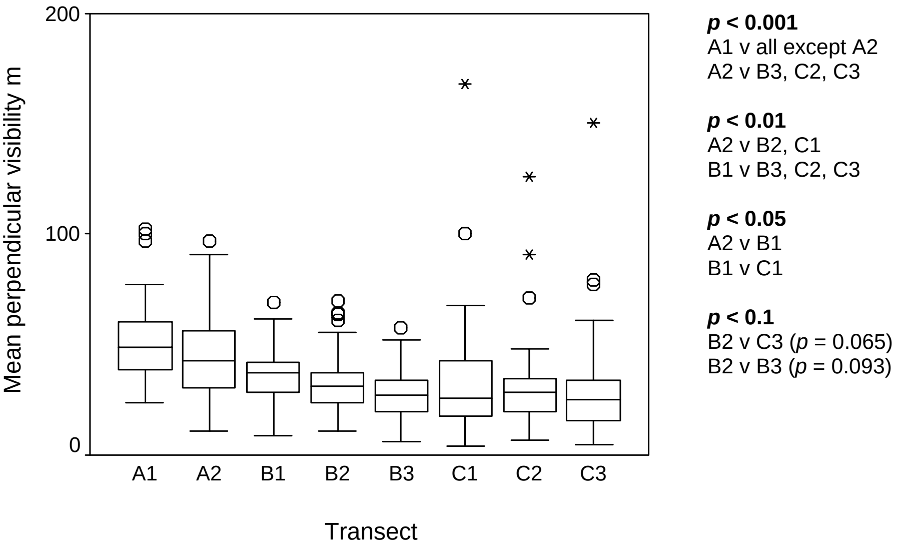

Figure 1. Box and whisker plots and Mann-Whitney *U*-tests, comparing visibility along eight 4 km transects in the Udzungwa Mountains (A, closed canopy forest in Magombera; B and C, semi-open and heavily logged forest in Matundu). Visibility was the horizontal distance to the furthest visible vegetation, on both sides of each transect, at 100m intervals. Boxes show median and interquartile range, with whiskers showing maximum and minimum values, excluding outliers (○ and ∗ = outliers more than 1.5 and 3 times the interquartile range).

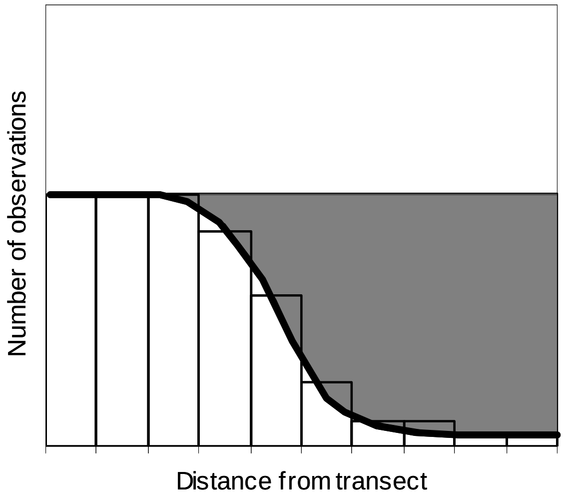

Figure 2. Diagrammatic representation of detection function curve used for estimating density from line-transect distance sampling. To allow for declining observations with increasing perpendicular distance, a histogram like this is plotted, and the decline in observations is modelled (curve) to predict of the number of observations missed due to visibility/detectability (shaded area).

Points of Contention

Field researchers have experimented with many methods, some of which have been rejected following debate and empirical testing (e.g. Robinette et al. 1974; National Research Council 1981). In this review we consider the LTDS methods that still remain in use for clustered animals.

For these methods, the continuing debate surrounds a) the use of animal-observer distance (Struhsaker 1975 & 2002; Chapman et al. 1988 & 2000), versus perpendicular distance to the transect (Burnham et al. 1980; Whitesides et al. 1988; Buckland et al. 1993 & 2001; Plumptre & Cox 2006), b) whether to determine individual densities by use of cluster sizes estimated during census walks (Plumptre & Reynolds 1994; Plumptre 2000), independent cluster counts (e.g. Defler & Pintor 1985; Struhsaker 1997), or counts of only those individuals seen during transect walks (Plumptre & Cox 2006), and c) whether or not to incorporate information on cluster spread (Whitesides et al. 1988; Plumptre & Cox 2006).

Decisions regarding LTDS methods must be made by a wide range of people, including conservation managers, field assistants and scientific researchers. Some of these people do not have access to the many journals and books in which this methodological debate continues. Deciding on methods is further complicated by mixed messages in the recent literature (e.g. Chapman et al. 2000 versus Plumptre & Cox 2006). This is despite a number of articles that have provided discussions of the alternative methods, suggesting conditions where each can be applicable (Robinette et al. 1974; National Research Council 1981; Brockelman & Ali 1987; Fashing and Cords 2000). Some have used more than one method to produce a range of density estimates (e.g. Oates et al. 1990; Plumptre 2000). However, with careful consideration of site conditions, animal behaviour, available time/resources and literature review, researchers should be better positioned to decide on a single most appropriate method.

Aims and Objectives

The following paper has been adapted from a conference talk presented at the XXIst Congress of the International Society for Primatology (Marshall 2006). It aims to summarise four alternative LTDS methods for estimating density from direct counts of primates. In achieving this we discuss the applicability of the various methods using published sources, personal observations from tropical forests, and field data from forests of the Udzungwa Mountains of Tanzania. Our overall aim is to develop a simple procedure for method selection.

The focus is on the unresolved issues of measuring cluster location, and estimating cluster size and spread. The review assumes that only one or two observers are available to make counts, and that animals can be detected from direct observations along line-transects. The methods have been developed for medium-to-large diurnal primates, however the review is relevant for any clustered animals in poor visibility habitats.

Assumptions and Limitations

One of the difficulties of estimating density by LTDS, is that there are several assumptions and limitations. In this section, we present a brief discussion of the key requirements from the literature (Burnham et al. 1980; Buckland et al. 1993 & 2001; Buckland pers. comm.). Points (a) to (e) are applicable to all four of the LTDS methods discussed in this review. Of these, points (a) and (b) are largely out of the control of the researcher, while (c) to (e) can often be achieved with careful planning. Assumptions (f) and (g) are more problematic, and the four methods discussed later aim to address these in different ways, with mixed success.

a) Objects are Detected at Their Initial Location

All distances must be measured before they are influenced by human presence. The observer may be able to reduce his/her influence by treading carefully, wearing inconspicuous clothing, or clearing the path of dry vegetation that may crunch under foot. However where primates are hunted, or where there is tangled vegetation, there is increased probability that they detect the observer first and begin fleeing. This may be the case in most tropical forests, where hunting by humans causes an increased flight response (Struhsaker pers. comm.). Solitary individuals are also a particular problem, as they are able to flee more quietly than a whole cluster, although if they are few in the population, these will not have a major effect.

b) Sightings are Independent

A second assumption is that sightings should be independent. Among many animals, especially primates, clusters are usually non-independently distributed, due to e.g. inter-specific associations, fission-fusion foraging strategies, and inter-group competition. However, although this is listed as an assumption, LTDS methods are robust to this and it is not a concern (Buckland et al. 2001).

c) Observer Walks Faster than the Animals Being Counted

Thirdly, the observer must walk faster than the animals, so that animals do not pass into the area being searched. Violation of this assumption would lead to overestimation of density due to additional groups entering the study area. The assumption also ensures that animals are not double counted. However, in practice, the speed of line-transect walks is limited by the need to detect sufficient animals, and to maintain observer stealth.

d) Transects are Placed at Random with Respect to the Distribution of the Animals

Fourthly, where population estimates are required for extrapolation to a larger survey area, transects must be placed in a random way, to avoid bias from clumped distributions. This means that for some animals, density estimation will be affected where features such as paths or ridges are used (e.g. duikers: Struhsaker 1997). Stratified random sampling may be employed to control for habitat variation, however this requires knowledge of the abundance and distribution of habitats prior to survey, which is often unavailable. For some studies, the research question may not require extrapolation of density from transect to the entire study area. In these cases, this assumption is not relevant (e.g. Ross & Reeve 2003; Rovero et al. 2006).

e) Sufficient Sightings are Made to Estimate the Detection Function or Strip Width

There must also be sufficient sightings so that the detection function or strip width can be estimated with certainty. This is not an assumption, rather a requirement for obtaining a reliable assessment of the decline in observations with increasing distance. Typically, at least 40 sightings are required, but preferably 60 to 80 (Buckland et al. 1993 & 2001). In more extreme cases, 15-30 observations have proved sufficient (Peres 1999 in Brugiere & Fleury 2000), but up to 100 observations may be needed (Bibby et al. 2000). LTDS can therefore be problematic in low density habitats. For example, along one heavily disturbed 4 km transect in lowland Udzungwa (Mkungusi, Matundu Forest), only one cluster of red colobus monkeys was seen in ten repetitions (Chapter 5). Given this encounter rate, 1600 km of survey would be required along this transect, to reach the minimum 40 observations. In this kind of situation, line-transects are impractical as a method for density estimation.

f) Objects on or Near the Line are Detected with Certainty

One of the two most difficult assumptions is that all animals on or near the transect line must be detected with certainty. Figures 3a-c highlight the issue, using diagrams and hypothetical data in cases of decreasing visibility / detectability. Where visibility is 100% within a known distance, no clusters are missed by the observer, and therefore observations do not decrease with distance from the transect (Fig. 3a). More typically, visibility and the number of observations decline with increasing distance from the transect, producing the classic detection function curve (Fig. 3b). Where visibility / detectability is reduced sufficiently that clusters are missed on the transect line, the implications are serious. The result is that the histogram bars and curve are pulled downwards, thus reducing the overall density estimate (Fig. 3c). In dense habitats such as tropical forests, the potential for missing individual animals on the transect line is high. For cluster-living animals, clusters are therefore the more popular sample unit, as they are less likely to be missed. However requirement (a) is relevant here, as clusters may move away from the transect line in response to an observer.

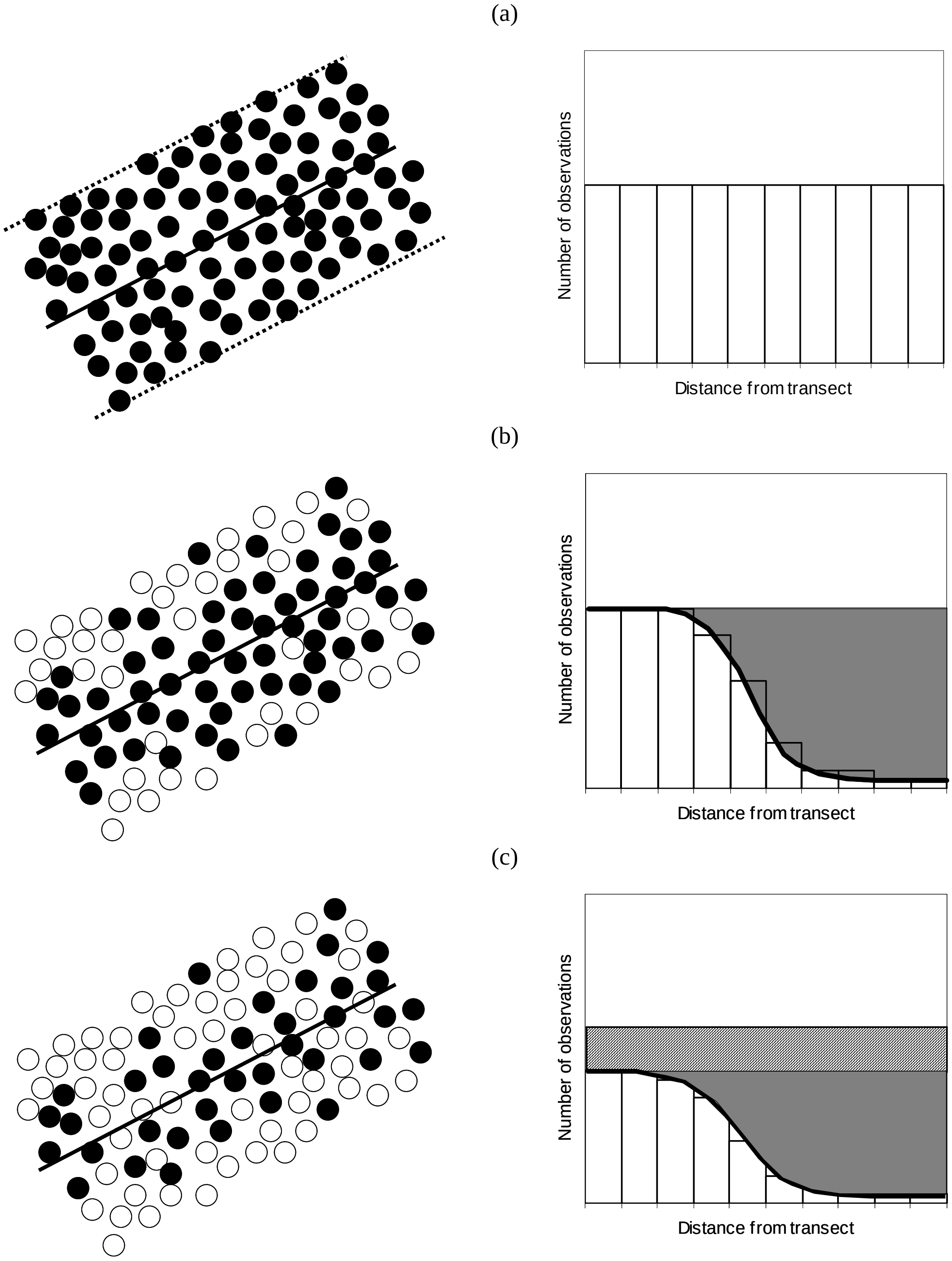

Figure 3. Diagrammatic representation of the effect of declining visibility on detection functions. (a) = perfect visibility (i.e. strip transect shown by dashed lines), (b) = visibility declining with distance from the transect, (c) = poor visibility with individuals missed on the transect line. Diagrams on the left represent the locations of all clusters seen (●) or missed (○) during census walks. Diagrams on the right show how the pattern of missed clusters in left-hand diagrams would affect the resulting histograms and detection function curves. Shaded areas in (b) and (c) show the number of clusters estimated to be missed for each model, and the hatched area in (c) shows the underestimation caused by individuals missed on the transect line.

g) Measurements are Exact

The second difficult assumption for reliable density estimation is that all measurements must be measured accurately. Estimating distances visually may have led to some serious overestimates in primate density (Brugiere & Fleury 2000). A laser rangefinder and compass are essential, and observers should be thoroughly trained in data collection. This is reasonably easy to achieve, however a more difficult consideration is the point of measurement. We have already seen above, that individuals are not suitable for LTDS of clustered animals, as some will almost certainly be missed on the transect line and may move before detection by the observer. It is also impractical to measure the location of every individual due to the large number that can associate together at any one time. For example, the Udzungwa red colobus *Procolobus gordonorum*, has associations up to 83 individuals, with mean cluster size of 41.6 in closed canopy forest (Struhsaker et al. 2004). This emphasises that the cluster is a more appropriate sample unit.

Cluster Parameters

A major complication for the assumption that all measurements are exact, is that the use of clusters as the sample unit requires two parameters, namely cluster size and location of cluster centre. Because of these potential sources of error, these two correction factors are at the centre of the debate for determining the most appropriate methods for estimating density, and will be discussed briefly before making comparisons between methods below.

Cluster Size

We have already reasoned that it is advisable to use clusters rather than individuals as the point of measurement during line-transect walks. In order to convert cluster density into the more useful figure of individual density, it must be weighted by the mean number of individuals per cluster (but see also method (b) below). Where possible these should be counted during walks, so that the distance data correspond exactly to the cluster size data (Plumptre 2000). Including a second or third observer may help to achieve this (Buckland pers. comm.), however time is a major limiting factor. In fact, it is rare that reliable counts of cluster size can be made during census walks of primates (Defler & Pintor 1985; Brugiere & Fleury 2000). Complete group counts of red colobus *Procolobus tephrosceles*, in Kibale forest (Uganda), required 10-60 hours of observation, and counts of redtail monkeys *Cercopithecus ascanius schmidti*, can require hundreds of hours (Struhsaker 1997). Selection of clusters for counting independently from line-transect walks, should be a representative sample and should not concentrate on the largest or most habituated (Plumptre 2000). They should also only consider those individuals associating at the time of encounter, so as to simulate the conditions of census walks. Cluster size may also vary within or between transects, or with time of day, however weighting for these would require considerable effort, and their effect on accuracy of density estimates will depend on field conditions.

Cluster Centre / Spread

Also critical for the assumption (g) that all measurements are exact, is that researchers must determine an appropriate point of measurement. For traditional distance sampling and strip transect methods, the point of measurement must be the centre of the cluster (Burnham et al. 1980; Buckland et al. 1993 & 2001). These methods therefore assume that clusters are well defined. Given that one cannot distinguish the orientation of a cluster from the notes in a datasheet, measurement to the cluster centre at the time of data collection is preferable (Plumptre 2000). However, estimating the location of cluster centre introduces subjectivity (and therefore interobserver bias) and becomes unreliable where animals are not in tight-living clusters, where visibility is poor, or where animals are not habituated (pers. obs.). In most situations, this is not possible and independent determination of mean cluster spread is therefore required.

Calculation of mean cluster spread assumes that clusters are approximately circular in shape (Whitesides et al. 1988). This is often untrue for an individual cluster (Struhsaker 1997; Fig. 4). However, cluster spread may in some cases be more circular than linear (Fashing & Cords 2000). Also it has been suggested that the mean cluster spread may be approximately circular (Fashing & Cords 2000; Fig. 4), although this has not been shown empirically, and is still doubted by some (Struhsaker pers. comm.). Because the orientation of the group relative to the transect is unknown during line-transect walks, spread should be measured from as many angles as possible across the cluster, at regular intervals (e.g. 30 mins; Plumptre 2000). Low sample size is likely to result in low precision of density estimates, especially for clusters with spread that deviates from the assumption of circularity. It is therefore important to obtain sufficient samples, determined for example by power analysis (Lenth 2001), or precision analysis (National Research Council 1981; Mitani et al. 2000). For animals that are not well habituated, the influence of human presence should also be considered, and measurements should only be taken before the spread has been affected. This may not be possible at all for unhabituated animals or animals with high cluster spread such as Sykes monkeys *Cercopithecus mitis*.

Because of the error involved, and daily variation in cluster spread, Plumptre (2000) advises against using cluster spread. Determining the mean spread of clusters may be unreliable, prone to subjectivity, and requires a considerable amount of field time in addition to time spent conducting transect walks. However, it should be noted that the few empirical tests to date show that cluster spread adjustments give accurate density estimates compared to known densities of primates (Whitesides et al. 1988; Fashing & Cords 2000).

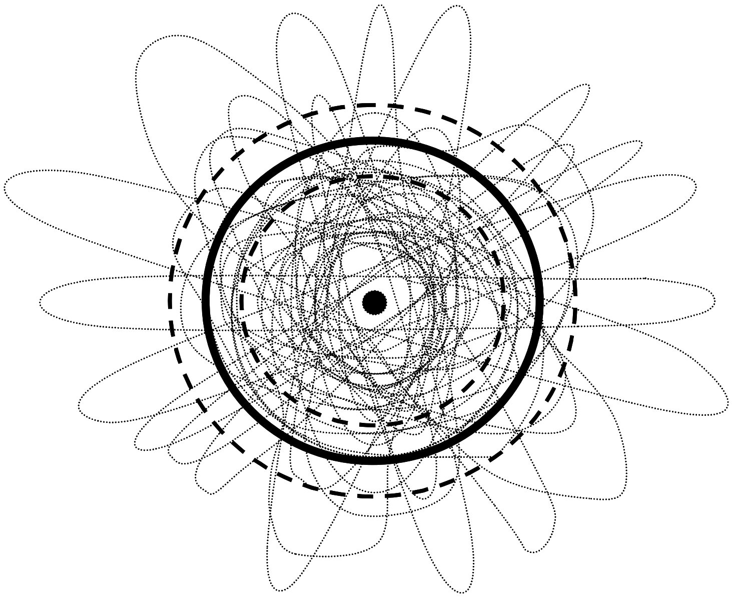

Figure 4. Diagrammatic representation of the assumption of circular cluster spread. Given sufficient samples of individual cluster spreads (dotted lines), the best approximation of spread may be a circle (solid line). The amount of error (dashed lines) will depend strongly on sample size.

"Accepted" Methods

The basic procedure for making counts along line-transects is reasonably consistent across the literature. Data suitable for modelling both perpendicular and animal-observer distances can even be collected simultaneously (Fashing & Cords 2000). Typically for primates, the observer walks at a pace of 1-2 kmh^{-1} (Ross & Reeve 2003), for 2-4 km, starting early in the morning (or more rarely in the late afternoon). The horizontal distance and bearing to all observations are measured, and where possible the perpendicular distance to the transect (Burnham et al. 1980; National Research Council 1981; Buckland et al. 1993 & 2001). The methods vary however, in how to determine the point of measurement for each observation, how to determine the area surveyed, and how to weight the observations to give individual density rather than cluster density. In this section, four methods (a-d), that have been considered appropriate for primates, are compared in terms of bias, accuracy, violation of assumptions, number of estimations, and applicability in the field. Although all four of these methods have been used in the literature, considerable debate surrounds their use; hence the use of inverted commas around the word *accepted* in the section heading. Here we discuss the methods in order of complexity, beginning with the most complex, and ending with the simplest.

Perpendicular Distance To Cluster Methods

a) Perpendicular Modelling of Cluster Centres (Traditional Detection Function Modelling)

The traditional modelling method for estimating density from LTDS data involves creating a detection function of perpendicular distance from cluster centre to the transect, for example using the program *Distance* (Burnham et al. 1980; Whitesides et al. 1988; Oates et al. 1990; Thomas 1991; Buckland et al. 1993 & 2001; Plumptre & Reynolds 1994). The *Distance* software commonly used for calculating perpendicular models, is beneficial as it also includes tools for sampling design, calculation of 95 % confidence intervals, effective strip width, spatial modelling and many other useful features (Buckland et al. 1993 & 2001). Access to *Distance* is further facilitated by training courses and technical support (www.creem.st-and.ac.uk).

For perpendicular modelling of cluster centres, various detection function models are fitted onto histograms of perpendicular distance versus frequency of observations. From this, density is estimated by allowing for those individuals missed (Burnham et al. 1980; Buckland et al. 1993 & 2001; Fig. 2). Alternative detection function models include the Fourier series, hazard-rate and half normal (Burnham et al. 1980; Buckland et al. 1993 & 2001), of which the hazard-rate has so far proved the best fit to the frequency distribution of perpendicular distances for primates (Plumptre & Reynolds 1994), except for where samples are low (less than about 30; Whitesides et al. 1988). Detection function modelling has the advantage over methods using a single cut-off distance, in that most of the data are used to make the density estimate. Empirical studies comparing density estimates from such models to estimates based on focal group follows, show a reasonable level of accuracy (Whitesides et al. 1988; Fashing & Cords 2000).

This method is highly dependent on reliable estimates of cluster size and spread, and therefore prone to the errors discussed above. Estimation of cluster location is the major concern (Struhsaker 1997; Chapman et al. 1988; Plumptre 2000; Plumptre & Cox 2006). Where cluster centre cannot be determined during census walks, it is determined by summing the distance from the observer to the edge of the cluster, and the mean cluster radius (Whitesides et al. 1988). Using the bearing to the edge of the cluster, the perpendicular distance is then estimated using basic trigonometry (Whitesides et al. 1988; Fig. 5a). However, defining the edge of a cluster is rarely easy. Using the first individual seen as the point of measurement, assumes that the first individual seen is on the side of the cluster nearest to the observer, and that it is in direct line from the observer to cluster centre in any given cluster (Fig. 5a). This is unlikely to be the case for any given cluster. Using the nearest individual seen to the observer is also not a good estimate as this would artificially place many clusters at zero distance to the transect line, and is reliant on the observer having a good feel for the spread of a given cluster (pers. obs.). Determining the edge of a cluster really therefore requires good visibility, and habituated or tightly-spread clusters. These situations are rare and so the method can often only be considered a minimum estimate of density, and will have low precision without detailed information on cluster spread.

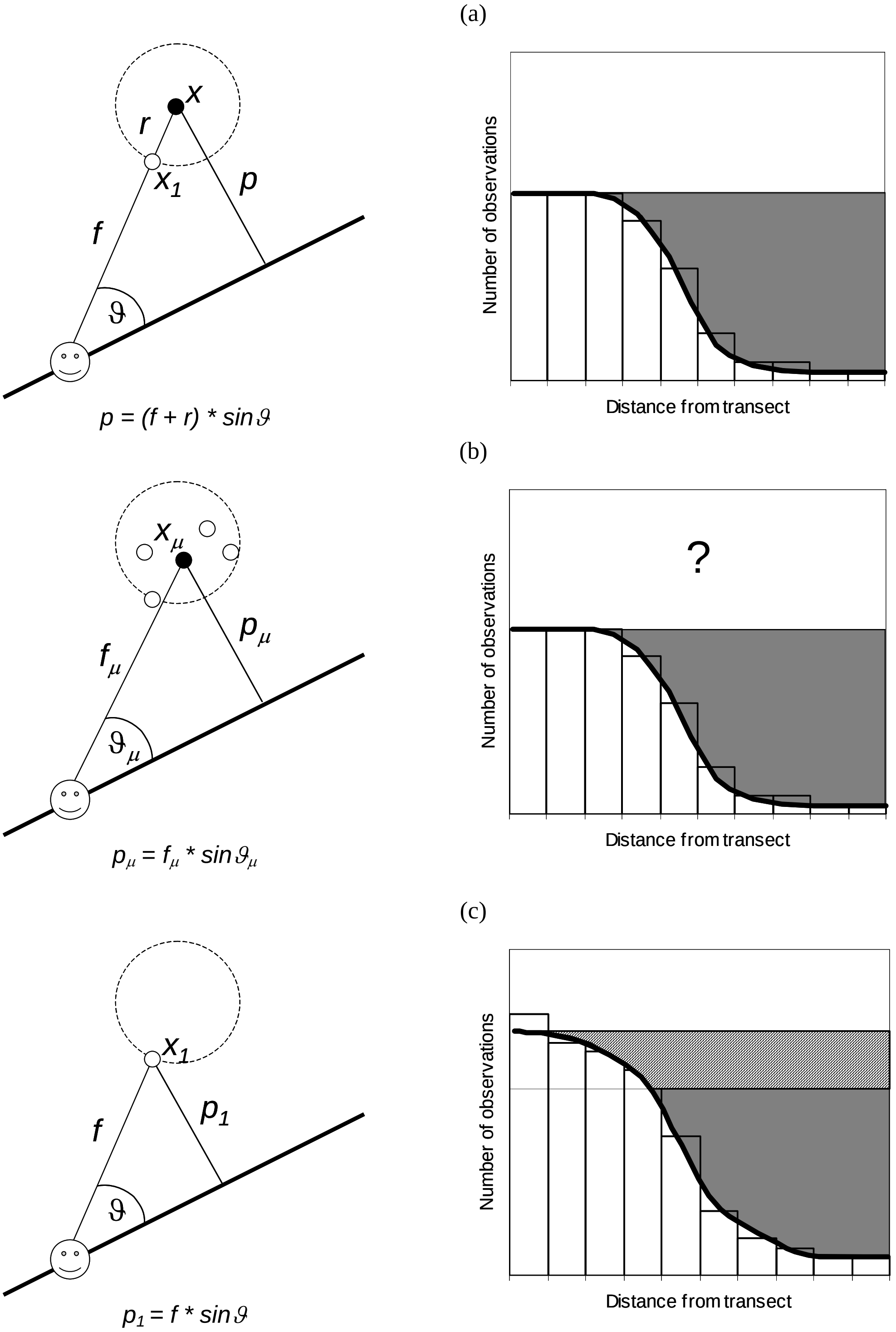

Figure 5. Comparison of expected models from estimating perpendicular distance as (a) cluster centre x, (b) geometric centre of measurable individuals in a cluster x_μ and (c) first individual seen x_1. On the left are schematic diagrams showing the calculations involved. Diagrams on the right show the expected effect on the detection functions. Shaded areas show the number of clusters estimated to be missed, and the hatched area in (c) indicates overestimation by use of the first individual seen. The detection function for method (b) has been assumed not to differ from method (a) (Plumptre & Cox 2006), however the question mark indicates that this remains to be tested.

b) Perpendicular Modelling of Centre of Measurable Individuals

Because cluster size and spread are rarely determinable during transect walks, Plumptre & Cox (2006) use the centre of only those individuals whose initial location can be determined and measured during a transect walk (Fig. 5b). Consequently, only a proportion of each cluster is used to make density estimates. This method is a recent development and remains to be tested against known densities, however it may reduce the problem of bias associated with estimating cluster size and spread. It also allows density estimates to be made from line-transect walks alone, without the need for added time spent making independent assessment of clusters. Although defining the centre of measurable individuals introduces a degree of subjectivity, it is thought to be at least as accurate as estimating the centre of the cluster (Plumptre & Cox 2006).

Methods for density estimation should keep correction factors to a minimum (Plumptre 2000). However, despite avoiding the need for cluster size and centre estimation, two additional correction factors are incorporated in the *Distance* program, for correcting errors in data derived from the centre of measurable individuals (Buckland et al. 1993 & 2001). Firstly, because large clusters are easier to detect than small clusters, corrections are also required for their higher detectability, particularly as distance from the transect increases (Plumptre & Cox 2006). Secondly, because individuals are often missed on the transect line, the method risks violation of assumption (f) above (objects on or near the line are detected with certainty).

Missing individuals on the transect line may be remedied by having two observers walking together, with one concentrating solely on detecting individuals on the transect. The proportion of individuals missed on the transect by the first observer compared to the second observer, is then used to estimate the probability of an observer missing individuals on the transect, using similar calculations to mark-recapture studies (Buckland et al. 1993 & 2001; Plumptre & Cox 2006). This introduces another source of bias, and is highly dependent on the second observer seeing more individuals on the line than the first observer. For this reason, like perpendicular modelling, this method may become difficult in low visibility habitats or for unhabituated animals. These factors may also mean that during transect walks, only one or two individuals may be seen at their initial location in most clusters (pers. obs.). This would give poor quality data for assessing cluster size and the number of individuals missed on the transect line.

c) Strip Transects (Truncated Distance Method or Kelker Method)

Early methods estimated animal densities from line-transects by determining a cut-off distance beyond which observations were excluded (Robinette et al. 1974). Despite the development of mathematical models for estimating detection functions, studies during the last 20 years have continued to employ modified versions of these strip transect methods (Chapman et al. 1988; Whitesides et al. 1988; Butynski 1990; Oates et al. 1990; Lawes 1992; McGraw 1994; White 1994; Rosenbaum et al. 1998; Brugiere 1998; Brugiere & Fleury 2000; de Thoisy 2000; Dvoskin et al. 2003; McConkey & Chivers 2003). The general principle is that of the Kelker method, whereby the cut-off distance is defined as the perpendicular distance beyond which the number of observations begins to decrease (reference in Robinette et al. 1974). An alternative is to only record observations within a fixed-width of the transect. However, this assumes that there is reliable information on the distance within which all groups can be detected with certainty. It also makes the unlikely assumption that the spread of all groups in relation to the transect and fixed-width distance, can be determined with certainty. Finally, unlike the Kelker method, it also does not analyse the pattern in declining observations, and therefore the reliability of the chosen fixed-width cannot be determined. For these reasons we do not make further discussion of this method.

There are a range of methods for determining an appropriate cut-off distance (Robinette et al. 1974; National Research Council 1981). Although rather arbitrary, the most popular method for primates is the 50 % rule, where the data are arranged into 10 m distance intervals. Data are then excluded beyond the interval where the number of observations decreases by half or more in the next one (or sometimes two) intervals (Marsh & Wilson 1981; Chapman et al. 1988; Whitesides et al. 1988; Oates et al. 1990; Lawes 1992; McGraw 1994; White 1994; Brugiere 1998; Muchaal & Ngandjui 1999; Brugiere & Fleury 2000; Chapman et al. 2000). So that observations are not excluded, the 50 % rule has been developed further to produce an “effective distance” or “effective strip width”. For this method, the sample area for all observations is determined as N_t / N_f × cut-off distance (where N_t = the total number of observations, and N_f = the number of observations below the cut-off distance; Whitesides et al. 1988; Buckland et al. 1993 & 2001).

An important assumption of all methods for determining cut-off distance, is that clusters can be detected with 100 % certainty, within the chosen distance from the transect (Fig. 3a). In fulfilling this assumption, a certain amount of subjectivity is required to ensure that the correct cut-off distance is chosen, rather than to rely heavily on an arbitrary cut-off point. The subjectivity involved has been a source of criticism (Brockelman & Ali 1987). However it is preferable to employ some subjectivity based on visual observation of the data, than to rely on an arbitrary percentage cut-off that is sometimes incorrect (see Fig. 7 for animal-observer method below). Also experimentation with a range of histogram bin widths (e.g. 5 to 10 m), may help to better detect a reliable cut-off rather than relying on the popular, yet arbitrary, bin width of 10 m (e.g. Chapter 5). This is built into the *Distance* program, but can also easily be calculated using standard spreadsheets and/or graphics packages.

As for perpendicular distance modelling, cluster locations must be measured to the centre of each cluster. Where centres cannot be determined in the field, the cut-off distance is obtained by adding a cluster radius adjustment to the cut-off determined from first individual distances. This adjustment is usually half of the mean cluster spread (“transect-width estimation” method of Whitesides et al. 1988; Fig. 6), but a quarter or a third of the mean cluster spread have also been employed (Brockelman & Ali 1987 [Janson & Terborgh unpublished data]). The half mean cluster spread method has shown good concordance with known primate densities (Whitesides et al. 1988;

Oates et al. 1990; Lawes 1994; White 1994; Brugiere & Fleury 2000). One study of *Colobus satanus* in Gabon, found this method to overestimate density, however distances were estimated rather than measured and the authors considered them to be potentially inaccurate, thus violating assumption (g) that measurements are exact (Brugiere & Fleury 2000).

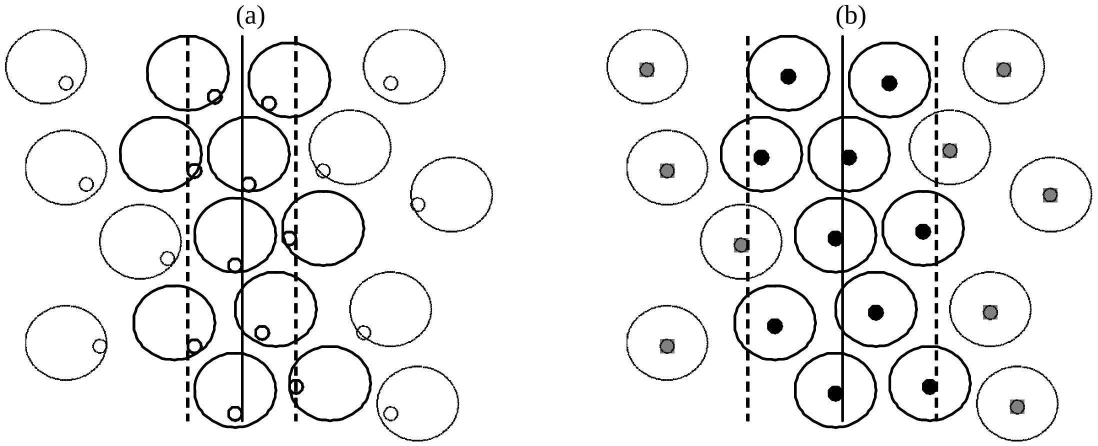

Figure 6. Diagram of strip transect width determination based on (a) the first individual seen, versus (b) first individual seen plus mean cluster radius (“transect-width estimation” method of Whitesides et al. 1988). Dashed lines represent estimated transect width, solid circles represent clusters (and first individual location ○, or centre ●) within the cut-off distance, and dotted circles represent clusters beyond the cut-off distance. Strip (a) would be expected to overestimate density due to underestimation of transect width.

The continued use of strip transects over detection function modelling by some studies, may be partly due to their simplicity, and lack of expertise or software. However, it is also largely because some researchers have found that data on cluster centre or centre of measurable individuals, cannot be accurately obtained under certain field conditions. For example, where visibility is poor, or animals are shy, the centre of the cluster cannot be determined, and having a second observer does not improve the number of sightings (pers. obs.). Also, in difficult terrain, transects are not straight, and so some perpendicular distances must be measured by hand from maps, introducing error (National Research Council 1981). This error is likely to be high given the poor satellite coverage for mapping using global positioning systems under forest canopy. The error is further increased if perpendicular distances have to be adjusted by mean cluster spread. The result is that every point used for creating a detection function model, would have some unknown error due to uncertainty in mapping and spread/orientation of any given cluster. This violates assumption (g) above (measurements are exact).

As with perpendicular modelling of cluster centres, strip transect sampling is susceptible to bias in estimating cluster size and spread. In addition, there are other concerns unique to this method. Firstly, it can be inefficient, as a lot of data may have to be discarded beyond the cut-off point, which leads to low precision where sample size is low (Burnham et al. 1985). Because of these concerns for strip transect methods, perpendicular distance modelling has often been preferred over strip transect methods, so long as the assumptions are met (Burnham et al. 1985; Brockelman & Ali 1987; Whitesides et al. 1988; Buckland et al. 1993 & 2001).

Perpendicular Distance to First Individual Methods

Some have criticised the strip transect method based on estimation of cluster centres, because it can produce a strip about double the size of one based on the perpendicular distance to the first individual seen (Struhsaker 1997). While this may seem extreme, it simply emphasises the large error involved in using the perpendicular distance to the first individual seen. Many studies have estimated density using strip widths or perpendicular models, based on the first individual seen of each cluster rather than cluster centre (Struhsaker 1975; Chapman et al. 1988; Brugiere & Fleury 2000; Chiarello 2000; de Thoisy 2000; Fashing & Cords 2000; Palacios & Peres 2004). This method avoids the difficulty of estimating cluster centre, however it is seriously flawed (Whitesides et al. 1988; Fashing & Cords 2000; National Research Council 1981) and we are not including this as an “accepted” method in our discussion.

The primary fault in this method, is that one would expect the first individual seen to be located nearer to the transect (National Research Council 1981; pers. obs.) and/or the observer (Whitesides et al. 1988; pers. obs.), than the geometric centre of the cluster. This has the effect of underestimating the perpendicular distance of each cluster and therefore increasing the frequency of clusters in the lowest distance bands (National Research Council 1981; Figs. 5c and 6a), and probably explains previous overestimates (Whitesides et al. 1988; Fashing & Cords 2000). Therefore when using perpendicular distance methods, even an inexact measure incorporating cluster spread, is preferable to use of the perpendicular distance to the first individual seen, so that the transect width is increased and that overestimation of density is lessened (Fashing & Cords 2000).

Non-Perpendicular Distance Method

d) Animal-Observer Distance Method (King’s Method)

While perpendicular distance methods based on the first or nearest individual seen have now been rejected by most researchers, a method based on the animal-observer distance to the first individual (or “sighting distance”), continues to appear in the literature (Robinette et al. 1974; National research council 1981; Defler & Pintor 1985; Chapman et al. 1988 & 2000; McGraw 1994; Struhsaker 1997; Rovero et al. 2006). A variation on this, using not the first individual, but the animal-observer distance to estimated cluster centre has also been employed (Freese et al. 1982). Use of these animal-observer methods have proved controversial, however we include them in our discussion as they are still accepted by some researchers. As for perpendicular distance modelling above, histograms are plotted of distance versus frequency. Clusters for analysis are then determined as for strip transects above, or by using the *TransAn* program (Struhsaker 1997). As for the strip transect method above, we suggest that determination of cut-off distance requires some subjectivity, as complete reliance on mathematical procedures may lead to error. Instead of having a set rule, the observer could select the cut-off point as the distance beyond which there is a large and sustained fall in observations. We illustrate this point using the 50 % rule (Fig. 7).

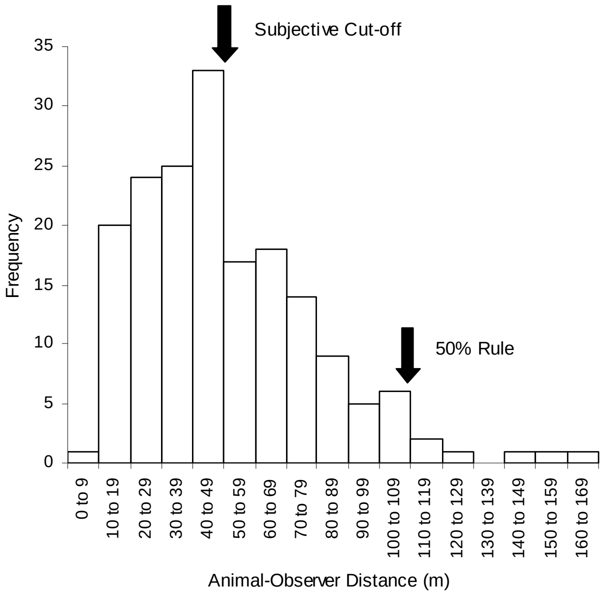

Figure 7. Subjective versus 50 % Rule determination of cut-off point, using the animal-observer distance method for estimating density of Sykes monkeys in Matundu forest, Tanzania. By visual observation, there is a clear drop in observations at 50 m, however this drop from 33 to 17 observations is only a 48 % decrease, and therefore not detected using the 50 % Rule.

The pattern of decline in observations with distance to the observer can be considered a true detection function because the actual sighting distance is used rather than distance to the transect. The method is similar to strip transects above, however because the measurement used is to the observer, it does not identify a strip. This means that although all observations are used in determination of the cut-off point, some can be discarded from calculation of density, because they have been seen from a long way ahead. There were a few examples of this in our 2004-2006 data from the Udzungwa mountains, including one *P. gordonorum* cluster recorded from a distance of 160 m from the observer, whereas the nearest individual was only 22 m from the transect line. The animal-observer method therefore does not define a physical survey area from which clusters are selected for density estimation. It has been described as a means of data reduction, with no mathematical basis (Plumptre & Cox 2006). For these reasons, LTDS methods and assumptions, have been developed for use with perpendicular distances, as these are the measurements directly relevant to density (Burnham et al. 1980; Brockelman & Ali 1987; Plumptre & Cox 2006). However this does not mean that the animal-observer method is obsolete, as we shall demonstrate.

The animal-observer method has made good approximations to known densities in several studies of primates and other animals (Robinette et al. 1974; National Research Council 1981; Defler & Pintor 1985; Chapman et al 1988; Struhsaker 1997; Fashing & Cords 2000). Despite this, some researchers have strongly criticised the method and suggest that it should not be used due to the mathematical uncertainties (Brockelman & Ali 1987; Plumptre & Cox 2006). However, only one published study has compared known primate density to animal-observer methods versus perpendicular methods based on cluster centre (Fashing & Cords 2000). They found that the strip transect method weighted by cluster spread (as described above; Fig. 6), produced only narrowly better estimates for *Colobus guereza* than the animal-observer method (and probably no statistically significant difference, but no tests were used). The strip transect method however performed better than the animal-observer method for *Cercopithecus mitis*. From these observations, this study concluded that, "… if mean spread cannot be determined… the [animal-observer] method provides a reasonable alternative [but is] prone to providing overestimates of density for species whose groups spread out over large areas". Given the inherent error in measuring cluster spread (Plumptre 2000, and discussion above), the animal-observer method may actually therefore be widely applicable. The recent assertion that Fashing & Cords (2000) "advise against" using this method (Plumptre & Cox 2006), is misleading.

Comparison of Methods

A summary of the above discussion of methods is presented in Table 1. The methods are summarised using five method selection criteria (number of correction factors, survey components, whether the physical survey area can be defined [mathematical justification], empirical support and whether or not special software or training are required). From this, it can be seen that perpendicular modelling methods, followed by strip transects, have the best mathematical justification (as they have a definable physical sample area), whereas the animal-observer method is the most practical (as it is simple and does not require many correction factors). Method selection will be strongly dependent on field conditions, and the choices required for deciding upon the appropriate method are considered in the discussion section.

An additional factor not included in Table 1, is the sample size required for each method. Some studies have rejected perpendicular modelling methods in favour of strip transect methods due to insufficient sample size for modelling (Brugiere & Fleury 2000; McConkey & Chivers 2004). However, given that strip transects and the animal-observer method require sufficient sample size for estimation of reliable cut-off distance, sample size is a concern for all methods. In fact, Burnham et al (1985) reject the use of strip transects, for the very reason that they can perform worse than perpendicular distance modelling under low sample sizes. Employment of the "effective distance" method for strip transects, described above, may however deal with this (Whitesides et al. 1988).

Table 1. Advantages and disadvantages of four methods for estimating density from line-transects.

	Method			
	Perpendicular distance methods			
Selection criteria	Detection function models (cluster centre)	Detection function models (centre of measurable individuals)	Strip transect	Animal-observer distance cut-off
Correction factors required	Detection function; Mean cluster size; Mean cluster radius; Cluster centre estimation; Map location*; Perp. distance*	Detection function; Cluster centre visual estimation; Individuals missed; Cluster size versus detection error; Map location*; Perp. distance*	Cut-off point; Mean cluster size; Mean cluster radius	Cut-off point; Mean cluster size
Survey components	3 (Transects; Cluster size and radius)	1 (Transects)	3 (Transects; Cluster size and radius)	2 (Transects; Cluster size)
Physical survey area definable	Yes	Yes	Yes	No
Empirical support	Yes	No	Yes	Yes
Software/training required	Yes	Yes	No	No

* Additional correction factors required for non-straight transects

General Discussion

Method Selection

From the information provided above, it is clear that making a decision as to what method to employ is not simple. The many assumptions and correction factors required by perpendicular methods (Table 1), mean that the resulting density estimates contain unknown error. The lack of mathematical basis for the animal-observer method means that the assumptions and error of this method are also unknown. Method selection is therefore a compromise that should aim to minimise bias by full consideration of the field conditions, available resources and personnel. To assist with method selection, a choice chart is presented including the key decisions for determining the most appropriate method for estimating density (Fig. 8). This chart is designed as an extension to the choice chart of Ross & Reeve (2003), who give guidance on where line-transects are applicable, but do not differentiate between different line-transect methods. To assist decision-making we speculate the likelihood of the various conditions of each method being met from our observations in the Udzungwa Mountains (Fig. 8 and subsequent discussion).

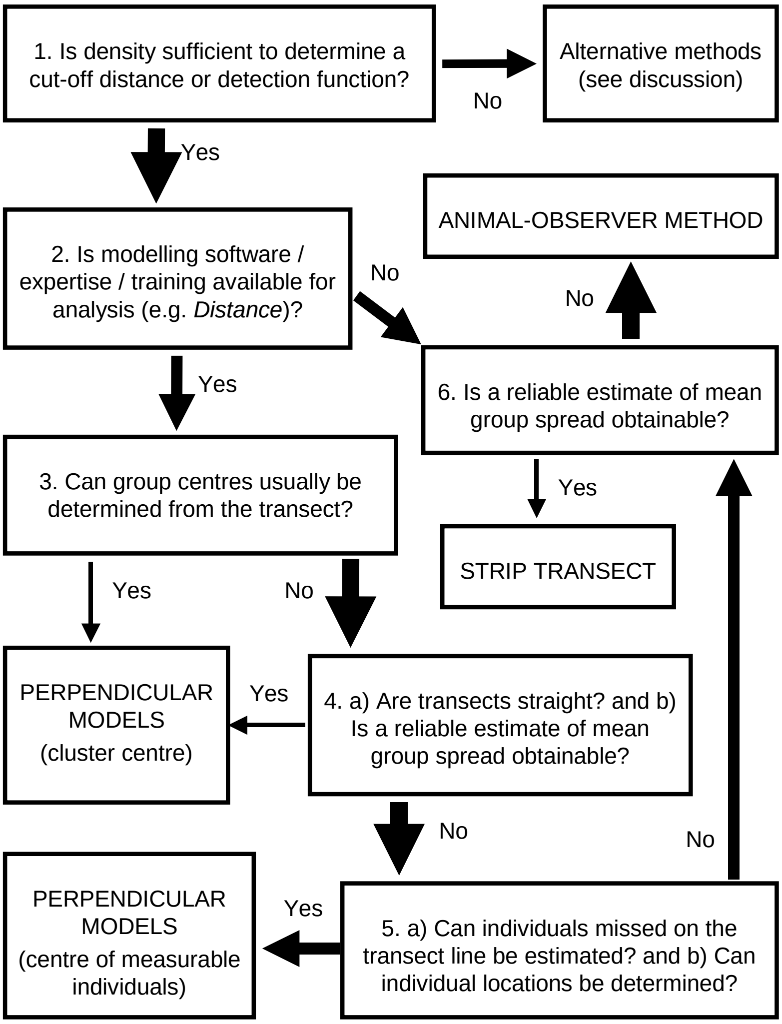

Figure 8. Choice chart for deciding between different line-transect distance sampling methods for estimating primate density. Arrow width represents our perception of the relative likelihood of each choice, from our observations in tropical forests with difficult terrain (see text).

Given the strong mathematical justification and technical support for perpendicular modelling methods, and the many useful features of the *Distance* program, these methods are very attractive given conditions where the assumptions are met and the correction factors can be measured with certainty. Firstly however, the researcher needs access to the appropriate software and requires training in its use. We have highlighted the international training courses that are available, and the software that can be downloaded from the internet. However, while this is achievable for most researchers in western countries, managers and researchers on small projects with limited budgets, or from the world's poorer nations, are unlikely to have the necessary computer literacy, resources, and/or access to training.

Having met the technological requirements for conducting perpendicular modelling, a researcher must determine whether either of the two alternative perpendicular modelling methods are feasible (cluster centre versus centre of measurable individuals). The many assumptions and correction factors mean that these methods require caution. At this stage it is difficult to determine which of these two alternatives is the most desirable. The advantage of models based only on measurable individuals is that they avoid error associated with cluster spread. However, without information on the relative bias of the several correction factors required for the two methods, this is not conclusive (Plumptre & Cox 2006). In particular, the error in estimating the number of individuals missed on the transect line is unknown, and cannot be tested without independent counts of cluster size.

Without information on the relative bias of the two perpendicular methods, the two most difficult choices in Fig. 8 are numbers 4 and 5. In situations where there is good visibility and animals are fairly well habituated, the cluster centre may be estimable, and thus the advantage of using the centre of measurable individuals is removed (Fig. 8; choice 3). However these situations are probably rare in tropical forests, as most have been impacted by humans, and contain tangled habitats or unhabituated animals. In these cases, and where cluster centres have to be estimated by mapping (e.g. due to non-straight transects), or where mean cluster spread is unknown, we suggest that the additional error involved makes this method less desirable (Fig. 8; choice 4). Finally, where a trained second observer is unavailable, where the second observer is unable to detect more individuals than the first (e.g. due to visibility), or where visibility or animal behaviour precludes measurement to more than one or two individuals per cluster, models using the first individual seen are also undesirable (Fig. 8; choice 5).

For these reasons, despite their mathematical advantages, the perpendicular modelling methods have not been universally accepted. Thus, where the assumptions cannot be met, and the correction factors cannot be measured with accuracy (including many primate species in tropical forests; pers. obs; Struhsaker pers. comm.), researchers must consider the alternatives. The strip transect method described above has been the most popular in the literature. We have highlighted the facts that the method is simple and has provided accurate density estimates for primates and other taxa (Robinette et al. 1974; Whitesides et al. 1988; Fashing & Cords 2000). It also has the advantage over perpendicular modelling that correction factors for strip width do not have to be applied to every single observation. Instead only a single correction factor is required to increase the sample width (Fig. 6). The main criticism however, is the error in measuring cluster spread, which can rarely be obtained with accuracy.

Following the rejection of other methods, Fig. 8 shows that we are left with the animal-observer method. Plumptre & Cox (2006) suggest that the animal-observer method should never be used due to its lack of mathematical justification, and others that it should only be used where other methods are impractical (Brockelman & Ali 1987; Fashing & Cords 2000). However, we have presented arguments for the continued use of the animal-observer method and like several previous studies (Robinette et al. 1974; National Research Council 1981; Brockelman & Ali 1987; Fashing & Cords 2000), we suggest that it may be considered where the assumptions of perpendicular methods are violated (Fig. 8). Rapid surveys of primates may also not have the time or resources to collect data required to fulfil all of the assumptions of perpendicular methods, or to consider the various correction factors (Table 1). The lack of mathematical justification for the animal-observer method is of course concerning, as the errors and assumptions are therefore unknown. However in the absence of alternatives, empirical evidence of accurate density estimates suggests that the method is adequate. Given that poor visibility, unhabituated animals, and difficult terrain, are common features of tropical forests, this method may be widely applicable.

We do not want to completely dismiss any of the four methods, because all have proved accurate estimates of density in the literature (with the exception of perpendicular modelling of the centre of measurable individuals, which remains to be tested; Table 1). More empirical comparisons are required for methods to be fully accepted/rejected, so for now methodological planning should use the available literature, which we have aimed to synthesise and simplify here. Preliminary surveys are also essential, for determining field conditions, and for seeking advice from mathematicians and field researchers. Given the polarised views that exist, full justification should be given for any choice of method. Where there is uncertainty in cut-off distance, we stress the importance of presenting a range of densities (National Research Council 1981). We also suggest that uncertainty in cluster spread and cluster size could be dealt with in the same way. The required level of accuracy or statistical power, will depend on the aims of the study and should be considered prior to conducting fieldwork (e.g. Plumptre 2000; Lenth 2001). Presentation of basic encounter rates can be especially useful to indicate broad trends and to allow the reader to see the raw data. If visibility is thought to vary widely, but the assumptions of distance methods are not fulfilled, analyses could consider incorporating measures of visibility (e.g. Fig. 1) as covariates in any statistical analysis of encounter rates. As we have mentioned, this does not account for animal behaviour, however it may serve as an approximate index.

Alternative Methods

Where populations are too low for reliable estimation of density, alternative methods to LTDS must be found (Burnham et al. 1980; Bibby et al. 2000; Buckland et al. 1993 & 2001; Brugiere et al. 2002; Fig. 8 – choice 1). Due to continuing habitat loss, reduction, degradation, and hunting, this is a perpetual problem. There are many alternatives, and like LTDS methods, deciding upon the best method will require consideration of many factors. A few possibilities include point sampling (Hanya et al. 2003), non-invasive mark-recapture (Petit & Valiere 2006), presence-absence / time-to-encounter (Pollock 2006), non-random sampling (Mèsochina & Ostrowski in press) and expert opinion (van der Hoeven et al 2004). Alternative line-transect methods to distance sampling could also be considered, including the 2-belt method (Lammertink 2003), encounter rates (Seber 1982; Mitani et al. 2000; Marshall et al. 2005; Rovero et al. 2006), casual walks (Dinesen et al. 2001), or given enough manpower, sweep census (Marsh & Wilson 1981; Whitesides et al. 1988; Tutin et al. 1997; Mbora & Meikle 2004). All these alternative methods have their own complications, and these should also be considered when deciding upon which to use. However this is beyond the scope of this review, as there have been few studies of methods for low sample sizes, and more work is needed.

There are also some populations that are simply not conducive to gaining accurate density estimates. For example, *Cercopithecus mitis* populations from a number of locations have provided poor estimates of density (Struhsaker 1997; Fashing & Cords 2000; Plumptre & Cox 2006; Marshall unpublished data). There are probably two reasons for this. Firstly, groups tend to be very spread out, sometimes over one hundred metres (Struhsaker & Leland 1979; pers. obs.). This means that estimating cluster spread is very difficult, and estimating cluster centre is impossible. Secondly, the species tends to move quickly and quietly through the canopy (pers. obs.). This means that in areas where animals are unhabituated (in fact they are often hard to habituate due to conflict with humans for crops), it is hard for an observer conducting a transect walk, to track their movements, and therefore a cluster may be inadvertently counted twice.

For difficult populations, one indirect method for assessing population status has also been shown to be highly effective. We have already reasoned how cluster counts independent of transect walks introduce a certain amount of error. However, cluster size/composition data has uses beyond conversion of cluster density to individual density. They have been particularly useful for inferring population viability in primates, e.g. through group size, fecundity, recruitment, juvenile survivorship and age-sex ratios (Struhsaker 1975 & 1997; Struhsaker et al. 2004). More lengthy group follows can reveal even more information, including behavioural changes that may be associated with population stress, such as fission-fusion foraging, dietary or range shifts. Given the high error that may arise when estimating density in certain situations, these alternatives have the potential to be an excellent substitute.

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Chapter 5 – Monkeys as Indicators in Lowland Udzungwa

Monkeys as Indicators in Lowland Udzungwa

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Abstract

Degradation of the world’s tropical forests is a major concern for conservation biology, however basic units for measurement of habitat quality are lacking. By determining species or communities that are indicators of ecosystem health, managers have a simple means of determining conservation priorities. Monkeys have potential as an indicator community as most are dependent on tropical forests and different species can be surveyed simultaneously along line transects. Because they are easier to observe than most forest animals, they also have potential to act as indicators through their behaviour. We therefore compare relative group abundance, density, social group size and species richness of monkeys along a gradient of disturbance in a large lowland forest in the Udzungwa Mountains of Tanzania. Group counts and relative group abundance are determined along six 4 km transects positioned to sample the full range of habitat degradation. Coarse-scale pairwise comparison between heavily disturbed and less disturbed habitats reveals that group size and density of two colobus monkeys is significantly reduced by disturbance. Fine-scale multivariate analysis then shows how the endemic Udzungwa red colobus *Procolobus gordonorum*, is related to many habitat variables, but particularly vegetation structure and composition. Black and white colobus *Colobus angolensis palliatus*, showed fewer significant relationships than the red colobus, and Sykes monkeys *Cercopithecus mitis*, were little affected by disturbance. Comparisons with a less disturbed lowland forest further support the relative effect of habitat disturbance on these species. The results suggest that those areas in the Udzungwa lowlands that contain high densities and large groups of red and black and white colobus monkeys contain the best quality forest in terms of vegetation structure and composition. Those containing mainly Sykes monkeys are the poorest quality. There is little evidence that any species reflects plant biodiversity. However, conservation management must consider many factors beyond diversity, as emphasised by the high population of Udzungwa red colobus in this disturbed forest.

Key words: *generalised linear model, generalist, primate, selective logging, specialist.*

Introduction

Most of the world’s natural forests have been impacted by human disturbance. In tropical forests, selective logging causes habitat degradation up to 19,823 square kilometres each year (Asner et al. 2005). Degradation of tropical forests is a global concern as they contain more than half of the world’s species (WRI 1992). Appreciating the impacts of habitat degradation on tropical forest species is therefore a major aim for conservation biology. However defining habitat quality, and collecting habitat data necessary for identifying trends can be labour intensive. Furthermore, managers and biologists frequently lack basic systems for determining progress towards global conservation goals (Balmford et al. 2003). For assessment of habitat quality following disturbance, indicators may be used as a measure of ecosystem health (e.g. Landres et al. 1988; Caro & O’Doherty 1999; Gregory et al. 2005). Determining the response of species to habitat variation however requires rigorous testing, yet full consideration of the many interacting variables is rare (Lindenmayer 1999; Harcourt et al. 2001; Rovero & Struhsaker in press; Chapter 2). For tropical forests, this is partly because these data are rarely available.

The responses of primates to forest disturbance are species-specific, leading to the definitions of “mature-forest specialist” and “secondary-forest generalist” guilds (Skorupa 1986 & 1988). The different responses of individual primate species makes it hard to generalise about the importance of conserving primates as a taxon (Lovett & Marshall 2006), and also about their potential as indicators (Plumptre & Reynolds 1994). In other taxa, e.g. rainforest trees and coral reef fish, the effect of disturbance is most clear at the community level, where colonizing, mixed or climax communities have been loosely defined (Eggeling 1947; Connell 1978; Townsend et al. 2003). Bird communities have also been used as an indicator community (“multi-species indicator”; Gregory et al. 2005) and can exist on “a very well defined gradient” of species occupying specialist versus generalist niches (Julliard et al. 2006). From the primates, we suggest that monkeys offer the greatest potential as an indicator community for three reasons: 1) different species can be surveyed simultaneously, 2) they are directly observable and therefore diverse and subtle changes in behaviour are detectable, arguably more than for any other taxa, and 3) most live in tropical forests, where there are more threatened species than any other terrestrial biome (Ricketts et al. 2005).

Species richness has been an important indicator for prioritising management of communities (Desmet & Cowling 2004; McCarthy et al. 2006; Chapter 2). For primates, species richness has been negatively related to habitat loss and increasing fragmentation in many areas (Cowlishaw 1999; Harcourt & Doherty 2005; Chapter 2). There are also many other indicators for making conservation priorities. Primate abundance has been closely linked to habitat in several species (Johns & Skorupa 1987; Cowlishaw & Dunbar 2000). The conspicuous nature of diurnal primates further allows investigation into behavioural responses to disturbance. Impoverished environments may lead to increased competition and disruption of social organisation. Large social groups may be unsustainable where there is low resource availability, and therefore in some species social group size has been closely related to habitat quality (e.g. Struhsaker 1975 & 1997; Struhsaker & Leland 1979; Skorupa 1986 & 1988; Dunbar 1988; Janson 1988; Janson & Goldsmith 1995; Gillespie & Chapman 2001; Struhsaker et al. 2004; Marshall et al. 2005). Most of these analyses of primate abundance and social grouping have been pairwise comparisons between disturbed and undisturbed areas. Fine-scale multivariate analyses have been comparatively rare (Rovero & Struhsaker in press).

Species vary in their vulnerability to extinction threats such as habitat disturbance (Isaac & Cowlishaw 2004; Cardillo et al. 2005). Several biological attributes may predispose species to the risks of extinction (e.g. Purvis et al. 2000). Theory predicts that specialised species have evolved in response to stability, and generalists in response to lack of stability (Futuyma & Moreno 1988; Wilson & Yoshimura 1994). Species are therefore vulnerable to becoming rare or extinct if they are highly specialised (Harcourt 2002; Sol et al. 2002). The positive relationship between geographic range and extinction risk is also widely held (IUCN 2001), but not consistently true (Mace & Kunin 1994). Here we evaluate the individual and community responses of four monkey species (Udzungwa red colobus *Procolobus gordonorum*, Angolan black and white colobus *Colobus angolensis palliatus*, Sykes monkey *Cercopithecus mitis* subsp. and yellow baboon *Papio cynocephalus*; all monkey latin names in this paper follow Grubb et al. 2003) to disturbance in Matundu forest, in the Udzungwa Mountains of Tanzania. From dietary studies of the four study species and closely related taxa (Oates 1974; Struhsaker 1975 & 1997; Clutton-Brock 1975; Wasser 1993; Kingdon 1997), and knowledge of their geographic range (Kingdon 1997; Chapter 2), we expect red colobus to be the most susceptible to habitat loss, followed by black and white colobus and then Sykes monkeys. Yellow baboons are more adapted to non-forest habitats (Altmann 1970), and are therefore unlikely to be affected by forest disturbance. Indeed, this pattern has been seen in previous studies of these species (Marshall et al. 2005; Rovero et al. 2006; Rovero & Struhsaker in press). Measures of specialisation of the Udzungwa monkeys besides diet are not yet available.

Aim and Objectives

The aim of this study is to determine the response of a threatened monkey community to habitat disturbance. In achieving this our objectives are to determine; 1) the degree to which community structure is affected by habitat disturbance (composition, species richness); 2) species-specific responses to disturbance; 3) components of the habitat that are important in these relationships; and 4) relative abundance, density and population size of the study site compared to published estimates for less disturbed forests. The results are used to discuss the potential of monkeys as an indicator community, and to guide conservation management.

Methods

Study Area

Data were collected in the Matundu forest, Tanzania, between September 2003 and April 2005 by ARM. The plants and animals of this forest are poorly known even though it is part of an internationally recognised biological hotspot. The Eastern Arc Mountains of Kenya and Tanzania are a centre for species diversity and endemism, are a crucial water catchment, and contain most of Tanzania's montane and submontane forest (Burgess et al. 2006). The Udzungwa Mountains in the southern end of the Eastern Arc chain, contain the only forests with full legislative protection in the Eastern Arc (the Udzungwa Mountains National Park). While around two-thirds of the Udzungwa Mountains remain poorly protected, there still remains around 1,500 km^2 of natural forest (Chapter 2; Fig. 1), at elevations from approximately 300 to 2600 m. The Udzungwa Mountains have many rare and restricted-range species, including the recently discovered kipunji monkey (*Rungwecebus kipunji*; Jones et al. 2005; Davenport et al. 2006) and Sanje mangabey (*Cercocebus galeritus sanjei*; Homewood and Rodgers 1981).

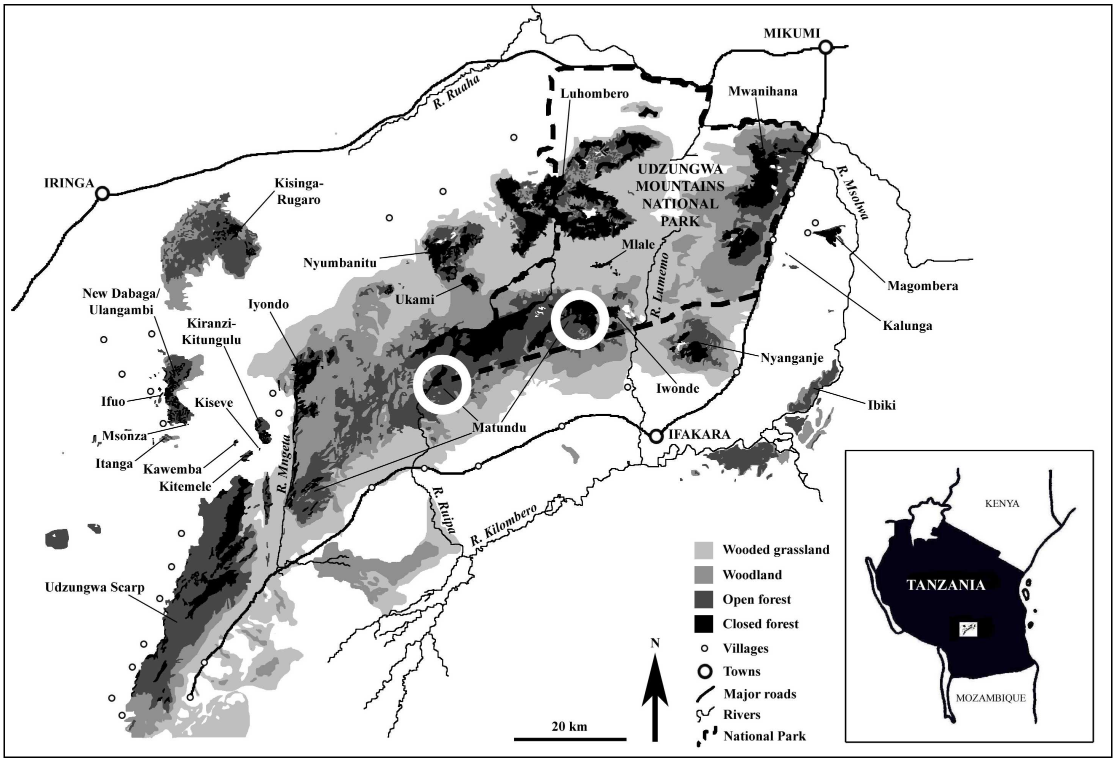

Figure 1. Map of the Udzungwa mountains showing locations of study sites (white circles) for monkey census walks and social group counts in Matundu forest (from Chapter 2).

Because of the large area of evergreen forest, and high numbers of Eastern Arc endemic and IUCN red-listed species, the mountainous forests of Mwanihana, West Kilombero and Udzungwa Scarp, have been given high priority for conservation research in the Udzungwas (Dinesen 1998; Dinesen et al. 2001; Fig. 1). The larger and more extensive forest of Matundu has been considered lower priority, as it has lower elevation range (approximately 273 to 800 m), has suffered from high levels of human disturbance, and has only two restricted-range bird species (Dinesen 1998; Dinesen et al. 2001). However it contains more than two-thirds of the forest in the Udzungwa Mountains (522 km^2; Dinesen et al. 2001; Chapter 2). It is now known that Matundu contains the IUCN vulnerable Abbott’s duiker (*Cephalophus spadix*; Rovero unpublished data), Udzungwa red colobus monkey (*Procolobus gordonorum*), rare and restricted range viverrids (Rovero unpublished data), plus several IUCN listed and Eastern Arc and coastal forest endemic plants, including a newly discovered species of *Coffea* (Marshall Chapter 3 and unpublished data). It forms the only potential corridor between the north-eastern and south-western Udzungwa forests (Fig. 1), and between the only known populations of the IUCN endangered Sanje mangabey (*Cercocebus galleritus sanjei*). Matundu also contains the main routes to dry season forest refugia, for large mammals of the Kilombero-Selous ecosystem to the south.

Approximately half of the Matundu forest is within the Udzungwa Mountains National Park, and at the time of study had very limited ongoing human impact. The remainder of the forest has Forest Reserve status, as Iyondo and Matundu Forest Reserves. Forest Reserve status however offers little practical protection from illegal exploitation, and the forest is under intense human pressure in the area west of the Ruipa river. However east of the river, human activity is currently low. Around 80 % of Matundu contains heavily degraded forest with an open canopy and dominated by tangled climbers (Fig. 1; Chapter 2). Only the most remote parts of Matundu in the far north and north-east contain closed canopy forest. This is largely due to logging by various companies and co-operatives, which occurred until the 1980s. Given the 15-20 year period since logging, we expect that the monkey community has had time to respond to this disturbance.

Transect Walks and Density Estimation

Monkeys were counted along six line transects, positioned to capture the main habitat variations within Matundu. Three transects were placed in moderate-to-heavily logged forest in the vicinity of the Ruipa river in central Matundu (Mkungusi, Lusolwa and Machumbo; Fig. 1), at elevations 290 to 385 m. Three more transects were placed in the east of Matundu (Bwawani, Itula and Isaula; Fig. 1), comprising heavily logged to unlogged forest, at elevations of 355 m to 700 m. The six transects comprise a gradient in tree communities from heavily disturbed semi-deciduous lowland forest to closed canopy semi-evergreen lowland/submontane forest (Chapter 3). The predominant habitat was semi-deciduous forest. Two transects (Machumbo and Bwawani) contained areas of ridgetop deciduous forest, however these were too small to examine deciduous habitat selection by the monkeys.

Line transects consisted of narrow paths 4 km in length, marked with metal tags and a line of red paint at 50 m intervals. Transects were cut as straight as possible, however difficult terrain and irregularly-shaped habitat meant that transects contained many turns. Transect walks were repeated until the mean encounter rate for each species had reached an asymptote (10-12 repetitions per transect; total combined distance 269 km). Transect walks were temporarily halted during rain because it affects the detectability of monkeys. On some rare occasions, walks were stopped short of 4 km due to dangerous herds of elephants, or prolonged rain. Walks were never conducted on consecutive days, to avoid the influence of human presence.

Transects were walked at a pace of 1 km h^{-1}, beginning as soon as possible after dawn. Upon observing any monkey, the location of the observer was noted and the horizontal distance and bearing to the first individual seen were measured using a laser rangefinder and compass. Perpendicular distances to the first individual were also measured. Where this was not possible, they were determined later using the field measurements above and maps made using a handheld global positioning system. For each observation, the number of individuals in the group was counted where possible, moving a short distance from the transect line if necessary. However, complete counts were rarely possible due to visibility and time constraints.

Group and individual density of the three species were also estimated using the animal-observer, or King’s method (Robinette et al. 1974; National Research Council 1981; Chapter 4). We chose this method using the rationale of Chapter 4. Primarily, we did not have reliable information on group spread, and tangled vegetation often prevented reliable estimation of group centre or presence of individuals on the transect line. In addition, this method minimises the number of correction factors required (Chapter 4), and has been shown to give reasonably accurate density estimates for monkeys and other animals (Robinette et al. 1974; Chapman et al. 1988; Struhsaker 1997; Fashing & Cords 2000). We also experimented with use of a strip transect method adjusted by our estimates of mean group spread for each species (Whitesides et al. 1988). This produced very similar estimates to the animal-observer method for the two colobines, however for Sykes monkeys the estimate was substantially lower. We do not however have much basis for our estimates of groups spread and therefore do not consider these estimates useful for this study.

Total population in Matundu forest was estimated by extrapolating the mean density estimate for the transects to the 522 km^2 area of Matundu forest as a whole. To account for different proportions of habitat between transects versus Matundu forest, densities and group sizes were calculated separately for areas of transect with heavy disturbance (Lusolwa, Mkungusi, and Bwawani 2000-4000m), and those with moderate-to-low disturbance (Bwawani 0-2000m, Machumbo, Itula and Isaula; sometimes referred to as “less disturbed” in the text). These categories were defined loosely according to canopy openness, dominance by climbers, and proximity to continuous canopy forest in the general area of each transect. We also use these to make coarse-scale comparison of group sizes and density before carrying out more fine-scale analyses. The resulting population estimates were then weighted using the estimated ratio of these habitats in Matundu (4:1 from Chapter 2). These should only be considered very crude estimates, due to the very high level of extrapolation from survey areas 0.54 %, 0.36 % and 0.45 % of the size of Matundu forest for red colobus, black and white colobus and sykes monkey respectively. However we felt that this would improve on the published population estimate of 3,130 red colobus, which were based on casual walks without consideration of habitat variation (Dinesen et al. 2001).

Social Group Size

Counts of social group size of the two colobine monkeys were made opportunistically both during transect walks (ARM 19 counts), and independently from transect walks (ARM: 22 counts; TTS with ARM: 2 counts). Opportunities for counting Sykes monkey groups were rare due to their behaviour and spatial distribution, and only one reliable count was made of 18 to 19 individuals. No effort was made to count yellow baboon social groups. In making counts, observers searched within 100 m of all transect lines until a monkey group was encountered. Once encountered, the observer waited for the group to move and counted the number of individuals as they crossed a clearly visible point. Where counts were made by a lone observer, a dictaphone was used to record the count details. This allowed the observer to make notes and view the monkeys through binoculars simultaneously. Notes were then transcribed to a notebook immediately afterwards. Previous studies show that group counts made during transect walks, are often of poor quality (Defler & Pintor 1985; Brugiere & Fleury 2000). However in rare cases (19 out of 429 observations), we found that counts during transect walks were possible where groups were clearly visible and fled in full view upon detection.

For all counts, both during and following the count, the observer checked that monkeys had not been missed within at least a 50 m radius of the group. The mean time taken to make a complete count of a group was 65 minutes, and the maximum was 265 minutes, however for many groups a complete count was not possible in a single day. Groups were not habituated and individuals were only occasionally recognisable, and thus it was not possible to make counts of groups over several days. So although most counts are likely to be from entire social groups, some may have been temporary associations (e.g. foraging parties). Where a count was made at a location within 250 m of previous counts, and of approximately similar size (and therefore potentially a repeat count), we used the most reliable of the counts for our analysis. Only complete counts were used, however where a count was considered very nearly complete, we used the mean of the number counted and our maximum estimate of the number missed (following Struhsaker et al. 2004).

Habitat Variables

Habitat variables for analysing fine-scale trends in the distribution and group size of monkeys, were measured for 200 m sections along all transects. The 200m intervals were chosen as a compromise between minimising the number of plots with zero monkey observations, and maximising sample size. A number of variables are used, as one variable alone was considered insufficient for describing the complex habitat mosaic of Matundu, and for considering all potential confounding factors. We include data on topography, disturbance and vegetation. Topographic variables were measured at all 50 m markers and averaged for each 200 m section. They were selected either for previous evidence of association with monkey distributions (slope: Caldecott 1980; streams/rivers: Mbora & Meikle 2004, Palacios & Peres 2004; swamp: Oates 1978), or for their suspected effects on vegetation composition (Chapter 3). Slope was measured using a clinometer. The presence of swamps and rivers/streams was recorded if present within 50 m of each plot. The presence of ridgetops and valley floors were recorded if extending at least 50 m through any plot. Elevation was taken from 1:50,000 topographic maps (Government of the United Republic of Tanzania 1983). Rainfall was not measured, however from our casual observations we expect that it varied little between sites.

The level of disturbance by humans was not directly measurable in the area as there are no records of logging rates. Instead, we estimated disturbance using the proportion of small trees smothered by woody climbers (≥50 % of canopy surface of each tree; Chapter 3). We also included trees that were broken, bent or deformed. Climber cover/damage is not a direct measure of human disturbance, as it incorporates disturbance by elephants and storms (e.g. Rice et al. 2004; Lawes & Chapman 2006). However given the extensive logging that has occurred in Matundu forest, the disturbance is thought to have been largely due to logging. Trees with <50 % climber cover/damage were not included in the index as a low density of climbers may be beneficial for species diversity, ecosystem diversity and biomass (references in Gerwing 2006). We also included an additional estimate of disturbance by large animals (primarily elephants), by noting large animal paths that extended for at least 50 m through any 200 m plot. Large animal paths in Matundu are associated with reduced rare tree species diversity, probably due to seed propagation or physical damage by large animals (Chapter 3). They may also produce a “tunnel effect” that may affect animal counts (Struhsaker 1997; pers. obs).

Vegetation was sampled by measuring and identifying trees with bole centre within 5 m either side of transects and at least 20 cm diameter at breast height (dbh; 1.30 m; Chapter 3). The dbh of the largest stem of all trees was measured using a dbh-calibrated tape measure, and height measured using a laser rangefinder (Bushnell Yardage Pro 500DX). From this we computed stem density and Simpson’s diversity. Mean stem volume was also approximated using the standard equation for the volume of a cone. While trees usually deviate from this geometric shape, we have preferred this approximate measure of volume to basal area or dbh, so that information on tree height could be incorporated. We also computed axis 1 scores from detrended correspondence analysis (DCA; Hill 1980) of the 120 plots. These DCA scores represent the broad gradient in tree community composition from heavily disturbed lowland semi-deciduous forest in the western sites, to old growth semi-deciduous/evergreen forest in the eastern sites (Chapter 3).

Analyses must however find a balance between maximising descriptive variables and over-complication (Vaughan & Ormerod 2003). Therefore, variables were removed due to autocorrelation ($r_s \geq 0.7$) with other variables (following Schadt et al. 2002). We chose to drop variables rather than merge variables using PCA, as the latter method would have made interpretation difficult. Where two variables correlated, we dropped the variable with the least relationship to the independent variable (following Schadt et al. 2002). Elevation was therefore dropped due to correlation with DCA axis 1 scores. In the case of multiple autocorrelation, we dropped the variable with the highest number of correlations. The total volume of stems was therefore not used due to correlation with stem density and mean volume.

Further information used for interpretation of monkey distribution and social group size, was included from dietary observations of all three species. Dietary data were very limited, however we include it due to the obvious importance of food, and due to previous evidence of food influencing monkey distributions in Udzungwa (Rovero & Struhsaker in press). While conducting group counts of monkeys, opportunistic observations were made of food items, including 32 observations for black and white colobus, 41 for red colobus and 10 for Sykes monkeys (Appendix 1). The observations were further supported by 106 records of tree species in which monkeys were perched, which closely reflected the observed ratio of dietary species (Appendix 1). While these additional observations were not direct evidence of diet, it is common for monkey groups to select perches that they also feed from (pers. obs.). Dietary data were collected during all seasons, and therefore were not affected by seasonal bias.

Each dietary species was only scored once during any given period of continuous observation of a group. For the two colobines, two dietary variables were used in the data analysis. These included the number of dietary species present in any 200 m plot, and the total volume of stems of the top two dietary species (red colobus: *Erythrophleum suaveolens* 19.5 % of feeding observations [and 21.1 % of perches] and *Khaya anthotheca* 12.2 % [7.8 % perches]; black and white colobus: *Celtis gomphophylla* [9.8 % perches] and *E. suaveolens* [20.7 % perches]; Appendix 1). Due to autocorrelation, the total volume of all dietary species was not used for either of the colobine monkeys. The total volume of the top two dietary species was not calculated for Sykes monkeys, due to insufficient data. Instead, for Sykes monkeys, only the volume of all dietary species was used. This was preferred to the number of dietary species, as it incorporates additional information on tree size.

Statistical Analyses

We used simple hypothesis testing to make comparisons between transects and between heavily disturbed and moderate-to-low disturbed habitats as defined above (Kruskal-Wallis and Mann-Whitney *U*-tests). Finer-scale analyses were used to test the relationship between monkey relative abundance and group size, versus habitat variables (adapted from Rovero & Struhsaker in press). Three methods for model selection were used due to the uncertainties of stepwise modelling (Whittingham et al. 2006). Generalised linear models (GLMs) were employed using the package *R* (version 2.2.1; http://cran.r-project.org/) using a Poisson error function and log link function (Maindolald & Braun 2003). To normalise and reduce skewness, $\log_{10}$ transformation was applied to mean tree volume, and square root transformation was applied to the volume of the top 2 dietary species. Variables making significant ($p < 0.05$) contribution to GLMs were determined from 1) full (global) models, and 2) backwards stepwise regression, using Akaike Information Criteria (AIC). Final multivariate models were also tested against a null model using ANOVA, and were rejected if they did not significantly improve on this (Maindonald & Braun 2003).

The third fine-scale method used multiple univariate Spearman rank correlation tests. To correct for multiple testing we used Hochberg corrected alpha values (Hochberg 1988). The Hochberg method was preferred over other multiple endpoint adjustments (e.g. Bonferroni and Holm correction), due its increased power (Wright 1992). The predictive power of independent variables for GLM and Spearman analyses, was considered strong if identified as significant by two or more methods, and weak if only identified by one. We also highlight near significant results ($p < 0.1$) as potential relationships that require further testing.

For the fine-scale analysis of monkey relative abundance we used the number of sightings of social groups per 200 m section (plot) of transect (following Rovero & Struhsaker in press). To account for visibility, species-specific cut-off points were selected by visual determination of the reliable perpendicular distance, i.e. the drop-off point in histograms of frequency versus perpendicular distance, using a range of bin widths. These were determined as 40 m for red colobus, 41 m for black and white colobus and 31 m for Sykes monkeys. Species-specific cut-offs were preferred to habitat-specific cut-offs to best account for the behaviour of the animals, rather than making assumptions about the visibility of groups. Analysis of group counts versus habitat variables was similar to that for relative abundance, however habitat data were combined into 600 m plots, using the three nearest 200 m plots to each group count.

Results

Coarse-Scale Distribution

Encounter rates of 429 observations of monkey social groups along the six transect walks are shown in Table 1. The encounter rates of red colobus and black and white colobus, were significantly different between transects (Kruskal-Wallis: red colobus $\chi^2 = 31.98$, $p < 0.001$; black and white colobus $\chi^2 = 22.07$, $p < 0.001$), but not Sykes monkey or yellow baboon (Kruskal-Wallis: Sykes monkey $\chi^2 = 5.10$, $p = 0.404$; yellow baboon $\chi^2 = 8.31$, $p = 0.140$; Table 1). Along the most disturbed transects, Sykes monkey groups were significantly more abundant than the two colobines. (Kruskal-Wallis: Lusolwa $\chi^2 = 23.78$, $p < 0.001$; Mkungusi $\chi^2 = 30.78$, $p < 0.001$; Table 1). Black and white colobus groups, were significantly more abundant than red colobus on the extremely disturbed Mkungusi transect (Table 1), where the only observations of red colobus during transect walks, were one small group and two solitary individuals. Red colobus and yellow baboons were the least common monkey on both of the heavily disturbed transects (Table 1).

The relative abundance of the four species was also significantly different for the four less disturbed transects (Kruskal-Wallis: Isaula $\chi^2 = 30.59$, $p < 0.001$; Itula $\chi^2 = 24.37$, $p < 0.001$; Bwawani $\chi^2 = 23.32$, $p < 0.001$; Machumbo $\chi^2 = 23.14$, $p < 0.001$). However the ratio of the four monkeys was not consistent, although yellow baboons were the least abundant in all areas (Table 1). Red colobus groups were significantly more abundant along all of the less disturbed transects than the two heavily disturbed transects, but the abundance of other monkeys relative to heavy disturbance is unclear without more focused analyses (Table 1; see below).

Density estimates were imprecise and could not be calculated for all transects (Table 1) due to insufficient observations. To increase sample size and to allow coarse comparison of habitats, we pooled transects into heavy disturbance (Lusolwa, Mkungusi, and Bwawani 2000-4000m) and moderate-to-low disturbance (Bwawani 0-2000m, Machumbo, Itula and Isaula; Mann-Whitney U-test; Fig. 2), as defined above. Both red colobus and black and white colobus had significantly lower group density along heavily disturbed transects than the less disturbed transects (Red colobus: 1.02 ± 0.89 groups km^{-2} versus 3.26 ± 1.30, $p = 0.001$, $U = 8.0$; Black and white colobus: 1.55 ± 1.57 versus 3.15 ± 1.85, $p = 0.036$, $U = 22.5$). Sykes monkeys had equivalent group density for both disturbance levels (3.91 ± 1.86 versus 3.63 ± 1.41, $p = 0.940$, $U = 49.0$). In the heavily disturbed areas, Sykes monkeys had significantly higher group density than the two colobines (Red colobus: $p = 0.04$, $U = 93.0$, Black and white colobus: $p = 0.012$, $U = 108.0$; Fig. 2). Black and white colobus group density was not significantly greater than red colobus ($p = 0.892$, $U = 195.0$; Fig. 2). Yellow baboons were too few to make density estimations.

Table 1. Mean ± standard deviation monkey group encounter rates per km transect (and group density km^{-2} in parentheses for transects with 20 or more groups). The data are non-parametric however these summary data are preferred medians and quartiles for consistency with previous studies. Letters in superscript indicate results of Kruskal-Wallis tests with Mann-Whitney posthoc tests, between transects per species (a-q), and species per transect (r-y). Encounter rates with similar letters were significantly different ($p < 0.05$; * and ** denote significant differences to all other data in rows and columns respectively).

Transect	Disturbance	Red colobus	Black and white colobus	Sykes monkey	Yellow baboon
Eastern sites					
Isaula	Low	^{a,b} 0.62 ± 0.31 (3.00 ± 2.30)	**, ^{m} 0.85 ± 0.36 (4.00 ± 2.41)	^{m} 0.56 ± 0.19 (2.55 ± 2.18)	* 0.00 ± 0.00
Itula	Low/moderate	^{c,d,n} 0.57 ± 0.30 (2.85 ± 1.87)	^{i,n,o} 0.26 ± 0.19	^{o} 0.88 ± 0.46 (4.16 ± 3.11)	* 0.10 ± 0.20
Bwawani	Moderate/high (forest edge)	^{e,f} 0.59 ± 0.32 (3.57 ± 3.05)	^{j} 0.34 ± 0.23	0.54 ± 0.35 (3.62 ± 2.29)	* 0.00 ± 0.00
Western sites					
Machumbo	Moderate/high (isolated)	^{g,h} 0.48 ± 0.29 (2.31 ± 1.91)	^{i,j,k,l} 0.67 ± 0.45 (5.10 ± 4.62)	0.61 ± 0.39 (4.29 ± 2.96)	* 0.02 ± 0.07
Lusolwa	High	^{a,c,e,g} 0.15 ± 0.21	^{k,p} 0.33 ± 0.26	* 0.73 ± 0.30 (4.59 ± 2.34)	^{p} 0.025 ± 0.08
Mkungusi	High	^{b,d,f,h,q,r} 0.03 ± 0.08	^{l,q,s} 0.43 ± 0.29	^{r,t} 0.66 ± 0.28 (4.39 ± 2.78)	^{s,t} 0.00 ± 0.00

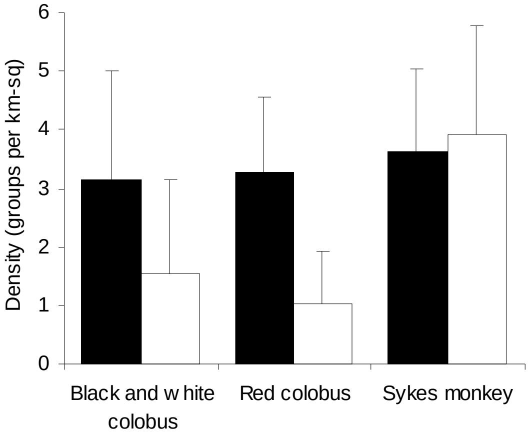

Figure 2. Mean and standard deviation monkey group density in heavily disturbed forest (open bars) versus less disturbed forests (black bars).

Fine-Scale Distribution

Monkey groups were seen in 110 of the 120 plots, of which 101 were within the designated cut-off points. Generalized linear models and Spearman rank correlation versus habitat variables show that red colobus, black and white colobus and Sykes monkeys had very different distributions among the plots (Table 2). For all three species, backwards stepwise models based on AIC produced the models with the best descriptive power compared to other models (ANOVA; Table 2). The number of red colobus groups per plot was the species most related to the habitat variables, with models explaining 23.1 % to 24.4 % of deviance, compared to 11.0 % to 12.9 % in black and white colobus and 9.4 % in Sykes monkey (Table 2).

By far the strongest relationship for red colobus was with the main gradient in tree community composition, from heavily disturbed lowland deciduous forest, to less disturbed lowland/submontane semi-deciduous/evergreen forest (as measured by DCA axis 1 scores; Table 2). Red colobus also showed a strong negative relationship with swamp presence/absence, and a strong positive relationship with presence/absence of rivers and streams (Table 2). There was weak evidence for a positive relationship between red colobus and the number of tree stems and presence/absence of valleys, and a negative relationship with slope (Table 2). Near-significant results included a positive relationship with stem diversity and negative relationships with climber cover and presence/absence of ridges.

In contrast, the number of black and white colobus was best predicted by the combined volume of the two main dietary species, *E. suaveolens* and *C. gomphophylla*, with weak evidence for a positive relationship with tree stem density (Table 2). There was also a near significant result for a negative relationship with slope (Table 2). All models for black and white colobus explained a smaller proportion of the variance than for red colobus, however this was low for both species (<15% versus <25%; Table 2). Only one significant model was produced for Sykes monkey distribution, providing weak evidence for negative relationships with climber cover, the log mean volume of stems, and DCA axis 1 score, and a positive relationship with slope. Yellow baboons were too few in number for this fine-scale analysis.

GLM and Spearman rank correlation analyses of the distribution of species richness in 200m plots versus habitat variables did not reveal any significant relationships. However, Spearman rank correlation found that the number of species per plot had a near-significant positive relationship with stem density ($r_s = 0.249$, $p = 0.006$ [Hochberg adjusted alpha = 0.0045]), and a near-significant negative relationship with climber coverage ($r_s = -0.211$, $p = 0.021$ [Hochberg adjusted alpha = 0.0050]). GLM analysis by backwards stepwise regression using AIC, also suggested a weak negative relationship with climber coverage (AIC = 335.4, % deviance explained = 3.81, $p = 0.063$), although the model was narrowly not a significant improvement over a null model (ANOVA: $F = 3.49$, $p = 0.062$). The unreduced (full) GLM model did not reveal any significant relationships ($p \geq 0.3$ for all variables), and also did not improve over a null model (ANOVA: $F = 0.55$ $p = 0.870$), and was therefore rejected.

Table 2. Significant (and near significant) correlates from multivariate GLM tests and Spearman correlation tests, on the number of monkey groups versus habitat variables, in 120 plots along six transects. GLM models are only shown if significantly different from a null model using ANOVA. Square brackets show GLM model statistics including Akaike Information Criterion (AIC) and percentage of deviance explained (%D; $100 \times [1 - \text{Residual Deviance} / \text{Null Deviance}]$). Variables are listed in order of the strength of relationship (most significant first). "+" = positive trend, "–" = negative trend, "p/a" = presence/absence, "√" = square root. Bold text indicates variables that are "strong predictors", i.e. significant in at least two models.

Test	Red colobus	Black and white colobus	Sykes monkey
ANOVA*	AIC > (Full > Null)	AIC > (Full > Null)	AIC > (Full = Null)
GLM - Full	**DCA axis 1 score** $^+$ **Swamp p/a** $^-$ **River/Stream p/a** $^+$ (Slope $^-$) [AIC 264.51, %D 24.37]	(√ Volume top 2 diet species $^+$) [AIC 285.63, %D 12.87]	No significant model
GLM - AIC stepwise	**DCA axis 1 score** $^+$ **River/Stream p/a** $^+$ Slope $^-$ Valley p/a $^+$ **Swamp p/a** $^-$ (Simpson diversity $^+$) (Ridge p/a $^-$) (Stem density $^+$) [AIC 256.55, %D 23.10]	**√ Volume top 2 diet species** $^+$ Stem density $^+$ [AIC 270.27, %D 11.03]	Slope $^+$ Climber cover $^-$ Log_{10} mean tree volume $^-$ DCA axis 1 score $^-$ [AIC 286.41, %D 9.36]
Spearman correlation - Hochberg correction	**DCA axis 1 score** $^+$ Stem density $^+$ (Climber cover $^-$) (Swamp p/a $^-$)	**√ Volume top 2 diet species** $^+$ (Stem density $^+$) (Slope $^-$) (Simpson diversity $^-$)	None significant or near significant

* ANOVA tests between GLMs: ">" = $p < 0.05$, "=" = $p > 0.05$.

Social Grouping

Counts of social groups (excluding solitary individuals) for both red and black and white colobus were within the range of published group sizes (red colobus mean group size ± standard deviation = 21.47 ± 10.00, $n = 31$; black and white colobus 10.12 ± 2.75, $n = 13$; versus published counts for *P. gordonorum*: 28.90 ± 16.48 [mean ± s.d. of Struhsaker & Leland 1980, Decker 1994, Struhsaker et al. 2004, Marshall et al. 2005 and Marshall unpublished data; $n = 103$]; and *Colobus angolensis*: 8.14 ± 3.52 [mean ± s.d. of Decker 1994, Marshall et al. 2005 and Marshall unpublished data; $n = 25$], 2-16 [range; Groves et al. 1973; $n = 37$], 5-20 [range; Rodgers 1981; n = unknown], 2-13 [range; Anderson et al. in press; n = 136]).

Group sizes of both colobines were significantly smaller in heavily disturbed areas than in other areas (Red colobus 11.83 ± 5.45 [$n = 9$], versus 25.41 ± 8.68 [$n = 22$]: $U = 18.0$, $p < 0.001$; Black and white colobus 8.3 ± 1.35 [$n = 5$], versus 11.25 ± 2.85 [$n = 8$]: $U = 5.0$, $p = 0.028$). In 600m plots, red colobus group size was best predicted by log mean tree volume (Table 3; Fig. 3). There was also strong support for a positive relationship with stem density, and negative relationships with DCA axis 1 score, presence/absence of valleys and dietary species richness (Table 3). Weaker support was seen for a relationship between red colobus group size and climber cover, and there was near-significant support for a positive relationship with the presence/absence of ridges (Table 3). No significant relationships were seen for black and white colobus group size (Table 3), however Spearman rank correlation showed near-significant negative relationships with climber coverage and presence/absence of rivers and streams (Table 3).

Density and Population

Estimates of group density for Matundu forest, weighting by the ratio of heavily disturbed to less disturbed forest (approx 4:1, Chapter 2; Fig. 2), are presented in Table 4. For the two colobines, these are converted to individual densities using mean group sizes for the same habitats from above. Extrapolating these densities gives a crude population estimate for Matundu of 13,705 red colobus. However the level of precision is very low given the high level of extrapolation (Table 4).

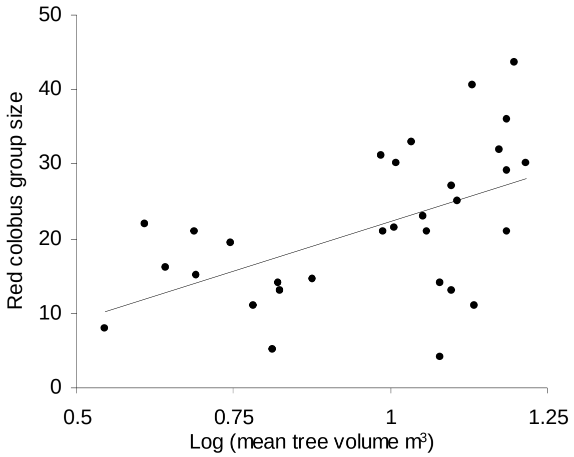

Figure 3. Red colobus group size versus $\log_{10}$ mean tree volume. Trendline produced from linear regression ($r = 0.52$, $p < 0.01$).

Table 3. Significant (and near significant) correlates from multivariate GLM tests and Spearman correlation tests, on social group size versus habitat variables, for 31 red colobus and 13 black and white colobus groups. GLM models are only shown if significantly different from a null model using ANOVA. Square brackets show model statistics including Akaike Information Criterion (AIC) and percentage of deviance explained (%D; 100 × [1 – Residual Deviance / Null Deviance]). Variables are listed in order of the strength of relationship (most significant first). "+" = positive trend, "–" = negative trend, "p/a" = presence/absence, "√" = square root. Bold text indicates variables that are "strong predictors", i.e. significant in at least two models.

Test	Red colobus	Black and white colobus
ANOVA*	AIC > (Full > Null)	AIC = (Full = Null)
GLM – Full	**Log$_{10}$ mean tree volume** $^{+}$ **Stem density** $^{+}$ **Valley p/a** $^{-}$ **DCA axis 1 score** $^{-}$ **Dietary species richness** $^{-}$ [AIC 224.69, %D 64.53]	No significant model
GLM - AIC stepwise	**Log$_{10}$ mean tree volume** $^{+}$ **Stem density** $^{+}$ **DCA axis 1 score** $^{-}$ **Valley p/a** $^{-}$ **Dietary species richness** $^{-}$ [AIC 216.30, %D 62.08]	No significant model
Spearman correlation - Hochberg correction	Climber cover $^{-}$ **Log$_{10}$ mean tree volume** $^{+}$ (Stem density $^{+}$) (Valley p/a $^{-}$) (DCA axis 1 score $^{-}$) (Dietary species richness $^{-}$) (Ridge p/a $^{+}$)	(Climbers $^{-}$) (River/Stream p/a $^{-}$)

* ANOVA tests between GLMs: ">" = $p < 0.05$, "=" = $p > 0.05$.

Table 4. Density and population estimates for monkeys in Matundu forest. Group and individual densities were calculated for heavily disturbed and less heavily disturbed forests along transect lines and then weighted by the estimated ratio of these habitats in Matundu forest as a whole (4:1; Chapter 2). Total group and individual estimates for Matundu, should only be considered crude as they are extrapolated from the survey areas (0.54 %, 0.36 % and 0.45 % of the size of Matundu forest) to the 522 km^{2} area.

	Red colobus	Black and white colobus	Sykes monkey
Groups km^{-2}	1.47 ± 0.86	1.87 ± 1.47	3.86 ± 1.34
Individuals km^{-2}	26.26 ± 12.92	17.38 ± 12.90	Unknown
Total groups	768 ± 451	976 ± 765	2,012 ± 703
Total individuals	13,705 ± 6,746	9,070 ± 6,732	Unknown

Discussion

Responses to Forest Disturbance

The data presented here support our hypothesis for the relative response of the four study species to habitat disturbance, based on ecological theory and previous empirical studies. Namely, we have shown that the Udzungwa red colobus group density and social group size is the most closely linked to habitat, followed by black and white colobus and then Sykes monkeys, with yellow baboons uncommon throughout. We here discuss the reasoning for this conclusion, and the key habitat features that are important for each species. Subsequently, we discuss the degree to which community structure is affected by habitat disturbance, and the potential for monkeys as an indicator community. Finally we discuss the practical and theoretical implications of the results.

1) Specialists

From coarse-scale analysis we have shown that Udzungwa red colobus are fewest and have their smallest group sizes in heavily disturbed areas of Matundu forest (Table 1; Fig. 2). From the fine-scale analysis, the principal variables associated with abundance and social group size of red colobus, are related to vegetation structure and composition (Tables 1 to 3; Figs. 2 and 3). The strongest fine-scale relationships are positive trends for relative group abundance versus tree community composition (DCA axis 1 scores; Table 2), and for group size versus both stem density and $\log_{10}$ mean tree volume (Table 3). Other weaker trends with vegetation composition and structure include the positive relationship between relative group abundance and stem density, near-significant positive relationship with Simpson diversity, near-significant negative relationship with climber cover (Table 2) and significant negative relationship between group size and climber cover (Table 3).

Some other relationships seen from the fine-scale analyses are also probably indirectly related to vegetation. Red colobus in the study area were found away from swamps (Table 2), where habitat diversity is lower than surrounding areas due to dominance by *Bridelia micrantha* (Chapter 3). We did not observe red colobus eating this species, nor did a previous dietary study in Mwanihana forest (Wasser unpublished data). However *B. micrantha* is common in the diet of closely-related Zanzibar red colobus *P. kirkii* (Struhsaker pers. comm.), so the negative relationship with swamps may be for other reasons (e.g. poor nutritional quality of foliage). The strong support for an association between red colobus and rivers/streams (Table 2), may also be due to the characteristic riverine community. Tree species *Afrosersalisia cerasifera*, *Treculia africana* and *Bersama abyssinica* are associated with streams and rivers along our transects (Chapter 3). *A. cerasifera* is a common dietary species of red colobus in Mwanihana forest (Wasser 1993), however we cannot verify this for Matundu. Also we have observed red colobus monkeys perched in *T. africana* but cannot verify that it is eaten. Valleys, ridgetops and steep slopes also have distinct vegetation, and may further explain the weak and near-significant results for these variables versus red colobus relative group abundance. For instance, red colobus dietary species *Anthocleista grandiflora* and *Shirakiopsis elliptica* are typically found in valleys (Chapter 3). However for all the dietary speculations made in this discussion, it is difficult to draw conclusions due to our very limited dietary data (Appendix 1). The high productivity of valleys compared to steep-sided slopes and ridgetops may also be a factor, however this has been little studied (Pinto et al. 1993).

It is also interesting to note some more unexpected relationships with red colobus group size. The significant negative relationships with DCA axis 1 scores, dietary species richness, valley presence/absence, and near-significant positive relationship with ridetop presence/absence, are opposite to those seen for relative group abundance. The reason for this is unclear. It may be that following logging, competition for the few remaining areas of closed-canopy forest has been especially great, therefore leading to increased group density but increased intragroup competition and therefore decreased social group cohesion. We have made a similar observation in the small forest of Magombera where population density is high following rapid compression, and yet social group size is lower than the nearby forest of Mwanihana (Marshall unpublished data).

From this evidence, the Udzungwa red colobus is considered a “late-successional” or “forest specialist” species. It is extremely vulnerable to habitat degradation (Struhsaker et al. 2004; Marshall et al. 2005; this study; Rovero & Struhsaker in press) and loss (Chapter 2). These insights gained from the Udzungwa red colobus may help to explain the vulnerability of red colobus across Africa (Struhsaker 2005), most of which are in too low densities for this kind of study. The few previous studies on other red colobus make similar observations of declining density and group size with declining habitat quality (*P. rufomitratus*, Tana River, Kenya: Mbora & Meikle 2004; *P. rufomitratus tephrosceles*, Kibale, Uganda: Skorupa 1986 and 1988; Struhsaker 1975 and 1997; Chapman & Chapman 1999 and 2000). Red colobus are therefore excellent indicators of forest health (Struhsaker 2005). Management that encourages protection or growth of closed-canopy, old growth forest is clearly important for the survival of this sensitive genus.

Like the red colobus, black and white colobus have reduced relative group abundance, group density and group size in heavily disturbed habitats (Table 2, Fig. 2 and results text), suggesting that they are also forest specialists. In the most disturbed areas of Matundu (Mkungusi and Lusolwa), their relative group abundance is however greater than the red colobus, suggesting that they are more tolerant of habitat disturbance (Table 2). From fine-scale analysis of relative group abundance, the number of significant habitat variables was also fewer than for the red colobus. The only strong relationship was with the total volume of the top two dietary species *Celtis gomphophylla* and *Erythrophleum suaveolens*, with weak support for a positive relationship with stem density (Table 2). Other near-significant relationships with relative group abundance and group size require further testing (Tables 2 and 3).

Colobus angolensis density in forest fragments of south-east Kenya has also been affected by habitat disturbance, including logging of major food trees and reduction in forest area (Anderson et al. in press). However, other previous studies have shown that group size and relative group abundance of this species are affected by habitat disturbance to a lesser degree than the Udzungwa red colobus (Marshall et al. 2005; Rovero & Struhsaker in press). The relative vulnerability of *Colobus* and *Procolobus,* is similar for other species of this genus (Struhsaker 1975 & 1997; Chapman et al. 2000; Oates 1974). However, *Colobus angolensis* appears to be less tolerant than the secondary-growth specialist *C. guereza*, which has benefitted from forest disturbance in Kibale forest (Skorupa 1986 and 1988; Struhsaker 1997). However, *C. guereza* does have a dietary preference for *Celtis gomphophylla* (= *C. durandii*; 50 % of diet, Oates 1974), suggesting some similarity with our limited dietary data for *C. angolensis* (Appendix 1).

For all models of group abundance of both colobines, the proportion of deviance explained was low (<25%D; Table 2). There may therefore be unmeasured variables that are influencing monkey group abundance. However given the narrow width of our vegetation plots, we suspect that this would increase with more complete sampling of the habitat.

2) Generalists

Sykes monkeys in Matundu are equally common in heavily disturbed and less disturbed forest, and dominate the monkey community in heavily disturbed areas (Table 1; Fig. 2). Their resilience to habitat disturbance is further supported by the lack of descriptive power of the full GLM model over a null model, and the lack of significant relationships for Spearman rank correlation (Table 2). Weak support for relationships between Sykes monkey relative group abundance and both $\log_{10}$ mean tree volume and DCA axis 1 scores are opposite to those seen for red colobus (Table 2), further suggests that Sykes monkeys may benefit from limited habitat disturbance. These observations support earlier studies in the Udzungwa Mountains that suggest that Sykes monkeys are generalists (Marshall et al. 2005; Rovero et al. 2006; Rovero & Struhsaker in press). They also show an opposite relationship to red colobus versus slope (Table 2), further suggesting that the habitat requirements of these two species are different. However the negative relationship between relative group abundance and climber coverage (our broad index of human disturbance), suggests that they still require at least some forest structure. Dependence on forest is further supported from their reduced abundance in low diversity deciduous woodland near to Mwanihana (Rovero & Struhsaker in press) and their absence from deciduous woodland areas south of Matundu forest (pers. obs.).

Our results also show that the fourth species in our study, the yellow baboon, is rare in all forest habitats of Matundu, with no significant relationship to forest disturbance (Table 1). In Udzungwa and elsewhere it is a generalist adapted to non-forest habitats (Altmann 1970; Rovero et al. 2006; Rovero & Struhsaker in press).

Monkeys as Indicators

The results give some support for the use of community species richness as an indication of habitat disturbance, with near-significant relationships between species richness and both climber cover and stem density. However the community response to disturbance is clearer when considered together with species-specific responses. From the above discussion we suggest that red colobus relative group abundance and group size are strong indicators of forest habitat quality. We further suggest that black and white colobus have potential as weak indicators, as they show responses in density and group size to coarse classification of habitat disturbance, yet have few significant relationships with features of microhabitat. We consider Sykes monkeys to be poor indicators of forest habitat quality, however from the discussion of previous studies, we suggest that they are at least associated with the presence of forest tree species. Yellow baboons are more indicative of non-forest habitats. When considered together, these conclusions suggest that the monkey community is related to forest habitat disturbance as shown in Fig. 4. From this we suggest that this four-species community is a reasonable indicator of forest habitat disturbance. The pattern in relative abundance of specialists and generalists in response to habitat disturbance may be further applicable to forests elsewhere, and could easily be tested using existing data.

Comparing our results to relative abundances in the less disturbed Mwanihana forest (Rovero et al. 2006), echoes our comparisons within Matundu, again supporting our hypothesis of relative response of the four species to forest habitat disturbance. The mean encounter rate for red colobus along the six transects (mean 0.41 ± 0.25 standard deviation groups km^{-1}), was lower than for previous estimate for Mwanihana (0.59 ± 0.27; Rovero et al. 2006). The mean density of 1.47 red colobus groups km^{-2} (26.26 individuals km^{-2}) is also considerably lower than estimated for the less disturbed Mwanihana forest (3-4 groups km^{-2}; or 180-245 individuals km^{-2}; Rovero et al. 2006). No previous density estimates exist for black and white colobus or Sykes monkeys. The encounter rate was similar to Mwanihana for black and white colobus (0.48 ± 0.30 versus 0.43 ± 0.26) and baboons (0.02 ± 0.06 versus 0.08 ± 0.11), but much higher for Sykes monkeys (0.66 ± 0.33 versus 0.35 ± 0.25).

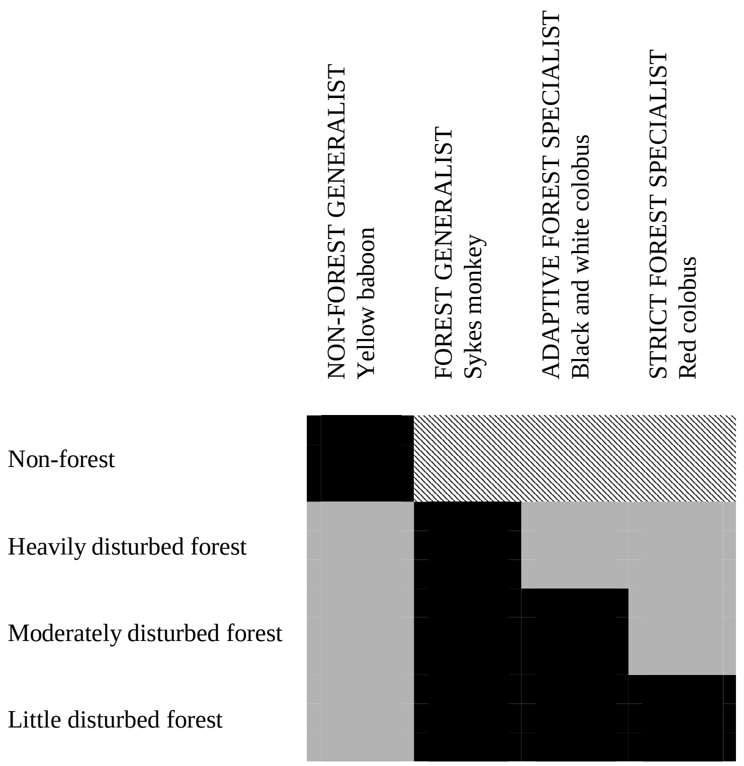

Figure 4. Monkeys as an indicator community in lowland Udzungwa, using results from this study, Rovero et al. (2006) and Rovero & Struhsaker (in press). Black = high group density, grey = low group density (and/or small groups for colobines), hatched = limited (e.g. seasonal) use when in near vicinity of forest.

We have shown how a combined assessment of social group size, relative abundance, density and community composition can closely reflect forest habitat quality. In the Udzungwa lowlands, habitats containing high densities and large groups of red colobus monkeys are likely to be of high quality, and therefore of greatest importance for conservation. Conversely, those habitats where Sykes monkey groups are the most common, where red colobus are absent, and/or where black and white colobus are only found in small groups or low density, are likely to require considerable habitat management. Determining monkey relative abundance and social group size requires considerable field time. However the parameters are all reasonably simple to determine as the species are easily recognisable and both groups and group abundance can be determined with basic training. This is appreciable when compared to the expertise and logistical effort required to collect and identify the many hundreds of plants that the habitat represents.

An ideal indicator should reflect trends in the broad habitat and act as a surrogate for ecosystem health (Caro & O’Doherty 1999), typically by its relationship with biodiversity (Gregory et al. 2005). Although we have shown that monkey relative abundance and social grouping may closely represent forest habitat structure, there is little support from Matundu (this study) or Mwanihana (Rovero & Struhsaker in press), for a relationship between Udzungwa monkeys and plant biodiversity (here measured using Simpson diversity). However given the global threats to tropical forests, management to conserve these habitats, rather than to conserve biodiversity, must be the priority for conservation management in the Udzungwa Mountains.

Conservation of Matundu Forest

From the fourfold increase in population from the only previous estimate (13,705 Table 4, versus 3,130 Dinesen et al. 2001), it appears that Matundu forest is more important for red colobus conservation than previously thought. We acknowledge that the high level of extrapolation has resulted in very low precision, however even the lower tail of the standard deviation is double the previous estimate, for which no indication of precision was given. This discordance has probably occurred due to previous focus on poorer quality habitats near to the Ruipa river, and/or density estimation based on casual walks rather than measured transects (Dinesen et al. 2001). This highlights the danger of non-systematic surveys of wildlife populations. The current overall population estimate for Udzungwa red colobus (15,400; Dinesen et al. 2001), has also clearly been underestimated. However, any renewed density estimate would not affect the classification as vulnerable on the IUCN red-list, as the limited geographic range of the red colobus is still within the criteria (Chapter 2). No previous estimates exist for the population of Sykes monkeys or black and white colobus in Matundu or Mwanihana.

Although it contains some restricted range species, Matundu does not contain as many Eastern Arc endemic species as the adjacent montane forests. Prioritisation of conservation efforts should not however be based solely on rare species richness, but on a landscape approach, considering threats, protected status, and habitat continuity (e.g. Primack 1998). The monkey community indicators have shown that much of Matundu forest has been negatively impacted by heavy disturbance. Furthermore, given its size, location, large population of Udzungwa red colobus, restricted tree growth and threats to habitat west of the Ruipa river, Matundu is emerging as a forest of high importance for conservation management. However the practicalities of encouraging regeneration old growth forest in an area of high elephant activity are difficult, and may preclude active clearance of restricting vegetation as a potential management strategy. Instead effective conservation of existing habitats, and monitoring of regeneration, are likely to be the best management strategies.

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Appendices

Appendix 1. Observations of diet and perch selection for monkeys in Matundu forest.

Red colobus foods	Feeding observations	%	Perching observations	%
Erythrophleum suaveolens (Guill. & Perr.) Brenan	8	19.5	19	21.1
Khaya anthotheca (Welw.) C. DC.	5	12.2	7	7.8
Unknown climbers	3	7.3	4	4.4
Xylopia parviflora Spruce	2	4.9	6	6.7
Antiaris toxicaria Lesch.	2	4.9	2	2.2
Ricinodendron heudelotii (Baill.) Heckel	2	4.9	1	1.1
Unknown trees	2	4.9	1	1.1
Margaritaria discoidea (Baill.) G.L. Webster	2	4.9	0	0.0
Milicia excelsa (Welw.) C.C. Berg	1	2.4	5	5.6
Anthocleista grandiflora Gilg	1	2.4	3	3.3
Zanha golungensis Hiern	1	2.4	1	1.1
Breonadia salicina (Vahl) Hepper & J.R.I. Wood	1	2.4	0	0.0
Celtis gomphophylla Baker	1	2.4	0	0.0
Vitex doniana Sweet	1	2.4	0	0.0
Pteleopsis myrtifolia (M.A. Lawson) Engl. & Diels	1	2.4	0	0.0
Parkia filicoidea Welw. ex Oliv.	1	2.4	0	0.0
Strombosia scheffleri Engl.	1	2.4	0	0.0
Millettia semseii J.B. Gillett	1	2.4	0	0.0
Brachystegia spiciformis Benth.	1	2.4	0	0.0
Quassia undulata (Guill. & Perr.) D. Dietr.	1	2.4	0	0.0
Shirakiopsis elliptica (Hochst.) Esser	1	2.4	0	0.0
Ficus strangler (?*natalensis*/*thonningii*)	1	2.4	0	0.0
Unknown understorey/ground vegetation	1	2.4	0	0.0
Black and white colobus foods				
Celtis gomphophylla Baker	9	28.1	8	9.8
Erythrophleum suaveolens (Guill. & Perr.) Brenan	5	15.6	17	20.7
Antiaris toxicaria Lesch.	3	9.4	3	3.7
Entada rheedei Spreng.	3	9.4	0	0.0
Xylopia parviflora Spruce	1	3.1	8	9.8
Milicia excelsa (Welw.) C.C. Berg	1	3.1	4	4.9
Funtumia africana (Benth.) Stapf	1	3.1	4	4.9
Khaya anthotheca (Welw.) C. DC.	1	3.1	2	2.4
Parkia filicoidea Welw. ex Oliv.	1	3.1	1	1.2
Morus mesozygia Stapf	1	3.1	1	1.2
Albizia gummifera (J.F. Gmel.) C.A. Sm.	1	3.1	1	1.2
Ricinodendron heudelotii (Baill.) Heckel	1	3.1	1	1.2
Celtis gomphophylla Baker or Mswehile	1	3.1	0	0.0
Tabernaemontana pachysiphon Stapf	1	3.1	0	0.0
Unknown tree	1	3.1	0	0.0
Unknown climber	1	3.1	0	0.0
Sykes monkey foods				
Unknown climbers	2	20.0	13	54.2
Khaya anthotheca (Welw.) C. DC.	2	20.0	5	20.8
Erythrophleum suaveolens (Guill. & Perr.) Brenan	2	20.0	1	4.2
Ficus sycomorus L.	1	10.0	3	12.5
Antiaris toxicaria Lesch.	1	10.0	2	8.3
Parkia filicoidea Welw. ex Oliv.	1	10.0	0	0.0
Unknown tree/climber	1	10.0	0	0.0

Chapter 6 – Summary Discussion

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The monkeys and trees of Udzungwa have shown many and diverse responses to disturbance, most of which are negative. Given that confounding variables have been controlled for throughout by use of multivariate methods, the observed relationships can be considered reliable. The following discussion considers the relevance of the major findings, including some speculations that may be investigated by subsequent research. I begin by considering the consequences of disturbance for the conservation status of species and the potential of trees and monkeys as habitat indicators. I then look further into the underlying environmental relationships, before finally discussing the future directions for conservation in the Udzungwas.

Summary of Relationships to Habitat Disturbance and Loss

Disturbance in Matundu has led to opening of the forest canopy, and the predominance of smothering climbers through much of this large area. In turn, this has affected the tree community composition, structure (density of large stems), and rare tree species diversity (Chapter 3). The effect on rare species is of particular concern, given their restricted range and extremely low densities even in good quality habitat (Chapter 3; Table 5). The disassociation between rare plant diversity and large animal (mainly elephant) paths, is also interesting (Chapter 3; Table 6). Due to their destructive behaviour, the incompatibility between elephant conservation and forest habitat regeneration has been noted previously (e.g. Eggeling 1947; Lawes & Chapman 2006). However to my knowledge this is the first evidence for their negative impact on rare species, and will pose difficulties for management.

The monkeys in Matundu have shown some ability to adapt to the high level of forest disturbance, as seen by the moderate numbers of both black and white colobus and Sykes monkey groups in the most disturbed habitat of Mkungusi (Chapter 5; Table 1). However, black and white colobus are still clearly affected by habitat degradation as seen from their reduced group size and density, from coarse-scale analysis of heavily disturbed versus less disturbed habitats (Chapter 5; Fig. 2 and results text), and from the relationship between relative group abundance and both stem density and dietary species from fine-scale analysis (Table 2). Moreover, from many significant relationships, red colobus group size and density are very closely linked to habitat structure and species composition (Tables 1 and 2; Figs. 2 and 3). This relationship is the biggest concern for conservation given that they are endemic to the Udzungwa Mountains.

Species richness of Udzungwa monkeys is probably affected by both habitat disturbance and loss. The relationship between species richness and both stem density and climber cover/damage are narrowly not significant (Chapter 5), perhaps due to differences in species-specific responses to disturbance. This is also partly due to our conservative choice of statistical tests, which some may regard as over-conservative (Perneger 1998; Garcia 2004). Without Hochberg correction for multiple testing, both stem density and climber coverage become significant for Spearman rank correlation tests. The effect of forest fragmentation on species richness in the Udzungwa Mountains is more apparent, with a clear species-area relationship (Chapter 2). Importantly, the two rare mangabey species are only associated with the largest fragments. A log-linear relationship between species richness and forest area suggests that a forests of over 150 km^2 are the most important for conservation of monkey diversity. Small forests are likely to have lower habitat diversity than larger fragments and are more susceptible to human impacts such as hunting, especially when considered in relation to isolation.

Overall the results suggest that conservation management of large areas of closed canopy forest is paramount for the conservation of rare and restricted range species.

Indicators

The criteria for selecting indicator species must be clearly defined and rigorously tested (Lindenmayer 1999; Hilty & Merenlender 2000). An ideal indicator species is easily recognisable, easy to locate, found in reasonable densities, not highly mobile, shows a high degree of specialisation and is representative of ecosystem health (Caro & O’Doherty 1999; Hilty & Merenlender 2000). The definition of ecosystem health is a sticking point in defining the utility of indicators, as the term indicator may have many meanings (Gregory et al. 2005). Biodiversity is closely associated with ecosystem health (Cardinale et al. 2006). However we have shown here that disturbance is damaging to forest structure and species composition, threatens the survival of rare species, but does not necessarily affect biodiversity (Chapter 3). Use of biodiversity alone (or indicators that measure biodiversity alone) to reflect ecosystem health, is therefore not always a suitable indicator for conservation management. Prioritisation of conservation efforts should not be based solely on biodiversity but on a landscape approach, considering threats, protected status, habitat continuity and rare/endemic species (e.g. Struhsaker 1981; Primack 1998; Harcourt et al. 2002; Orme et al. 2005; McCarthy et al. 2006; Chapter 3). Areas selected for conservation by global strategies using biodiversity alone, have shown no relationship with species endemism or threat (Orme et al. 2005).

The Udzungwa red colobus arguably has the best potential as an indicator of forest habitat quality (but not biodiversity), of any of the many taxa found in the Udzungwa Mountains. They are easily recognisable and are conspicuous due to their frequent squealing calls and loud, jumping movement through vegetation. They also occur in high numbers when the habitat is suitable, and rarely venture far from forest habitats. The close association between red colobus and intactness of forest habitats is also strong. Significant positive relationships between forest quality and both group size and relative group abundance have been demonstrated by several studies of this species

(Struhsaker et al. 2004; Marshall et al. 2005; Rovero et al. 2006; Rovero & Struhsaker in press; Chapters 2 and 5), and closely related species of the same genus (Struhsaker 1975 and 1997; Struhsaker & Leland 1979; Skorupa 1986 and 1988; Chapman & Chapman 1999 & 2000; Chapman et al. 2000; Mbora & Meikle 2004). This contradicts previous assertions that single taxa are not good indicators of ecosystem health (Hilty & Merenlender 2000). In the absence of red colobus, black and white colobus may serve as an approximate indicator, but its relationship with habitat disturbance is less clear (Chapter 5).

We have also reasoned that the monkey community composition closely reflects forest habitat quality (Chapter 5; Fig. 4). The most intact forest habitats contain high group densities of red colobus, black and white colobus, and Sykes monkeys, including large groups of red and black and white colobus. The poorest quality habitats are dominated by Sykes monkey groups, with low densities of black and white colobus in small groups, and with red colobus largely absent. However, the practical use of this observation is unclear. Firstly it is a qualitative observation and it is hard to quantify given the uncertain habitat requirements of Sykes monkeys and black and white colobus. Noting the proportion of groups seen of each species can give a good preliminary impression of habitat, but it is perhaps no more useful than that. Furthermore, the community composition provides no more indication of habitat quality than using red colobus alone. This is because the relative response of three species to disturbance is consistent. Namely, there are no forests containing red colobus that do not contain black and white colobus, and likewise there are no forests that contain black and white colobus that do not contain Sykes monkeys. Tall old growth forests in the Udzungwa lowlands on average contain higher densities of red colobus and larger social groups than heavily disturbed forests contain few or no red colobus.

The observation that the Udzungwa red colobus is a good indicator perhaps has most practical relevance for monitoring. Managers could for example set conservation targets in the Udzungwa lowlands: 1) to achieve/maintain relative group abundance that is equivalent to the mean between less disturbed habitats in Chapter 5, and that of Rovero et al. (2006) in Mwanihana forest (0.60 groups per km), and 2) group size mean between the less disturbed habitats presented here and of Struhsaker et al. (2004) (29 individuals per group). Monitoring of both relative group abundance and group size is advisable, as relative group density may be artificially inflated where groups have split into foraging parties (see discussion in Chapters 4 and 5). Using a density estimation method based on the centres of individuals seen could account for this, but there are many caveats to this (Plumptre & Cox 2006; Chapter 4). Relative group abundance does not account for visibility, but for monitoring temporal changes may be considered preferable to estimating density due to the many uncertainties and assumptions (e.g. Struhsaker 1997; Mitani et al. 2000; Rovero et al. 2006; Chapter 4). More work is needed to determine the potential of red colobus as indicators in high elevation areas of Udzungwa, particularly due to their decreased density and high levels of hunting.

The advantage of using red colobus as indicators rather than forest trees is that their ecology has been well tested in many situations and by many studies. Also identification of red colobus over other similar species requires less training, resources, and technical expertise than it would for tropical forest trees. However, monitoring programs that use a number of indicator species together are more likely to reflect ecosystem health (Hilty & Merenlender 2000). We have therefore also suggested some potential indicator tree species (Chapter 3). Of these, *Parinari excelsa* is common across the Udzungwa Mountains at most elevations, and is easily recognisable from the ground and air. It therefore has potential for use in rapid aerial surveys for assessing forest health across the Udzungwa Mountains. Another alternative is *Funtumia africana*, which is a fast-growing tree. From my observations of dense stands of *F. africana* appearing within areas of tangled climbers, it seems that this is one of the first trees to penetrate the layer of climbers caused by disturbance. It may therefore be a key species for indicating commencement of forest canopy regeneration. My observations of taller and more sparse *F. africana* trees together with large *Dialium holtzii*, *Erythrophleum suaveolens*, *Vangueria volkensii* and *Xylopia parviflora*, lead me to believe that these are the next canopy tree species to regenerate, before growth of massive trees like *P. excelsa*, *Milicia excelsa*, *Khaya anthotheca* and *Quassia undulata*. This subjective observation of forest canopy succession however needs testing by monitoring regeneration and is certainly oversimplified.

The final indicator discussed in the thesis is the use of climber coverage of trees < 20 cm dbh to indicate habitat disturbance. This is supported by previous observations that disturbance causes increased growth of woody climbers (Gerwing 2006). In Mwanihana forest, Rovero & Struhsaker (in press) also found that climber coverage correlates with structural features of the habitat and is associated with gaps and disturbed areas. Similarly from our data, climber cover/damage showed significant correlation with stem density (Chapter 3). Furthermore our use of only the smallest trees and only of trees with > 50 % coverage reduces the chance of including climbers with sparse coverage that add to the biodiversity value of the forest. Use of climbers as an indicator also fits with subjective impressions of disturbed habitats (e.g. compare relative cover of climbers in habitat photographs Chapter 1; Fig. 1). Although it is likely to also represent natural disturbance e.g. by storms and elephants, the high level of past logging suggests that the dominance of climbers in Matundu has largely resulted from human activity.

Environmental Relationships

The underlying environmental relationships shaping the communities and species in Matundu forest are easy to overlook given the high level of habitat disturbance. However, from the various analyses we have seen a number of significant relationships with environmental variables. We have shown that streams and swamps have a distinct vegetation community (Chapter 3; Table 2 and Fig. 4). We have also shown that ridgetops and north-facing slopes have high stem density (Chapter 3;

Table 4). Rare species diversity is also high on north-facing slopes, but they are negatively associated with ridgetops (Chapter 3; Table 6). However, recurrent significant relationships show that elevation and angle of slope are the most significant environmental determinants of vegetation composition and structure in Matundu forest (Chapter 3; Tables 2 and 4; Fig. 4), with both stem density and diversity decreasing with elevation, yet increasing with slope. The trend of decreasing diversity with elevation concords with traditional theory (Richards 1979). The elevation trends for both density and diversity are however contrary to trends previously seen in the Udzungwa Mountains and elsewhere in the Eastern Arc, over longer elevation gradients (470-1700 m; Lovett 1996 and 1999; Lovett et al. 2006).

The environmental relationships on the vegetation have subsequently affected the monkey community. Red colobus group sighting rate was positively related to streams and rivers, yet negatively related to swamps (Chapter 5; Table 2). There is also evidence that they are negatively associated with steep slopes, and evidence from one model that they are positively associated with valley floors (Chapter 5; Table 2). The avoidance by red colobus of steep slopes fits my subjective impressions from earlier work in high elevation forests. Given the association between vegetation community composition and both slope angle and valley (Chapter 3), this may be a response to dietary species availability. The increased locomotor cost of moving along steep slopes (Caldecott 1980), may also be a factor. Monkeys may therefore minimise time spent on steep slopes to save energy. A human observer struggling up a line transect on steep slopes can certainly appreciate this (Marshall pers. obs. of Tom Struhsaker!). Environmental effects on the remaining monkey species are unclear, however there is also weak evidence that black and white colobus have a negative association with slope, while Sykes monkeys have a positive relationship (Chapter 5; Table 2), however these are only supported by single models. The environmental effects on monkey species richness are unclear from our analyses (Chapters 2 and 5). This is probably because responses to vegetation are largely species-specific and therefore best analysed at the species level.

The trend in increasing red colobus abundance with DCA axis 1 scores (and therefore also elevation) in Matundu, is opposite to that in the mountains as a whole, where monkey abundance decreases at high elevations (Marshall et al. 2005). This may partly be due to the higher level of disturbance at the lowest elevations in Matundu, but may also reflect changes in vegetation composition (Chapter 3; Tables 2 and 3; Fig. 4). For example, over the small elevation range in Matundu (273 to 800 m), large evergreen trees were more common in highest elevation sites (e.g. *Funtumia africana* and *Parinari excelsa*; Chapter 3), although deciduous trees were common at all elevations. This is unlike the broad vegetation elevation gradient in the Udzungwa Mountains, where deciduous trees are rare at high elevation.

This leads me to speculate about the relationship between Udzungwa red colobus monkey abundance and deciduousness. Where the habitat is undisturbed, red colobus relative group abundance is highest in habitats comprising both deciduous and evergreen trees (Mwanihana forest mean 0.59 ± 0.27 standard deviation, Rovero et al. 2006; Magombera forest 1.17 ± 0.34, Marshall unpublished data, and Isaula transect 0.62 ± 0.31, Chapter 5, Table 1), yet low in evergreen forest (New Dababa / Ulangambi 0.24 ± 0.18, Ndundulu 0.48 ± 0.17, Marshall et al. 2005; Udzungwa Scarp 0.20, Ndundulu 0.44 Pedersen & Topp-Jørgensen 2000). Red colobus can be found in deciduous woodland, but only in areas near to semi-deciduous or evergreen forest (e.g. miombo woodland adjacent to Mwanihana forest, Rovero et al. 2006, and north of the Lumemo village adjacent to gallery forest, pers. obs.). They are not however known from entirely deciduous areas (e.g. extensive miombo woodland south of Matundu forest, pers. obs. near to Lumemo and Namwawala villages). From these observations we speculate that in the absence of disturbance, the relationship between red colobus monkeys and deciduousness resembles that shown in Fig. 1.

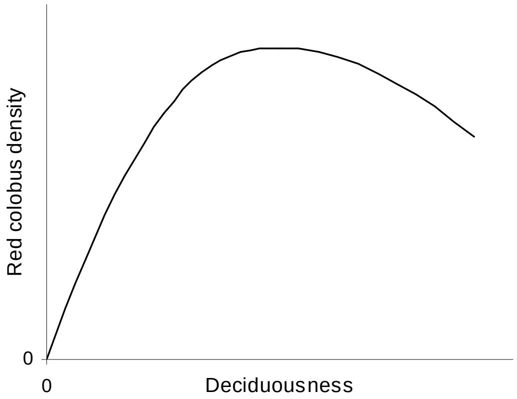

Figure 1. Speculation of relationship between red colobus density and deciduousness in the Udzungwa Mountains. Note that the x-axis has no scale as the optimum proportion of deciduousness has not been quantified.

The reason for a peak in red colobus abundance at intermediate levels of deciduousness is unknown. Plants in tropical forests have many chemical and physical adaptations to combat folivory (Coley & Barone 1996). Accordingly, colobus monkeys have been shown to select young leaves over mature leaves, for their nutritional value and digestibility (Oates 1974; Clutton-Brock 1975; Struhsaker 1975; Oates et al. 1990; Dasilva 1994; Chapman & Chapman 2002). The annual cycle of young leaves produced by deciduous trees, may therefore provide a more plentiful supply of nutritional leaves than an evergreen environment consisting mainly of mature leaves. In the Udzungwa Mountains, the asynchronous phenology of different tree species means that leaf flushing by deciduous trees lasts around six months (Marshall unpublished data), and may therefore be an advantage to folivores. The benefits of non-synchronisation of leaf sprouting by deciduous trees in the tropics, has been noted previously (references in Heymann 2001). However studies in the Kibale forest of Uganda have also found that at least some evergreen trees have year-round production of young leaves (Struhsker 1997). For now it is therefore hard to draw conclusions and this is as a possible avenue for future research.

Future Directions for Udzungwa

The fact that the range of the Udzungwa red colobus is now more or less known (Chapter 2), highlights that all of the main Udzungwa forest fragments have now been visited by researchers. This itself is a major development from the situation in the late 1970s, when the only population of red colobus known to researchers was that in Magombera, and the species was considered to be under serious threat of extinction. However the ecology of the Udzungwas is still extremely poorly known. The diverse habitats and topography, and wealth of rare and restricted range species, offer great potential for future ecological research. Research has increased markedly in recent years, and this is set to continue with the opening of the new Udzungwa Ecological Monitoring Centre, in the same week that I submitted this thesis. However to finish I would like to discuss the conservation of the Udzungwas, as this is the issue of most practical importance and most relevant to the aims of the thesis.

Connectivity

As I see it there are three major issues for the various management authorities of the Udzungwa Mountains: 1) connectivity, 2) temporal changes, 3) increasing human population pressure, and 4) collaboration between stakeholders. Chapter 2 highlighted the importance of large forests for primate conservation. Presently however, connectivity between most of the various fragments is hampered by bushfires that annually pass through the intervening habitats. A study at the forest-bushland interface between Nyumbanitu and Ndundulu (Luhombero) forests, found that these fires prevent regeneration and forest expansion, resulting in a sharp division between forest edge and adjacent habitats (Marshall et al. 2001). However despite knowledge of the negative impacts of bushfires, they continue to be lit, mostly to assist visibility for hunting.

Temporal Trends

Knowledge of the temporal changes in Udzungwa habitats and animal populations are limited. Matundu (and much of lowland Udzungwa) contains forest in a state of recovery from past logging. The ability of these forests to regenerate is however in doubt, due to the prevalence of tangled climbers. Given the size of the area and disturbance by elephants, active management to clear climbers is probably impractical. The best management strategy may therefore be to monitor progress. Experimental removal of climbers from some areas may also assist managers in determining the potential for this management strategy. Monitoring of changes in monkey populations will also be useful, both as indicators of habitat change, and to investigate lag times in responses to disturbance. The response of primates to disturbance may not be instant (e.g. Skorupa 1988; Struhsaker 1997; Cowlishaw 1999). In Udzungwa this is most apparent in the forest of Magombera where extremely high densities of red colobus are probably the result of recent compression (Marshall unpublished data). In this forest the population currently appears to be stable, but may be liable to crash in the future.

Increasing Human Population Pressure

The human population in and around the Udzungwa Mountains is increasing. Current management activities are not however addressing this increase, nor the added pressure that it is putting on the forests. Influx of people to the Kilombero valley east of the Udzungwa National Park, is particularly high, yet there are now very few resources in this valley to sustain the population growth. Firewood and building poles are in short supply in this area and there are no local plantation forests, from which these resources can be obtained. The Udzungwa Scarp Forest Reserve is another forest that continues to be degraded by pitsawing and has high levels of hunting. This is seriously threatening one of the only two populations of the Sanje mangabey, and one of the most important areas for amphibian conservation in Tanzania (Rovero and Menegon pers. comm.). The village of Udekwa in the northeast of the Udzungwa Mountains is also expanding at an alarming rate, putting added pressure on the forest of Nyumbanitu. Community-based management projects in this and other northeastern villages, have also failed to control unsustainable hunting, leading to the decline and loss of forest mammals in some fragments (Marshall et al. 2005; Neilsen 2006; Chapter 2).

Collaboration

Safeguarding the future of the Udzungwa Mountains will require close collaboration between the various management authorities, and close consultation with the people living in the area. However, management authorities still disagree about some issues, and discussion between the various stakeholders is limited. Two workshops held in Tanzania began to redress this situation, leading to some important decisions for collaboration and future projects. These include social development in the Kilombero valley, investigations into connectivity between Udzungwa and adjacent conservation areas, a feasibility study for National Park extension to incorporate the Udzungwa Scarp Forest Reserve, and incorporation of Magombera forest into the Selous Game Reserve (Sumbi et al. 2005). A further issue given little attention is the lack of definable biological targets for conservation, particularly for the forests that lie outside of the Udzungwa Mountains National Park. Given that these areas are of international value for conservation of biodiversity and endemic species, inclusion of such criteria seems imperative for the success of any management project. Indicators such as the Udzungwa red colobus may be useful for evaluating conservation success, and I hope that the information presented in this thesis can therefore be of use in developing such criteria.

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